

Anxiety Body Odors as Context for Dynamic Faces: Categorization and Psychophysiological Biases

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Abstract

Body odors (BOs) can convey social information. In particular, their effects are maximal when their presence is paired with meaningful social contexts. Static faces have been widely used as social stimuli. However, they miss a key feature of our phenomenological experience, characterized by multisensory dynamic stimulations. Here, we investigate how BO sampled from

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individuals experiencing a transitory anxiety state, (a) induce a stress response and (b) bias the recognition of dynamic facial expressions, compared with BO of relaxed individuals. Participants (n=46) categorized the emotion of a face, morphing from a neutral expression to either an angry or happy expression, during exposure to either BO condition. In addition, their cardiac activity was measured. Exposure to anxiety BO increased the accuracy of dynamic facial recognition and reduced cardiac parasympathetic activity. These results suggest that in social situations that simulate part of the multisensory and dynamic features of real-life social contexts, anxiety BOs will induce a stress response in recipients, modulating both arousal and cognitive-emotional skills but facilitating emotional facial processing.

Keywords

dynamic facial expressions, anxiety body odors, heart rate variability, olfaction, stress

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Introduction

In the social dimension, our phenomenological experience is characterized by dynamic, multisensory stimulations. Among humans, faces are prominent social signals and, for that reason, have been extensively used as experimental stimuli (Adolphs, 2002). However, and contrary to real-life stimulations, most experiments have investigated how humans interact with static faces in uninformative contexts (Ekman, 1972). Static presentation paradigms miss to evaluate the contribution of informative and essential parameters compared with viewing dynamic facial expressions, such as facial motion (Kappas & Descôteaux, 2003) and contextual information (Hassin, Aviezer, & Bentin, 2013). The use of dynamic presentation paradigms provides several beneficial effects to the observer in terms of behavioral (e.g., improves emotion recognition accuracy; Lander & Bruce, 2000; Recio, Schacht, & Sommer, 2013) and emotional vividness (Ambadar, Schooler, & Cohn, 2005). Moreover, it heightens the discriminability of fake expressions (Kätsyri, Klucharev, Frydrych, & Sams, 2003; Wallraven, Bülthoff, Cunningham, Fischer, & Bartz, 2007) and induces greater facial mimicry (Sato, Fujimura, & Suzuki, 2008) and neural responses (e.g., activation of regions associated with social and emotional information processing such as the superior temporal sulcus, amygdala, and insula; Arsalidou, Morris, & Taylor, 2011; Kilts, Egan, Gideon, Ely, & Hoffman, 2003). This supports the idea that, viewing dynamic facial expressions, is an experience that more closely resembles everyday life and it follows its own processing rules, which are distinct from the requirements necessary to elaborate static information (Collignon et al., 2008). To date, face-context combinations have mostly been studied within the visual domain. However, there are examples of nonvisual cues providing informative socioemotional contexts to facial expressions (Johnstone & Scherer, 2000).

Besides the most common pairing of facial expressions to voices (e.g., De Gelder & Bertelson, 2003), body odors (BOs) can reliably, and with no conscious effort, communicate socioemotional information among conspecifics (Lübke & Pause, 2015; Lundstrom & Olsson, 2010; Parma et al., 2017). In addition to conveying information about stable personal traits (e.g., Mitro, Gordon, Olsson, & Lundström, 2012), BOs transmit transitory affective states, among which fear and anxiety have been the most studied (de Groot & Smeets, 2017; Parma et al., 2017). The exposure to anxiety BOs reduces the pleasantness of target objects when judged following the priming of a static happy face, as compared with

when the odor context is emotionally neutral (Pause, Ohrt, Prehn, & Ferstl, 2004). Furthermore, when facial information is ambiguous—such as when a happy face is not presented at the peak of its intensity—exposure to anxiety BOs renders the face less positive, as compared with when exercise sweat is smelled (Zernecke et al., 2011), and it increases the recognition accuracy for angry faces (as well as neutral faces, Mujica-Parodi et al., 2009). In line with these observations, ambiguous facial expressions (morphed from happy and fearful) are evaluated as more fearful when recipients are exposed to fear-related BOs (Zhou & Chen, 2009). Contextual effects of anxiety BOs have also been extended to psychophysiological (Albrecht et al., 2011; Prehn, Ohrt, Sojka, Ferstl, & Pause, 2006) and neurophysiological correlates (Prehn-Kristensen et al., 2009). The chemosensory perception of human anxiety BO magnifies startle responses (Prehn et al., 2006) and seems to automatically recruit areas involved in the processing of attentional and empathy-related resources compatible with anxiety (Prehn-Kristensen et al., 2009). Taken together, these findings suggest that anxiety BOs are able to bias behavioral and physiological responses to facial expressions, in a way compatible with stress responses (Parma et al., 2017), and in line with emotional contagion mechanisms (Semin & de Groot, 2013). Although these findings suggest that anxiety BOs bias behavioral and physiological responses to facial expressions in a way compatible with stress responses (de Groot & Smeets, 2017; Parma et al., 2017), an assessment of anxiety BO's modulation of cardiac activity beyond blood pressure and heart rate is currently lacking (Albrecht et al., 2011). Hence, it remains open to determine whether cardiac indices that are more sensitive to indicators of anxiety, such as heart rate variability (HRV) parameters (Elliot, Payen, Brisswalter, Cury, & Thayer, 2011), could reflect BO-transmitted anxiety.

The aim of the present study was to determine the influence of anxiety BO—expected to induce a stress response—in biasing facial emotion recognition when presented dynamically. In addition, to assess whether anxiety BO impact cardiac activity, we isolated the parasympathetic influence of cardiac activity (the percentage of high frequency [HF%]; Task Force of the European Society of Cardiology, 1996), a HRV index reliably detecting stress responses and anxiety (Licht, de Geus, van Dyck, & Penninx, 2009; Thayer, Hansen, Saus-Rose, & Johnsen, 2009), but not accurate in revealing modulations induced by happiness or anger (Kop, Synowski, Newell, Schmidt, Waldstein, & Fox, 2011). Based on the idea that dynamic information improves identification of facial affect, especially for degraded stimuli (Krumhuber, Kappas, & Manstead, 2013). Participants exposed to BO (henceforth, recipients) were asked to categorize short videos of faces gazing directly toward them. The faces were morphed from a neutral expression to an angry expression, a reliable indicator of threat (Adams, Gordon, Baird, Ambady, & Kleck, 2003; Sander, Grandjean, Kaiser, Wehrle, & Scherer, 2007), or a happy expression, in the context of either anxiety or neutral BOs. If exposure to anxiety BOs induces a stress response, we should be able to measure it via the use of accurate measures of cardiac activity, known to reflect even subtle indicators of stress responses (Elliot et al., 2011). We hypothesize that participants will display a significant reduction in HF% of the total HRV in the absence of the concurrent reduction of total spectrum power (Hjortskov et al., 2004). Further, we expect such reduction to be evident primarily during the exposure to anxiety BOs, as compared with neutral BOs, and not present when participants smell clean air. If this is the case, we further foresee that such stress response will affect recipients' ability to categorize dynamic facial expressions. With respect to reaction time (RT) performance, we outline two alternative hypotheses. On the one hand, if anxiety BOs produce a generalized stress response, then we expect the response time to accurate responses to be prolonged for both angry and happy faces. In other words, we expect the induced stress response to increase the cognitive and

emotional load (e.g., vigilance) on the recipients resulting in a general poor emotion categorization performance (Blanchette & Richards, 2003). This would be in line with data on static images from de Groot, Smeets, and Semin (2015) in which visual search task performance was decreased during fear odor exposure only when the task was difficult, and with the Yerkes–Dodson law (Yerkes & Dodson, 1908), which postulates that performance increases with increments in arousal until a tipping point is reached. Increments in arousal past that point would correspond to decrements in performance. Alternatively, we can foresee the emergence of an affective congruency effect, based on the affective negativity shared by the angry-face or anxiety-BOs combination. If this is the case, we expect that being exposed to anxiety BOs will selectively reduce the categorization speed to angry faces (Richards et al., 2002), given that angry faces will be faster disambiguated based on the negative emotional state of the donor (as it happens in the case of fear faces in Zhou & Chen, 2009). A third option would be a faster responding to all faces, which would be indicative of a heightened vigilance in virtue of the exposure to anxiety-BOs.

Materials and Methods

Particibants

Of the initial 54 female university students who volunteered to take part in the study, 46 were included in the final analyses (mean age: 23.2 years old; SD = 3.4; range= 19-33 years old). Four were excluded due to technical problems, the performance of three participants emerged as outliers in the psychophysiological analyses (more than 20% of trials represented an outlier performance), as defined by the outlier labeling rule (Hoaglin & Iglewicz, 1987), and one participant was excluded for abnormal RT data. We only included heterosexual women, based on self-report, to avoid possible bias of sex and sexual orientation (Martins et al., 2005). Furthermore, women have been suggested to be more sensitive to fear-related chemosignals, both when they are produced by men and when they are produced by women (de Groot, Semin, & Smeets, 2014). Participants were asked to refrain from eating gum, drinking coffee, smoke, or using any scented products that could interfere with their ability to smell on the day of the testing. As per their report, recipients did not suffer from any mental, metabolic, or neurological diseases and were screened for normal olfactory function using a shorted version of the Sniffin' Sticks test (Burghart Instruments, Wedel, Germany), a test using odorous pens to assess, among others, odor identification abilities. Participants who correctly identified (upon provision of four verbal labels) less than five out of seven odor pens were excluded from the sample. Recipients' perceived stress level was assessed via Visual Analogue Scales (VAS, from 0 to 100) before the experiment. Participants were randomly assigned to two groups: those smelling the anxiety BOs and those smelling the neutral BOs. As evident in Table 1, the two groups were comparable for self-reported anxiety measures.

All experimental procedures were approved by the ethics committee of the University of Aveiro, Portugal, and are compliant with the Declaration of Helsinki. All participants (recipients and donors) provided written informed consent and were rewarded for their participation with a10 Euro-voucher to be used at a nearby mall.

Olfactory Stimuli

BOs collected from six self-reported heterosexual females (M=20 years; SD = 0.7 years, range = 19–21) were used as olfactory stimuli. We only included female donors to avoid

Table 1. Descriptive Statistics and Difference Between	Groups in Relation to Sociodemographic Data and
Questionnaire Scores.	

	Neutral group Mean (SD)	Anxiety group Mean (SD)	$Var\!\sim\!Group\;eta$	95% CI	Þ
Age	23.22 (4.30)	23.21 (2.36)	-0.02	[-2, 1.96]	.99
STAI-T	34.14 (6.64)	35.21 (7.54)	1.07	[-3.05, 5.19]	.61
FNE	89.41 (8.41)	93.00 (8.53)	3.59	[-1.31, 8.49]	.16
SIPAAS					
Distress anxiety	95.64 (19.37)	97.13 (20.86)	1.49	[-10.18, 13.15]	.80
Avoidance	81.14 (23.38)	81.50 (22.98)	0.36	[-13.04, 13.77]	.96
Total	176.82 (39.03)	178.63 (41.61)	1.81	[-21.57, 25.18]	.88

Note. SIPAAS = Social Interaction and Performance Anxiety and Avoidance scale; FNE = Fear of Negative Evaluation Scale; STAI-T = Spielberger's State-Trait Anxiety Inventory.

 $Var \sim Group$ indicates that the linear mixed model calculated the effect of group on each dependent variable reported in Column I.

sex effects generated by smelling the odor of a potential sexual partner (given that all participants were heterosexual; e.g., Herz & Inzlicht, 2002; Martins et al., 2005). To be included, female donors had to be nonsmokers, medication free and not report any physical, metabolic, or mental health disorder. They should also score in the normal range of the Spielberger's State-Trait Anxiety Inventory (M = 36.16; SD = 3.43). The same donors participated in two sessions of sweat collection, which sweat was collected in either an anxiety-provoking (oral exam with an evaluative component) or emotionally neutral situation (attending a regular class) during a period of 90 min. The State-Trait Anxiety Inventory (Spielberger, 1983) and a 100-mm VAS were used to assess donors' awareness about their levels of anxiety. Donors reported both significantly higher levels of subjective stress and rated state anxiety (p < .05) and anxiety for both moments during the anxiety session as compared with the neutral session. This suggests that the emotion induction method was successful (see Supplementary Material for further details on the BO collection procedure and detail information about donors' stress and anxiety levels). Please note that emotional tone of the BO collection was counterbalanced across donors.

Visual Stimuli

Photos of 12 individuals (6 females) expressing anger and happiness were selected from the Karolinska Directed Emotional Faces database (Lundqvist, Flykt, & Öhman, 1998); 15-s videos were created with the neutral version of the face morphing into a full-intensity angry or happy face. Each participant was exposed to 12 videos during practice (involving 1 female and 1 male actor, repeated three times each). These actors used in the practice trials were different from those used in the main task. In the main task, 80 videos (each original video was repeated four times) were used. For further details, please refer to the Supplementary Materials.

Heart Rate Recording

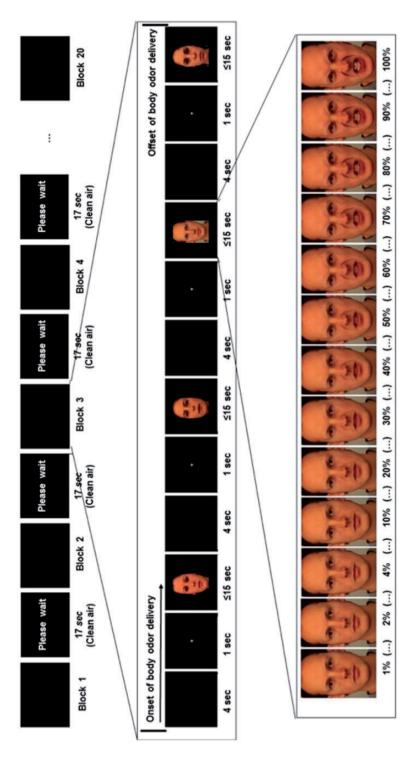
Electrocardiographic activity was recorded from three electrodes (EL503 by BIOPAC) placed in lead-II configuration, following skin cleaning with alcohol. The three electrodes were connected to the BIOPAC ECG amplifier (ECG100C), set to a sampling frequency of 2000 Hz.

Procedure

Participants were connected to the electrocardiogram equipment and then started the emotion categorization task. Participants were instructed to watch each video while exposed to an olfactory stimulus, and their task was to categorize the emotion as angry or happy by pressing either of two keys on the keyboard ("z" or "m") as fast as possible (bottom panel, Figure 1). To prevent laterality effects, the keys on the keyboard were reversed for half of the recipients. Recipients underwent a training session including three blocks of four trials before the main task began. The main task included 20 blocks of four trials each, spaced by 17-s clean air presentation to lower potential odor adaptation or habituation and carry-over effects (top panel, Figure 1). In each trial, the odor delivery started while a black screen (4 s) was presented. The odor was initiated before the visual stimuli to provide contextual information for the visual processing. Subsequently, a 1-s fixation cross was displayed which indicated the beginning of each video. Following the participant's response or at the end of the 15-s period, a new trial began (middle panel, Figure 1). A 4-channel olfactometer was used to deliver the BOs and clean air through a birhinal nasal cannula (flowrate 2.5 l/min) into the participant's nostrils (Lundström, Gordon, Alden, Boesveldt, & Albrecht, 2010). To avoid habituation effects, each participant was exposed to two different supradonors within the same BO condition over the course of the session. The two different supradonors were presented alternatively between blocks, that is, the supradonor was not presented for two blocks in a row. After the emotion categorization task, the electrodes were carefully removed (25 min). Subsequently, the recipients rated the BOs and clean air for intensity, pleasantness, and familiarity using a 100-mm VAS. Each odor presentation would start with a 5-s countdown. Then, a fixation cross was presented indicating the delivery of the odor. The recipients were instructed to breathe naturally at the presentation of the fixation cross. An experimenter visually inspected the compliance of this rule from a window. Hence, the experimenter was not in the room with the recipient. No recipient was excluded from the sample for this reason. The odors were rated consecutively for three times, to obtain an average rating value. The full experimental session lasted approximately 20 min.

Data Analysis

First, frequency- and time-domain HRV analyses were performed using the Kubios software (Tarvainen, Niskanen, Lipponen, Ranta-aho, & Karjalainen, 2014, University of Eastern Finland, Kuopio, Finland), which deals with artifact correction based on threshold (set at medium; please refer to the Kubios manual for further details [http://www.kubios. com/downloads/Kubios HRV Users Guide.pdf]). HRV measures were extracted for each block. To calculate frequency-domain measures, we conducted power spectrum analysis on the interbeat intervals (see Trinder et al., 2001 for details). The measures of interest were as follows: total power (reflecting total HRV, ms²), HF (an index of pure vagal tone, expressed as absolute power in arbitrary units), and percentage of HF (0.15–0.40 Hz) over total power. To exclude that, this frequency band may be confounded by body movements and yawning, an experimenter monitored the data collection. No trials had to be excluded for these reasons. Using a time domain approach, the time interval between consecutive R-waves, reflecting the myocardial contraction frequency (ms), was calculated. To correct for nonnormality, HRV variables were log transformed. Second, to evaluate the presence of possible individual differences among the recipients and differences across odor conditions, linear mixed models (LMMs) were performed with subject identification as a random factor and group as predictor to assess questionnaire scores. Third, explorative data analyses were



Middle panel: Each block included the presentation of four videos during the exposure to one BO; each trial was constituted by a 4-s black background, a 1-s fixation cross, and one video presentation. Bottom panel: Each video was presented for 15 s and showed a faced morphed progressively from a neutral to an Figure 1. Graphical depiction of the emotion categorization task. Top panel: The main task included 20 blocks, clean air was presented for 17 s between blocks. angry or happy emotional face.

Table 2. Summary of HRV Analyses.

	Neutral group Mean (SD)	Anxiety group Mean (SD)	$\begin{aligned} & Var \sim Group \times \\ & Sex \; Face \; \times \\ & Emotion \; Face \; \beta \end{aligned}$	95% CI	Þ
Clean air					
Session duration (s)	146.07 (25.08)	147.67 (22.21)	1.60	[-12.07, 15.26]	.82
Mean RR log (s)	6.61 (0.14)	6.59 (0.16)	-0.03	[-0.11, 0.06]	.57
HF log (ms ²)	6.19 (1.60)	5.74 (1.37)	-0.44	[-1.3, 0.42]	.32
HF%	37.78 (19.14)	29.87 (20.10)	-8.92	[-20.28, 2.45]	.13
Total power log (ms ²)	7.34 (0.95)	7.22 (0.94)	-0.12	[-0.67, 0.43]	.66
Odor stimulation					
Session duration (s)	1040.57 (88.31)	1002.812 (95.29)	-37.756	[-91, 15.48]	.17
Mean RR log (ms)	6.60 (0.14)	6.60 (0.12)	0.001	[-0.07, 0.08]	.97
HF log (ms ²)	6.02 (1.56)	5.56 (1.14)	-0.465	[-1.25, 0.32]	.25
HF%	25.88 (13.77)	17.16 (6.67)	-8.724	[-15.31, -2.13]	.01*

Note. HF = high frequency; RR = R-waves.

performed on the accuracy and the RT data to ascertain the ability and the speed at which recipients categorized a face morphing from neutral to angry or happy. An outlier analysis applying the so-called boxplot outlier labeling rule was conducted (Hoaglin & Iglewicz, 1987), which is based on multiplying the interquartile range by a factor of 2.2. This procedure is accurate for both large and small sample sizes and was hereby performed on a subject-by-subject basis (Iglewicz & Banerjee, 2001). It identified 35 (0.84%) upper limit outliers in 4,160 cells. Those trials were removed from analyses. Traditional RT analyses were performed by using LMMs on accurate RTs to determine the effect of odor (two between-subject levels), sex (two within-subject levels), and emotion (two within-subject levels), as fixed factors, whereas subject identification was treated as a random factor on the model. Analyses were performed with the RStudio 0.99.484. Significance was set for all test at alpha <0.05, and the tests were considered as two tailed.

Results

Smelling Anxiety BOs Induce Stress-Like Cardiac Activity

To evaluate potential BO-dependent stress induction on cardiac activity, we assessed the effect of group on the collected heart rate measures. The results showed that the absolute HF, as well as total power, did not reveal any significant differences between groups in the BO condition (Table 2).

However, for HF% over the total power, a significant main effect of group emerged, $\beta = -8.724$, p = .01, 95% CI [-15.31, -2.13] (Figure 2). In line with our hypothesis, we found that the group smelling the anxiety BOs demonstrated lower vagal activity, as compared with the group smelling the neutral BOs. To assess if these results were mediated by factors other than the BOs features itself, a manipulation check was initially performed via LMM on the duration of the categorization time. This revealed no significant differences between the two groups while participants were smelling clean air only, $\beta = 1.598$, p = .82, 95% CI [-12.07, 15.26]. Similarly, none of the frequency- and time-domain HRV measures significantly differentiates between groups when no odor was presented (aka, the HF% parameter

^{*}p < .05.

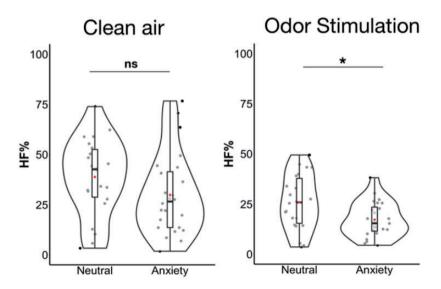


Figure 2. Percentage of HF in the group exposed to the anxiety and neutral BOs. The red dot indicates the mean value per group. The violin plot represents the smoothed distribution of data. HF = high frequency; *ns* = not significant.

per se did not reveal any difference between groups). Please refer to Table 2 for details. Moreover, the duration of the session did not differ between groups, even in the experimental session, when each group was exposed to either the anxiety BOs or the neutral BO, $\beta = -37.756$, p = .17, 95% CI [-91, 15.48]. Thus, in light of the findings of the training session, such results cannot be accounted for only by individual differences. It is also worth noting that the amount of vagal activity in both the anxiety and the neutral BOs group does not depend on reduced total power.

Smelling Anxiety BOs Increase Accuracy Rate to All Facial Expressions During Emotional Categorization

To assess the recipients' ability to correctly categorize a face morphing from a neutral to an angry or happy emotion, accuracy data were analyzed within and between groups by means of chi-squared tests. The analyses of the accuracy data showed a high percentage of accurate responses (96.84%) and a low percentage of inaccurate responses (3.16%). For the 112 trials, out of the total 3,549, the emotion categorization was incorrect. Given the ceiling effects for the accurate responses, an explorative data analysis was run for inaccurate responses in relation to the Yerkes–Dodson law (Yerkes & Dodson, 1908). Considering only the inaccurate responses, the analyses revealed that the group smelling the neutral BOs committed 70 inaccuracies (78.4%), whereas only 42 (21.6%) were committed by the anxiety BOs group. A two-sample test for equality of proportions with Yates continuity correction revealed that this difference was significant, $\chi^2(1, N=112)=13.018$, p=.0003, 95% CI [0.11, 0.39]. The inaccuracies were homogeneously divided across facial expressions, $\chi^2(3, N=112)=3.05$, p=.38.

Faster Detection of Happy Compared With Angry Faces

The results of the speed at which recipients correctly categorized both angry and happy faces revealed a significant two-way interaction, group by emotion, $\beta = -238.81$, p < .04, 95% CI

[-469.65, -7.98]. Post hoc analyses with TUKEY adjustments revealed that this significant interaction seems to be explained by the main effect of emotion, $\beta = 960.48$, p < .0001, 95% CI [793.38, 1127.58], indicating that the recipients, irrespective of odor exposure, were faster in categorizing happy (2785 ms), as compared with angry facial expressions (3749 ms). No other significant effects were found (Figure 3).

Anxiety BOs Were Not Perceptually Different From the Neutral BOs

Lastly, we evaluated whether the above-outlined behavioral and psychophysiological results could result from possible differences in the percept of the odors itself. As evident from three separate LMMs, including the ratings of clean air as covariate to control for rating behavior, recipients from the anxiety and the neutral BOs groups perceived the BO conditions to be comparable in respect of rated intensity, $\beta = -4.29$, p = .46, 95% CI [-15.66, 7.09], pleasantness, $\beta = 3.10$, p = .44, 95% CI [-4.77, 10.98], and familiarity, $\beta = 2.35$, p = .69, 95% CI [-9.07, 13.76]. Thus, given this result and that the BOs samples were produced by the same donors across groups, it is unlikely that the perceptual features of the odors (when evaluated explicitly) are the factors driving the differences emerging in psychophysiological and behavioral data.

Discussion

The central question of the present study focused on whether and how being exposed to anxiety BOs facilitate dynamic facial emotion recognition. In particular, our hypotheses were tailored to assess whether smelling anxiety BOs would induce a stress response affecting the accuracy and processing speed of the categorization of dynamic facial expressions.

As predicted, recipients smelling the anxiety BOs showed lower HF%, independent of any preodor exposure difference between the groups. Furthermore, HF% difference across

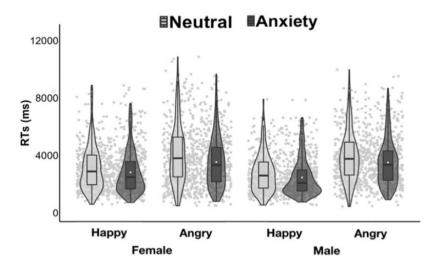


Figure 3. Traditional reaction times analysis performed only on accurate responses. The white diamond indicates the mean value per group, per condition, whereas the box plot indicates the quartiles of each distribution. Each box plot is surrounded by violin plots representing the smoothed distribution of data. Gray dots represent single data points. RT = reaction time.

groups during the task was not dependent on interindividual characteristics, given that the HF\\(^{9}\) while smelling clean air did not significantly differentiate the groups. This observation is further strengthened by the fact that the two groups neither differed across the various self-reports used to assess anxiety, nor on the perceptual ratings to the odor conditions, indicating again that interindividual differences are unlikely to play a key role in the significance of the behavioral and psychophysiological findings. Although this result may seem in contrast with Albrecht et al. (2011), who do not report an effect of heart rate and blood pressure difference across participants in the anxiety and no anxiety conditions, here we used a more sensitive indicator of cardiac activity able to isolate the parasympathetic influence on heart rate measures (Task Force of the European Society of Cardiology, 1996). We interpret the decrement in HF% as the reduction in parasympathetic (vagal) cardiac activity induced by the exposure to the anxiety BOs. This olfactory-dependent emotional contagion effect (Semin & de Groot, 2013) is compatible with numerous studies reporting decreased vagal activity in relation to anxiety (Friedman, 2007) and, more generally, to stress (Thayer, Ahs, Fredrikson, Sollers, & Wager, 2012). Although this is the first time that HRV analyses are applied to the investigation of BOs effects, this result align with previous physiological evidence suggesting that anxiety BOs induce stress responses. The startle reflex, an independent peripheral psychophysiological measure modulated by stressful events (Grillon & Baas, 2003), has previously been demonstrated to be potentiated by anxiety BOs (Pause, Adolph, Prehn-Kristensen, & Ferstl, 2009; Prehn et al., 2006). Similarly, the cardiac activity elicited by anxiety BOs is compatible with the prefrontal activity found while experiencing stress or anxiety (Prehn-Kristensen et al., 2009), given that the activity of the prefrontal cortex correlates with the vagal component of HRV in emotional contexts (Lane, Reiman, Ahern, & Thayer, 2001). Furthermore, the prefrontal cortex, as well as the amygdala—an area considered to be part of the olfactory network (Price, 2003) and central in behavioral responses to threats (Mobbs et al., 2009)—emerged in a recent meta-analysis on the relationships between HRV and neural activity as the integration centers of autonomic and neural activity during stress (Thayer et al., 2012). The odor-induced experience evident in the recipients seems to have been associated with the specific stress status of the donors (and was not due to the mere presence of BOs). Indeed, donors reported to feel more anxious and stressed during the anxiety than the neutral BOs collection, which confirmed that the anxiety induction to which they were subjected during BOs collection generated differential levels of anxiety across conditions and determined that our manipulation was successful.

The psychophysiological evidence was complemented by behavioral findings of a stress response induced by performing dynamic facial expression categorization in the context of anxiety BOs. With respect to accuracy, the analysis of accurate responses (~95%) suggests that the task was well understood and rather easy (Wieser & Brosch, 2012), with ceiling effects in the accuracy performance emerging. However, accuracy data analysis allows us to indirectly test the strength of the BO-induced stress response in relation to the Yerkes–Dodson law (Yerkes & Dodson, 1908). The analysis of inaccurate responses revealed that the group smelling the anxiety BOs correctly categorized dynamic facial expressions significantly more often than the group smelling the neutral BOs. No specific facial expression effects emerged. This pattern of result suggests that such a generalized increment in performance may be linked to a moderate stressing power of the anxiety BO (Yerkes & Dodson, 1908), which favors the allocation of attentional resources. Such attentional facilitation is not selective to affective-compatible facial expressions (i.e., angry faces), but it is generalized to both emotions.

Such reasoning can be extended to the results produced by the analysis of the RTs since angry faces were not faster recognized under a congruent affective BO context compared with happy faces. The present results contradict previously research showing that anxiety BOs, as well as fear (Zhou & Chen, 2009), tend to modulate responses to negative emotional static faces (Pause et al., 2004; Rubin, Botanov, Hajcak, & Mujica-Parodi, 2012; Zernecke et al., 2011), which is in line with the evidence proposed by de Groot et al. (2015), who showed that classification speed for neutral, fearful, happy, and disgusted faces was modulated by the exposure to fear BO. However, whether such differences in results are determined by a difference in the message embedded in the anxiety versus fear BO, or if it reflects a difference between the use of static and dynamic stimuli or if it is related to different possible sensory acquisition mechanisms (e.g., De Groot et al., 2012) cannot be teased apart with the present study and needs to be further assessed.

Recipients from both groups were faster categorizing happy compared with angry facial expressions, which is consistent with studies using dynamic stimuli and reporting the so-called *happy face advantage* (Ambadar et al., 2005), namely faster RTs to categorize happy faces over negative emotional faces. One possible explanation for the absence of an affective congruent context on both accuracy and RTs could be the nature of the stimulus used, since studies reporting the happy advantage effect pointing low-level perceptual features, such as the exposed teeth of a smile (e.g., Recio et al., 2013), as a key factor driving the effect.

Although this article provides a novel use of dynamic facial expressions in association with BOs and a thorough evaluation of body odor-induced cardiac activity, it is not free from limitations. First, the duration of the unfolding of the facial expressions should be reduced in future studies, as to more closely match real-life dynamics of facial expressions. This could also help increase the difficulty of the task and let olfactory effects emerge more prominently. Interestingly, this approach will also provide information on whether visuoolfactory interactions require a particular temporal course. Second, the use of within-subject designs and baseline and BO-exposure phases of similar duration would help to confirm this phenomenon. Using the current study to calculate an informed effect size, future experiments will allow to test whether the effects reported here stand on samples with a power of at least 80%. Third, although unlikely, due to the long-odor stimulations, the use of respiratory measures may be included to check whether the breathing rate of the subjects may have impacted on the HRV measures, and to assess whether the anxiety BO could have modulated sensory acquisition strategies. Fourth, while succeeding in the attempt of proposing an experimental design that allows us to get a step closer in the characterization of our phenomenological experience, the present study still suffers from lab restrictions, necessary to control for possible confounders. Above all, participants evaluated facial expressions presented on a screen. Fifth, a complementary study using fear facial expressions could be used to disentangle if the effects of the anxiety BOs are generalized to perception of threat (anger and fear) or whether there would specific fear or anxiety effect that we were not able to capture here.

We consider this work as a first step to develop experimental protocols able to directly study the perception of social information in real-life situations, for instance, including portable eye-tracking devices and wearable sensors measuring psychophysiology. Finally, to be fully generalizable, these observations should be extended also to the male population.

Altogether, these results indicate that performing the dynamic facial categorization task in the context of anxiety BO increased the recognition accuracy. At the physiological level, the anxiety BO context induced in the recipients a vagal activity compatible with a stress response. Furthermore, such odor-induced anxiety experience in the recipients was not due

to the mere exposure to BOs, but it specifically reflected the emotional experience of the donors. These findings are taking the field of social chemosignal communication a step forward by demonstrating BO-dependent emotional and cognitive effects in more ecological valid social contexts, such as the one provided by the dynamic facial expressions.

Author Contributions

Marta Rocha and Valentina Parma contributed equally to this work.

Declaration of Conflicting Interests

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Supplementary Material

Supplementary material for this article is available online.

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