The Function of Fear Chemosignals: Preparing for Danger

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Abstract

It has been shown that the presence of conspecifics modulates human's vigilance strategies as is the case with animal species. Mere presence has been found to reduce vigilance. However, animal research has also shown that chemosignals (e.g., sweat) produced during fear-inducing situations modulates individuals' threat detection strategies. In the case of humans, little is known about how exposure to conspecifics' fear chemosignals modulates vigilance and threat detection effectiveness. The present study (N= 59) examined how human fear chemosignals affect vigilance strategies and threat avoidance in its receivers. We relied on a paradigm that simulates a "foraging under threat" situation in the lab, integrated with an eye-tracker to examine the attention allocation. Our results showed that the exposure to fear chemosignals (vs. rest chemosignals and a no-sweat condition) while not changing vigilance behavior leads to faster answers to threatening events. In conclusion, fear chemosignals seem to constitute an important warning signal for human beings, possibly leading its receiver to a readiness state that allows faster reactions to threat-related events.

Keywords

Vigilance; Fear chemosignals; Olfaction; Threat detection; Eye-tracking

Introduction

Avoiding threat constitutes a paramount adaptive process for human beings, with direct implications in our daily lives (see Öhman & Mineka, 2001). An examination of how conspecifics influence our threat avoidance strategies represents a remarkable step to understanding human behavior in social contexts. Recent research (Gomes & Semin, 2020) has shown that the mere presence of conspecifics influences humans' threat monitoring strategies. Other factors that can influence others' threat monitoring strategies involve the emission of diverse sensory cues (e.g., facial expressions of fear). Such factors alert receivers to possible danger (Tipples, 2006). The present study was designed to explore the particular role that olfactory danger signals, namely sweat produced during fear-inducing situations, play in preparing human beings to be vigilant. In order to frame this research question, we integrated the literature on vigilance on social species (Beauchamp, 2015) and research on human olfactory danger signals (i.e. fear-related chemosignals; see de Groot & Smeets, 2017).

In order to survive, animal species evolved optimal trade-off strategies balancing between their intake activities and vigilance behavior to avoid danger (e.g., Beauchamp, 2015; Creel et al., 2014). The balance of this trade-off has been seen to be shaped by the presence of conspecifics. Group situations have been documented to reduce stress (Hawlena & Schmitz, 2010; Voellmy et al., 2014) and consequently to decrease vigilance (e.g., van Schaik et al., 1983). The reduction of vigilance releases resources that can be invested in other survival-relevant activities such as foraging (see Beauchamp, 2015). Several mechanisms driving this safety increment have been postulated (e.g., "many-eyes effect" or "risk-dilution"; Bertram, 1978; Caraco et al., 1980). Among the most prominent ones is the so-called 'mutual warning' mechanism (or "collective detection"; e.g., Lima, 1995). This mechanism posits that in a group situation, individuals who do not detect a threat source can

nevertheless rely on other group members to warn them of a dangerous stimulus. Consequently, individuals in group contexts can reduce their vigilance levels without compromising their safety. Interestingly, a recent study from our lab (Gomes & Semin, 2020) pointed for similar modulatory effects of the presence of conspecifics in humans' vigilance. Human beings in a co-presence condition sacrificed their vigilance allocating more resources to intake activities than subjects performing the experiment in an individual condition (Gomes & Semin, 2020; see also Barash, 1972; Wawra, 1988; Wirtz & Wawra, 1986).

Notably, a central aspect of a 'mutual warning' mechanism is the transfer of information between threat detectors and non-detectors. Animal research has confirmed this communication skill in many different species, involving the most variated sensory cues, such as visual (e.g., alert body postures in fish; Brown et al., 1999), acoustic (e.g., alarm calls in prairie dogs; Hoogland, 1979), mechanical (e.g., vibrations in the ground, transmitted between foot-drumming mammals; Randall, 2001), or even olfactory danger signals (e.g., alarm pheromones released by rats; Kikusui et al., 2001). The question is does 'mutual warning' play a role in shaping the behavior of our own species? Although not often framed in terms of 'mutual warning' a considerable amount of research has revealed that humans are able to produce and perceive conspecifics' visual and acoustic alarm signals. Several studies illustrate how humans communicate danger with, for example, fear facial expressions (e.g., Bannerman et al., 2009; Mogg et al., 2007; Pourtois et al., 2004), fear body postures (e.g., Bannerman et al., 2009; De Gelder, 2006; Stienen & de Gelder, 2011), fear prosody (e.g., Dolan et al., 2001) or crying (e.g., Giardino et al., 2008). Moreover, exposure to these alarm signals has been shown to trigger defensive strategies in their receivers (see De Gelder, 2006; Öhman & Mineka, 2001). These studies support a 'mutual warning' phenomenon in human beings.

It is only recent that olfactory danger cues (i.e. fear chemosignals; de Groot & Smeets, 2017) have been shown to trigger threat avoidance processes in human beings as in the case of other animal species (e.g., Kikusui et al., 2001). In particular, exposure to fear chemosignals (i.e. sweat collected during fear-inducing conditions) activates facial muscles associated with facial expressions of fear (*medial frontalis* and *corrugator supercilii*; de Groot et al., 2014; Gomes et al., 2020; Kamiloğlu et al., 2018). These muscles are associated with increased sensory acquisition (Susskind et al., 2008), manifested in a widening of the eye aperture, speeding up of ocular movement, and increasing inhalation volume (de Groot et al., 2012). Moreover, fear-related chemosignals also facilitate the processing of emotional faces (e.g., Kamiloğlu et al., 2018; Silva et al., 2020; Wudarczyk et al., 2016; Zhou & Chen, 2009), trigger withdrawal behaviors (enhance the startle reflex; Prehn et al., 2006), reduce cardiac parasympathetic activity (Rocha et al., 2018), and activate brain areas associated with threat processing (e.g., amygdala; Mujica-Parodi et al., 2009). Thus, fear chemosignals appear to act as an "alarm" signal, increasing sensory acquisition, and preparing its receivers to deal with potential threats (e.g., de Groot et al., 2012; Parma et al., 2017).

However, there is no empirical study on the effects of being exposed to fear chemosignals in humans and the types of threat avoidance mechanisms they activate. Do they modulate threat monitoring (i.e. vigilance)? To what extent do they influence the reaction to threatening events? In the present study, our aim was to examine (a) how fear chemosignals shape the trade-off between intake activities (benefits) and vigilance behavior to avoid danger (threat avoidance), and (b) modulate the reaction to threat-related events (threat coping). We examined this with an innovative "foraging-vigilance" task integrated with an eye-tracker to explore participants' attention allocation. Specifically, this paradigm (see Gomes & Semin, 2020) motives participants with monetary rewards to solve a central letter discrimination task (i.e. foraging simulation) and simultaneously makes them 'suffer' stronger monetary

punishments if they do not detect and avoid peripheral changes (i.e. threat simulation; Kameda & Tamura, 2007; Löw et al., 2008; Schlund & Cataldo, 2010). This simulation of foraging under threat risk provides us with a tool to examine not only threat monitoring but also the effectiveness in "escaping" to threatening events across chemosignal conditions (fear vs. neutral vs. clean air) in the laboratory.

It is possible to deduce several outcomes from the literature on 'mutual warning' research with animals and research on olfactory danger chemosignals (fear). One possible scenario is that the exposure to fear chemosignals signals the imminence of danger. An outcome that this scenario would suggest is that participants exposed to fear chemosignals will be more vigilant compared to participants exposed to rest chemosignals or clean air (i.e. no-sweat condition). This will result in more time spent scanning the targets in their peripheral visual field, fewer correct and more no responses to the central letter discrimination task (H1). Additionally, an increment in vigilance behavior may result in (H2) a higher number of avoided threatening changes (see Gomes & Semin, 2020). At the same time, besides modulating threat monitoring, fear chemosignals may prepare receivers for a defensive reaction. In this scenario, we expect to observe (H3) faster reaction times to avoid threat compared to exposure to either rest chemosignals or the no-sweat. Since no study to date explored such phenomenon, the question remains whether all or a subset of the possible outcomes mentioned above will be confirmed.

Method

Sweat collection

Eight healthy Portuguese Caucasian males, aged between 18 and 34 (M = 25.00 years; SD = 5.81), gave their informed consent and participated voluntarily in the sweat collection. All participants were non-smokers, heterosexual, did not report any neurological of psychological disorders, and were not under medication at the time of the collection. Only

males were recruited as sweat donors due to their larger and more active apocrine glands (compared to females; see de Groot et al., 2015; Zhou & Chen, 2009). Following the guidelines of previous studies, only heterosexual males were included as sweat donors because the participants of the study were heterosexual females, which seem to evaluate sweat from homosexual and heterosexual males differently (Martins et al., 2005). Each participant received monetary compensation to donate sweat.

Sweat was collected over two sessions (fear-inducing and rest sessions; sessions order was counterbalanced across participants) separated by a week's interval. As in previous studies (de Groot et al., 2015; Gomes et al., 2020), in the two days preceding the sweat collection, sweat donors were instructed to follow a strict protocol to avoid sweat contamination. Donors were instructed to shave their armpits and not allowed to consume alcohol, have sexual intercourse, consume odorous food (e.g., garlic, chili, asparagus), practice excessive exercise, sleep in the same bed as their partner or pet, and also from using any type of perfumed personal care products. Fragrance-free personal care products (i.e. soap, shampoo, and deodorant) were given to the participants to use on these two days. On the collection day, participants were not allowed to wear any type of personal care products, and two hours before each sweat collection were instructed not to eat or drink anything other than water.

Sweat was collected using absorbent non-woven pads (70% viscose, 30% polyester; Wells, Sonae SA, Portugal), attached by the experimenter under the participants' armpits using hypoallergenic tape. Donors were then seated in an individual cubicle (temperature kept between 23-25 ºC). To induce a fear or a rest state, sweat donors watched fear-inducing or neutral video clips (previously piloted and used in Gomes et al., 2020) for approximately 30 minutes. Sweat pads were then removed by the experimenter and stored at -23 ºC,

separately in Amber glass vials. Following de Groot and colleagues (2012), clean absorbent non-woven pads were stored at the same temperature to be used in the no-sweat condition.

As an emotion-inducing manipulation check, two variables were recorded: (a) the subjective feelings of the sweat donors during each session – sweat donors were asked to report, using 0 - 10 separated visual analogue scales, to what extent they felt angry, fearful, happy, sad, disgusted, neutral, surprised, calm, and amused during each sweat collection session; (b) the weight of the produced sweat in each session - calculated by subtracting the weight of the pads before the sweat collection from the weight of the pad after the sweat collection session (using a *Precisa* scale model: BJ 100M with .001g precision).

The procedure for the sweat collection was approved by the host institution ethics committee and was conducted in accordance with the guidelines of the declaration of Helsinki.

Sweat receivers

Participants

Sixty-five Portuguese female university students gave their informed consent and participated on a voluntary basis in the experiment. Six participants were excluded due to psychological related disorders or misunderstanding the experimental rules. Thus, 59 participants, aged between 18 and 31 (M = 20.98 years; SD = 3.27), were randomly distributed across the 3 chemosignal conditions: 21 participants (age range: 18-27; M = 20.14 years; SD = 2.17) took part in the fear chemosignals condition; 19 participants (age range: 18-31; M = 21.47 years; SD = 3.50) performed the experiment in the rest chemosignals condition; and 19 participants (age range: 18-30; M = 21.42 years; SD = 3.95) participated in the no-sweat condition. All participants were Caucasian, non-smokers. They reported no psychological or neurological disorders, no respiratory diseases, no illness, cold or allergy, no

uncorrected vision problems, and no medication intake. All participants were also tested for the absence of severe olfactory problems by identifying three clear odors: cinnamon, fish odor, and banana (see Lötsch et al., 2016). Following previous studies using emotional chemosignals (e.g., de Groot et al., 2015; Zhou & Chen, 2009), only females were included due to their higher sensitivity towards emotional signals and a better sense of smell compared to men. Only heterosexual women were included because research has shown that women perceived male sweat differently as a function of both the donors' and their own sexual orientation (Martins et al., 2005).

Sample size was determined à priori with a power analysis (using G-Power 3.1.9.3; Faul et al., 2007) for a one-way MANOVA (*Pillai's Trace* = .177, power = .80, α = .05). The value of the *Pillai's Trace* was obtained from a previous study from our LAB, examining the effects of being in a group in humans' vigilance behavior (Gomes & Semin, 2020). The power analysis revealed that a minimum of 18 subjects would be needed in each of the experimental conditions (i.e. fear, rest, and no-sweat). This resulted in a minimum total sample of 54 subjects.

The experiment was approved by the host institution ethics committee and was conducted following the guidelines of the Declaration of Helsinki.

Design

The present study has a 3 chemosignals conditions design: Fear chemosignals vs. rest chemosignals vs. no-sweat condition (between subjects). Participants were randomly assigned to the 3 sweat conditions. Neither the participants nor the experimenter were aware of the conditions (i.e. double-blind experiment).

Materials and measures

Composition of the sweat stimuli: Following previous studies (de Groot et al., 2015; Gomes et al., 2020), to reduce possible effects of interindividual variability in the sweat production, pad pieces of different sweat donors were combined to create "super-donors", to which the receiver participants were exposed. Each sweat pad, obtained in the sweat collection phase, was divided into 8 equal parts. Using a custom-made randomization script, four pad parts (2 from right and 2 from left armpits) were combined to create a "super-donor". The same combination of donors was used to create fear and the rest "super-donors".

As already mentioned, clean absorbent non-woven pads were stored at the same temperature as the sweat stimuli (i.e. -23ºC) to be used in the no-sweat condition.

Foraging-vigilance task: This vigilance task - developed and previously used in our Lab (see Gomes & Semin, 2020) - constitutes a laboratory simulation of the evolutionary trade-off between foraging and avoiding threat, which represents the ideal context to study vigilance behavior (Beauchamp, 2015).

In each trial, participants were presented with three-by-four letter matrices consisting of 12 random letters per matrix. In these letters was always included one of two target letters (q or p). Around the letter matrices, 8 circular Gabor patches (with a diameter of 1.25 visual degrees) were displayed equidistantly from the center of the screen by 8 visual degrees (see Figure 1).

Figure 1: Example of a letter matrix surrounded by 8 Gabor patches. The arrow illustrates a possible change in one of the 8 Gabor patches.

Participants were instructed to find as many target letters as possible during each trial. When a participant gave an answer, a new letter matrix was automatically displayed. If there

was no answer after 1.5 seconds, the letter matrix automatically changed to a new one. For each correct response, participants received an additional 0.02€ in their final reward – foraging simulation. However, in 40% of the trials, one of the 8 Gabor patches narrowed down (its width was gradually reduced to about a third of its original size). This lasted for 4 seconds and occurred randomly between 2 seconds after the start of the trial and 4 seconds before its end. Participants were instructed to press an escape key (SPACE) as fast as possible when they notice that a change was occurring. If the escape key was not pressed, they receive a feedback message informing them that they lost 0.50€ from their final reward, which constituted the threat simulation. When they pressed the escape key, the change immediately disappeared from the screen and the participants were asked to identify, using the mouse, which Gabor patch changed during the trial. Each trial ended after 20 seconds or when a change occurred. In total, each participant performed 50 trials (including 20 change trials). The task had a mandatory break in the middle of the experiment. The average duration of the "foraging-vigilance" task was approximately 25 minutes.

In this experimental situation, when a participant increases her vigilance level also increases the likelihood of avoiding danger (i.e. detecting the changes in the Gabor patches) (Gomes & Semin, 2020). However, an increment in vigilance results in the sacrifice of the foraging activity, creating the referred trade-off between the two survival activities.

Stress Rating: As a subjective measure of the participants' stress feeling during the experimental task, they were asked to assess, on a 10 points visual analogue scale (ranging from 'not stressed at all' to 'very stressed'), how stressed they felt during the experiment.

Sweat Ratings: At the end of the experiment, and after an approximately 5-min break (to reduce habituation effects), participants were told that they will assess how intense and pleasant an odor stimulus was. They did not receive the information that this odor stimulus

was the same that they were exposed to during the experiment and were asked to wear a blindfold in order to preclude them from seeing the amber glass vial and the pad portions in it. Then the experimenter asked them to smell the vial and rate from 0 meaning ‘not at all’ to 7 meaning ‘very much’ how intense or pleasant the stimulus was, writing down the participants' answer. The procedure was then repeated for the remaining rating (the order of these two ratings was counterbalanced between participants). Contrary to the other employed scales in the current study, which were 10-point visual analogue scales, a 7-point Likert scale was used here to allow participants to give their answers verbally without removing the blindfold.

Display

The experiment was programmed using Experiment Builder (Version 1.10.1630, SR Research, 2016). To display the experiment an Asus VX238H 23” Full HD LED monitor (1920×1080) with a refresh rate of 60 Hz, connected to a Dell OptiPlex 755 were used.

To record participants’ ocular movement data, we used an Eyelink 1000 plus eye tracker (SR Research) with a sampling rate of 1000 Hz. The eye tracker was calibrated, using a standard 5-point calibration procedure, to the participants' right eye. Between trials, a drift correction procedure was used to ensure that the participants started each trial with their gaze focused on the center of the monitor.

Participants’ responses were collected using a standard keyboard.

In order to restrict participants’ head movement and to ensure a constant viewing distance of 55 cm, a chin and forehead rest was used.

Procedure

Each experimental session began by thawing the sweat sample an hour prior to the start of the experiment. After entering the lab, participants were asked to sign an informant consent and then instructed to fill out a demographic questionnaire (e.g., age, sexual orientation). Participants received the instructions for the "foraging-vigilance" task. They were informed that their final reward would be contingent upon their performance in the experiment: they would receive a course credit or 5€ for the participation, but they could win up to 5€ more. They were also informed about the value of the monetary rewards and punishments during the task. The instructions were exactly the same across the 3 sweat conditions.

Participants were asked to place their head on the chin and forehead rest. An amber glass vial (volume: 60 cm^3; aperture diameter: 28 mm) containing one of the three sweat conditions (i.e. fear, rest, or no-sweat) was placed 2 cm below the participants' nostrils and opened by the experimenter, who left the room immediately. No information was given regarding the content of the vials. Participants performed 15 practice trials, followed by the main task (50 trials of which 20 were change-trials).

At the end of the experiment participants assessed how stressed they felt during the experiment. Then, after a short pause (≈ 5 minutes) – during which the experimenter calculated rewards - participants were asked to rate the pleasantness and intensity of the sweat sample to which they were exposed. Lastly, they were paid in accordance with their performance.

In total the experimental procedure had an average duration of 45 minutes.

Data Preparation

In order to detect and correct for possible calibration problems, the eye-tracker data were visually inspected trial-by-trial for all participants. Trials with clear calibration problems were corrected by manually adjusting all the fixations and saccades (< 7% of the trials).

After the correction procedure the mean percentage of time per trial that the participants' gaze was focused outside of the central letter discrimination task was computed (i.e., the mean percentage of vigilance time; see Figure 2). In other words, the percentage of vigilance time concerns the time that the participant's gaze was located outside the central orange rectangle displayed in Figure 2, which represents the area where the letter matrices were displayed.

Figure 2: An example of a representative trial as viewed in the software used to extract and analyze the eye-tracker data (i.e., DataViewer; SR Research). The small blue circles represent each fixation of the participant (the blue numbers are the duration of each fixation in milliseconds). The elements in orange represent the interest areas. The outer orange circle concerns the limit of the task area. Any fixation or saccade outside of this area was considered spurious. The central rectangle delimits the area where the letter matrices were displayed. Vigilance time concerns the percentage of time that the participant's gaze was focused outside of the letter discrimination task, represented in this image by the small blue circles out of the central orange rectangle.

As in Gomes & Semin (2020), only no-change trials (30 trials) were considered to compute the vigilance time because these are the ones that had a fixed 20s duration. Due to the randomization of the moment that the changes start happening, change trials had random

durations. Thus, considering them to compute the percentage of vigilance time could have created a confound.

Regarding the central letter discrimination task (i.e. the foraging activity), the mean number of correctly identified target letters, as well as the mean number of no-answers, per trial were computed (once again, only the no-change trials were considered due to the same reasons mentioned earlier).

Concerning the capacity to avoid the threatening changes, the percentage of correctly detected changes, and the mean reaction time in pressing the escape key were computed per participant.

All the recorded variables were checked for outliers per chemosignals condition, identified as values exceeding 2.5 median absolute deviations (Leys et al., 2013). The outlier values (≤ 5% of data in all the analyzed variables) were then replaced to be one unit above the next extreme score on that variable (Field, 2014).

All the computed variables were extracted using DataViewer (SR Research).

All data will be made available upon request.

Statistical analysis

Sweat Donors

Regarding the sweat weights, and because the assumption of normality was not verified, a non-parametric Wilcoxon signed-ranks test was used to examine whether the distinct emotion-induction sessions resulted in different amounts of produced sweat. Possible differences in the room temperature between the 2 sweat collection sessions were also examined using a Wilcoxon signed-ranks test.

As for the self-reported affect, and because the data was not normally distributed, separated non-parametric Wilcoxon signed-ranks tests were conducted to examine possible

differences in the several dependent variables, across conditions. Considering the descriptive nature of this data, no p-value adjustments for multiple comparisons were performed.

Sweat Receivers

Due to the possible correlation between the different recorded variables, we examined the possible differences in vigilance behavior between different chemosignals conditions (the hypothesis regarding vigilance strategies; H1) using a one-way MANOVA. The chemosignal conditions (fear, rest, and no-sweat) were used as the between-subjects factor, and the mean percentage of vigilance time (eye-tracker data), the mean number of correctly identified target letters, as well as the mean number of no-answers, per trial, were entered as dependent variables. Regarding the threat avoidance hypotheses (H2 and H3), another one-way MANOVA was used to examine possible differences between chemosignal conditions. Once again, the chemosignal conditions (fear, rest, and no-sweat) were used as the between-subjects factor. The percentage of detected changes and the mean reaction time in pressing the escape key constituted the dependent variables. For both MANOVAs, if a significant multivariate main effect of the chemosignal conditions were revealed, then we examined each dependent variable using separate one-way ANOVAs. Post-hoc comparisons were performed using the Bonferroni correction procedure.

Additionally, Bayesian hypothesis testing was used to quantify the relative strength of evidence for either the null or the alternative hypotheses (e.g., Faulkenberry, 2018). Thus, one-way Bayesian ANOVAs were used to examine each dependent variable. These ANOVAs were performed using non-informative prior settings (*r scale fixed effects* = .5; *r scale random effects* = 1). The interpretation of the Bayes factor (BF) was conducted following the classification proposed by Lee and Wagenmakers (2013).

Moreover, to explore possible differences in the participants' perceived stress between the chemosignal conditions, a one-way ANOVA was conducted.

Lastly, to examine possible differences in the perceived intensity of the sweat samples (the data were not normally distributed) – a Kruskal-Wallis test, using the chemosignal conditions as a between-subjects factor, was performed. Regarding the perceived pleasantness, possible differences between chemosignal conditions were examined using a one-way ANOVA.

The researcher who analyzed the data was not aware of the chemosignal conditions. All the analyses were run using the JASP (JASP Team, 2020) and IBM SPSS (version 25.0; IBM Corp., Armonk, NY).

Results

Sweat Collection

Considering the sweat weight, a non-parametric Wilcoxon signed-ranks test showed significant differences between the fear and the rest condition (N = 8; Z = -2.52; p =.008). Specifically, participants produced significatively more sweat in the fear condition (*Mdn* = .20g; *IQR* = .16 – .24) than in the neutral condition (*Mdn* = .09g; *IQR* = .05 – .15), indicating that the emotional manipulation directly influenced the sweat production (see Figure 3). Moreover, regarding room temperature, another non-parametric Wilcoxon signed-ranks test revealed no significant differences (Z = -.18; p = 1.000) between the fear and the rest sweat collection sessions, ruling out the role of temperature in sweat production.

Figure 3: Mean sweat production, in milligrams, per sweat collection. Error bars represent 95% within-subject confidence intervals.

With regard to the self-reported feelings (see figure 4), non-parametric Wilcoxon signed-rank tests revealed that, participants reported significatively more fear (N = 8; Z = -2.52; p = .008) in the fear condition (*Mdn* = 7.25; I*QR* = 4.63 – 7.73) than in the rest condition (*Mdn* = .00; *IQR* = .00 – .13). On the other hand, participants in the rest condition (*Mdn* = 9.00; *IQR* = 2.33 – 10.00) reported significatively more calmness (N = 8; Z = -2.52; p = .008), than participants in the fear condition (*Mdn* = 1.05; *IQR* = .20 – 1.78). Thus, these results point to a successful emotional manipulation during the sweat collection. Surprisingly, no statistically significant differences were observed in the reported neutral affect between the fear and the rest conditions (N = 8; Z = -1.58; p = .156). Moreover, the results showed significant differences in the reported disgust (N = 8; Z = -2.37; p = .016), amusement (N = 8; Z = -2.53; p = .008), and happiness (N = 8; Z = -2.37; p = .016). Explicitly, participants reported more disgust in the fear (*Mdn* = 3.20; *IQR* = 1.95 – 5.15) than in the rest condition (*Mdn* = .00; *IQR* = .00 – .03), and more amusement and happiness in the rest (amusement: *Mdn* = 6.25; *IQR* = 5.13 – 7.23; happiness: *Mdn* = 7.75; *IQR* = 6.35 – 9.10), than in the fear condition (amusement: *Mdn* =.70; *IQR* = .00 – 1.85; happiness: *Mdn* = .15; *IQR* = .00 – .90). No statistically significant differences were observed for the reported anger (Z = -1.36; p = .29), surprise (Z = -1.12; p = .313) and sadness (Z = -.34; p = .781).

Figure 4: Mean reported feelings by sweat donors, per sweat collection. Error bars represent 95% within-subject confidence intervals.

Sweat receivers

Regarding vigilance behavior (H1), a one-way MANOVA revealed no significant main effect of the chemosignal conditions [*Pillai's Trace*= .07, $F(6, 110)= .63$, $p= .707$, $\eta^2p= .03$], indicating that the vigilance behavior was similar across the 3 different conditions. In other words, the exposure to the 3 chemosignal conditions did not modulate the mean percentage of vigilance time (eye-tracker data) or the foraging activity (central letter discrimination task). Moreover, Bayesian one-way ANOVAs revealed moderate evidence in favor of the null hypothesis for all the 3 dependent variables (mean percentage of vigilance time: BF_{01} = 3.21 ± 3.80%; mean number of correctly identified letters: BF_{01} = 5.81 ± 2.90%; mean number of no-answers: BF_{01} = 4.95 ± 3.1%). The mean values of each dependent variable per chemosignal condition can be found in Table 1.

Concerning the threat avoidance hypotheses (H2 and H3), as expected, a one-way MANOVA revealed a significant main effect of the chemosignal conditions [*Pillai's Trace*= .23, $F(4, 112)= 3.62$, $p= .008$, $\eta^2p= .12$], suggesting that the capacity to avoid the threatening changes differed across the 3 conditions. A one-way ANOVA regarding the accuracy in detecting threatening changes revealed no significant differences between the 3 chemosignal conditions [$F(2, 56)= 1.08$, $p= .346$, $\eta^2p= .04$]. A Bayesian one-way ANOVA showed moderate evidence in favor of the null hypothesis (BF_{01} = 3.31 ± 3.00%), confirming that the exposure to the different chemosignal conditions had no effect on the number of avoided threatening events (for the mean percentage of avoided threatening changes per chemosignal condition see Table 1).

Table 1: Mean values and standard deviations (in parenthesis) of each non-significant dependent variable per chemosignal condition.

However, concerning the reaction time in pressing the 'escape' key (H3), a one-way ANOVA revealed a significant main effect of the chemosignal condition [$F(2, 56)= 5.97$, $p= .004$, $\eta^2p= .18$]. A Bayesian one-way ANOVA confirmed that there was moderate (near to strong) evidence in favor of the alternative hypothesis ($BF_{10} = 9.91 \pm 1.60\%$). In line to what was hypothesized, post hoc tests showed that participants exposed to fear chemosignals pressed the escape key significantly faster ($M= 2502.37$ ms; $SD= 223.92$) than participants exposed to rest chemosignals ($M= 2736.29$ ms; $SD= 196.04$; $p= .009$; *95% CI* [-419.52; -48.32]) or those in the no-sweat condition ($M= 2712.43$ ms; $SD= 285.24$; $p= .021$; *95% CI* [-396.16; -24.95]). No significant differences were observed between the rest chemosignals and the no-sweat condition ($p= 1.000$; *95% CI* [-166.82; 213.55]) (see figure 5).

Figure 5: Mean reaction time (in milliseconds) in pressing the escape key. Participants in the fear condition pressed the escape key significantly faster than participants in the rest and no-sweat conditions. No statistically significant differences were observed between the rest and no-sweat conditions. * $p < .05$; ** $p < .01$; n.s. $p > .05$.

Moreover, regarding the subjective stress feeling, no significant differences were observed between the chemosignal conditions [$F(2, 55)= .37$, $p= .690$, $\eta^2p= .01$], indicating that there were no distinct subjective stress experiences between conditions.

Lastly, regarding the perceived intensity, results revealed no significant differences between the chemosignal conditions [$X^2_{KW}(2)= .85$, $p= .655$]. Similarly, concerning the

perceived pleasantness, results also revealed no significant differences between the chemosignal conditions [$F(2, 56)= .35$, $p= .709$, $\eta^2 p= .01$] (see table 2).

Table 2: Means and standard deviations (in parenthesis) of the subjective ratings of the sweat stimuli.

Discussion

The study reported here was designed to examine how the exposure to fear chemosignals shape (a) the trade-off between intake activities (benefits) and vigilance behavior (threat monitoring), and (b) the effectiveness in avoiding threatening events. To examine this, we relied on a vigilance paradigm (Gomes & Semin, 2020) that simulates in the laboratory a "foraging under threat" scenario, which is thought as the ideal context to study vigilance (see Beauchamp, 2015; Gomes & Semin, 2020). This paradigm was used in conjunction with an eye-tracker, allowing us not only to examine the participants' effectiveness in detecting and reacting to the threat-related events but also to explore how they allocate their attentional resources.

Considering the possible predicted outcomes, the obtained results revealed that the exposure to fear chemosignals (compared to rest chemosignals and no-sweat) modulated neither the participants' vigilance strategies nor the number of threatening changes they avoided. Instead, the results indicate that the fear chemosignals speeded up their responses to the threat-related events. In other words, the exposure to fear chemosignals revealed its effects not by modulating participant's threat-monitoring strategies, but by inducing faster answers when a threat-related event was identified. An interesting implication of these findings is that they suggest that olfactory danger cues may play a role in 'mutual warning' in the human species. This 'mutual warning-like phenomenon' seems not to be driven by a

higher number of threatening events that are avoided but rather by the fact that individuals exposed to the danger signal respond faster to threatening events than those who did not receive it (for a similar argument in animal research see, for instance, Martín et al., 2006). Thus, in addition to previous research pointing fear chemosignals as an alarm cue that increases sensory acquisition in its recipients (e.g., de Groot et al., 2012, 2014, 2018), our results suggest a practical advantage of being exposed to fear chemosignals in coping with danger events (i.e. faster threat avoidance reactions).

From an evolutionary perspective, this capacity to communicate warning signals through olfaction may have been advantageous in terms of survival. As already mentioned, 'mutual warning' involves transferring information between conspecifics (see Beauchamp, 2015). Hence, environmental factors (e.g., visual barriers; light conditions; noisy environments) that interfere with information transfer decrease the effectiveness of the mutual warning. However, olfactory communication, by remaining reliable in the presence of such factors (i.e., when other senses are blocked; see Lundström & Olsson, 2010), may have constituted a source of information capable of overcoming environmental impediments.

Interestingly, the perceived intensity and pleasantness between the chemosignals conditions revealed no significant differences, ruling out the possibility that either dimension could have contributed to the observed effects. Following previous studies (e.g., de Groot et al., 2014; 2015; Radulescu & Mujica-Parodi, 2013), this suggests that the observed data pattern was not driven by consciously perceived characteristics of the chemosignals but by the emotional information that they carry.

The faster defensive reactions that were seen in the fear chemosignals condition may be explained by a readiness (or preparedness) state triggered by this olfactory warning signal. In fact, fMRI data from a study using anxiety body odors (i.e. sweat collected from humans awaiting an academic examination; Prehn-Kristensen et al., 2009) have shown that exposure

to this type of olfactory stimulus (compared to exercise sweat) results in the activation of brain areas responsible for, among others, the regulation of emotional responses and actions (e.g., posterior cingulated cortex; see Cato et al., 2004) and attentional control (e.g., anterior cingulated cortex; Botvinick et al., 1999). Another fMRI study employing sweat from individuals experiencing high levels of stress (i.e. sweat collected during first time skydiving; Mujica-Parodi et al., 2009) reported that the exposure to this specific type of body odors (compared to exercise sweat) results in the activation of the amygdala, a threat detection-related brain area (e.g., LeDoux, 1996; Morris et al., 1999). On one hand, the activation of this network involving attention, emotion, and threat detection-related areas suggests that this type of olfactory stimulus is processed in a privileged fashion being treated as a warning stimulus. On the other hand, this activation pattern indicates that fear-related chemosignals can signal an imminent source of danger and possibly prepare its receiver to process and react to it. This preparatory state induced by anxiety/high-stress sweat (compared to exercise sweat) also seems to be confirmed by studies using event-related potential (ERPs). For instance, Rubin and colleagues (2012) revealed that exposure to this specific type of olfactory danger signals was associated with heightened late positive potentials (LPPs) to not only angry faces but also neutral and emotionally ambiguous facial expressions (Rubin et al., 2012). Following the authors' reasoning, these results indicate that this olfactory stimulus may modulate humans' attention, enhancing attentiveness to otherwise irrelevant stimuli. We speculate that the results obtained in our study are likely to be driven by a similar mechanism. Exposure to fear chemosignals increases the attentiveness of the participants (i.e. readiness state) to the small changes in the peripheral Gabor patches, allowing them to identify the threat-related events faster than participants exposed to rest chemosignals or no-sweat. In fact, it is even possible that this hypothetical readiness state triggered by fear-related chemosignals is not danger-specific. That is, exposure to danger-related olfactory cues may

increase attentiveness in general or just to peripherally presented stimuli (as suggested by the activation of facial muscles involved in displaying fear facial expressions, which increase the size of the visual field; see de Groot et al., 2012; Susskind et al., 2008). Further research manipulating the visual location, where both the rewarding and threat-related events are presented, may be valuable to unriddle the specific attentional mechanisms behind the observed effects.

An important question that needs to be clarified is why the exposure to fear chemosignals (compared to rest chemosignals and no-sweat) does not modulate participants' vigilance behavior. Vigilance, as an alertness state that governs risk monitoring, tends to increase as the perceived threat risk increases, which consequently results in an increment of the stress levels (see Beauchamp, 2015). Indeed, some animal studies have shown that vigilance behavior is influenced by stress hormone levels (cortisol and norepinephrine; e.g., Hawlena & Schmitz, 2010; Voellmy et al., 2014; but see Tkaczynski et al., 2014). We argue that in the reported study the exposure to fear chemosignals did not increase the perceived threat risk (i.e. the participants' alertness) – as shown by the absence of significant differences between chemosignals conditions in the reported stress felt during the experiment. This resulted in the absence of significant differences in vigilance behavior. Instead, the exposure to fear chemosignals just modulated participants' behavior in a more basic way increasing, as already mentioned, their attentiveness to otherwise non-relevant changes. However, this remains mere speculation that needs to be addressed in future research.

An important limitation of the current study is the fact the 3 chemosignal conditions were manipulated using a between-subjects' design, which by definition leads to weaker conclusions than a within-subjects comparison. Taking into account that the current study is one of the first steps taken to explore the role of fear chemosignals in modulating vigilance and threat detection efficacy, these results should be interpreted with caution. It is also

important to note that, in the current study, vigilance behavior was operationalized as the percentage of time that the participants' gaze was allocated to scan the surroundings. However, this is just one of several possible measures that can be considered to describe risk-monitoring strategies (e.g. scan duration and frequency; see Beauchamp, 2015). To improve our understanding of how fear chemosignals modulate on human risk monitoring and threat detection strategies, we need different vigilance indicators. Also, controlling receivers' menstrual cycles and hormonal contraceptives intake, which have been shown to alter the perception and effects of body odors (e.g., Hornung et al., 2019; Nabergoj et al., 2020; Parma et al., 2012) may strengthen such research.

Taken together, our results indicate that fear chemosignals may constitute an important warning signal for human beings driving a 'mutual warning-like phenomenon'. The current findings suggest that exposure to fear chemosignals is advantageous to cope with threat-related events not by modulating threat monitoring, but by preparing receivers for faster reactions.

Conflict of interests

None.

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Figure Captions

Figure 1: Example of a letter matrix surrounded by 8 Gabor patches. The arrow illustrates a possible change in one of the 8 Gabor patches.

Figure 2: An example of a representative trial as viewed in the software used to extract and analyze the eye-tracker data (i.e., DataViewer; SR Research). The small blue circles represent each fixation of the participant (the blue numbers are the duration of each fixation in milliseconds). The elements in orange represent the interest areas. The outer orange circle concerns the limit of the task area. Any fixation or saccade outside of this area was considered spurious. The central rectangle delimits the area where the letter matrices were displayed. Vigilance time concerns the percentage of time that the participant's gaze was focused outside of the letter discrimination task, represented in this image by the small blue circles out of the central orange rectangle.

Figure 3: Mean sweat production, in milligrams, per sweat collection. Error bars represent 95% within-subject confidence intervals.

Figure 4: Mean reported feelings by sweat donors, per sweat collection. Error bars represent 95% within-subject confidence intervals.

Figure 5: Mean reaction time (in milliseconds) in pressing the escape key. Participants in the fear condition pressed the escape key significantly faster than participants in the rest and no-sweat conditions. No statistically significant differences were observed between the rest and no-sweat conditions. * $p < .05$; ** $p < .01$; n.s. $p > .05$.

	Fear		Rest		No-sweat	
Variables						
Mean % of vigilance Time	.18	(.06)	.20	(.07)	.17	(.07)
Mean number of identified target letters	12.84	(2.23)	12.44	(2.58)	13.07	(2.57)
Mean number of no-answers	4.32	(1.38)	4.55	(1.44)	4.05	(1.65)
Accuracy in detecting threat (%)	.42	(.17)	.50	(.14)	.44	(.21)

	Fear		Rest		No-sweat	
Subjective ratings of sweat stimuli						
Intensity (1 = very weak to 7 = very strong)	2.00	(.89)	2.11	(1.24)	1.84	(1.12)
Pleasantness (1 = very unpleasant to 7 = very pleasant)	3.95	(1.43)	4.11	(1.56)	4.32	(1.11)

Figure 1

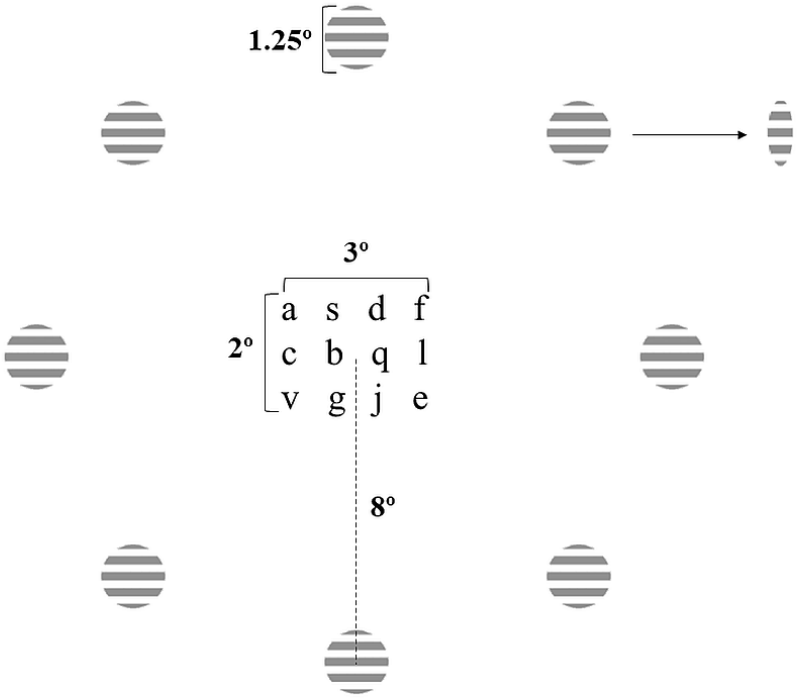

Figure 2

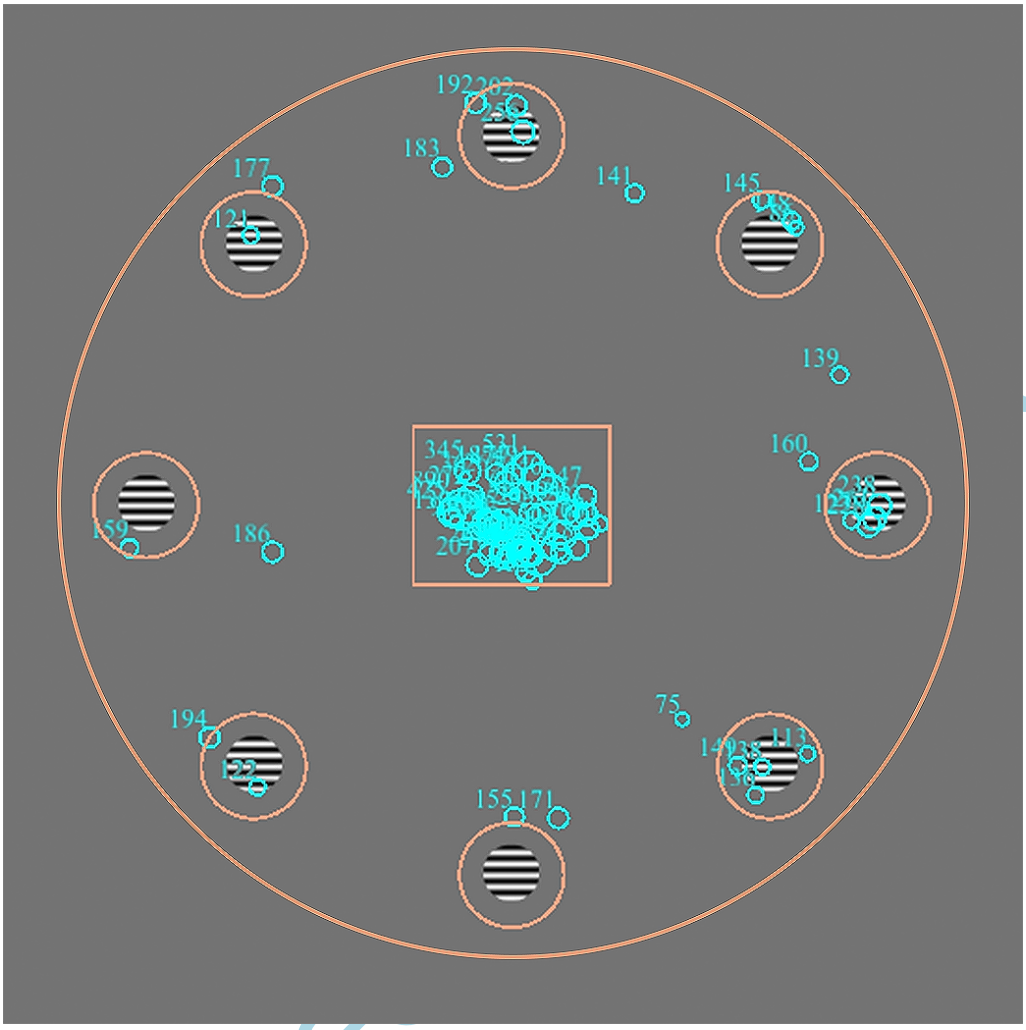

Figure 3

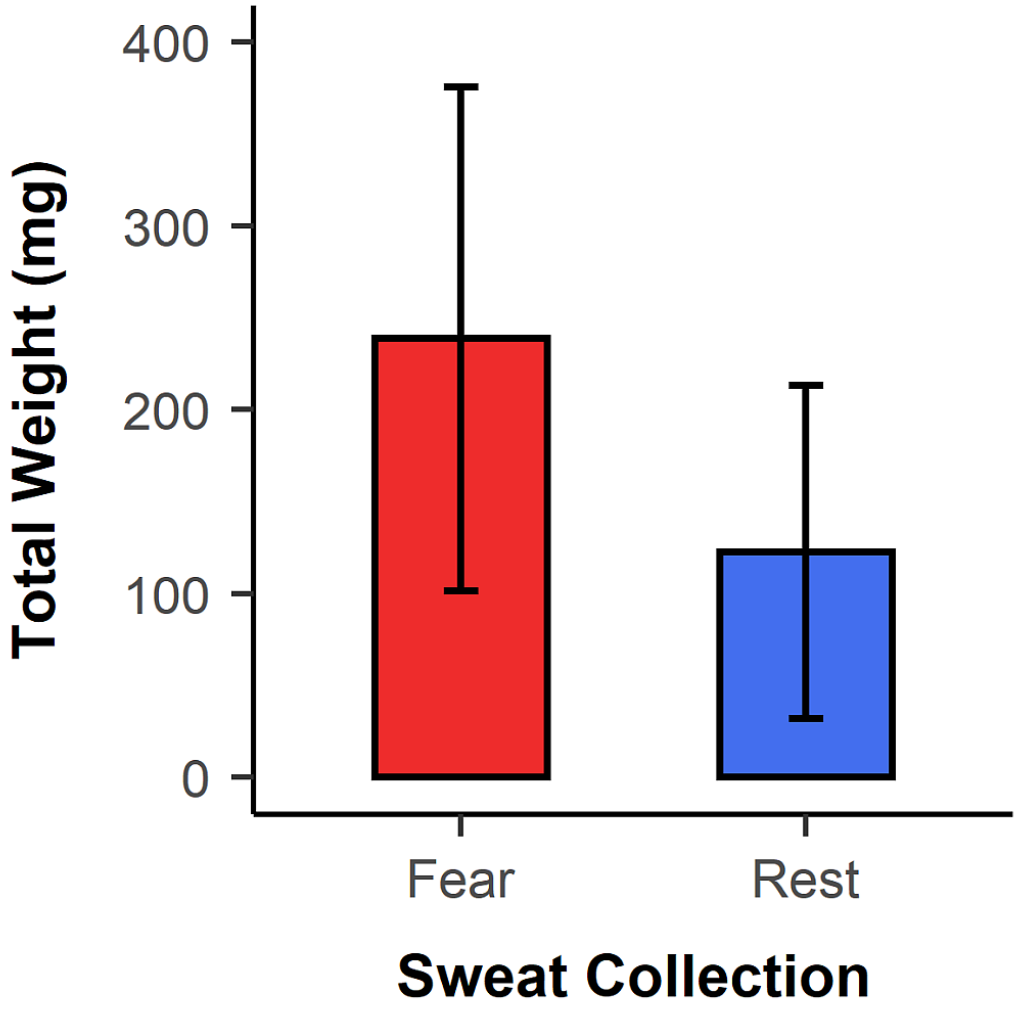

Figure 4

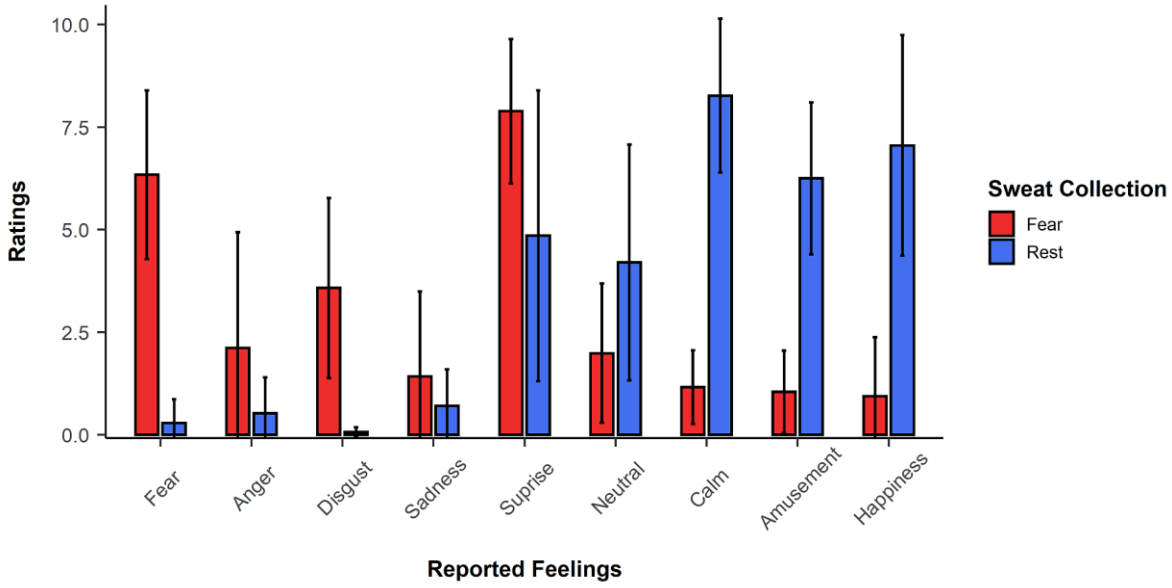

Figure 5