MODULATING VIGILANCE:
THE DIFFERENTIAL CONTRIBUTIONS OF FEAR CHEMOSIGNALS AND GROUP CONTEXTS

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To Rita Costa
for all the unconditional support and words of encouragement during this long journey

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RESUMO

Noutras espécies sociais que não a humana, as estratégias individuais de monitorização de risco (i.e. vigilância) e a capacidade de detetar e evitar estímulos ameaçadores são moduladas pelos co-específicos. Por um lado, a presença de co-específicos resulta numa diminuição dos recursos atencionais alocados pelo indivíduo à vigilância, permitindo um maior investimento noutras atividades (e.g., procura de alimento). Por outro lado, co-específicos expostos a uma fonte de perigo, emitem pistas sensoriais (e.g., sons ou odores corporais) que alertam/preparam o indivíduo para lidar com eventos ameaçadores. Pretende-se, no presente trabalho, explorar o papel direto (pela presença) e indireto (através de odores corporais de medo) que os co-específicos assumem ao modular estratégias individuais de vigilância e deteção de ameaça na espécie humana.

No primeiro estudo, investigou-se se os humanos usariam estratégias de vigilância semelhantes a outras espécies sociais. Com recurso a um paradigma que permite o estudo das estratégias de vigilância mediante a utilização de um *eye-tracker*, demonstrou-se que a presença de co-específicos (vs. condição individual), tal como noutras espécies sociais, diminui os recursos alocados à vigilância, permitindo um investimento maior noutras atividades, embora prejudicando a capacidade de detetar/evitar ameaças.

No segundo estudo foi investigado se, tal como noutras espécies, a redução de vigilância poderia estar associada a um sentimento acrescido de segurança despoletado pela presença dos outros. Os resultados obtidos parecem confirmar este efeito, na medida em que para um indivíduo, imaginando-se na presença de co-específicos (2 amigos ou 2 estranhos vs. sozinho), era menor o sentimento de ameaça assim como a probabilidade percebida de sair magoado de situações ambíguas de perigo.

O terceiro estudo centrou-se nos efeitos modulatórios de diferentes contextos de grupo nas estratégias de vigilância. Os resultados obtidos indicam que perceber co-específicos como cooperadores ou competidores (vs. mera presença) não modula, de forma distinta, o comportamento de vigilância. Sob a égide de literatura anterior, é possível especular que o efeito destes contextos de grupo poderá ser observado tão-somente perante situações em que indivíduo e co-específicos presentes podem observar-se e interagir entre si.

No quarto estudo, que visou compreender de que forma a exposição a odores corporais de medo poderia modular estratégias de vigilância e a capacidade de detetar e evitar eventos ameaçadores, concluímos que esta pista sensorial (vs. odores corporais neutros e ausência de odores) não modula diretamente as estratégias de vigilância, mas parece induzir um estado de preparação/prontidão nos seus recetores, levando-os a detetar e reagir mais rapidamente a eventos ameaçadores.

O último estudo replica literatura anterior, demonstrando que a exposição a odores corporais de medo ativa mecanismos associados a um aumento da aquisição sensorial. Evidenciou-se ainda que amostras de suor podem ser reutilizadas após uma primeira utilização de 20 minutos, permitindo especular sobre as propriedades de volatilidade das moléculas que transportam informação associada ao medo.

Em conclusão, os resultados obtidos nesta tese sugerem que co-específicos modulam, direta e indiretamente, as estratégias individuais de vigilância e deteção de ameaça. Destaca-se assim a importância de variáveis sociais para o estudo e aprimoramento da monitorização do risco nas sociedades contemporâneas.

ABSTRACT

In non-human social species, risk-monitoring strategies (i.e. vigilance) and an individuals' capacity to detect and avoid threat stimuli are modulated by conspecifics. On the one hand, the presence of conspecifics results in a reduction of the attentional resources allocated to vigilance, which allows higher investment in other activities (e.g., foraging). On the other hand, conspecifics exposed to a source of danger release sensory cues (e.g., sounds or body odors) that alert/prepare the individual to deal with a possible threatening event. The main goal of the present thesis was to explore the direct (through their presence) and indirect (through fear body odors) role of conspecifics in modulating the individual strategies of vigilance and threat detection in human beings.

In the first study, we investigated whether humans use vigilance strategies similar to other social species. Employing a paradigm designed to study vigilance using an eye-tracker, we showed that the presence of conspecifics (vs. an alone condition) reduced the attentional resources allocated to vigilance. As in other social species, this vigilance reduction allowed a higher investment in other activities but impaired the participants' capacity to detect and avoid threatening events.

In the second study, following animal research, we investigated whether the vigilance reduction observed in the first study might be associated with an increased safety feeling triggered by conspecifics' presence. The results seem to confirm this effect, showing that by envisioning themselves in the presence of conspecifics (either two friends or two strangers vs. alone) participants reduced their feelings of being threatened and their perceived probability of being harmed in danger situations that are ambiguous.

In the third study, we explored if different group contexts modulate vigilance strategies. The obtained data indicated that perceiving conspecifics as cooperators or competitors (vs. mere presence) did not modulate vigilance behavior differently. Drawing on earlier literature, it is possible to speculate that the role of these different group contexts governing vigilance emerges only when conspecifics can observe and interact among them.

The fourth study focused on the role of being exposed to fear body odors in modulating vigilance strategies and the capacity to detect and avoid threatening events. Our data showed that fear body odors (vs. rest body odors or a blank) did not modulate vigilance *per se* but triggered in receivers a preparedness/readiness state that allows them to detect and react quickly to threatening events.

In the fifth study, we replicated previous literature evidencing that the exposure to fear body odors triggers mechanisms associated with an increased sensory acquisition. We also evidenced that samples of fear body odors can be re-used after a first use of 20 minutes. This allowed us to speculate about the volatility of the molecules involved in carrying the fear-related information.

In sum, the results obtained in the current thesis suggest that conspecifics modulate directly and indirectly individuals' vigilance strategies and threat detection. These findings highlight the critical role of social variables in studying and improving risk-monitoring in modern societies.

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Chapter I:

Introduction and Overview

Introduction

During ancient and modern times, exposure to harmful events has been a repeated feature of animal life. As a result, strategies and mechanisms to efficiently avoid getting harmed were and continue to be crucial for present-day survival and well-being. Human beings, as an animal species, are no exception. Many physical and behavioral characteristics displayed by humans are thought to be the result of several adaptations, sculpted by evolutionary pressures (e.g., Seligman, 1971), that evolved to cope with different danger sources (e.g., predators, noxious stimuli). Such adaptation seems to be still a pivotal part of our daily lives (e.g., Öhman & Mineka, 2001). This becomes obvious when we consider that, despite living in modern societies filled with mechanisms designed to increase and maintain our safety (e.g., solid buildings, police, traffic rules, animal control), we are still continuously exposed to threatening events in diverse contexts. Harmful animals (e.g., snakes; Kasturiratne et al., 2008), irresponsible drivers, high toxic pollution, fragile financial markets, and aggressive conspecifics constitute just a few examples of daily events threatening the individual and collective and are best avoided (for a similar argument see Kameda & Tamura, 2007).

Notably, the first and paramount step to succeed in avoiding harmful events is the rapid detection of cues indicating that a dangerous event is about to occur. In fact, as noted by Kameda & Tamura (2007) and exemplified in Reason (1997) and Slovic (1987, 1999), this requires constant and efficient monitoring. When monitoring fails, then the likelihood of an early detection of dangerous events is considerably reduced and can lead to serious and often irretrievable damage to an individual or groups of humans. Thus, identifying factors that could impair or improve risk monitoring and help avoid threatening events constitutes an essential research question that remains without clear answers.

Although very little is known about how risk monitoring is modulated in humans, some speculation can be made if one considers findings from animal behavior research. In non-human animals, the need to avoid dangerous events is considered to be the evolutionary base of vigilant behavior (hereinafter referred to just as vigilance), which is considered a central mechanism for danger avoidance across many animal species (for a detailed review see Beauchamp, 2015). In animal research, vigilance has been defined and operationalized as the duration and frequency of scanning the surrounding environment for danger (e.g., Beauchamp, 2008). Hence, in order to stay safe and healthy, a wide range of animal species seem to constantly trade-off vigilance activity with other homeostasis-relevant activities (e.g., foraging, mate searching, sleep) (see Beauchamp, 2015). In other words, an increment in vigilance enhances the chances to avoid an approaching danger at the cost of resources (i.e. time) that are relevant for other survival-relevant activities, such as foraging. Thus, the key to maintain homeostasis seems to be, at least in part, developing strategies that maximize monitoring efficacy without neglecting other relevant activities (e.g., intake activities) (e.g., Caraco, 1979; Lima, 1987). This was pivotal in the evolutionary pathway of different species (e.g., Creel et al., 2014), and is central to understanding risk monitoring. In solitary species, the aforementioned trade-off is straightforward, being regulated individually (Bednekoff & Lima, 1998) and explained by factors that directly compromise an individuals' safety (e.g., the presence of predators). In other words, vigilance levels in solitary species can be explained by considering only individual variables (e.g., the threat-risk associated to each subject). However, when it comes to social species, the adjustment of such trade-off becomes more intriguing, as it is also modulated by variables such as the presence of conspecifics. In fact, vigilance research in animal herds has shown that the mere presence of conspecifics can affect vigilance in different ways. For instance, the presence of conspecifics can signal increased safety or increased danger, which can lead to reducing or enhancing an individuals' vigilance. Additionally, conspecifics can also emit sensory cues (i.e. visual, auditory, mechanical, and/or olfactory signals), signaling the presence of threat sources. These sensory signals can alert (i.e. enhancing vigilance) and prepare (i.e., modulating danger avoidance responses) proximal individuals to deal with the presence of dangerous stimuli (see Beauchamp, 2015). Hence, to study vigilance and danger avoidance in social species, it is crucial to consider the group's many roles in modulating individual behavior.

Humans are inherently social species and there is a wide range of documented phenomena (e.g., conformity, Asch, 1956; emotional contagion, Hatfield et al., 1993; social facilitation, Guerin, 1986; Triplett, 1898; Zajonc, 1965), especially social psychological research showing that the direct (e.g., being in group vs. individual situations; Zajonc, 1965) or the indirect (e.g., being exposed to sensorial cues such as emotional body odors; de Groot et al., 2017) presence of others can strongly affect individual behavior. However, when the subject is danger monitoring and avoidance in humans, then the role of conspecifics' presence – with the exception of a handful of observational studies (e.g., Barash, 1972; Dunbar et al., 2002; Wirtz & Wawra, 1986) – seems to have been neglected, leaving behind a number of open questions. For instance, to what extent do humans perform differently in a group compared to individual situations when it comes to detect and avoid threatening events? Are humans capable of alerting and influencing conspecifics to react to danger? If so, what are the different sensorial cues that carry such information? Answering those questions could have tremendous practical implications, constituting one of the first steps to understand and improve risk monitoring in the most varied contexts in modern society (e.g., air traffic controller situations, financial monitoring, riot control, etc.). Thus, throughout this thesis, I intend to shed light on these issues. My aim is to explore how human beings, in individual or group scenarios, trade-off their attentional resources between vigilance and intake activities (i.e. foraging), and modulate the capacity of nearby conspecifics, through emotional (fear) body odors (i.e. chemosignals), in dealing with imminent threatening events. Although olfaction is not the sensorial modality that immediately comes to mind, this medium of communication has been substantially overlooked in research despite its potential role in monitoring danger and co-alerting others. It was selected here due to its primordial role in passing on survival information (Huart et al., 2013; Pause, 2012; Strausfeld & Hildebrand, 1999). In fact, this chemical sensorial modality, widely neglected regarding communication in human beings until recently (Parma et al., 2017), seems to have clear advantages when threat detection and mutual warning are considered. For instance, we are, even unconsciously, constantly sampling information of the surrounding environment through olfaction (breathing never ceases as long as we are alive). This information sampling is functional even when the other senses are blocked (i.e. volatiles can carry information in the darkness, noisy environments, or even surpass some environmental barriers; see Pause, 2017). Additionally, this form of communication is outside the control of both the sender and the receiver and therefore operates automatically. Warning chemosignals are released unintentionally when their sender is in a dangerous situation and processed unconsciously by their receiver (Semin & Gomes, under review). Additionally, communication through chemosignals sends out a message to the “herd”, or the collective, rather than to the individual. That is, once a chemosignal is released, it is not directed to someone in particular but becomes available to all individuals that can sample it. Chemosignals transmit their information even to conspecifics that are not aware of its sender. Taking this into account, olfaction constitutes a powerful yet subtle mean to communicate peril-relevant information, having potential advantages for survival in social species.

In the following sections of this chapter, I first provide an overview of animal and human research on the trade-off between vigilance and intake activities in group (compared to individual) situations, as well as the recent research in human communication through emotional (fear) chemosignals and their impact on vigilance and threat detection. I shall then introduce our main goals and questions, moving to a brief overview of the issues addressed in each of the following chapters. A description of the novel paradigm developed in our lab that allows us to examine vigilance in human beings with the aid of eye-tracker technology is also provided.

Vigilance: a danger avoidance behavior modulated by conspecifics' presence

Vigilance behavior and its modulation by the presence of conspecifics constitute one of the most studied phenomena in non-human animal species. In fact, the first published references to it can be found more than 100 years ago in the work of prominent Victorian British naturalists such as Henry Bates (1863), Thomas Belt (1874), and Francis Galton (1871, 1883). The latter, Galton – better known for his very controversial work in eugenics (e.g., Gillham, 2001) – had put forward one of the first descriptions of vigilance in social species. In his widely cited book "*Inquiries into human faculty and its development*", Galton (1883, pp. 51, 52), describing his own observations of the Damara cattle's behavior in contemporary Namibia's savanna, wrote (as quoted by Beauchamp, 2015, p. 1):

> *"…the cattle have to take care of themselves against the wild beasts, and they would infallibly be destroyed by them if they had not safeguards of their own… When he is alone it is not simply that he is too defenceless, but that he is easily surprised. …cattle are obliged in their ordinary course of life to spend a considerable part of the day with their heads buried in the grass, where they can neither see nor smell what is about them. A still larger part of their time must be spent in placid rumination, during which they cannot possibly be on the alert. But a herd of such animals, when considered as a whole, is always on the alert; at almost every moment some eyes, ears, and noses will command all approaches, and the start or cry of alarm of a single beast is a signal to all his companions. To live gregariously is to become a fibre in a vast sentient web overspreading many acres; it is to become the possessor of faculties always awake, of eyes that see in all directions, of ears and nostrils that explore a broad belt of air; it is also to become the occupier of every bit of vantage ground whence the approach of a wild beast might be overlooked. The protective senses of each individual who chooses to live in companionship are multiplied by a large factor, and he thereby receives a maximum of security at a minimum cost of restlessness."*

As I will further explore, although he did not explicitly use the word "vigilance" – firstly employed by Cameron (1908) 25 years later – Galton had pointed out in his report the most prominent factors governing risk monitoring (i.e. vigilance) in social species.

Similar to what was already mentioned in the previous section, Galton's report highlighted that monitoring the surrounding environment (i.e. being vigilant) is necessary for the survival of many animal species. This monitoring activity relies on the animal's different sensorial modalities, which may be vision (e.g., Wallace et al., 2013) audition (e.g., Basile et al., 2009), vibrotactile (e.g., Castellanos & Barbosa, 2006), and olfaction (e.g., Blumstein et al., 2008).

Galton’s reasoning then took into consideration the fact that vigilance is a costly activity in terms of attentional and, more specifically, time resources. He then considered that vigilance was not the only necessary activity for the animals’ survival. If animals allocate all their time and resources to vigilance, they will certainly detect a higher percentage of threatening events in their surroundings. However, they will also increase their chances of dying, for instance, by starvation. Thus, a constant trade-off between vigilance and other homeostasis-relevant activities, such as foraging for food, is a paramount component of animal life. Due to their relevance to understanding risk monitoring, the drivers of such trade-off have constituted the main subject of research regarding vigilance in non-human species (see Beauchamp, 2015). From this research, it is possible to conclude that the time invested in vigilance appears to be influenced by a multiplicity of intrinsic and extrinsic factors. Examples are energy demands (e.g., Bednekoff & Woolfenden, 2003), availability of food resources (e.g., Beauchamp, 2014; Krebs, 1974; Lazarus, 1978), environmental factors (e.g., light levels; Hilton et al., 1999), and - obviously, as a danger avoidance tactic - perceived threat risk (e.g., the presence of predators; Caraco et al., 1980a; Creel et al., 2014; Périquet et al., 2012). The latter is supposed to play one of the most prominent roles in modulating vigilance (i.e. especially when anti-predator vigilance is considered; Beauchamp, 2015). Hence, variables that affect the perception of threat risk must have a strong influence on vigilance.

Indeed, as noted earlier on, in Galton’s report and confirmed by a considerable volume of research – especially after the publication of the first mathematical model of anti-predator vigilance by Pulliam (1973) – one of these crucial variables is the presence of conspecifics. In social species (e.g., species that forage in groups) the presence of conspecifics appears to be, in general, understood as a signal of lower threat-risk (i.e. safety). This can be explained by many different hypothetical mechanisms. One of such mechanisms, not only described by Galton (1883) in the aforementioned report but also noticed in the work about the behavior of bird flocks by Bates (1863) and Belt (1874), is usually termed as the “many-eyes effect” (Caraco et al., 1980b). This mechanism, central to many models predicting vigilance reduction when in the presence of conspecifics, posits that the number of possible threat detectors is higher in group situations. In the words of Galton (1883, p. 51), when an individual is in the presence of conspecifics, then there is at “*…every moment some eyes, ears, and noses…”* monitoring the surrounding environment. This multiplicity of possible threat detectors increases the probability of detecting an approaching danger. Evidently, the many-eyes effect does not provide an increased safety without a related mechanism known as “collective detection” (also termed “mutual warning”). As also described in the aforementioned Galton’s quote, when a possible threat is detected, the threat detector can warn other group members for imminent danger. Thus, in a group situation, an individual can detect a threat himself or rely on other group members to warn him of an imminent dangerous encounter (e.g., Lima, 1990). Thus, both the many eyes-effect and the consequent collective detection increase the individual probability to avoid danger, allowing individuals to relax vigilance without compromising their safety.

Another competing hypothesis explaining the increment of safety in group situations is “risk dilution”. Contrary to the previous ones, risk dilution is not related to faster/efficient detection of threat sources provided by being in a group situation. This mechanism relies on a lower probability to be the target of a danger source when conspecifics are present. Considering a predator attack as an example, risk dilution posits that the more conspecifics are present in the vicinity, the lower the individual probability of being targeted (Bertram, 1978). In other words, the multiplicity of possible targets automatically reduces the individual’s likelihood of being chased by a predator, increasing in such a way the safety of group situations. This reduced the time allocated to vigilance.

Regarding the previously summarized mechanisms, although they have different natures and assumptions, all reach similar conclusions and predictions: the presence of conspecifics generally reduces the individual threat-risk. Consequently, the resources allocated to vigilance behavior tend to decrease as a function of the number of conspecifics in the vicinity (a phenomenon also known as group size effect; e.g., Bertram, 1980; Quenette, 1990; van Schaik, van Noordwijk, de Boer, et al., 1983). These resources can then be invested in other homeostasis-relevant activities (e.g., foraging), increasing individuals’ fitness. Interestingly, the effects of the presence of conspecifics’ are considered to be one of the main precursors of the evolution of group living, and consequently the sociality, in animal species (Pulliam & Caraco, 1984). In fact, although not clearly described or named, the different mechanisms hypothesized behind an increased safety in group conditions are presented as the basis of the most prominent theories regarding the evolution of group living. One example can be observed in Galton’s report (1871). Inspired by the *“Theory of Evolution by Natural Selection”* proposed by his cousin Charles Darwin (1859), Galton concluded that the evolution of gregariousness might have occurred to increase safety due to the many-eyes effect and collective detection. Another relevant approach was put forward by George C. Williams (1966) in his successful book titled *“Adaptation and Natural Selection”*. Briefly, the author defended that living in a group could be beneficial because individuals can use others as protection against predators (i.e. risk dilution effect). Furthermore, the author also hypothesized that the capacity to perceive conspecifics' alarm signals, acting defensively (i.e. collective detection), might have had a great adaptive value (Williams, 1966). Williams' idea gave rise, 5 years later, to another influential theory sketched by William D. Hamilton (1971) in his widely cited paper titled *"Geometry for the Selfish Herd"*. Using geometric models, the author explored the idea that the presence of conspecifics (i.e. risk-dilution) and a more central physical position in the group (see also Vine, 1971), shape the decreased probability of being targeted during a predator attack. The author concluded that, even in non-sociable species, natural selection may favor individuals that are in the presence of other conspecifics.

Independent of the mechanism thought to be driving it, a considerable volume of behavioral animal research has confirmed that vigilance rates tend to decline as group size increases. This phenomenon can be observed, for instance, in invertebrates (Fordyce & Agrawal, 2001), several bird species (e.g., Beauchamp & Livoreil, 1997; Lazarus, 1978; Radford & Ridley, 2007; Rieucau et al., 2010), and also mammals (e.g., Blumstein, 1996; Blumstein et al., 1999), including non-human primates (Gosselin-ildari & Koenig, 2012; van Schaik et al., 1983; but see Treves, 2000;). Interestingly, hormonal research in animals species has also shown that vigilance rates seem to be positively related to stress hormone levels (e.g., cortisol, Hawlena & Schmitz, 2010; but see Tkaczynski et al., 2014), which apparently decrease in animals (i.e. sheep) living in larger groups (Michelena et al., 2012). This supports the fact that vigilance decrement is indeed related to a perceived safety increment when in the presence of conspecifics.

However, does the presence of conspecifics always mean increased safety? Animal research mainly conducted with primate species (see Treves, 2000), revealed that the answer to this question may not be as straightforward as one would expect. As is the case with other animal species, primates seem to have reduced their predation problem by living in groups (Shultz et al., 2004; van Schaik, van Noordwijk, Warsono, et al., 1983). Nevertheless, living gregariously apparently brings a set of distinct complications. In fact, data from non-human primates showed that they can face more severe threats from conspecifics (e.g., intragroup aggression, infanticide; Treves, 1998) than several other taxa. The threat provided by conspecifics in primate groups, especially in highly competitive environments (e.g., Treves, 1999), is frequent and often lethal (e.g., Collins et al., 1984; Dittus, 1980; Goodall, 1986). In these cases, it is clear that the presence of conspecifics does not represent increased safety. Consequently, it is not expected that the presence of conspecifics results in lower vigilance levels in such group contexts (see Treves, 2000). Especially in competitive environments, primate species, besides monitoring predators, spend a considerable amount of time monitoring conspecifics as well (also known as within-group vigilance or social vigilance; see Beauchamp, 2015). This precludes the observation of a decrease in vigilance in several large group contexts (e.g., Barbosa, 2002; Blumstein & Daniel, 2002; E. Z. Cameron & Du Toit, 2005; Keverne et al., 1978). These results highlight that vigilance, as a danger avoidance tactic, does not serve only monitoring interspecies threat (e.g., predators). Vigilance is further allocated to monitor threats that could come from group members (e.g., aggressive conspecifics). In such a way, variables such as the context where the data collection is conducted (e.g., threatening vs. non-threatening situations) and the group context where the individuals are inserted (e.g., highly competitive or cooperative) seem to be paramount to fully unravel the dynamics behind danger monitoring across animal species.

Human beings are animals too, and as mentioned in the introductory section of this chapter, they are continuously exposed to diverse threat sources. Hence, as in the case of other animal species, this daily threat exposure demands a proper balance between intake/foraging-like activities and efficient risk/threat monitoring (analogous to vigilance behavior; see Kameda & Tamura, 2007). However, despite the relevance of risk monitoring in our daily lives, and although we are one of the most social species in the animal kingdom, little is known about human vigilance and the modulatory effects introduced by the presence of conspecifics. Specifically, do humans rely on similar vigilance strategies as other social species? Does the presence of conspecifics modulate human vigilance behavior? Does it still serve threat avoidance purposes?

The first study trying to address these questions was conducted by the present-day emeritus professor of psychology David P. Barash (Barash, 1972). Probably inspired by earlier work on vigilance behavior in animal species, Barash, observing the behavior of college students at a snack bar in the state University College at Oneonta, New York, concluded that: (a) solitary individuals tend to select tables significantly closer to walls compared to more central tables (a pattern that was not observed in groups of individuals); (b) solitary individuals evidence a higher frequency of vigilance behavior (which the author named as *"looking-ups"*) while eating than individuals in group situations. In what the author called the *"Snack-bar Security Syndrome"*, Barash speculated that the pattern that he observed in human beings resulted from a need for physical security while eating, which was modulated by the presence of conspecifics (i.e. group situations). In other words, solitary individuals, feeling more unprotected than individuals in group situations, selected more sheltered tables (i.e. close to walls), also evidencing a higher frequency of monitoring behavior (i.e. vigilance). Following the author’s reasoning, although the data were collected in a predator-free environment, this search for security may be a product of the selective pressure exerted by the necessity to avoid predator raids through our evolutionary pathway (Barash, 1972). In his own words: *“Human culture has evolved at a fantastic rate relative to our genetic evolution and it seems entirely plausible that we have carried such behavioral anachronisms into the 20th Century.”* (Barash, 1972, p. 578). Following Barash’s study, 14 years later, Peter Wirtz and Monika Wawra (1986) decided to explore the group size effect observed in other animal species on humans’ vigilance. Using a similar observational methodology as Barash (1972), Wirtz and Wawra (1986) reached the main conclusion that, as in other animal species, the frequency and duration of scanning the surrounding environment (i.e. vigilance) also correlates negatively with the group size (1-5 elements) in our own species. The authors also showed that females (compared to males) display a more rapid reduction in vigilance as group size increases. These results were replicated and extended 2 years later by Wawra (1988), who additionally pointed that the scanning behavior seems not to be coordinated between individuals (but see Kameda & Tamura, 2007; Kuroda & Kameda, 2019), and it is independent of the level of conversation within groups. As with Barash (1972), these authors (i.e. Wawra, 1988; Wirtz & Wawra, 1986) argued that this behavior was an artifact of evolution that remains until the present-day. This hypothesis, known as *ghost-of-predation-past* theory (see Beauchamp, 2015), is based on the assumption that traits, like vigilance, although not fully useful in the present, can persist in the population if they are not too costly, or if the evolutionary pressures driving such traits changed just recently (see Lahti et al., 2009).

Unfortunately, no further progress was made until 2002, when the British anthropologist Robin Dunbar – better known for his work in the *“the social brain hypothesis”* (see Dunbar, 1998) – and his colleagues conducted a study aiming to examine alternative explanations to the *ghost-of-predation-past* (Dunbar et al., 2002). Observing the behavior of human individuals and groups in large refectories and open parks, Dunbar and colleagues (2002) replicated the data from previous studies (i.e. Wawra, 1988; Wirtz & Wawra, 1986) evidencing a negative correlation between vigilance and group size. Nevertheless, further exploring their data, they also showed that the motivation for human vigilance (operationalized as the frequency of scanning behavior) in a threat-free situation appeared to be directed more to members of their own species (i.e. mate searching) instead of monitoring the surroundings for possible danger sources. These results suggest that vigilance can be tuned into the light of individuals’ current necessities, serving purposes other than threat detection (e.g., mate searching) when the individuals are in a threat-free environment. As already suggested in animal research, Dunbar and colleagues’ (2002) data highlight that when vigilance is studied, context variables (e.g., threat risk) should be considered. In fact, the authors suggested that if the studies had been conducted in a threat-rich environment, they might have found a relation between vigilance and threat avoidance (Dunbar et al., 2002).

Kameda and Tamura (2007) simulated a ‘foraging under threat risk’ situation using a virtual task. In this task, participants were financially rewarded for solving problems and punished if they did not detect a signal. Their results confirmed the relation between vigilance and threat avoidance predicted by Dunbar and colleagues (2002) in human subjects. They showed that individuals tend to allocate more resources (i.e. time) to vigilance as the cost of failing to detect threat increased, hence reducing their foraging activity. As is the case with other animal species, human beings also faced a trade-off between foraging/intake-related activities and vigilance when in a threat-rich environment. This may have strong implications for understanding risk monitoring in our own species (see Kameda & Tamura, 2007).

This relation between vigilance and threat avoidance was reinforced recently by Beauchamp (2020), employing a virtual task that simulates foraging under threat risk. This task consisted of a virtual scenario where participants were asked to decide how much time they spend collecting food rewards or trying to avoid a virtual predator attack. His results showed that human vigilance behavior is modulated by the frequency of threat encounters. When the frequency of threat encounters (i.e. the virtual predator attack) increased, the time allocated to vigilance also increased, resulting in reduced foraging activity (Beauchamp, 2020). In sum, when assessed in a threat-rich scenario, human vigilance appears to serve threat detection purposes, being modulated not only by the costs of failing to detect a threat stimulus but also by the probability of a threat encounter (Beauchamp, 2020; Kameda & Tamura, 2007). Therefore, in order to study the relevance of vigilance behavior to danger monitoring and avoidance in our own species, one should consider assessing vigilance in a context where it seems to have evolved: in a threat-rich environment where a trade-off between foraging and vigilance needs to be achieved in order to maintain the individual’s safety and well-being (see Beauchamp, 2015).

Despite the research summarized above and the promising role of vigilance in human risk monitoring, it is still unclear how the presence of conspecifics in a threatening environment affects vigilance and the humans’ capacity to detect threatening cues in different group contexts.

Emotional (fear) chemosignals: A collective detection mechanism in human beings?[1]

One of the mechanisms thought to be behind the increased safety perceived in group contexts is collective detection (e.g., Lima, 1990). Briefly, collective detection proposes that the transfer of information between conspecifics warns non-vigilant individuals that a dangerous event is about to occur, presenting protection from a potential inquiry. Thus, individuals in a group situation can reduce their vigilance level without compromising their safety (for a review see Beauchamp, 2015). Obviously, the collective detection mechanism is dependent on an efficient information transfer between conspecifics (for the sake of simplicity, hereinafter termed as communication[2]). Interestingly, research in non-human animal species has shown that such communication can rely on the most diverse sensorial signals, which can be 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).

Given the importance of collective detection in other animal species, a question that can naturally arise is: does “collective detection” play a role in shaping human behavior? Although not often framed in terms of collective detection, research has shown that our own species developed the capacity not only to emit sensory cues signaling that a dangerous situation is occurring (or may occur; i.e. fear or anxiety-related situations) but also to perceive and react in accordance to these sensory cues emitted by conspecifics (see De Gelder, 2006; Öhman & Mineka, 2001). Notably, this communication of danger-related information in humans can also rely on many sensory modalities. One of these sensory modalities is vision. Vision plays a prominent role in navigating the surrounding environment. A colossal volume of research in psychology and neurosciences has evidenced that we are highly susceptible to visual stimuli signaling that a conspecific is in a threatening situation. A prominent example of such stimuli is facial expressions of fear (e.g., Mogg et al., 2007; Pourtois et al., 2004). This highly relevant visual stimulus is preferentially processed by our brain (in comparison to threat-unrelated faces; e.g., Mogg et al., 2007). In fact, fearful faces quickly grab our visual attention (e.g., Pourtois et al., 2004), being detected and perceived faster when compared, for instance, to neutral faces (e.g., Fox et al., 2007; Yang et al., 2007). Moreover, fearful faces also seem to orient our gaze to their gaze's location to a greater extent than neutral faces (e.g., Gallup et al., 2014). The same

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[1] This section is partially based on a literature review reported in: Semin., G. R., & Gomes, N. (under review). Human Emotion Chemosignals: A Functional Activation-Articulation Model.

[2] which *“... occurs when a signal produced by an individual causes a change (reaction) in another organism, where both the signal and the reaction have been designed for these purposes”* (Scott-Phillips, 2015, p. 30)

seems to be true for fear body postures (see De Gelder, 2006). These stimuli also grab human attention (Bannerman et al., 2009) and are perceived in a privileged way (e.g., Stienen & de Gelder, 2011) in comparison to non-threatening body postures. Interestingly, this communication of danger signals is not exclusive to vision. Acoustic danger cues, such as fear prosody (e.g., Dolan et al., 2001) or cry (e.g., Giardino et al., 2008), also play a role in transferring information about dangerous events in human beings. They seem to guide our attention (e.g., Rigoulot & Pell, 2012) and to modulate the perception of visual threat cues (e.g., Stienen et al., 2011). Hence, this long tradition of research in psychology has demonstrated that a similar phenomenon to "collective detection" is relevant in humans, shaping our daily behavior.

Although completely uncharted until two decades ago, another sensory modality that constitutes a strong candidate for danger communication between humans is olfaction – which constitutes one of the pillars driving the present thesis. Contrary to common beliefs, it is now well-known that humans seem to have excellent olfactory abilities, being able to discriminate and detect an extraordinary range of odors (see McGann, 2017). Even more impressive is the fact that our sense of smell plays an important role in social communication through body odors (i.e. usually axillary sweat; see Semin & de Groot, 2013). Information about the senders' age (Mitro et al., 2012), gender (Penn et al., 2007), health status (Olsson et al., 2014), and familiarity (Lundström et al., 2009) constitute just a few examples of individual characteristics that can be communicated via body odors (i.e. chemosignals). Interestingly, in addition to the communication of information about relatively stable individual characteristics, chemosignals carry information about transient emotion-related states. This was firstly explored 20 years ago by Denise Chen and Jeannette Haviland-Jones (2000). In this pioneering work, Chen and Haviland-Jones evidenced that humans were somehow able to identify chemosignals produced under fear and happy-inducing situations above chance, suggesting that there must be some differences in the released body odor. Their work constituted the forerunner to more than 30 studies exploring the effects of emotion-related chemosignals on their receivers. This line of research confirmed that human beings unknowingly adjust the chemical composition of their chemosignals as a function of their emotional state (Smeets et al., 2020). Even more interesting for research in psychology, an extensive volume of evidence has also indicated that the exposure to such chemically distinct chemosignals – i.e. produced during happiness (de Groot et al., 2018; de Groot, Smeets, & Semin, 2015), disgust (de Groot et al., 2012; Zheng et al., 2018), and alertness-related emotional states (fear, anxiety, or high-stress conditions; e.g., de Groot et al., 2012, 2014a, 2014b, 2018; de Groot, Smeets, Rowson, et al., 2015; Kamiloğlu et al., 2018; Mujica-Parodi et al., 2009; Pause et al., 2004; Prehn et al., 2006; Rocha et al., 2018; Silva et al., 2020) – seem to modulate their receivers' behavior in accordance with the emotional condition in which they were produced. For the purposes of the present thesis, the literature summarized below will focus only on the effects of being exposed to alertness-related chemosignals (i.e. high-stress, anxiety, and fear-related chemosignals; see de Groot et al., 2017; de Groot & Smeets, 2017), and their impact on the receivers' capacity (or preparedness) to detect and avoid threatening stimuli.

Considering the capacity of chemosignals to transmit emotion-related information, chemosignals released in an alertness-related condition (e.g., during fear or anxiety emotional states) should signal to their receivers that a nearby conspecific is (or recently was) in a threatening situation. Thus, assuming that a "collective detection-like" phenomenon has a role in shaping human beings' behavior, the exposure to this specific type of chemosignals must trigger a preparedness state in its receivers to detect and avoid threatening stimuli. Research using alertness-related chemosignals has pointed out that this is the case. Repeated research has shown, for instance, that exposure to fear-related chemosignals (i.e. apocrine axillar sweat sampled while participants watched horror movies) results in very subtle activations (compared to the exposure to sweat sampled while participants watched neutral movies) of the facial muscles *medial frontalis* and *corrugator supercilii* (e.g., de Groot et al., 2014a; Kamiloğlu et al., 2018). Interestingly, these are precisely the facial muscles responsible for displaying fear expressions (Fridlund & Cacioppo, 1986) As Susskind and colleagues (2008) have suggested, the activation of these muscles widens the eye aperture increasing the visual field, and consequently sensory acquisition (Lee et al., 2013). Congruently with this sensory acquisition increment, exposure to fear-related chemosignals also increased the sniffing volume, triggered a quick visual scan strategy, and increased target detection sensitivity (compared to the exposure to neutral and disgust-related chemosignals; de Groot et al., 2012).

Moreover, evidence in the literature further suggests that the exposure to fear-related chemosignals (compared to neutral chemosignals) biases visual perception, leading receivers to rate ambiguous facial expressions as more fearful (de Groot et al., 2020; Zhou & Chen, 2009). Fear-related chemosignals (compared to neutral chemosignals) are also known to reduce the time needed to classify fear expressions as negative (Kamiloğlu et al., 2018), and to accelerate access to awareness for fear facial expressions (Silva et al., 2020) or to faces in general (i.e. independent of their emotional content; de Groot et al., 2018). This perceptual bias was further supported by work using anxiety-related chemosignals (i.e. sweat collected during high-anxiety situations such as waiting for an academic examination). This research evidenced that the exposure to these chemosignals (compared to exercise sweat) increased the accuracy in discriminating between emotional morphed faces (Rocha et al., 2018; Wudarczyk et al., 2016). Mujica-Parodi and colleagues (2009) also confirmed the perception bias, evidencing that the exposure to high-stress chemosignals (i.e. sweat collected during first-time skydiving) resulted in enhanced discrimination of ambiguous anger faces (compared to the exposure to exercise sweat). Together these results indicate that exposure to alertness-related chemosignals biases visual perception, facilitating the assessment of risk information in facial stimuli, especially during demanding perceptual conditions.

In addition to increasing sensory acquisition and leading to a perceptual bias that facilitates risk assessment, research using anxiety chemosignals went further evidencing that they also prepare receivers to react to potentially threatening stimuli. In fact, the exposure to these chemosignals modulates receivers' cardiac activity in congruence with a stress response (i.e. reducing cardiac parasympathetic activity; Rocha et al., 2018), and pre-attentively priming motor defensive behaviors such as increasing the amplitude of the startle reflex (a well-known withdraw behavior; Prehn et al., 2006).

This relation between the exposure to alertness-related chemosignals and the modulation of threat detection and avoidance mechanisms is further supported by neuroimaging evidence. Although research on the neuronal mechanisms driving the processing of alertness-related chemosignals is still in its infancy, the few existing studies show that these chemosignals are processed similarly to other threat-related stimuli (e.g., fear facial expressions; for a review see Parma et al., 2017). An interesting illustration of this preferential processing of alertness-related chemosignals is the study conducted by Pause and colleagues (2010) using electroencephalography (EEG). Their results showed that exposure to anxiety-related chemosignals (compared with exposure to exercise sweat) results in P3 component's magnitude increment, located in the medial frontal brain areas. This specific increment of the neuronal activity in the frontal medial brain areas is commonly associated with exposure to potentially harmful odors (Laudien et al., 2008). The activation of this brain region (i.e. medial prefrontal cortex) is often related to emotional activation (Phan et al., 2002) and hypothesized to be related to flexible physiological adjustments in relevant situations (Damasio, 1994), involving the integration of sensory and cognitive information in order to adjust physiological activity (see Pause et al., 2010; Rolls, 1999). Hence, these results indicate not only that processing of alertness-related chemosignals require enhanced neuronal resources (compared to exercise chemosignals), but also point out that – considering the location of the increased neuronal activity – exposure to these specific sensory cues may trigger physiological adjustments and multisensory integration, which may be advantageous in reacting to imminent threatening stimuli.

In the same vein, a fMRI study with anxiety chemosignals (compared to exercise chemosignals) showed activation in the fusiform area, the insula, precuneus, cingulated cortex, thalamus, dorsomedial prefrontal cortex, and cerebellum (Prehn-Kristensen et al., 2009). As also described by the authors, the activation of structures like insula (Jabbi et al., 2007), precuneus (Cavanna & Trimble, 2006; Gobbini et al., 2004), and the anterior and posterior cingulated cortex (Völlm et al., 2006) are usually associated with empathy networks. Areas such as the fusiform cortex seem to be activated during the processing of socially relevant stimuli (e.g., faces; Vuilleumier & Pourtois, 2007). In turn, the activation of the thalamus (e.g., Snow et al., 2009) and cerebellum (especially the vermis; Schutter & Van Honk, 2005) are thought to be related to attention and emotional control, respectively. Additionally, the precuneus is deeply connected with, among others, the premotor and supplementary motor areas (Cavanna & Trimble, 2006). We speculate that this connection may drive the motor adaptations observed during the exposure to alertness-related chemosignals (i.e. the aforementioned fEMG effects and the modulation of withdrawal behaviors; e.g., de Groot et al., 2012; Prehn et al., 2006).

More recently, Wudarczyk and colleagues (2016) extended these findings in another fMRI study. They used an emotion recognition task with faces that were parametrically morphed from neutral to fear. The goal was to examine brain responses to changes in facial expressions while being exposed to anxiety-related chemosignals (in contrast to exercise chemosignals). In the anxiety chemosignal condition, the increase in the fearfulness of facial expressions corresponded to increased activity in the insula (usually implicated, among other functions, in producing an emotionally relevant context; e.g., Singer et al., 2009), and middle occipital gyrus extending into the fusiform gyrus (visual areas that were previously associated with a visual preparedness mechanism triggered by olfactory stimuli; e.g., Lundström et al., 2008). As already mentioned, the increased activations triggered by the anxiety chemosignals, co-occurred with participants rating the more discernible faces (i.e. faces in morph levels closer to neutral or fear facial expressions) as more fearful and neutral, respectively. Interestingly, the higher ratings of fearfulness also corresponded to an increment in hippocampus activity (a brain area associated with memory, e.g., Burgess et al., 2002). These results indicate that the exposure to alertness-related chemosignals facilitates face processing and may improve retrieval of fear faces by enhancing the emotional context.

Furthermore, contrasting sweat collected during a high-stress situation (i.e. first time skydiving) with exercise sweat, Mujica-Parodi and colleagues (2009) showed that exposure to high-stress chemosignals resulted in the activation of the amygdala - a brain area commonly associated with threat detection and coordination of appropriated defensive responses (suggesting a preparedness to deal with imminent danger) through its cortical feedback connections (e.g., Amaral, 2002; LeDoux, 2014). In line with this, Mujica-Parodi et al. (2009) reported that stress-related chemosignals enhanced the discrimination of ambiguous threatening (anger) faces, thus linking amygdala activation with a facilitated risk-assessment. Accordingly, using EEG, Rubin and colleagues (2012) showed that exposure to high-stress sweat (compared to exercise sweat) resulted in heightened late positive potentials (LPP) not only to angry faces but also neutral and emotionally ambiguous facial expressions. This suggests that, by enhancing attentiveness to otherwise non-relevant stimuli (like neutral and emotionally ambiguous faces), the exposure to high-stress sweat modulates sustained attention and perceptual salience-related electrocortical activity (see Rubin et al., 2012).

Additionally, in a very recent fMRI study, de Groot and colleagues (2020) examined whether sweat produced by donors exposed to different quantities (i.e., low, medium, and high; as categorized by the authors) of fear-related chemosignals resulted in distinct behavioral, physiological, and neural responses in receivers (compared to neutral chemosignals). Their results showed that exposure to fear-related chemosignals, independent of the “fear intensity” experienced by the sweat donor, resulted in: (a) a bias towards perceiving fear in ambiguous morphed faces; (b) an increment in sniffing response; and (c), as in the aforementioned studies employing anxiety-related chemosignals, the activation of the fusiform gyrus, as well as prefrontal areas (in this case the ventral medial prefrontal cortex). Additionally, the authors presented some evidence that the “fear intensity” experienced by the sweat donors seems to be partially coded on the receivers’ left amygdala. More relevant for our current purposes, de Groot and colleagues (2020) also found a relation between the level of left amygdala activity and the percentage of face morphs being perceived as fearful. This interesting result suggests the amygdala as a mediator structure for the perceptual bias triggered by alertness-related chemosignals.

Altogether, research on the effects of alertness-chemosignals has shown that exposure to specific sensory signals modulates sensory acquisition, attention, emotion, defensive behaviors, as well as activity in brain areas associated with threat-detection in human beings (e.g., de Groot et al., 2012; Mujica-Parodi et al., 2009; Prehn-Kristensen et al., 2009; Prehn et al., 2006; Rocha et al., 2018). This data pattern seems to support a “collective detection-like” phenomenon driven by alertness-related chemosignals that may modulate risk-monitoring and threat avoidance in our own species, contributing to individual and group safety. However, no research has hitherto directly explored the effects of being exposed to alertness-related chemosignals in humans' risk monitoring (i.e. vigilance), as well as in the capacity to detect and avoid threatening stimuli.

Thesis' Purpose and Specific Goals

In the previous section, I summarized animal and human research pointing out that risk monitoring and threat avoidance strategies in human beings are very likely to be directly (i.e. by the presence of conspecifics) or indirectly (i.e. through alarm sensory cues such as alertness-related chemosignals) modulated by conspecifics. Concretely, based on the research I reviewed, it is possible to argue that: (a) the presence of non-threatening and unfrightened conspecifics induces a feeling of safety leading to a reduction in vigilance, and an increment of intake activities (e.g., foraging); (b) however, this effect is not only modulated by the context where vigilance is activated (i.e. in threatening or threat-free environments), but also by the group context where the individuals are (i.e. safe or high competitive environments contexts); (c) besides the direct effects of their presence, conspecifics may also modulate individual's danger monitoring and threat avoidance strategies through alarm sensory cues transferred by, among other sensory modalities, olfactory signals. Nevertheless, and despite the importance that such arguments may have in governing danger avoidance in a range of contexts in our societies (e.g., air-traffic controllers; Blachman & Proschan, 1959), they were neglected in psychological research. In fact, no study has hitherto addressed the real impact of the presence of conspecifics and their olfactory danger signals on human vigilance strategies and their capacity to avoid threatening stimuli. In other words, notwithstanding the previously summarized research, no effort has been made to explore the real role that conspecifics play in modulating individual danger monitoring. It is precisely here that lies the novelty of the present thesis.

Therefore, across 5 studies, I intend to shed light on the influence of conspecifics in individual vigilance strategies and in the capacity to avoid dangerous events. Specifically, these studies examine the applicability of behavioral ecological models of animal vigilance to human beings in a (virtual) threatening environment, testing the following predictions: (a) human beings rely on vigilance strategies similar to those documented in animal species, namely the mere presence of conspecifics increases foraging activity at the expense of the time allocated to vigilance; (b) this vigilance decrement may be associated with a perceived safety increment when in the presence of conspecifics; (c) however, adverse group contexts (i.e. the presence of competitive conspecifics) should result in an opposite effect, increasing vigilance behavior; (c) when in a threatening environment, vigilance behavior serves threat detection purposes; and (d) alertness-related (i.e. fear) chemosignals drive a “collective detection-like” phenomenon, modulating their receivers’ vigilance behavior and capacity to avoid threatening events. In addition, my plan was also to explore possible concomitant effects of the presence of conspecifics in vigilance and threat-detection, while exposed to fear-related chemosignals. However, due to the current global pandemic (COVID-19), we were prevented from having more than one participant in the lab’s facilities at a time, impeding the execution of this last study.

It is also important to note that, regarding the modulatory effects of the presence of conspecifics on humans’ vigilance, the aim of this thesis was not to study what is known in animal research as “group size effect” (for a review see Beauchamp, 2015). That is, the number of conspecifics in the “co-presence condition” remained constant across studies. Moreover, in contrast to previous studies (see Kameda & Tamura, 2007; Kuroda & Kameda, 2019), we did not examine the effects of group dynamics (e.g., “producer-scrounger” games; see Giraldeau & Caraco, 2000), or the influence of conspecifics’ vigilance rates on individual vigilance (e.g., Sirot, 2006). Instead, we examined more fundamental phenomena, namely if the simple presence of conspecifics, (e.g., “neutral” conspecifics, or conspecifics perceived as competitors) was enough to change individual vigilance strategies and threat detection capacity.

Overview and main conclusions

Chapter II[3] reports an experimental study that constitutes one of the two pillars of the current thesis. The study was conducted to provide a proof of principle for vigilance behavior in human beings, its modulation by the presence of conspecifics, and its relationship to threat detection. This chapter introduces a novel paradigm developed in our lab, which is called “foraging-vigilance task”. This novel paradigm was created to allow the study of vigilance in the context in which it is likely to have evolved – namely, where the adjustment of a trade-off between the two survival activities (risk monitoring and foraging) is required to increase an individual’s “fitness”. In fact, employing such a trade-off constitutes a necessary condition to study the danger avoidance function of vigilance behavior (Beauchamp, 2015). This task constitutes a simulation of foraging under threat risk and is inspired by Kameda and Tamura's

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[3] Please note that Chapter I, as a general introduction to the current thesis, has overlapping information with the remaining chapters.

work (2007). Concretely, participants were told that their final reward would depend on their task performance. They received small monetary rewards for solving a central letter discrimination task (i.e. foraging simulation) but suffered strong monetary punishments for not detecting changes in their peripheral visual field (i.e. threat-simulation). Thus, participants had to decide how to distribute their attentional resources between the two tasks, which were incompatible with each other. That is, when participants focused on the letter discrimination task, they were not able to detect the peripheral threatening changes and vice-versa. In other words, to increase the probability of detecting the threatening changes presented peripherally, participants had to increase the time allocated to vigilance, which necessarily results in a sacrifice of their performance on the central letter discrimination task. Hence, a trade-off between foraging and vigilance had to be achieved in order to increase participants' fitness (i.e. to increase their final reward). This task was paired with an eye-tracker, allowing us to reliably measure the attentional resources (i.e. time) allocated to each independent "survival relevant activity" (i.e. foraging and vigilance).

In order to assess whether the presence of conspecifics had a direct impact on vigilance behavior and threat detection, participants performed the experiment in one of two conditions: an individual condition where they solved the task isolated in a cubicle, or a co-presence condition, where they were in the presence of two confederates performing the same task on two independent monitors. A between-subjects design was chosen to minimize learning effects between conditions and participants' tiredness. The results revealed that participants in the individual condition (compared to the participants in the co-presence condition) allocated more attentional resources to avoid threatening stimuli (i.e. vigilance), thereby sacrificing foraging, but increasing their likelihood of detecting threatening events. The results of this study not only confirmed that vigilance serves threat detection purposes in a threatening environment but also, as seen in studies with animal species, that the presence of conspecifics modulates this behavior, as shown by reduced vigilance rates.

Chapter III aimed to shed light on the mechanisms behind the observed decrease in vigilance when conspecifics are present - namely, the assumed safety increment triggered by the presence of conspecifics. Specifically, this study examined whether the presence of conspecifics (2 friends or 2 strangers), compared to an individual condition, reduces the perceived threat in ambiguous danger situations. In an online-based experiment, participants were asked to immerse themselves into several dangerous scenarios presented in small vignettes (involving either dangerous animals or harmful conspecifics; between-subjects factor). In each vignette, they had to imagine themselves alone, in the company of 2 friends, or 2 strangers (within-subjects factor). Their task was to assess how threatened they would feel and how likely they were to be harmed in each scenario. The results of this study showed that, irrespective of the threat source (i.e. dangerous animals or harmful conspecifics), the presence of conspecifics (2 friends or 2 strangers) reduced the perceived threat and probability of getting harmed when compared to the individual condition. These results supported the notion that the presence of conspecifics automatically increases perceived safety, which arguably results in fewer resources being dedicated to vigilance compared to individual conditions.

The research reported in **Chapter IV** was designed to shed light on how different co-presence conditions (i.e. mere presence vs. competition vs. cooperation; between-subjects design) shape human vigilance and threat detection capability when performing the “foraging-vigilance task”. Specifically, in this experiment, participants received distinct sets of instructions in accordance with the condition they were taking part. In the mere co-presence condition, participants were told that their tasks and their rewards were independent of the other participants. In the competition condition, participants were told that they only receive the final reward if they obtain a better performance result compared to the two other participants (confederates). In the cooperation condition, participants were informed that they constitute a team, being led to believe that their reward would be contingent on the performance of the team. The results showed that the different co-presence conditions neither modulated vigilance behavior nor threat detection capacity. These results suggest that, independent of the conspecifics being perceived as competitors or cooperators, their presence modulates vigilance levels and foraging activity in a similar way to just their mere presence. Arguably, competition or cooperation contexts may only play a role when the dynamics between group members are examined (e.g., Kameda & Tamura, 2007; Kuroda & Kameda, 2019) but not when the experimental contingencies do not allow interaction between participants as in the case of the experiment reported in this chapter.

The research reported in **Chapter V** constitutes the second pillar of the thesis. In this chapter, an experiment examining the effects of exposure to fear-chemosignals on vigilance and threat detection is reported. In this study, participants were exposed to one of three chemosignal conditions – fear-related chemosignals, rest chemosignals, and a clean air condition – while performing the “foraging-vigilance task”. The presence of conspecifics was not manipulated. Participants performed the experiment alone in an experimental cubicle. As in the study reported in chapter II, a between-subjects design was chosen to avoid learning and tiredness effects between odor conditions. Interestingly, the obtained results revealed that the exposure to fear-related chemosignals (compared to the rest chemosignals and the clean air condition) did not modulate vigilance behavior *per se* but led to faster reactions to threatening events. These results suggest that instead of increasing participants’ alertness, and modulating risk-monitoring, fear-related chemosignals induced in their receiver an unconscious danger-avoidance readiness state categorized by high attentiveness that allows faster reactions to threatening events.

Chapter VI constitutes a methodological component to the present thesis. It is designed to examine how to reduce the monetary and time cost of further planned research employing chemosignals. Unfortunately, as aforementioned, the final planned study involving chemosignals could not be conducted due to the restrictions imposed by the world pandemic situation. Nevertheless, this methodological study was still reported here due to the advantages that it can bring to future research on this field. The research reported in this chapter investigated if it is possible to reutilize fear chemosignals a second time. Specifically, replicating the methodology used in previous studies exploring what the authors termed emotional communication through body odors (e.g., de Groot et al., 2014a), my co-authors and I tested if fear and neutral sweat samples produce similar fEMG effects across two independent applications. Firstly, our results replicated the findings in the earlier literature. Exposure to fear chemosignals (compared to neutral chemosignals) results in stronger activation of the facial muscles involved in fear expressions (i.e. the *medial frontalis* and the *corrugator supercilii*; see Fridlund & Cacioppo, 1986). Moreover, this data pattern was similar across both sweat applications, underlining the feasibility of re-using fear sweat samples. Interestingly, these results also led to some speculation regarding the volatiles involved in the information transfer between sweat donors and receivers. As the data patterns were similar across applications, it is very likely that the volatiles carrying fear-related information are not high-volatile molecules that spread fast in the environment but low-volatile molecules, remaining in the location where they were released for longer periods of time.

Finally, **Chapter VII** constitutes a general discussion of the findings obtained in chapter II to VI and is divided into 3 sections. The first section focuses on the results related to the effects of the presence of conspecifics on vigilance and threat detection. A discussion about their relation with previous findings, as well as the added value of the present research to understand diverse social phenomena, is provided (e.g., social buffering; Kikusui et al., 2006). The second section focuses on the findings involving the effects of fear-related chemosignals on threat avoidance. In this section, the role of fear chemosignals in preparing receivers to avoid dangerous events (i.e. readiness state) is explored. The obtained results are integrated with a functional activation-articulation model elaborated recently by us (Semin & Gomes, under review). This model's core argument is that human emotional chemosignals do not directly induce emotional states. Instead, they activate a highly adaptive neural, muscular, attentional, and perceptual state of preparedness or readiness. The third section offers limitations of the studies reported on this thesis and directions for future research. A set of possible practical implications and some final remarks conclude this chapter. It is important to note that, as a general discussion of the findings obtained in the current thesis, chapter VII has overlapping information with chapters II-VI.

References

Amaral, D. G. (2002). The primate amygdala and the neurobiology of social behavior: Implications for understanding social anxiety. In *Biological Psychiatry* (Vol. 51, Issue 1, pp. 11–17). Elsevier Inc. https://doi.org/10.1016/S0006-3223(01)01307-5

Asch, S. E. (1956). Studies of independence and conformity: I. A minority of one against a unanimous majority. *Psychological Monographs: General and Applied*, *70*(9), 1–70. https://doi.org/10.1037/h0093718

Bannerman, R. L., Milders, M., de Gelder, B., & Sahraie, A. (2009). Orienting to threat: faster localization of fearful facial expressions and body postures revealed by saccadic eye movements. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1662), 1635–1641. https://doi.org/10.1098/rspb.2008.1744

Barash, D. P. (1972). Human Ethology: The Snack-Bar Security Syndrome. *Psychological Reports*, *31*(2), 577–578. https://doi.org/10.2466/pr0.1972.31.2.577

Barbosa, A. (2002). Does vigilance always covary negatively with group size? Effects of foraging strategy. *Acta Ethologica*, *5*(1), 51–55. https://doi.org/10.1007/s10211-002-0059-0

Basile, M., Boivin, S., Boutin, A., Blois-Heulin, C., Hausberger, M., & Lemasson, A. (2009). Socially dependent auditory laterality in domestic horses (Equus caballus). *Animal Cognition*, *12*(4), 611–619. https://doi.org/10.1007/s10071-009-0220-5

Bates, H. W. (1863). *The Naturalists on the River Amazons*. Murray Press.

Beauchamp, G. (2008). What is the magnitude of the group-size effect on vigilance? *Behavioral Ecology*, *19*(6), 1361–1368. https://doi.org/10.1093/beheco/arn096

Beauchamp, G. (2014). Antipredator vigilance decreases with food density in staging flocks of Semipalmated Sandpipers (Calidris pusilla). *Canadian Journal of Zoology*, *92*(9), 785–788. https://doi.org/10.1139/cjz-2014-0037

Beauchamp, G. (2015). *Animal vigilance : monitoring predators and competitors*. Academic Press.

Beauchamp, G. (2020). Predator attack patterns influence vigilance in a virtual experiment. *Behavioral Ecology and Sociobiology*, *74*(4). https://doi.org/10.1007/s00265-020-02833-0

Beauchamp, G., & Livoreil, B. (1997). The effect of group size on vigilance and feeding rate in spice finches (Lonchura punctulata) . *Canadian Journal of Zoology*, *75*(9), 1526–1531. https://doi.org/10.1139/z97-776

Bednekoff, P. A., & Lima, S. L. (1998). Re-examining safety in numbers: Interactions between risk dilution and collective detection depend upon predator targeting behaviour. *Proceedings of the Royal Society B: Biological Sciences*, *265*(1409), 2021–2026. https://doi.org/10.1098/rspb.1998.0535

Bednekoff, P. A., & Woolfenden, G. E. (2003). Florida Scrub-Jays (*Aphelocoma coerulescens*) are Sentinels More When Well-Fed (Even with no Kin Nearby). *Ethology*, *109*(11), 895–903. https://doi.org/10.1046/j.0179-1613.2003.00926.x

Belt, T. W. (1874). *The Naturalist in Nicaragua*. Murray Press.

Bertram, B. C. R. (1978). Living in groups: predator and prey. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural Ecology* (pp. 64–96). Blackwell Publishing Ltd.

Bertram, B. C. R. (1980). Vigilance and group size in ostriches. *Animal Behaviour*, *28*(1), 278–286. https://doi.org/10.1016/S0003-3472(80)80030-3

Blachman, N., & Proschan, F. (1959). Optimum Search for Objects Having Unknown Arrival Times. *Operations Research*, *7*(5), 625–638. https://doi.org/10.1287/opre.7.5.625

Blumstein, D. T. (1996). How much does social group size influence golden marmot vigilance. *Behaviour*, *133*(15–16), 1133–1151. https://doi.org/10.1163/156853996X00332

Blumstein, D. T., Barrow, L., & Luterra, M. (2008). Olfactory predator discrimination in yellow-bellied marmots. *Ethology*, *114*(11), 1135–1143. https://doi.org/10.1111/j.1439-0310.2008.01563.x

Blumstein, D. T., & Daniel, J. C. (2002). Isolation from mammalian predators differentially affects two congeners. *Behavioral Ecology*, *13*(5), 657–663. https://doi.org/10.1093/beheco/13.5.657

Blumstein, D. T., Evans, C. S., & Daniel, J. C. (1999). An experimental study of behavioural group size effects in tammar wallabies, Macropus eugenii. *Animal Behaviour*, *58*(2), 351–360. https://doi.org/10.1006/anbe.1999.1156

Brown, G. E., Godin, J. G. J., & Pedersen, J. (1999). Fin-flicking behaviour: A visual antipredator alarm signal in a characin fish, Hemigrammus erythrozonus. *Animal Behaviour*, *58*(3), 469–475. https://doi.org/10.1006/anbe.1999.1173

Burgess, N., Maguire, E. A., & O’Keefe, J. (2002). The human hippocampus and spatial and episodic memory. In *Neuron* (Vol. 35, Issue 4, pp. 625–641). Cell Press. https://doi.org/10.1016/S0896-6273(02)00830-9

Cameron, E. S. (1908). Observations on the Golden Eagle in Montana. *The Auk*, *25*(3), 251–268. https://doi.org/10.2307/4070518

Cameron, E. Z., & Du Toit, J. T. (2005). Social influences on vigilance behaviour in giraffes, Giraffa camelopardalis. *Animal Behaviour*, *69*(6), 1337–1344. https://doi.org/10.1016/j.anbehav.2004.08.015

Caraco, T. (1979). Time Budgeting and Group Size: A Theory. *Ecology*, *60*(3), 611–617. https://doi.org/10.2307/1936081

Caraco, T., Martindale, S., & Pulliam, H. R. (1980a). Avian flocking in the presence of a predator. *Nature*, *285*(5764), 400–401. https://doi.org/10.1038/285400a0

Caraco, T., Martindale, S., & Pulliam, H. R. (1980b). Avian Time Budgets and Distance to Cover. *The Auk: Ornithological Advances*, *97*(4), 872–875. https://doi.org/10.1093/auk/97.4.872

Castellanos, I., & Barbosa, P. (2006). Evaluation of predation risk by a caterpillar using substrate-borne vibrations. *Animal Behaviour*, *72*(2), 461–469. https://doi.org/10.1016/j.anbehav.2006.02.005

Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: A review of its functional anatomy and behavioural correlates. *Brain*, *129*(3), 564–583. https://doi.org/10.1093/brain/awl004

Chen, D., & Haviland-Jones, J. (2000). Human Olfactory Communication of Emotion. *Perceptual and Motor Skills*, *91*(3), 771–781. https://doi.org/10.2466/pms.2000.91.3.771

Collins, D. A., Busse, C. D., & Goodall, J. (1984). Infanticide in two populations of savannah baboons. In G. Hausfater & S. B. Hrdy (Eds.), *Infanticide: Comparative and Evolutionary Perspectives* (pp. 193–216). Aldine.

Creel, S., Schuette, P., & Christianson, D. (2014). Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology*, *25*(4), 773–784. https://doi.org/10.1093/beheco/aru050

Damasio, A. (1994). *Descartes' Error. Emotion, Reason and the Human Brain*. Avon Books.

Darwin, C. (1859). *On the origin of species by means of natural selection, or preservation of favoured races in the struggle for life*. John Murray.

De Gelder, B. (2006). Towards the neurobiology of emotional body language. In *Nature*

Reviews Neuroscience (Vol. 7, Issue 3, pp. 242–249). https://doi.org/10.1038/nrn1872

de Groot, J. H. B., Kirk, P., & Gottfried, J. A. (2020). Titrating the Smell of Fear: Initial Evidence for Dose-Invariant Behavioral, Physiological, and Neural Responses. *Psychological Science*, *21*(1), 1–9.

de Groot, J. H. B., Semin, G. R., & Smeets, M. A. M. (2014a). I can see, hear, and smell your fear: comparing olfactory and audiovisual media in fear communication. *Journal of Experimental Psychology. General*, *143*(2), 825–834. https://doi.org/10.1037/a0033731

de Groot, J. H. B., Semin, G. R., & Smeets, M. A. M. (2014b). Chemical communication of fear: A case of male-female asymmetry. *Journal of Experimental Psychology: General*, *143*(4), 1515–1525. https://doi.org/10.1037/a0035950

de Groot, J. H. B., Semin, G. R., & Smeets, M. A. M. (2017). On the Communicative Function of Body Odors: A Theoretical Integration and Review. *Perspectives on Psychological Science*, *12*(2), 306–324. https://doi.org/10.1177/1745691616676599

de Groot, J. H. B., & Smeets, M. A. M. (2017). Human fear chemosignaling: Evidence from a meta-analysis. *Chemical Senses*, *42*(8), 663–673. https://doi.org/10.1093/chemse/bjx049

de Groot, J. H. B., Smeets, M. A. M., Kaldewaij, A., Duijndam, M. J. a, & Semin, G. R. (2012). Chemosignals communicate human emotions. *Psychological Science*, *23*(11), 1417–1424. https://doi.org/10.1177/0956797612445317

de Groot, J. H. B., Smeets, M. A. M., Rowson, M. J., Bulsing, P. J., Blonk, C. G., Wilkinson, J. E., & Semin, G. R. (2015). A Sniff of Happiness. *Psychological Science*, *26*(6), 684–700. https://doi.org/10.1177/0956797614566318

de Groot, J. H. B., Smeets, M. A. M., & Semin, G. R. (2015). Rapid stress system drives chemical transfer of fear from sender to receiver. *PLoS ONE*, *10*(2), e0118211. https://doi.org/10.1371/journal.pone.0118211

de Groot, J. H. B., van Houtum, L. A. E. M., Gortemaker, I., Ye, Y., Chen, W., Zhou, W., & Smeets, M. A. M. (2018). Beyond the west: Chemosignaling of emotions transcends ethno-cultural boundaries. *Psychoneuroendocrinology*, *98*, 177–185. https://doi.org/10.1016/j.psyneuen.2018.08.005

Dittus, W. P. J. (1980). The social regulation of primate populations: a synthesis. In D. G. Lindburg (Ed.), *The Macaques: Studies in Ecology, Behavior and Evolution* (pp. 263–286). van Nostrand Reinhold.

Dolan, R. J., Morris, J. S., & de Gelder, B. (2001). Crossmodal binding of fear in voice and face. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(17), 10006–10010. https://doi.org/10.1073/pnas.171288598

Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology*, *6*(5), 178–190. https://doi.org/10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8

Dunbar, R. I. M., Cornah, L., Daly, F. J., & Bowyer, K. M. (2002). Vigilance in human groups: A test of alternative hypotheses. *Behaviour*, *139*(5), 695–711. https://doi.org/10.1163/15685390260136771

Fordyce, J. A., & Agrawal, A. A. (2001). The role of plant trichomes and caterpillar group size on growth and defence of the pipevine swallowtail *Battus philenor*. *Journal of Animal Ecology*, *70*(6), 997–1005. https://doi.org/10.1046/j.0021-8790.2001.00568.x

Fox, E., Mathews, A., Calder, A. J., & Yiend, J. (2007). Anxiety and Sensitivity to Gaze Direction in Emotionally Expressive Faces. *Emotion*, *7*(3), 478–486. https://doi.org/10.1037/1528-3542.7.3.478

Fridlund, A. J., & Cacioppo, J. T. (1986). Guidelines for Human Electromyographic Research. *Psychophysiology*, *23*(5), 567–589. https://doi.org/10.1111/j.1469-8986.1986.tb00676.x

Gallup, A. C., Chong, A., Kacelnik, A., Krebs, J. R., & Couzin, I. D. (2014). The influence of emotional facial expressions on gaze-following in grouped and solitary pedestrians. *Scientific Reports*, *4*(1), 1–4. https://doi.org/10.1038/srep05794

Galton, F. (1871). Gregariousness in cattle and in men. *Macmillan's Magazine*, *23*(136), 353–357.

Galton, F. (1883). *Inquiries into Human Faculty and Its Development*. McMillan.

Giardino, J., Gonzalez, A., Steiner, M., & Fleming, A. S. (2008). Effects of motherhood on physiological and subjective responses to infant cries in teenage mothers: A comparison with non-mothers and adult mothers. *Hormones and Behavior*, *53*(1), 149–158. https://doi.org/10.1016/j.yhbeh.2007.09.010

Gillham, N. W. (2001). Sir Francis Galton and the Birth of Eugenics. *Annual Review of Genetics*. https://doi.org/10.1146/annurev.genet.35.102401.090055

Giraldeau, L.-A., & Caraco, T. (2000). *Social Foraging Theory*. Princeton University Press.

Gobbini, M. I., Leibenluft, E., Santiago, N., & Haxby, J. V. (2004). Social and emotional attachment in the neural representation of faces. *NeuroImage*, *22*(4), 1628–1635. https://doi.org/10.1016/j.neuroimage.2004.03.049

Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behaviour*. Harvard University Press.

Gosselin-ildari, A. D., & Koenig, A. (2012). The Effects of Group Size and Reproductive Status on Vigilance in Captive Callithrix jacchus. *American Journal of Primatology*, *74*(7), 613–621. https://doi.org/10.1002/ajp.22013

Guerin, B. (1986). Mere presence effects in humans: A review. *Journal of Experimental Social Psychology*, *22*(1), 38–77. https://doi.org/10.1016/0022-1031(86)90040-5

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, *31*(2), 295–311. https://doi.org/10.1016/0022-5193(71)90189-5

Hatfield, E., Cacioppo, J. T., & Rapson, R. L. (1993). Emotional Contagion. *Current Directions in Psychological Science*, *2*(3), 96–100. https://doi.org/10.1111/1467-8721.ep10770953

Hawkley, L. C., & Cacioppo, J. T. (2010). Loneliness matters: A theoretical and empirical review of consequences and mechanisms. *Annals of Behavioral Medicine*, *40*(2), 218–227. https://doi.org/10.1007/s12160-010-9210-8

Hawlena, D., & Schmitz, O. J. (2010). Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *American Naturalist*, *176*(5), 537–556. https://doi.org/10.1086/656495

Hilton, G. M., Ruxton, G. D., & Cresswell, W. (1999). Choice of Foraging Area with Respect to Predation Risk in Redshanks: The Effects of Weather and Predator Activity. *Oikos*, *87*(2), 295. https://doi.org/10.2307/3546744

Hoogland, J. L. (1979). The effect of colony size on individual alertness of prairie dogs (Sciuridae: Cynomys spp.). *Animal Behaviour*, *27*(PART 2), 394–407. https://doi.org/10.1016/0003-3472(79)90174-X

Huart, C., Rombaux, P., & Hummel, T. (2013). Plasticity of the human olfactory system: The olfactory bulb. In *Molecules* (Vol. 18, Issue 9, pp. 11586–11600). Molecules. https://doi.org/10.3390/molecules180911586

Jabbi, M., Swart, M., & Keysers, C. (2007). Empathy for positive and negative emotions in the gustatory cortex. *NeuroImage*, *34*(4), 1744–1753. https://doi.org/10.1016/j.neuroimage.2006.10.032

Kameda, T., & Tamura, R. (2007). “To eat or not to be eaten?” Collective risk-monitoring in groups. *Journal of Experimental Social Psychology*, *43*(2), 168–179. https://doi.org/10.1016/j.jesp.2006.02.003

Kamiloğlu, R. G., Smeets, M. A. M., de Groot, J. H. B., & Semin, G. R. (2018). Fear odor facilitates the detection of fear expressions over other negative expressions. *Chemical Senses*, *43*(6), 419–426. https://doi.org/10.1093/chemse/bjy029

Kasturiratne, A., Wickremasinghe, A. R., De Silva, N., Gunawardena, N. K., Pathmeswaran, A., Premaratna, R., Savioli, L., Lalloo, D. G., & De Silva, H. J. (2008). The global burden of snakebite: A literature analysis and modelling based on regional estimates of envenoming and deaths. *PLoS Medicine*, *5*(11), 1591–1604. https://doi.org/10.1371/journal.pmed.0050218

Keverne, E. B., Leonard, R. A., Scruton, D. M., & Young, S. K. (1978). Visual monitoring in social groups of talapoin monkeys (Miopithecus talapoin). *Animal Behaviour*, *26*(PART 3), 933–944. https://doi.org/10.1016/0003-3472(78)90157-4

Kikusui, T., Takigami, S., Takeuchi, Y., & Mori, Y. (2001). Alarm pheromone enhances stress-induced hyperthermia in rats. *Physiology and Behavior*, *72*(1–2), 45–50. https://doi.org/10.1016/S0031-9384(00)00370-X

Kikusui, T., Winslow, J. T., & Mori, Y. (2006). Social buffering: Relief from stress and anxiety. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*(1476), 2215–2228. https://doi.org/10.1098/rstb.2006.1941

Krebs, J. R. (1974). Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (Ardea herodias). *BEHAVIOUR*, *51*(1–2), 99–131. https://doi.org/10.1163/156853974x00165

Kuroda, K., & Kameda, T. (2019). You watch my back, I’ll watch yours: Emergence of collective risk monitoring through tacit coordination in human social foraging. *Evolution and Human Behavior*, *40*(5), 427–435. https://doi.org/10.1016/J.EVOLHUMBEHAV.2019.05.004

Lahti, D. C., Johnson, N. A., Ajie, B. C., Otto, S. P., Hendry, A. P., Blumstein, D. T., Coss, R. G., Donohue, K., & Foster, S. A. (2009). Relaxed selection in the wild. In *Trends in Ecology and Evolution* (Vol. 24, Issue 9, pp. 487–496). Elsevier Current Trends. https://doi.org/10.1016/j.tree.2009.03.010

Laudien, J. H., Wencker, S., Ferstl, R., & Pause, B. M. (2008). Context effects on odor processing: An event-related potential study. *NeuroImage*, *41*(4), 1426–1436. https://doi.org/10.1016/j.neuroimage.2008.03.046

Lazarus, J. (1978). Vigilance, flock size and domain of danger size in the White- fronted Goose.

Wildfowl, *29*, 135–145.

LeDoux, J. E. (2014). Coming to terms with fear. *Proceedings of the National Academy of Sciences*, *111*(8), 2871–2878. https://doi.org/10.1073/PNAS.1400335111

Lee, D. H., Susskind, J. M., & Anderson, A. K. (2013). Social Transmission of the Sensory Benefits of Eye Widening in Fear Expressions. *Psychological Science*, *24*(6), 957–965. https://doi.org/10.1177/0956797612464500

Lima, S. L. (1987). Vigilance while feeding and its relation to the risk of predation. *Journal of Theoretical Biology*, *124*(3), 303–316. https://doi.org/10.1016/S0022-5193(87)80118-2

Lima, S. L. (1990). The influence of models on the interpretation of vigilance. In M. Bekoff & D. Jamieson (Eds.), *Interpretation and Explanation in the Study of Animal Behavior: Vol. 2. Explanation, Evolution and Adaptation.* (pp. 246–267). Westview Press.

Lundström, J. N., Boyle, J. A., Zatorre, R. J., & Jones-Gotman, M. (2008). Functional neuronal processing of body odors differs from that of similar common odors. *Cerebral Cortex*, *18*(6), 1466–1474. https://doi.org/10.1093/cercor/bhm178

Lundström, J. N., Boyle, J. A., Zatorre, R. J., & Jones-Gotman, M. (2009). The neuronal substrates of human olfactory based kin recognition. *Human Brain Mapping*, *30*(8), 2571–2580. https://doi.org/10.1002/hbm.20686

McGann, J. P. (2017). Poor human olfaction is a 19th-century myth. *Science*, *356*(6338), eaam7263. https://doi.org/10.1126/science.aam7263

Michelena, P., Pillot, M. H., Henrion, C., Toulet, S., Boissy, A., & Bon, R. (2012). Group size elicits specific physiological response in herbivores. *Biology Letters*, *8*(4), 537–539. https://doi.org/10.1098/rsbl.2012.0197

Mitro, S., Gordon, A. R., Olsson, M. J., & Lundström, J. N. (2012). The smell of age: Perception and discrimination of body odors of different ages. *PLoS ONE*, *7*(5). https://doi.org/10.1371/journal.pone.0038110

Mogg, K., Garner, M., & Bradley, B. P. (2007). Anxiety and orienting of gaze to angry and fearful faces. *Biological Psychology*, *76*(3), 163–169. https://doi.org/10.1016/j.biopsycho.2007.07.005

Mujica-Parodi, L. R., Strey, H. H., Frederick, B., Savoy, R., Cox, D., Botanov, Y., Tolkunov, D., Rubin, D., & Weber, J. (2009). Chemosensory cues to conspecific emotional stress activate amygdala in humans. *PLoS ONE*, *4*(7). https://doi.org/10.1371/journal.pone.0006415

Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review, 108*(3), 483–522. https://doi.org/10.1037/0033-295X.108.3.483

Olsson, M. J., Lundström, J. N., Kimball, B. A., Gordon, A. R., Karshikoff, B., Hosseini, N., Sorjonen, K., Olgart Höglund, C., Solares, C., Soop, A., Axelsson, J., & Lekander, M. (2014). The Scent of Disease: Human Body Odor Contains an Early Chemosensory Cue of Sickness. *Psychological Science*, *25*(3), 817–823. https://doi.org/10.1177/0956797613515681

Parma, V., Gordon, A. R., Cinzia, C., Cavazzana, A., Lundström, J. N., & Olsson, M. J. (2017). Processing of Human Body Odors. In A. Buettner (Ed.), *Springer Handbook of Odor* (pp. 963–986). Springer.

Pause, B. M. (2012). Processing of body odor signals by the human brain. *Chemosensory Perception*, *5*(1), 55–63. https://doi.org/10.1007/s12078-011-9108-2

Pause, B. M. (2017). Human Chemosensory Communication. In A. Buettner (Ed.), *Springer Handbook of Odor* (pp. 987–1010). Springer.

Pause, B. M., Lübke, K. T., Laudien, J. H., & Ferstl, R. (2010). Intensified Neuronal Investment in the Processing of Chemosensory Anxiety Signals in Non-Socially Anxious and Socially Anxious Individuals. *PLoS ONE*, *5*(4), e10342. https://doi.org/10.1371/journal.pone.0010342

Pause, B. M., Ohrt, A., Prehn, A., & Ferstl, R. (2004). Positive emotional priming of facial affect perception in females is diminished by chemosensory anxiety signals. *Chemical Senses, 29*(9), 797–805. https://doi.org/10.1093/chemse/bjh245

Penn, D. J., Oberzaucher, E., Grammer, K., Fischer, G., Soini, H. A., Wiesler, D., Novotny, M. V., Dixon, S. J., Xu, Y., & Brereton, R. G. (2007). Individual and gender fingerprints in human body odour. *Journal of the Royal Society Interface*, *4*(13), 331–340. https://doi.org/10.1098/rsif.2006.0182

Périquet, S., Todd-Jones, L., Valeix, M., Stapelkamp, B., Elliot, N., Wijers, M., Pays, O., Fortin, D., Madzikanda, H., Fritz, H., MacDonald, D. W., & Loveridge, A. J. (2012). Influence of immediate predation risk by lions on the vigilance of prey of different body size. *Behavioral Ecology*, *23*(5), 970–976. https://doi.org/10.1093/beheco/ars060

Phan, K. L., Wager, T., Taylor, S. F., & Liberzon, I. (2002). Functional neuroanatomy of emotion: A meta-analysis of emotion activation studies in PET and fMRI. In *NeuroImage*

(Vol. 16, Issue 2, pp. 331–348). Neuroimage. https://doi.org/10.1006/nimg.2002.1087

Pourtois, G., Grandjean, D., Sander, D., & Vuilleumier, P. (2004). Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cerebral Cortex*, *14*(6), 619–633. https://doi.org/10.1093/cercor/bhh023

Prehn-Kristensen, A., Wiesner, C., Bergmann, T. O., Wolff, S., Jansen, O., Mehdorn, H. M., Ferstl, R., & Pause, B. M. (2009). Induction of empathy by the smell of anxiety. *PLoS ONE*, *4*(6), e5987. https://doi.org/10.1371/journal.pone.0005987

Prehn, A., Ohrt, A., Sojka, B., Ferstl, R., & Pause, B. M. (2006). Chemosensory anxiety signals augment the startle reflex in humans. *Neuroscience Letters*, *394*(2), 127–130. https://doi.org/10.1016/j.neulet.2005.10.012

Pulliam, H. R. (1973). On the advantages of flocking. In *Journal of Theoretical Biology* (Vol. 38, Issue 2, pp. 419–422). J Theor Biol. https://doi.org/10.1016/0022-5193(73)90184-7

Pulliam, H. R., & Caraco, T. (1984). Living in groups: is there an optimal group size? In John R. Krebs & N. B. Davies (Eds.), *Behavioural Ecology* (pp. 122–147). Blackwell Scientific Publications.

Quenette, P. Y. (1990). Functions of vigilance behaviour in mammals: a review. *Acta Oecologica*, *11*(6), 801–818.

Radford, A. N., & Ridley, A. R. (2007). Individuals in foraging groups may use vocal cues when assessing their need for anti-predator vigilance. *Biology Letters*, *3*(3), 249–252. https://doi.org/10.1098/rsbl.2007.0110

Randall, J. A. (2001). Evolution and function of drumming as communication in mammals'. *American Zoologist*, *41*(5), 1143–1156. https://doi.org/10.1093/icb/41.5.1143

Reason, J. T. (1997). *Managing the Risks of Organizational Accidents*. Ashgate. https://doi.org/10.4324/9781315543543

Rieucau, G., Morand-Ferron, J., & Giraldeau, L. A. (2010). Group size effect in nutmeg mannikin: Between-individuals behavioral differences but same plasticity. *Behavioral Ecology*, *21*(4), 684–689. https://doi.org/10.1093/beheco/arq039

Rigoulot, S., & Pell, M. D. (2012). Seeing emotion with your ears: Emotional prosody implicitly guides visual attention to faces. *PLoS ONE*, *7*(1), 30740. https://doi.org/10.1371/journal.pone.0030740

Rocha, M., Parma, V., Lundström, J. N., & Soares, S. C. (2018). Anxiety Body Odors as

Context for Dynamic Faces: Categorization and Psychophysiological Biases. *Perception*, *47*(10–11), 1054–1069. https://doi.org/10.1177/0301006618797227

Rolls, E. T. (1999). *The Brain and Emotion*. Oxford University Press.

Rubin, D., Botanov, Y., Hajcak, G., & Mujica-Parodi, L. R. (2012). Second-hand stress: inhalation of stress sweat enhances neural response to neutral faces. *Social Cognitive and Affective Neuroscience*, *7*(2), 208–212. https://doi.org/10.1093/scan/nsq097

Schutter, D. J. L. G., & Van Honk, J. (2005). The cerebellum on the rise in human emotion. *Cerebellum*, *4*(4), 290–294. https://doi.org/10.1080/14734220500348584

Scott-Phillips, T. C. (2015). Speaking Our Minds. In *Speaking Our Minds*. Palgrave Macmillan. https://doi.org/10.1007/978-1-137-31273-0

Seligman, M. E. P. (1971). Phobias and preparedness. *Behavior Therapy*, *2*(3), 307–320. https://doi.org/10.1016/S0005-7894(71)80064-3

Semin, G. R., & de Groot, J. H. B. (2013). The chemical bases of human sociality. *Trends in Cognitive Sciences*, *17*(9), 427–429. https://doi.org/10.1016/j.tics.2013.05.008

Shultz, S., Noë, R., McGraw, W. S., & Dunbar, R. I. M. (2004). A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proceedings of the Royal Society B: Biological Sciences*, *271*(1540), 725–732. https://doi.org/10.1098/rspb.2003.2626

Silva, F., Gomes, N., Korb, S., & Semin, G. R. (2020). Not All Emotions Are Equal: Fear Chemosignals Lower Awareness Thresholds Only for Fearful Faces. *Chemical Senses*, *45*(7), 601–608. https://doi.org/10.1093/chemse/bjaa047

Singer, T., Critchley, H. D., & Preuschoff, K. (2009). A common role of insula in feelings, empathy and uncertainty. *Trends in Cognitive Sciences*, *13*(8), 334–340. https://doi.org/10.1016/j.tics.2009.05.001

Sirot, E. (2006). Social information, antipredatory vigilance and flight in bird flocks. *Animal Behaviour*, *72*(2), 373–382. https://doi.org/10.1016/j.anbehav.2005.10.028

Slovic, P. (1987). Perception of risk. *Science*, *236*(4799), 280–285. https://doi.org/10.1126/science.3563507

Slovic, P. (1999). Trust, emotion, sex, politics, and science: Surveying the risk- assessment battlefield. *Risk Analysis*, *19*(4), 689–701. https://doi.org/10.1023/A:1007041821623

Smeets, M. A. M., Rosing, E. A. E., Jacobs, D. M., van Velzen, E., Koek, J. H., Blonk, C., Gortemaker, I., Eidhof, M. B., Markovitch, B., de Groot, J. H. B., & Semin, G. R. (2020). Chemical fingerprints of emotional body odor. *Metabolites*, *10*(3). https://doi.org/10.3390/metabo10030084

Snow, J. C., Allen, H. A., Rafal, R. D., & Humphreys, G. W. (2009). Impaired attentional selection following lesions to human pulvinar: Evidence for homology between human and monkey. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(10), 4054–4059. https://doi.org/10.1073/pnas.0810086106

Stienen, B. M. C., & de Gelder, B. (2011). Fear Modulates Visual Awareness Similarly for Facial and Bodily Expressions. *Frontiers in Human Neuroscience*, *5*. https://doi.org/10.3389/fnhum.2011.00132

Stienen, B. M. C., Tanaka, A., & de Gelder, B. (2011). Emotional Voice and Emotional Body Postures Influence Each Other Independently of Visual Awareness. *PLoS ONE*, *6*(10), e25517. https://doi.org/10.1371/journal.pone.0025517

Strausfeld, N. J., & Hildebrand, J. G. (1999). Olfactory systems: Common design, uncommon origins? In *Current Opinion in Neurobiology* (Vol. 9, Issue 5, pp. 634–639). Current Biology Ltd. https://doi.org/10.1016/S0959-4388(99)00019-7

Susskind, J. M., Lee, D. H., Cusi, A., Feiman, R., Grabski, W., & Anderson, A. K. (2008). Expressing fear enhances sensory acquisition. *Nature Neuroscience*, *11*(7), 843–850. https://doi.org/10.1038/nn.2138

Tkaczynski, P., MacLarnon, A., & Ross, C. (2014). Associations between spatial position, stress and anxiety in forest baboons Papio anubis. *Behavioural Processes, 108,* 1–6. https://doi.org/10.1016/j.beproc.2014.08.006

Treves, A. (1998). Primate Social Systems: Conspecific Threat and Coercion-Defense Hypotheses. *Folia Primatologica*, *69*(2), 81–88. https://doi.org/10.1159/000021567

Treves, A. (1999). Within-group vigilance in red colobus and redtail monkeys. *American Journal of Primatology*, *48*(2), 113–126. https://doi.org/10.1002/(SICI)1098-2345(1999)48:2<113::AID-AJP3>3.0.CO;2-K

Treves, A. (2000). Theory and method in studies of vigilance and aggregation. *Animal Behaviour*, *60*(6), 711–722. https://doi.org/10.1006/anbe.2000.1528

Triplett, N. (1898). The Dynamogenic Factors in Pacemaking and Competition. *The American Journal of Psychology*, *9*(4), 507. https://doi.org/10.2307/1412188

van Schaik, C. P., van Noordwijk, M. A., de Boer, R. J., & den Tonkelaar, I. (1983). The effect of group size on time budgets and social behaviour in wild long-tailed macaques (Macaca fascicularis). *Behavioral Ecology and Sociobiology*, *13*(3), 173–181. https://doi.org/10.1007/BF00299920

van Schaik, C. P., van Noordwijk, M. A., Warsono, B., & Sutriono, E. (1983). Party size and early detection of predators in sumatran forest primates. *Primates*, *24*(2), 211–221. https://doi.org/10.1007/BF02381083

Vine, I. (1971). Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *Journal of Theoretical Biology*, *30*(2), 405–422. https://doi.org/10.1016/0022-5193(71)90061-0

Völlm, B. A., Taylor, A. N. W., Richardson, P., Corcoran, R., Stirling, J., McKie, S., Deakin, J. F. W., & Elliott, R. (2006). Neuronal correlates of theory of mind and empathy: A functional magnetic resonance imaging study in a nonverbal task. *NeuroImage*, *29*(1), 90–98. https://doi.org/10.1016/j.neuroimage.2005.07.022

Vuilleumier, P., & Pourtois, G. (2007). Distributed and interactive brain mechanisms during emotion face perception: Evidence from functional neuroimaging. *Neuropsychologia*, *45*(1), 174–194. https://doi.org/10.1016/j.neuropsychologia.2006.06.003

Wallace, D. J., Greenberg, D. S., Sawinski, J., Rulla, S., Notaro, G., & Kerr, J. N. D. (2013). Rats maintain an overhead binocular field at the expense of constant fusion. *Nature*, *498*(7452), 65–69.

Wawra, M. (1988). Vigilance Patterns in Humans. *Behaviour, 107*(1–2), 61–71. https://doi.org/10.1163/156853988X00197

Williams, G. C. (1966). *Adaptations and Natural Selection*. Princeton University Press.

Wirtz, P., & Wawra, M. (1986). Vigilance and Group Size in Homo sapiens. *Ethology, 71*(4), 283–286. https://doi.org/10.1111/j.1439-0310.1986.tb00592.x

Wudarczyk, O. A., Kohn, N., Bergs, R., Goerlich, K. S., Gur, R. E., Turetsky, B., Schneider, F., & Habel, U. (2016). Chemosensory anxiety cues enhance the perception of fearful faces – An fMRI study. *NeuroImage*, *143*, 214–222. https://doi.org/10.1016/j.neuroimage.2016.09.002

Yang, E., Zald, D. H., & Blake, R. (2007). Fearful Expressions Gain Preferential Access to Awareness During Continuous Flash Suppression. *Emotion*, *7*(4), 882–886. https://doi.org/10.1037/1528-3542.7.4.882

Zajonc, R. B. (1965). Social facilitation. *Science*, *149*(3681), 269–274.

https://doi.org/10.1126/science.149.3681.269

Zheng, Y., You, Y., Farias, A. R., Simon, J., Semin, G. R., Smeets, M. A. M., & Li, W. (2018). Human chemosignals of disgust facilitate food judgment. *Scientific Reports*, *8*(1), 1–10. https://doi.org/10.1038/s41598-018-35132-w

Zhou, W., & Chen, D. (2009). Fear-related chemosignals modulate recognition of fear in ambiguous facial expressions. *Psychological Science*, *20*(2), 177–183. https://doi.org/10.1111/j.1467-9280.2009.02263.x

Chapter II:
Mapping Human Vigilance: The Influence of Conspecifics

Chapter based on:

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Abstract

A considerable volume of animal research on detecting threat and foraging reveals that the co-presence of conspecifics reduces vigilance and enhances foraging. Monitoring threat is an adaptive process and is of considerable relevance to humans. It is therefore important to understand how the presence of others influences threat monitoring - namely vigilance - and consequently the capacity to detect threats. We examine this with a novel paradigm, that simulates a “foraging under threat” situation, with an eye-tracker (allowing the examination of the allocation of attention). Our results show, as predicted, that participants in the individual condition (versus co-presence) allocated more attentional resources to scanning the environment and thereby sacrificing foraging, which increased their likelihood of detecting threatening events. Thus, the presence or absence of others modulates vigilance strategies in humans. These findings highlight the heuristic value of animal vigilance models to understand humans threat monitoring with considerable applied relevance.

Keywords

Vigilance; Co-Presence; Threat-Detection; Eye-Tracking;

Introduction

A significant adaptive process across species is threat monitoring and not surprisingly, a process that is of considerable relevance for humans across diverse contexts (e.g., Reason, 1997). An important question about this process is understanding how threat monitoring in humans can be potentially influenced by others. How does the presence of others - compared to their absence - affect vigilance, namely the capacity to detect threats? The research reported here examines this question for the first time with a novel experimental paradigm. The paradigm simulates a situation that reproduces 'foraging under threat' and permits the examination of the allocation of attentional resources in such situations. This research is inspired by the considerable literature on vigilance in animal herds (see Beauchamp, 2015, for a review) to which we turn first, followed by an overview of the theoretical considerations driving the current research and the research paradigm.

Many animal species have evolved strategies to maximize a trade-off between foraging for food and scanning their surroundings by proportioning their attentional resources for danger (e.g., Creel, Schuette, & Christianson, 2014). This so-called 'anti-predator vigilance' has been the subject of considerable research in animal research (see Beauchamp, 2015). One of the central moderators for the 'anti-predator vigilance' process has been found to be the presence of conspecifics. In species that forage in groups (i.e. social species), individuals rely either on themselves or on others to detect a danger source (mutual warning; see Caraco, Martindale, & Pulliam, 1980; Galton, 1871; Lima, 1995). Moreover, another important aspect of conspecific presence in vigilance is risk dilution (Bertram, 1978). If a predator cannot attack all group members, then the presence of conspecifics will also reduce the individual probability of being targeted (which is inversely proportional to the group size; see Beauchamp, 2015).Thus, relying on others as additional threat detection sources (mutual warning) and as secondary targets for approaching predators (risk dilution), allows individuals to allocate more resources on foraging and to reduce their danger monitoring vigilance activity (see Beauchamp, 2015). Consequently, in social species, vigilance rates decline as a function of the number of conspecifics present (the so-called 'group size effect'; e.g., Bertram, 1980; van Schaik, van Noordwijk, de Boer, & den Tonkelaar, 1983; but see Treves, 2000).

There is little known about human vigilance behavior. Arguably, humans, even in modern societies, are exposed to adaptive challenges that demand a proper balance between foraging/intake activity and risk-monitoring (see Kameda & Tamura, 2007). However, do human beings rely on the same vigilance strategies as other social species, namely the influence of conspecifics' presence on vigilance? So far, a few observational field studies have tried to answer this question. These studies showed that, as with other animal species, vigilance behavior in humans tends to decrease with the presence of conspecifics (Barash, 1972; Dunbar, Cornah, Daly, & Bowyer, 2002; Wawra, 1988; Wirtz & Wawra, 1986). Notably, the conditions in these studies did not entail predatory dangers as in the case of the animal studies and therefore do not constitute examinations of the presence of conspecifics on vigilance in threatening situations. Indeed, whether vigilance in these studies can serve a threat detection purpose (e.g., Wirtz & Wawra, 1986) is debatable also because vigilance behavior could be directed towards same species members (e.g., mate searching; see Dunbar et al., 2002). Nevertheless, the authors argued that in a more threat-rich environment vigilance might be related with threat detection (Dunbar et al., 2002). In fact, this relation was supported by Kameda and Tamura (2007), where using a task that simulated foraging under threat, the authors demonstrated that individuals allocated more resources (i.e., time) to vigilance as the cost of failing to detect threat increased. However, despite this debate, no empirical study has hitherto directly examined the relation between vigilance behavior and avoiding threatening events by humans in the presence of conspecifics.

In the present study, our chief goal was to examine the effects of the presence of conspecifics (vs. being alone) on vigilance in a threatening context. Additionally, we examined the relation between vigilance behavior and the detection of threatening events. We created a new “foraging-vigilance” experimental paradigm, inspired by Kameda and Tamura (2007), and integrated it with eye-tracker technology. This task provides a laboratory simulation of foraging under threat. Concretely, participants receive small monetary rewards for solving a central letter discrimination task - foraging simulation - and suffer strong monetary punishments for non-detected changes occurring in their peripheral visual field - threat simulation (see Methods for detail). Note that monetary loss is widely used to induce threat and avoidance behavior (e.g., Kameda & Tamura, 2007; Löw, Lang, Smith, & Bradley, 2008; Schlund & Cataldo, 2010). It is also important to consider that in contrast to Kameda and Tamura (2007; see also Kuroda & Kameda, 2019), our aim in the present study is not to explore how group dynamics modulate vigilance rates (e.g., “producer-scrounger” game; Giraldeau & Caraco, 2000), or how individuals use vigilance rates of conspecifics to infer the imminence of threat. (e.g., Sirot, 2006). Instead, we sought to tackle a more basic phenomenon, namely if the mere co-presence of conspecifics is enough to modulate individual vigilance strategies.

Building upon the animal vigilance literature and also the limited studies with humans, we hypothesized that (H1) participants in the individual condition will be more vigilant compared to participants in the presence of conspecifics (co-presence) condition. This will result in more time spent scanning the targets in the peripheral visual field (compared to the co-presence condition). An increase in vigilance (in the individual condition) will be associated with a sacrifice of foraging activity, resulting in fewer correct responses and more missed responses in the central task (compared to the co-presence condition). Moreover, we anticipate that vigilance behavior is related to the human capacity to detect threatening changes, resulting in (H2) a higher number of detected changes in the individual condition.

Method

Participants

Ninety-six university students' participated in the experiment on a voluntary basis. Four participants had to be excluded due to anxiety-related disorders, neurological pathologies, or misunderstanding the experimental instructions. The final sample consisted of 92 participants (25 men), aged between 18 and 35 (M_{Age}= 20.95, *SD* = 4.00). All the participants had normal or corrected to normal eyesight, no psychiatric/neurologic medication intake, and no registered or observed symptoms of anxiety-related disorders.

Participants were randomly assigned to the individual or co-presence condition. Forty-five participants (13 males), aged between 18 and 35 (M_{Age}= 22.07, *SD* = 4.96), performed the experiment in the 'individual condition', and 47 (12 males) participants, aged between 18 and 28 (M_{Age}= 19.87, *SD* = 2.41), took part in the 'co-presence condition'.

Sample size was determined *à priori* with a power analysis (using G-Power 3.1.9.3; Faul, Erdfelder, Lang, & Buchner, 2007) for an independent one-tailed Student's t-test, using an effect size obtained from similar eye-tracking research investigating the effect of being in a co-presence condition (compared to an individual condition) on the latency from trial onset to the first fixation on a change location (Göl, Acartürk, & Semin, in preparation). Based on a *Cohen's d* of 0.54 (*power* = .80, *α* = .05), the power analysis revealed that a minimum of 44 participants would be needed in each experimental condition (i.e., a minimum of 88 participants in total).

Foraging-vigilance task

Inspired by the work of Kameda and Tamura (2007), we created a laboratory simulation of foraging under threat. In each trial, participants were presented with random letter matrices measuring three by four letters, which included one of two target letters, a "q" or "p". These matrices were surrounded by 8 circular Gabor patches (comprising 2.25° visual degrees of diameter) that were equidistant from the center of the screen by 8º visual degrees (i.e., presented in the participants near peripheral visual field; see Figure 1).

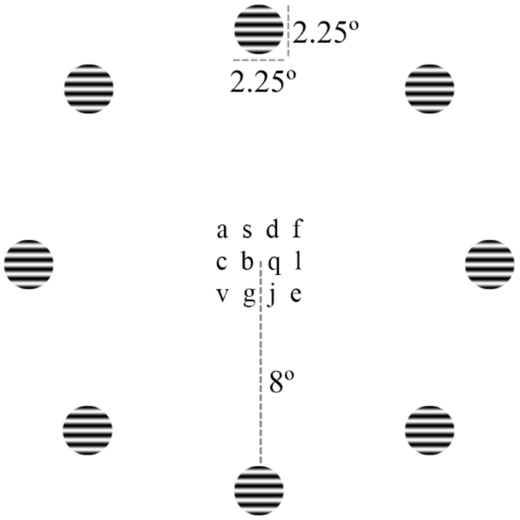

Figure 1: Example of a letter matrix surrounded by 8 Gabor patches.

Participants were asked to find as many target letters as possible during each trial (i.e., a central letter discrimination task). A new matrix was automatically displayed after a participant's response. If there was no answer after 1.5 seconds, then the matrix automatically changed to a new one. Notably, different letter matrices were presented until the end of each trial. Thus, each trial contained several letter matrices. For each correct response, participants received 0.02€ – **foraging simulation**. However, in 40% of the trials, one of the 8 Gabor patches changed in size (gradually reducing its width to about a third of its initial size). This change lasted 4 seconds and could occur at any time between 2 seconds after the start of the trial and 4 seconds before its end. When participants noticed the change, they were instructed to press an escape key (SPACE). If the escape key was not pressed, then they received feedback informing them that they just lost 0.50€ of their accumulated money - **threat simulation**. If they pressed the escape key then the change disappeared immediately from the screen, and the participant was asked to use the mouse to identify the location of the change (i.e., which Gabor patch changed during the trial). Importantly, when a false-alarm happened (i.e., the participant pressed the SPACE key when no change was occurring) no punishment was given. However, we recorded the number of false alarms to control for the frequency of spurious responses. The data revealed a negligible number of false-alarms per participant (only 10.9% of the participants had more than 2 false-alarms in the entire experiment).

Each trial ended after 20 seconds or when a change occurred.

In this task, participants could increase the likelihood of avoiding danger (i.e., detecting a change in a Gabor patch) by elevating their vigilance level. Choosing to do so, however (as the Gabor patches where presented in the peripheral visual field making it impossible or, at least, difficult to perform the central letter discrimination task at the same time) meant that participants had to sacrifice their foraging activity. Thus, this experimental paradigm permitted the simulation of a trade-off between the two survival activities of risk-monitoring and foraging, which, as mentioned in the introductory section, is necessary to study vigilance (see Beauchamp, 2015).

Design

The present study had a 2-level (individual versus co-presence) between participants design. Participants were randomly assigned to the 'individual' or 'co-presence' conditions. In the individual condition, participants performed the task isolated in an experimental cubicle. In the group condition, they sat together with two confederates (1 male and 1 female) who solved a similar task on two independent monitors.

Display

The experiment was performed using Experiment Builder (Version 1.10.1630, SR Research, 2016). The stimuli were displayed on an Asus VX238H 23" Full HD LED monitor (1920x1080) with a refresh rate of 60 Hz, connected to a Dell OptiPlex 755.

An Eyelink 1000 plus eye tracker (SR Research) with a sampling rate of a 1000 Hz was used to record the participants' eye movements. The eye tracker was calibrated to the participants' right eye, using a standard 5-point calibration procedure. 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.

A chin and forehead rest were used to restrict participants' head movements and to control the viewing distance to the screen at 55 cm. Responses were collected using a standard keyboard.

Procedure

All the procedures were conducted in line with the ethical guidelines of the host institution. Each experimental session was divided into 3 phases. Firstly, after an informed consent form was signed, participants were asked to fill out a questionnaire about their demographic details (e.g., age, sex, and education level). Then they received the task instructions. In both experimental conditions, participants received the same instructions and were told that their reward would be contingent upon their performance in the experiment: they would receive 5€ or course credit for their participation, but they could win up to 5€ more (depending on their performance). Participants were informed about the value of the monetary rewards and punishments during the task.

Second, they performed 15 practice trials followed by the main task, which consisted of 50 trials (including the 20 peripheral change trials). The task had a mandatory break in the middle of the experiment.

Lastly, at the end of the experiment, the participants' reward was calculated, and they were paid according to their performance.

Data Preparation

The ocular movement data were visually inspected (trial-by-trial; participant-by-participant), in order to detect and correct trials with calibrations problems. When a trial was clearly identified to have a calibration problem, then all the fixation and saccades were manually adjusted. In total, 2.13% of the trials were corrected.

Following the correction procedure, the mean percentage of time per trial that each participant spent scanning the peripheral targets across the trials where no change occurred (30 no-change trials) was computed. Note that we included only no-change trials because these are the ones that had a fixed 20 seconds duration. The trials where a change occurred (change trials) were designed to have random durations due to the randomization of the moment that the change started, thus having different durations within and between participants. Therefore, including the change trials in the 'vigilance time analysis', would have created a confound.

Regarding the behavioral data related to the central task (i.e., the foraging activity), the mean number of hits and misses of the target letters per trial was computed (only in no-change trials due to the same reasons mentioned earlier).

The capacity to detect peripheral threatening events was measured as the percentage of correctly detected changes per participant.

Lastly, all the recorded variables were checked for outliers that were identified as values exceeding 2.5 median absolute deviations (MAD) (Leys, Ley, Klein, Bernard, & Licata, 2013). These outlier values (< 2% of data in all the analyzed variables) were then altered to be one unit above the next extreme score on that variable (see Field, 2014).

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

Statistical analysis

Regarding the first hypothesis (i.e., vigilance hypothesis; H1), a 2 group design (experimental condition: individual vs. co-presence condition; between-subjects factor) one-way MANOVA – with the mean percentage of scanning time, the mean number of hits, as well as the mean number of misses to the central task, per trial, as dependent variables – was conducted in order to assess whether the participants in the co-presence condition displayed significantly different vigilance behavior from those in the group condition. Following a significant multivariate main effect of the experimental condition, each of the dependent variables was examined using independent one-tailed Student's t-tests.

As far as our second hypothesis (i.e., the threatening changes detection hypothesis; H2) is concerned, the percentage of detected changes were compared in an independent one-tailed Student's t-test using the experimental conditions (i.e., individual vs. co-presence condition) as the between-subjects factor[1].

Additionally, to confirm the existence of a trade-off between the two survival activities of risk-monitoring and foraging in the present study, we conducted 3 simple linear regressions. The goal was to assess the predictor effect of the mean percentage of scanning time on: (a) the mean number of hits (i.e., in the letter discrimination task); (b) the mean number of misses (i.e., in the letter discrimination task); and (c) the percentage of detected changes in the peripheral Gabor patches. Specifically, the later analyses allowed us to assess if a higher vigilance behavior directly translated to a foraging sacrifice.

Results

Regarding our first hypothesis, the one way MANOVA revealed a significant main effect of the experimental condition (*Pillai's Trace* = .18; $F(3, 88) = 6.30$, $p = .001$, $\eta_p^2 = .18$), indicating that participants in the individual condition displayed a distinct vigilance behavior compared to participants in the co-presence condition. In line with our hypothesis, participants in the individual condition were significantly more vigilant than participants in the co-presence condition, $t(79.81) = 3.01$, $p = .002$ (one-tailed), $d = 0.63$, 95% CI].023; +∞[, spending on average 21.08% ($SD = 9.56$) of the trial time scanning the peripheral targets, whereas the

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[1] Regarding our second hypothesis, we changed the pre-registered statistical analysis plan, including only one (percentage of detected changes) of the 4 proposed variables (reaction times in detecting the changes, and delay and velocity of participants' first saccade to the change location). Due to the general low accuracy in detecting the threatening changes, we were not able to compute the remaining variables because they were based in a low number of trials (particularly in the co-presence condition), hence not reflecting reliable values.

participants in the co-presence condition only scanned for 15.82% (*SD* = 6.90) of the time (see Figure 2).

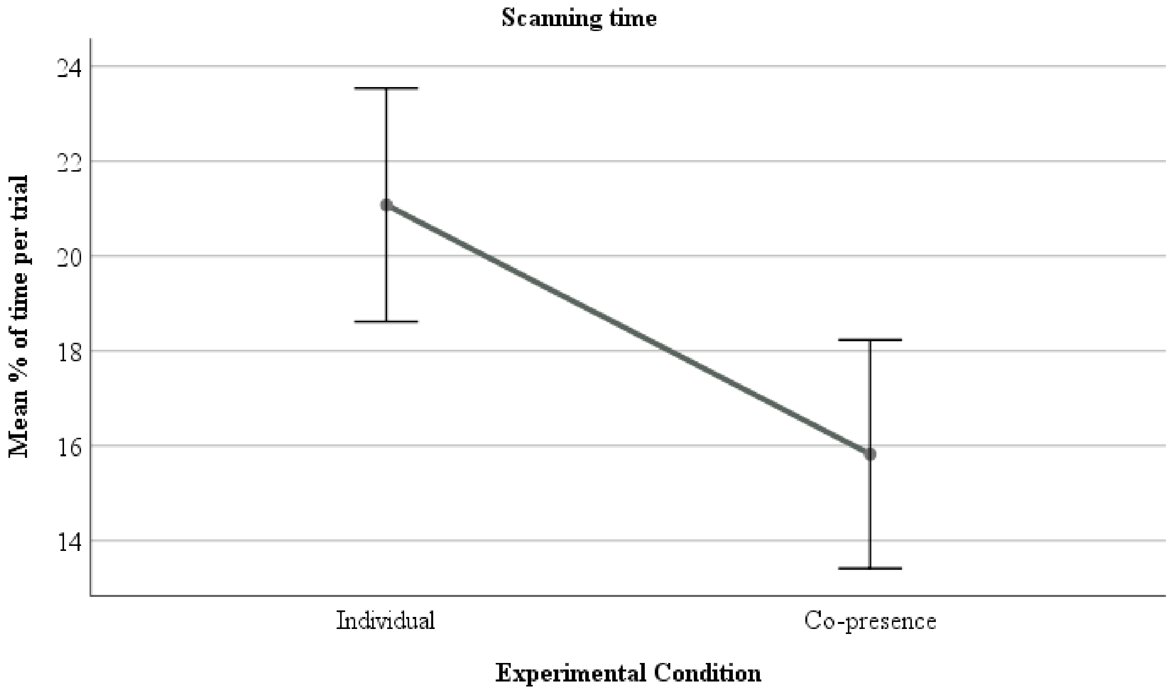

Figure 2: Mean percentage of time spent scanning the peripheral targets. Error bars represent 95% confidence intervals.

In line with the observed vigilance increment, and as predicted, the results revealed a foraging sacrifice in the individual condition. Specifically, participants in the individual condition evidenced a significantly lower number of correctly identified letters per trial (M = 11.30; SD =2.48) compared to the participants in the co-presence condition (*M* = 13.20; *SD* = 2.52; *t*(90) = -3.64, *p* < .001 (one-tailed), *d* = .76, 95% CI]-∞; -1.033[) (see Figure 3).

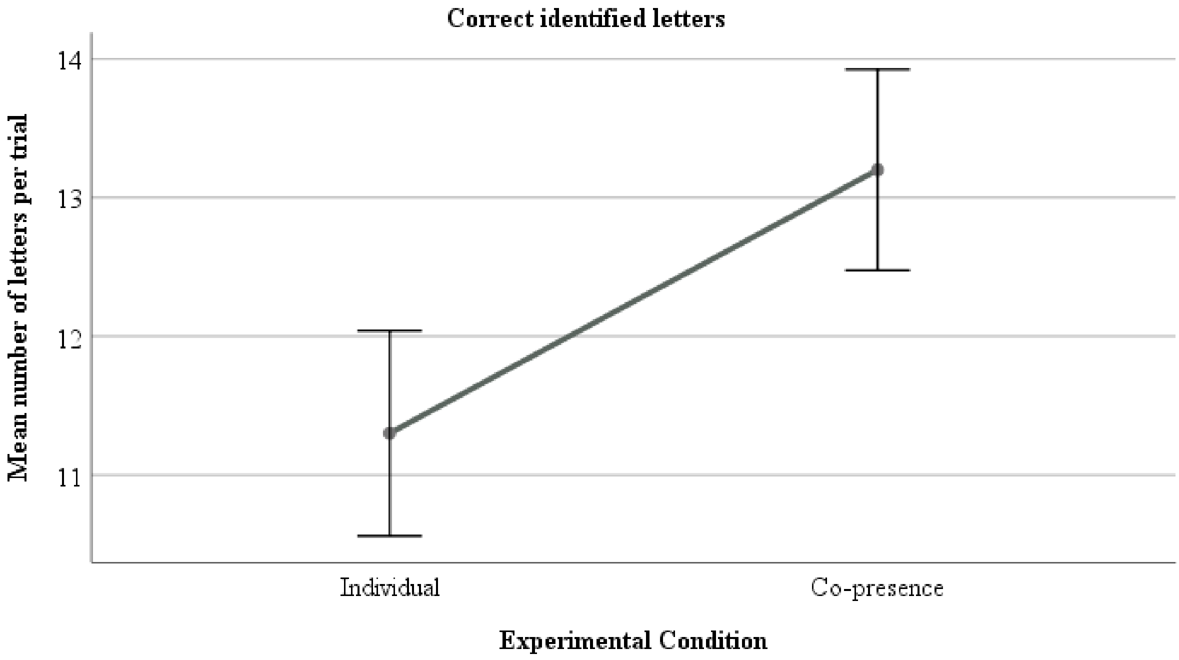

Figure 3: Mean number of correct identified letters per trial. Error bars represent 95% confidence intervals.

Moreover, and also in line with this decrease in foraging, participants in the individual condition also showed a higher number of non-identified letters per trial (*M* = 5.27; *SD* = 1.62) compared with participants in the co-presence condition (*M* = 3.92; *SD* = 1.56; *t*(90) = 4.08, *p* < .001 (one-tailed), *d* = .85, 95% CI].802; +∞[) (see Figure 4).

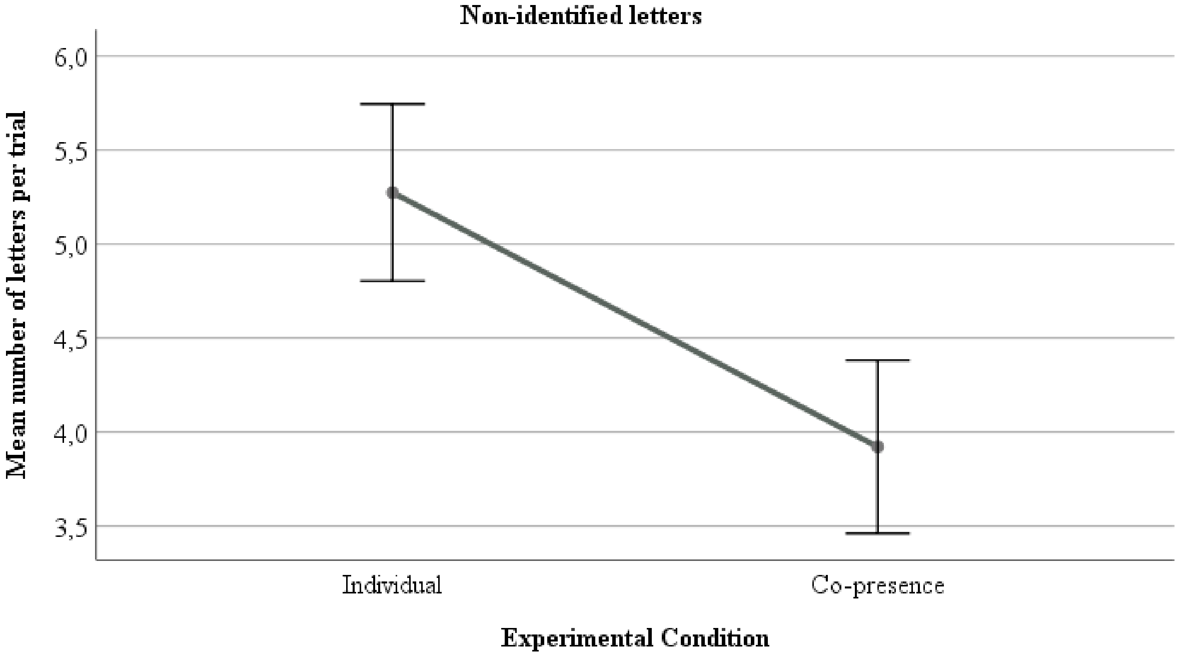

Figure 4: Mean number of non-identified letters per trial. Error bars represent 95% confidence intervals.

Regarding the change detection hypothesis (H2), the independent one-tailed Student’s t-test revealed that participants in the individual condition detected significantly more changes (M = 46.11%; SD = 17.96) than participants in the co-presence condition (M = 38.87%; SD = 17.11; *t*(90) = 1.98, *p* = .025 (one-tailed), *d* = .41, 95% CI].012; +∞[) (see Figure 5).

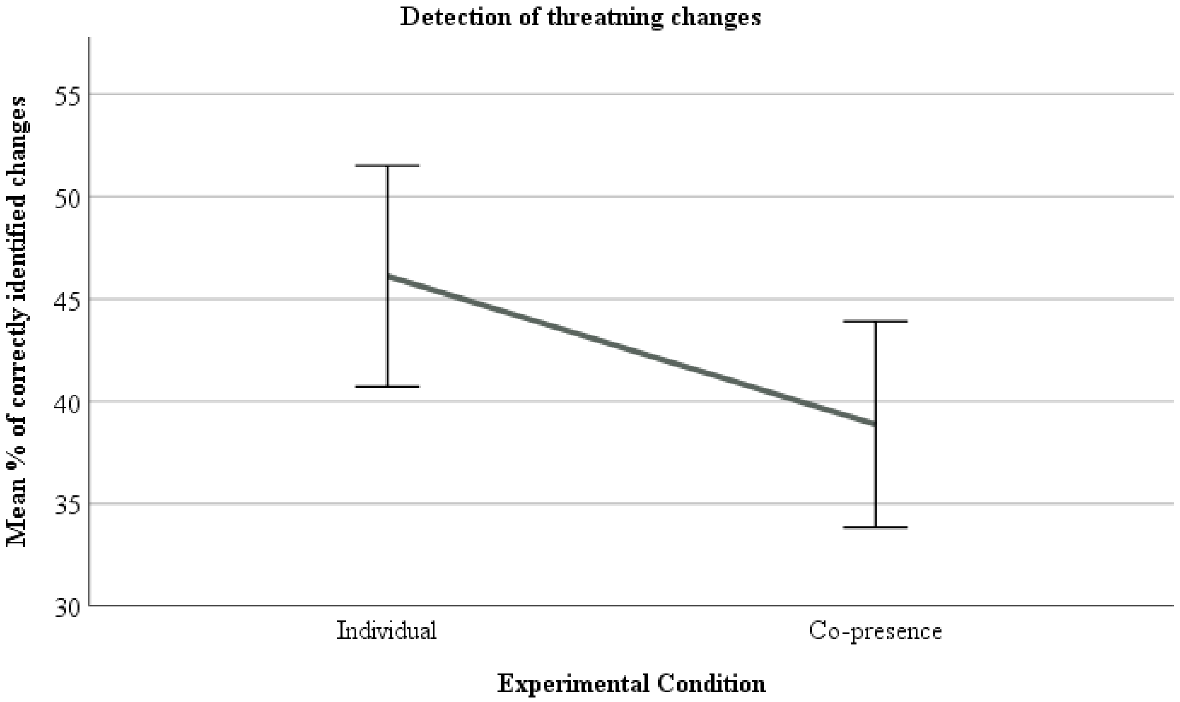

Figure 5: Mean percentage of correctly identified changes. Error bars represent 95% confidence intervals

Finally, concerning the existence of a trade-off between the two survival activities of risk-monitoring and foraging, the linear regression analyses revealed that the mean percentage of scanning time significatively predicts the mean number of hits ($R^2 = .15$, $F(1, 90) = 17.02$, $p < .001$), the mean number of misses ($R^2 = .21$, $F(1, 90) = 24.49$, $p < .001$), and also the percentage of detected changes ($R^2 = 0.37$, $F(1, 90) = 52.13$, $p < .001$). Moreover, when analyzing the standardized coefficients of the regression models it is possible to conclude that the higher the mean percentage of scanning time, the lower the mean number of hits ($\beta = -.40$), the higher the number of the mean number of misses ($\beta = .46$), and the higher the percentage of detected changes ($\beta = .61$).

Discussion

This experiment was designed to examine how vigilance behavior and the detection of threat are affected in the presence or absence of others. To this end, we developed a new, innovative experimental paradigm designed to produce a ‘foraging under threat’ scenario in order to examine attentional resources allocation. The results confirmed, as predicted, that higher vigilance levels were manifested in the individual condition compared to the co-presence condition. Moreover, increased vigilance was negatively correlated with foraging activity, namely participants in the individual condition devoted less resources (i.e. time) to the central letter discrimination task compared to participants in the co-presence condition. Notably, the increase in vigilance in the individual condition resulted in an enhanced capacity to detect peripheral changes that represent threatening events compared to the co-presence condition. Additionally, an increment in the time spent scanning the peripheral targets directly translates to an impairment of the participants' performance on the central letter discrimination task. This confirms the existence of a trade-off between the two survival activities of risk-monitoring and foraging in the present study, and consequently the suitability of our task in studying vigilance. The outline of these findings converges with the observational research in the animal behavior literature (see Beauchamp, 2015), and humans (Barash, 1972; Dunbar et al., 2002; Wawra, 1988; Wirtz & Wawra, 1986). However, the details of our findings, due to the sophisticated and innovative experimental paradigm, go far beyond these observational studies. They reveal the dynamic underlying the differentially vigilant behavior displayed in individual and co-presence conditions.

To understand the possible underlying mechanisms behind the observed effects, we must first consider previous research on animal behavior. Vigilance, as an alertness state that governs risk monitoring, appears to have been modulated, to some extent, by evolutionary regularities (e.g., Beauchamp, 2010). One of these contingences is related to the perceived threat in the surrounding environment. In many animal species, including human beings, the imminent occurrence of threatening events induces an increased alertness state (also defined as a fear-like state; see Öhman & Mineka, 2001), which enhances vigilance (see Beauchamp, 2015). This relation between alertness and vigilance is supported by many animal studies showing that vigilance is influenced by stress hormone levels, such as cortisol and norepinephrine (e.g., Hawlena & Schmitz, 2010; Voellmy, Goncalves, Barrette, Monfort, & Manser, 2014; but see Tkaczynski, MacLarnon, & Ross, 2014). This is further supported by studies showing that diazepam - a drug that lowers anxiety (and consequently the referred alertness state) in many vertebrates - significantly reduces the scanning behavior in laboratory mice (Choy, Yu, Hawkes, & Mayorov, 2012). Another evolutionary contingency relates to the presence of conspecifics. The regularities across the evolutionary pathway (e.g., group situations, due to mutual warning or risk dilution, are safer than individual situations; see Galton, 1871; Hamilton, 1971) may have shaped vigilance to automatically decrease in the presence of conspecifics (especially in situations when other sources of danger than predators are absent). Thus, the perception of threat (i.e., predation risk) in prey animals (a major stressor) decreases in large groups. This was supported, for instance, by Michelena and colleagues (2012), who evidenced that the amount of circulating cortisol – a hormone related with stress levels - decreased in sheep living in larger groups. Accordingly, and as already discussed previously, vigilance rates also tend to decrease as group size increases (group size effect; e.g., Caraco et al., 1980). Notably, this literature shows the effects of the presence of conspecifics. Hence, we suggest that the results obtained in our study are likely driven by a similar mechanism. The presence of conspecifics - due to evolutionary regularities, namely repeated reduction of vigilance and alertness in group situations, becomes functionally autonomous and is manifested in reduced alertness whenever conspecifics are present. In turn, this results in lower vigilance rates and higher foraging activity in the co-presence condition (compared to the individual condition).

One could also possibly argue that the pattern of results in the co-presence condition were due to a distraction effect induced by the presence of others (see Baron, Moore, & Sanders, 1978 for related accounts). One argument on the effects of the presence of others suggests that this constitutes a distraction (e.g., Muller, Atzeni, & Butera, 2004) because participants have to divide their attention between monitoring the other and the requirements of the task (see Baron, 1986). It is suggested that the presence of others leads to a narrowing of attentional focus. Thus, performance improves at the expense of peripheral distractor cues in tasks that require the allocation of attention to a central target (e.g., Muller et al., 2004). In our case, the referred distraction effect does not fit with the pattern of our findings if one takes into consideration our methodology and the ocular movement data. In our experiment, it was not possible for participants to perform both tasks simultaneously (i.e., participants had to allocate their attention to one task at a time). As such, what we observed in the conspecific condition cannot be due to reduced performance to the peripheral task. Instead, it reflects a different strategy employed towards the demands the participants faced (i.e., to what task should I pay most attention to). This is further attested by the gaze movement data showing that participants in the co-presence condition (compared to the individual condition) detected more target letters (more time spent at the central task) and spent less time searching for changes in their periphery.

One noteworthy constraint of the current study, when compared to the animal studies, is the relationship found with group size and vigilance – the group size effect (e.g., Beauchamp, 2008). The present study had only 3 participants in the group condition. We cannot therefore say anything about a group size effect in human groups. Nevertheless, the current experimental paradigm can be easily adapted to larger groups to examine how different group sizes might shape vigilance in human beings. Such effects could be of considerable relevance for the human risk-monitoring research field.

Moreover, this study examines a group situation in which the nature of the relationships does not have any relationship defining feature such as competition or cooperation. This was because we were concerned with the basic condition of co-presence alone. Obviously, additional variables such as the type of interdependences might affect vigilance behavior and the detection of threat (see Beauchamp, 2015). Thus, the current study constitutes an important starting point to examine such variations.

In conclusion, this study shows for the first time - using gaze movement data - that when in a threat-rich context, human beings rely on vigilance strategies and adapt to co-presence vigilance patterns similar to those observed in other social animal species (Barash, 1972; Dunbar et al., 2002; Wawra, 1988; Wirtz & Wawra, 1986). This research demonstrates that when in a threat-rich scenario, being alone leads to an increment in vigilance and translates directly to an improved threat detection capacity. Taken together, these conclusions highlight the heuristic value of animal behavioral models to study risk-monitoring in human beings, with a wide range of applications, such as in the case of air-traffic controllers (e.g., Blachman & Proschan, 1959).

References

Barash, D. P. (1972). Human Ethology: The Snack-Bar Security Syndrome. *Psychological Reports*, *31*(2), 577–578. https://doi.org/10.2466/pr0.1972.31.2.577

Baron, R. S. (1986). Distraction-Conflict Theory: Progress and Problems. *Advances in Experimental Social Psychology*, *19*, 1–40. https://doi.org/10.1016/S0065-2601(08)60211-7

Baron, R. S., Moore, D., & Sanders, G. S. (1978). Distraction as a source of drive in social facilitation research. *Journal of Personality and Social Psychology*, *36*(8), 816–824. https://doi.org/10.1037/0022-3514.36.8.816

Beauchamp, G. (2008). What is the magnitude of the group-size effect on vigilance? *Behavioral Ecology*, *19*(6), 1361–1368. https://doi.org/10.1093/beheco/arn096

Beauchamp, G. (2010). A comparative analysis of vigilance in birds. *Evolutionary Ecology*, *24*(5), 1267–1276. https://doi.org/10.1007/s10682-010-9358-5

Beauchamp, G. (2015). *Animal vigilance : monitoring predators and competitors*. Academic Press.

Bertram, B. C. R. (1978). Living in groups: predator and prey. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural Ecology* (pp. 64–96). Oxford: Blackwell Publishing Ltd.

Bertram, B. C. R. (1980). Vigilance and group size in ostriches. *Animal Behaviour*, *28*(1), 278–286. https://doi.org/10.1016/S0003-3472(80)80030-3

Blachman, N., & Proschan, F. (1959). Optimum Search for Objects Having Unknown Arrival Times. *Operations Research*, *7*(5), 625–638. https://doi.org/10.1287/opre.7.5.625

Caraco, T., Martindale, S., & Pulliam, H. R. (1980). Avian Time Budgets and Distance to Cover. *The Auk*, *97*(4), 872–875. https://doi.org/10.1093/auk/97.4.872

Choy, K. H. C., Yu, J., Hawkes, D., & Mayorov, D. N. (2012). Analysis of vigilant scanning behavior in mice using two-point digital video tracking. *Psychopharmacology*, *221*(4), 649–657. https://doi.org/10.1007/s00213-011-2609-5

Creel, S., Schuette, P., & Christianson, D. (2014). Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology*, *25*(4), 773–784. https://doi.org/10.1093/beheco/aru050

Dunbar, R. I. M., Cornah, L., Daly, F. J., & Bowyer, K. M. (2002). Vigilance in human groups: A test of alternative hypotheses. *Behaviour*, *139*(5), 695–711.

https://doi.org/10.1163/15685390260136771

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*(2), 175–191. https://doi.org/10.3758/BF03193146

Field, A. (2014). Discovering Statistics Using SPSS, Second Edition. *SAGE Publication*. https://doi.org/10.1111/j.1365-2648.2007.04270_1.x

Galton, F. (1871). Gregariousness in cattle and in men. *Macmillan's Magazine*, *23*(136), 353–357.

Giraldeau, L.-A., & Caraco, T. (2000). *Social Foraging Theory*. Princeton NJ: Princeton University Press.

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, *31*(2), 295–311. https://doi.org/10.1016/0022-5193(71)90189-5

Hawlena, D., & Schmitz, O. J. (2010). Physiological Stress as a Fundamental Mechanism Linking Predation to Ecosystem Functioning. *The American Naturalist*, *176*(5), 537–556. https://doi.org/10.1086/656495

Kameda, T., & Tamura, R. (2007). "To eat or not to be eaten?" Collective risk-monitoring in groups. *Journal of Experimental Social Psychology*, *43*(2), 168–179. https://doi.org/10.1016/j.jesp.2006.02.003

Kuroda, K., & Kameda, T. (2019). You watch my back, I'll watch yours: Emergence of collective risk monitoring through tacit coordination in human social foraging. *Evolution and Human Behavior*, *40*(5), 427–435. https://doi.org/10.1016/J.EVOLHUMBEHAV.2019.05.004

Leys, C., Ley, C., Klein, O., Bernard, P., & Licata, L. (2013). Detecting outliers: Do not use standard deviation around the mean, use absolute deviation around the median. *Journal of Experimental Social Psychology*, *49*(4), 764–766. https://doi.org/10.1016/J.JESP.2013.03.013

Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, *49*(1), 11–20. https://doi.org/10.1016/0003-3472(95)80149-9

Löw, A., Lang, P. J., Smith, J. C., & Bradley, M. M. (2008). Both predator and prey: emotional arousal in threat and reward. *Psychological Science*, *19*(9), 865–873. https://doi.org/10.1111/j.1467-9280.2008.02170.x

Michelena, P., Pillot, M.-H., Henrion, C., Toulet, S., Boissy, A., & Bon, R. (2012). Group size elicits specific physiological response in herbivores. *Biology Letters*, *8*(4), 537–539. https://doi.org/10.1098/rsbl.2012.0197

Muller, D., Atzeni, T., & Butera, F. (2004). Coaction and upward social comparison reduce the illusory conjunction effect: Support for distraction–conflict theory. *Journal of Experimental Social Psychology*, *40*(5), 659–665. https://doi.org/10.1016/J.JESP.2003.12.003

Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, *108*(3), 483–522. https://doi.org/10.1037/0033-295X.108.3.483

Reason, J. T. (1997). *Managing the Risks of Organizational Accidents*. Ashgate. https://doi.org/10.4324/9781315543543

Schlund, M. W., & Cataldo, M. F. (2010). Amygdala involvement in human avoidance, escape and approach behavior. *NeuroImage*, *53*(2), 769–776. https://doi.org/10.1016/j.neuroimage.2010.06.058

Sirot, E. (2006). Social information, antipredatory vigilance and flight in bird flocks. *Animal Behaviour*, *72*(2), 373–382. https://doi.org/10.1016/J.ANBEHAV.2005.10.028

Tkaczynski, P., MacLarnon, A., & Ross, C. (2014). Associations between spatial position, stress and anxiety in forest baboons Papio anubis. *Behavioural Processes*, *108*, 1–6. https://doi.org/10.1016/j.beproc.2014.08.006

Treves, A. (2000). Theory and method in studies of vigilance and aggregation. *Animal Behaviour*, *60*(6), 711–722. https://doi.org/10.1006/anbe.2000.1528

van Schaik, C. P., van Noordwijk, M. A., de Boer, R. J., & den Tonkelaar, I. (1983). The effect of group size on time budgets and social behaviour in wild long-tailed macaques (Macaca fascicularis). *Behavioral Ecology and Sociobiology*, *13*(3), 173–181. https://doi.org/10.1007/BF00299920

Voellmy, I. K., Goncalves, I. B., Barrette, M.-F., Monfort, S. L., & Manser, M. B. (2014). Mean fecal glucocorticoid metabolites are associated with vigilance, whereas immediate cortisol levels better reflect acute anti-predator responses in meerkats. *Hormones and Behavior*, *66*(5), 759–765. https://doi.org/10.1016/j.yhbeh.2014.08.008

Wawra, M. (1988). Vigilance Patterns in Humans. *Behaviour*, *107*(1–2), 61–71. https://doi.org/10.1163/156853988X00197

Wirtz, P., & Wawra, M. (1986). Vigilance and Group Size in Homo sapiens. *Ethology*, *71*(4), 283–286. https://doi.org/10.1111/j.1439-0310.1986.tb00592.x

Chapter III:

Feeling Safer: The influence of conspecifics on threat appraisals

Chapter based on:

Gomes, N., & Semin, G. R. (in preparation). Feeling Safer: The influence of conspecifics on threat appraisals.

Abstract

Research on risk-monitoring in human beings has shown that the presence of conspecifics (compared to individual conditions) reduces the attentional resources allocated to vigilance, increasing the investment in other survival-relevant activities (e.g., foraging). As suggested by several studies in diverse animal species and proposed by distinct theories on the beginning of animal gregariousness, this vigilance reduction may be explained by a perceived increase in safety in group conditions. In the present study, we aimed to explore this effect in human beings, assessing whether the presence of conspecifics (compared to an alone condition) results in lower threat feelings during ambiguous, dangerous situations. Additionally, we also examined the modulatory effects of distinct threat sources (i.e. dangerous animals or harmful conspecifics) and different presence conditions (i.e. the presence of 2 friends or 2 strangers) on the phenomenon mentioned above. In an online-based study, we asked participants to envision themselves (either alone, in the company of 2 friends, or in the presence of 2 strangers) in several dangerous scenarios and then rate how threatened they would feel and how likely they would get harmed in each situation. As predicted, our results showed that participants (regardless of the threat source) rated the different scenarios as less threatening when they imagined themselves in the presence of conspecifics compared to when they imagined themselves alone. These findings support the hypothesis that the presence of conspecifics reduces vigilance behavior by increasing the participants' feeling of safety.

Keywords

Risk-perception; Threat; Co-presence; Safety.

Introduction

Efficiently monitoring the surrounding environment looking for potentially dangerous stimuli (i.e. vigilance) without neglecting other fitness-relevant activities (e.g., foraging) is extremely important for many animal species' survival. Human beings are no exception. They face a similar attentional trade-off in diverse modern contexts (see Kameda & Tamura, 2007). As verified in other social animal species (see Beauchamp, 2015), an interesting feature of this trade-off in human beings is that conspecifics strongly modulate it (e.g., Barash, 1972; Wawra, 1988; Wirtz & Wawra, 1986). Attentional resources (i.e. time) allocated to vigilance tend to decrease when humans are in the mere presence of conspecifics (compared to when they are alone), reducing their efficacy in avoiding dangerous events. Nevertheless, by reducing vigilance, individuals in the presence condition (compared to an alone condition) could invest more attentional resources in an intake activity analogous to foraging (see Gomes & Semin, 2020). In the research reported here, we aimed to go a step forward, exploring a possible mechanism behind the modulatory effects of the presence of conspecifics on the trade-off mentioned above between vigilance and other survival-relevant activities. Specifically, inspired by a considerable volume of animal research (e.g., Michelena et al., 2012), the present study examines the hypothesis that the presence of conspecifics automatically induces a feeling of increased safety (i.e. lower threat risk). Arguably this safety increment reduces the individuals' alertness and, consequently, the resources allocated to vigilance (for a similar argument, see Gomes & Semin, 2020). In the following, we first summarized the animal and the few human findings on the role of conspecifics modulating threat monitoring and coping, turning then to an overview of the theoretical considerations driving the current research.

Notably, the idea that conspecifics' presence represents an increased safety stems from the beginnings of the research on gregariousness and vigilance. From the first descriptions of what is nowadays known as vigilance (e.g., Galton, 1871) until the most influential theories regarding the beginning of gregariousness in animal species (e.g., the *"Geometry for the selfish herd"*; Hamilton, 1971), group contexts (compared to individual situations) were thought to represent safer scenarios. Although based on different mechanisms, these theories posit that when in the presence of conspecifics, an individual can either rely on others as additional threat detection sources (*"many-eyes effect"* and *"mutual warning"*; e.g., Caraco et al., 1980; Galton, 1871; Lima, 1995) and/or as secondary targets for approaching danger (*"risk dilution"*; e.g., Bertram, 1978). Hence, in group situations, an individual's probability of getting injured by a dangerous stimulus is hypothetically reduced, allowing them to invest less attentional resources to danger monitoring without compromising safety (see Beauchamp, 2015). This "lower threat risk" (i.e. increased safety) is commonly hypothesized as behind the observed vigilance reduction in group contexts across a wide range of different animal species. These may be invertebrates (Fordyce & Agrawal, 2001), birds (e.g., Rieucau et al., 2010), or mammals (e.g., Blumstein et al., 1999) even including non-human primates (e.g., Gosselin-ildari & Koenig, 2012). Studies showing that active stress hormones (associated with vigilance levels; e.g., Hawlena & Schmitz, 2010) are reduced in animals living in larger groups (e.g., sheep; Michelena et al., 2012) constitute further support for this relation between safety and vigilance rates.

Arguably, a similar mechanism may also explain the vigilance reduction observed in human subjects when in the presence of conspecifics. As we hypothesized (Gomes & Semin, 2020), this regularity of reduced threat risk in group contexts (compared to individual situations) may have shaped threat detection mechanisms throughout our evolutionary history. Hence, group situations may be automatically assessed, even nowadays, as safer than when we are alone (see also Barash, 1972; Wirtz & Wawra, 1986). Consequently, vigilance can be automatically relaxed, which allows the allocation of more attentional resources to other survival-relevant activities, increasing individuals' fitness. If this is the case, human subjects should assess ambiguous danger situations as less threatening when in the presence of conspecifics (compared to when alone).

Although no study has hitherto directly explored how the presence of conspecifics shapes threat appraisals, some supportive evidence for its role in coping with threat situations can be found in human studies on social support and social buffering (see Epley, 1974; Hornstein & Eisenberger, 2018; Kikusui et al., 2006). Research on these fields has shown that the presence of conspecifics playing a supportive social role (e.g., friends, romantic partners, parents, etc.,), but not strangers, reduces or mitigates psychological and physiological responses to threat (e.g., Kiyokawa et al., 2007; Thorsteinsson & James, 1999). Additionally, social support figures' presence also affects fear learning processes by reducing fear acquisition and enhancing fear extinction (see Hornstein et al., 2016, 2018). As Hornstein and Eisenberger (2018) argue in an analogy to the preparedness theory[1] (Seligman, 1971), social supporters seem to constitute an innate stimulus category that automatically signals safety (i.e. preparedness for safety; see Jacobs & LoLordo, 1977). Hence, their presence dampens the responses to dangerous stimuli (see Hornstein & Eisenberger, 2018). However, this research neither explores

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[1] Which posits that stimuli that provided threats to the survival of our phylogenetic ancestors (e.g., deadly predators, heights, or wide-open spaces) are more likely to be feared than contemporary threats (e.g., weapons, motorcycles, or damaged electric equipment) frequently found in our environment (Seligman, 1971).

the modulatory effects of conspecifics on threat appraisals nor provides a concrete explanation for reducing vigilance rates observed in our previous study. In Gomes and Semin (2020), the mere presence condition was manipulated, leading the participants to perform the experiment in the presence of two strangers (i.e. confederates) that did not represent social support figures.

Hence, in the present study, our goal was to shed light on the modulatory effects of the presence of conspecifics (compared to individual situations) in threat appraisals during ambiguous, dangerous situations (i.e. scenarios where a threatening event is about to occur). The distinct modulatory roles of social support figures (i.e. friends) and strangers and the effects of different threat sources (i.e. animal versus socially dangerous stimuli) were also explored. To achieve our goal, we asked participants to envision themselves in several dangerous scenarios by exposing them to short threatening vignettes (involving either dangerous animals or potentially harmful conspecifics). In each scenario, they had to imagine themselves alone, in the company of 2 friends, or in the presence of 2 strangers. Their task was to rate (1) how threatened they would feel and (2) the likelihood of getting harmed in each situation. Although these two questions may be highly correlated, our aim in using both was to collect across the three presence conditions: (1) a subjective measure of threat (i.e. feeling threatened); and also (2) a measurement of the participants' perception about the objective consequences of being exposed to dangerous stimuli (i.e. probability of getting injured).

Importantly, we acknowledge that a scenario study (also known as imagery; e.g., J. D. Mayer et al., 1995) constitutes an inherently different situation compared to an experiment in vivo. The imagery case seems to depend on the participants’ imagination and interpretation of the different scenarios' content, which may not result in equally vivid experiences for all the subjects (see Zhang et al., 2014). However, a wide range of research has shown that imagery is a robust method to induce emotional/alertness states (see Siedlecka & Denson, 2019). Several studies have shown that inducing fear (a threat-related emotional state; e.g., Adolphs & Andler, 2018) with this method not only increases participants feelings of fear but also modulates startle response, respiration rate, heart rate, and skin conductance consistent with a fear response (e.g., Cuthbert et al., 2003; Vrana & Lang, 1990). Moreover, previous research on threat appraisals in different contexts also confirmed that imagery is effective in triggering threatening feelings in the participants (e.g., Muris et al., 2008; Reuman et al., 2015).

Building upon the animal vigilance research and the observed vigilance reduction in human groups, we hypothesized (H1) that participants will judge a dangerous situation that is ambiguous less threatening if the situation involved the presence of conspecifics compared to being in the situation alone. Relying on earlier work on social support, we also hypothesized

(H2) that if the co-presents are friends rather than strangers, participants will express less threat (e.g., Hornstein & Eisenberger, 2018). Finally, we made no predictions regarding the potential sources of danger (i.e. dangerous animals or harmful conspecifics).

Method

Participants

One hundred and sixty volunteers gave their informed consent to participate in an online experiment. Three participants had to be excluded because their native language was not Portuguese, leaving 157 participants (63 females) aged between 18 and 35 (M_{Age} = 23.40 years; *SD* = 4.02). All participants were recruited through the Prolific Academic crowdsourcing platform and were pre-screened for current psychiatric/neurological disorders.

Participants were randomly assigned to one of two threat source conditions: 82 participants (33 females), aged between 18 and 35 (M_{Age} = 23.23 years; *SD* = 3.95), were given vignettes with dangerous animals; 75 participants (30 females), also aged between 18 and 35 (M_{Age} = 23.58 years; *SD* = 4.11) were given vignettes with harmful conspecifics.

We could not estimate *a priori* an effect size as there were no previous studies on the influence of the presence of conspecifics on threat appraisals. Instead of a formal power analysis, we defined our minimum sample size based on Brysbaert's (2019) guidelines. Considering our effect of interest (i.e. a main effect of the presence condition; a within-subjects factor with 3 levels, where 2 of these levels were expected to have similar data patterns), and assuming a d = .4 and a power of .8, we established a minimum of 75 participants per threat source condition.

The study was approved by the local ethics committee and followed the guidelines of the Declaration of Helsinki.

Design and manipulation

The current study employed a mixed 2x3 factorial design with the threat source (dangerous animals, harmful conspecifics) as a between-subjects factor and the presence condition (alone, with 2 friends, with 2 strangers) as a within-subjects factor.

Vignettes preparation

To create the dangerous scenarios in which participants were asked to immerse themselves, we prepared 24 ambiguous threatening vignettes (12 describing events involving potentially dangerous animals and 12 involving potentially harmful human beings; the full set of vignettes appears in appendix A).

The vignettes' effectiveness in inducing a threatening feeling was tested, comparing them to their neutral version (created by replacing the dangerous event with a neutral one) in a pilot study. Specifically, 54 participants (39 men), aged between 18 and 34 (M_{Age} = 22.80 years; *SD* = 3.74), were asked to immerse themselves in 16 (randomly selected) of the possible 48 scenarios (24 threatening and 24 neutral vignettes). Their task was to assess, using a 0-100 slider (ranging from *'Not at all threatened'* to *'Very threatened'*), how threatened they were likely to feel in each scenario. Each vignette was rated 18 times, which were then averaged to create a threatening score per vignette. A dependent Student's t-test revealed that threatening vignettes (*M*= 81.32; *SD*= 9.85) were rated as significantly as more threatening ($t(23)$= 25.42, $p < .001$, *95% CI* [64.21; 75.64]) than their neutral versions (*M*= 11.37; *SD*= 8.49). Moreover, all threatening vignettes presented average scores higher than 63 points, indicating that they did induce an above-average feeling of threat in the participants.

It is also important to note that participants were asked to imagine themselves being alone in all these vignettes. In the main experiment, the vignettes could contain additional information indicating the presence of either 2 friends or 2 strangers.

Procedure

Participants were randomly assigned to one of the threat source conditions (i.e. vignettes involving dangerous animals or harmful conspecifics) after giving their informed consent and completing a short sociodemographic questionnaire. Each participant was exposed to 12 vignettes corresponding to the threat source condition in which he/she was taking part. The 12 vignettes were randomly distributed by the 3 presence conditions so that each participant had 4 vignettes in each presence condition. The same vignette was never presented in more than one presence condition.

Participants' task was to immerse themselves in the scenario described in each vignette and attend to all the details of the story. Then, using separated sliders (0-100 points), they had to assess (1) how threatened they would feel and (2) how likely it would be for them to get harmed in each situation.

After assessing all the vignettes, participants were asked to identify the task's goal to understand whether they were aware of the study's objective and hypotheses. Less than 12% of the participants were able to determine what was being examined in the experiment. As their exclusion/inclusion in the final analyses did not change the observed data pattern, these participants were included in all the analyses.

Data was collected online using the experiment builder Gorilla (Anwyl-Irvine et al., 2020).

Statistical analysis

To examine our hypotheses, two separate linear mixed models (LMM; one for the subjective threat feeling and the other for the perceived probability of getting injured) were performed. The data's normality and homoscedasticity were examined using skewness and kurtosis values, and through a visual inspection of the residual plots, and found not to be violating these assumptions. For both LMMs, the subject ID was entered as a clustering variable, the participants' sliders responses constituted the dependent variable, and the threat source (i.e. dangerous animals vs. harmful conspecifics; between-subjects) and the presence condition (i.e. alone vs. 2 friends vs. 2 strangers; within-subjects) were the model predictors. As fixed effects in the models, the main effects of the threat source and the presence condition, as well as their interaction, were considered. As the random effect, and to adequately consider inter-individual variability, we consider random intercepts per subject. Moreover, post hoc comparisons were performed using the Bonferroni correction procedure.

The models were estimated using restricted maximum likelihood, and a Satterthwaite approximation of the degrees of freedom was considered (see West, 2009). The analyses were performed using the GAMLj module (Gallucci, 2019) implemented with the jamovi software (The jamovi project, 2019).

Results

Regarding the participants' subjective threat feeling (i.e. the answer to the question *"How threaten would you fell in this situation?"*), the LMM analysis ($R^2_{marginal}$ =.01; $R^2_{conditional}$ = .41) revealed a significant main effect for the presence condition [$F(2, 1723) = 14.85$; $p < .001$]. As predicted (H1), post hoc comparisons showed that participants imagining themselves alone reported feeling significantly more threatened ($M = 80.49$; $SE = 1.33$) than when they imagined themselves in the company of 2 friends (*M* = 77.03; *SE* = 1.33; *t*(1723) = 3.55; *p* = .001; *95% CI* [1.55; 5.37]) or in the presence of 2 neutral strangers (*M* = 75.27; *SE* = 1.33; *t*(1723) = 5.36; *p* < .001; *95% CI* [3.31; 7.13]). Nevertheless, contrary to what was hypothesized based on the social supported literature (H2), no significant differences were evidenced between the 2 friends and the 2 strangers conditions (*t*(1723) = 1.80; *p* = .215; *95% CI* [-.15; 3.67]), indicating that these two different presence conditions did not modulate participants' threat appraisals distinctively (see figure 1). Additionally, the LMM did not show a main effect of the threat source [*F*(1, 155) = .48; *p* = .490], or a significant interaction between the threat source and the presence condition [*F*(2, 1723) = 3.00; *p* = .123]. These results pointed out that the threat source (i.e. animal or social) did not influence participants' threat appraisals.

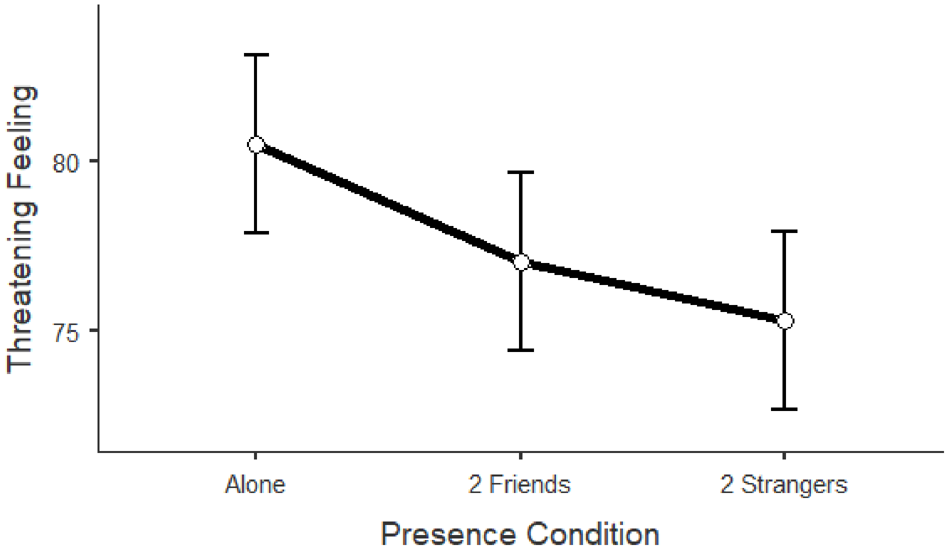

Figure 1: Mean threatening feeling per presence condition. Error bars represent 95% confidence intervals.

Concerning the participants' perceived probability of getting injured (i.e. the answer to the question *"How likely would it be for you to get harmed in this situation?"*), the LMM analysis ($R^2_{marginal}$ =.01; $R^2_{conditional}$ = .33) also showed a significant main effect of the presence condition [*F*(2, 1723) = 10.49; *p* < .001]. Similar to the previous presented results and confirming H1, post hoc comparisons showed that participants imagining themselves alone reported significantly a higher perceived probability of getting harmed (*M* = 64.90; *SE* = 1.50) than when in the company of 2 friends (*M* = 61.07; *SE* = 1.50; *t*(1723) = 3.09; *p* = .006; *95% CI* [1.40; 6.26]) or the presence of 2 neutral strangers (*M* = 59.35; *SE* = 1.50; *t*(1723) = 4.47; *p* < .001; *95% CI* [3.12; 7.97]). Once again, contrary to H2, no significant differences were found between the 2 friends and the 2 strangers conditions (*t*(1723) = 1.38; *p* = .501; *95% CI* [-.72; 4.14]), indicating that these two different presence conditions did not modulate distinctively participants' perceived probability of getting harmed (see figure 2). Moreover, no significant main effect of the threat source *F*(1, 155) = 1.10; *p* = .297], neither a significant interaction between threat source and presence condition *F*(1, 1723) = .37; *p* = .691] were found, indicating once again that the threat source (i.e. animal or social) did not influence the participants' perceived probability of getting harmed.

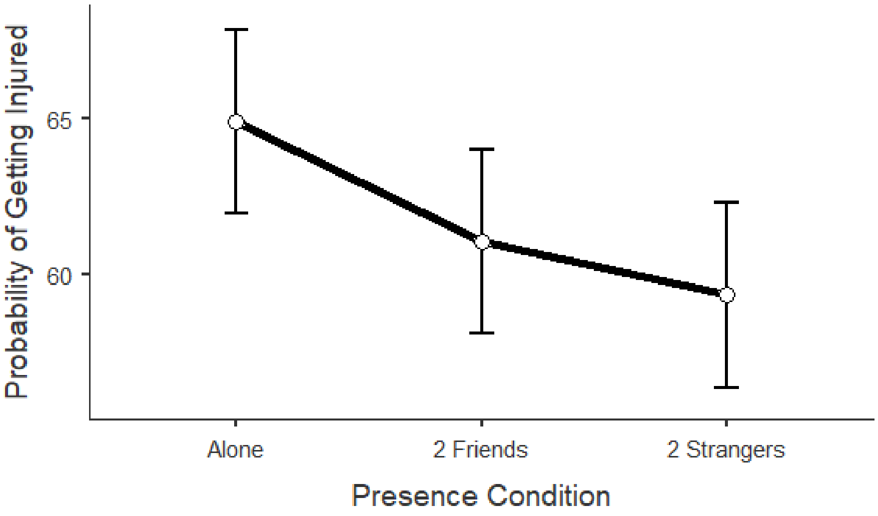

Figure 2: Mean perceived probability of getting harmed per presence condition. Error bars represent 95% confidence intervals.

Discussion

The present study was designed to examine the role of the presence of conspecifics (compared to an individual condition) in shaping threat appraisals of ambiguous, dangerous situations. Additionally, possible modulatory effects of different presence conditions (i.e. the presence of 2 friends or 2 strangers), as well as distinct threat sources (i.e. dangerous animals or harmful conspecifics), were also explored. To this end, participants on an online-based experiment were led to envision themselves alone, in the company of 2 friends, or in the presence of 2 strangers in several potentially dangerous scenarios (involving dangerous animals or harmful conspecifics). Their task was to rate how threatened they would feel and how likely they would get harmed in each situation.

The results showed that participants were less threatened when they imagined themselves in the presence of conspecifics compared to when they imagined themselves alone, confirming our main hypothesis (H1). These results support the notion that the presence of conspecifics is automatically perceived as a signal of increased safety. From an evolutionary point of view, and considering the case of our species, which have rather limited size, speed, and strength (when compared, for instance, to several predator species), living in a group context might have been a necessary step to increase our survival (Wilson, 2007). By living together in a group defending ourselves, we had the chance to spend more attentional resources (i.e. time) on survival-relevant activities (e.g., foraging and reproduction) aside from monitoring danger without compromising safety. This may have increased individual fitness and survival. Due to this regularity of lower threat-risk in group conditions throughout our evolutionary pathway, it is not surprising that the presence of conspecifics is still nowadays able to increase the feeling of safety (for a similar argument see Cacioppo et al., 2006). Arguably, this can reduce individuals' alertness and, consequently, the attentional resources allocated to defense strategies (e.g., vigilance behavior; Gomes & Semin, 2020; Wirtz & Wawra, 1986). Interestingly, the presence of others still seems to play a crucial role in our present-day well-being. Several studies have evidenced that perceptions of social isolation (i.e. loneliness) not only increase vigilance for social threat, heightening feelings of vulnerability but also are thought to be one of the causes of increased morbidity and mortality, also potentiating psychological (e.g., psychosis) and neurological (e.g., dementia) disorders in human beings (for a review see Hawkley & Cacioppo, 2010).

Additionally, our results showed that the observed effect of the presence of conspecifics on threat appraisals was neither modulated by distinct threat sources (i.e. inter or intraspecific threats; see E. Mayer, 1974) nor by the different conditions where conspecifics were present (i.e. the company of 2 friends or the presence of 2 strangers). Regarding threat sources (i.e. dangerous animals or harmful conspecifics), the absence of any significant results perhaps just indicates that the presence of conspecifics led to a general state of increased safety irrespective of what a dangerous stimulus may be. This is congruent with the different hypothetical mechanisms explaining a safety increment in group conditions. The presence of conspecifics is thought to reduce threat risk because others can act as additional threat detection sources (*"many-eyes effect";* e.g., Caraco et al., 1980; Galton, 1871; Lima, 1995) or secondary targets for danger *("risk-dilution";* Bertram, 1978). Thus, regardless of the threat source, the presence of non-dangerous conspecifics will result in a lower individual probability of getting injured, automatically resulting in a lower perceived threat risk when compared to individual situations.

Regarding the different conditions where conspecifics were present, the absence of significant differences between imagining themselves in the company of 2 friends or 2 strangers contradicts our second hypothesis (H2), and, at first sight, the literature on social support and social buffering (e.g., Epley, 1974; Hornstein & Eisenberger, 2018; Kikusui et al., 2006). As aforementioned, previous studies on these two overlapping research fields have pointed out that the presence of social support figures, but not strangers, reduce the participants' response to threatening events, mitigate their physiological consequences, and also impact the aversive (fear) learning processes (e.g., Hornstein et al., 2016, 2018; Kiyokawa et al., 2007; Thorsteinsson & James, 1999). However, in the present study, what was assessed was not the participants' coping response to a threatening event that already occurred, but their perception of the probability of an imminent danger affecting them (risk perception). Indeed, the distinction between these two processes may explain the absence of differences between the 2 presence conditions evidenced by our results. Concerning perceived risk and attending to the *"many-eyes"* and the *"risk-dilution"* effects, the presence of non-threatening conspecifics in general (either social supporters or strangers) can be considered as a source of increased safety. As already mentioned, they can either emit sensory cues alerting and preparing others for the presence of threat stimuli (e.g., Gomes & Semin, under review) or dilute the threat risk by acting as potential alternative targets for a possible danger source. However, once the dangerous event takes place affecting the individual (i.e. threat coping), the presence of stranger conspecifics may no longer mean increased safety or support. As strangers have no social connection to the individuals, they may focus on protecting themselves, in detriment of contributing to the safety of the species in general – an argument somehow compatible with the premises of the *"Selfish Gene"* proposed by Dawkins (1990)[2]. Consequently, the presence of stranger conspecifics may not aid the individual in coping with the threat source. On the other hand, humans seem to have evolved to form strong social connections to increase their survival chances (see Hawkley & Cacioppo, 2010). Thus, social supporters (e.g., friends), which are part of the individual's social network, may act to protect or help him cope with threat stimuli for the group's well-being (see Hornstein & Eisenberger, 2018). We believe that these differences between risk-perception and threat-coping processes may be the reason behind the presence of strangers being enough to reduce the perceived probability of danger but not to buffer the effects of a dangerous event that already took place. However, this argument remains purely speculative in need of future research to explore it.

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[2] As well described by Cacioppo and colleagues (2006; p. 1055): *"...the world of the selfish gene is generally one of savage competition, ruthless exploitation, and deceit. Even apparently collective actions that foster survival, such as fish swimming in schools, can be explained in terms of individual self-interest. When sardines are predated, they form a dynamic fish ball as a last means of defense. The emergence and unfolding of this collective action can be explained by a single, selfish rule: Swim to the middle".*

It is important to note that this study was conducted online, asking participants to envision themselves in different scenarios (i.e. imagery) rather than experience them in vivo. Although imagery (e.g., Siedlecka & Denson, 2019) has been proven to be a robust method to induce threat-related feelings, exposing participants to Lab controlled experiments with different simulations of threatening events (e.g., imminent monetary or electric punishments) might strengthen the confidence in our findings. Furthermore, all the participants' responses were obtained by self-report, being then subjective. Even though the subjective feelings are considered a critical part of the threat/emotional experience (e.g., Barrett, 2006), future studies should consider using physiological measures (e.g., galvanic skin response) to complement self-reported data. Additionally, taking into account the vigilance literature and the well-known group size-effect (i.e. the attentional resources allocated to risk-monitoring are inversely correlated to the number of conspecifics present; see Beauchamp, 2015), an interesting avenue for future research may also be to explore the effect of different group sizes on threat appraisals.

In conclusion, this study shows for the first time that the presence of conspecifics (i.e. strangers or friends) reduced the perceived threat risk (i.e. increased safety) in ambiguous, dangerous scenarios (either involving dangerous animals or harmful conspecifics). This finding supports the notion that, by triggering a feeling of increased safety, the presence of conspecifics (compared to individual conditions) arguably reduces individuals' alertness, and consequently, the resources devoted to vigilance in group conditions (see Gomes & Semin, 2020; Wirtz & Wawra, 1986).

Appendix A

Threat source	Portuguese Version	English Translation
Animal	Num encontro universitário fomos acampar num parque natural. Num dos dias decidi dar um passeio pela mata sozinho(a). Durante o passeio ouvi um som estranho na folhagem. Quando olhei com atenção estava uma cobra à minha frente a encarar-me…	At a university meeting, we went camping in a natural park. On one of the days, I decided to take a walk through the woods alone. During the walk, I heard a strange sound in the foliage. When I looked closely, there was a snake in front, staring at me …
Animal	Decidi participar numa corrida de orientação sozinho(a). Durante a prova, enquanto subia numa estrada de mato bastante inclinada reparei num movimento entre os arbustos. De repente estava um javali à minha frente…	I decided to participate in an orientation race alone. During the race, while climbing a fairly sloping bush road, I noticed a movement between the bushes. Suddenly, there was a boar in front of me …
Animal	Numa viagem à Austrália fiquei alojado num bungalow sozinho(a). Num determinado momento apercebi-me da presença de várias teias por baixo da cama. Olhando com atenção vi uma aranha enorme…	On a trip to Australia, I stayed in a bungalow by myself. At one point, I noticed the presence of several webs under the bed. Looking closely, I saw a huge spider ...
Animal	Durante uma caminhada num parque natural sozinho(a), ouvi uma agitação não muito longe de mim. As colunas do parque começaram então a emitir um aviso em que pediam a calma e informavam que um dos lobos da reserva tinha rompido a vedação e se encontrava solto…	During a walk in a natural park alone, I heard a stir not far from me. The columns of the park then began to issue a warning in which they asked for calm and informed that one of the wolves of the reserve had broken the fence and was loose…
Animal	Num fim de semana decidi fazer uma caminhada na Serra de Portalegre sozinho(a). Quando estava de regresso ouvi um barulho estranho atrás de mim. Quando olhei para trás, estava um lobo a encarar-me de frente…	One weekend I decided to go hiking in Serra de Portalegre alone. On my way back, I heard a strange noise behind me. When I looked around, a wolf was staring at me…
Animal	Durante as minhas férias de verão em Sintra, decidi fazer um trilho de bicicleta sozinho(a). A meio do caminho, um dos pneus ficou vazio. Saí da bicicleta e enquanto tentava reparar o pneu, vi um movimento entre os arbustos e, de forma repentina, apareceu um javali que começou a caminhar na minha direcção...	During my summer vacation in Sintra, I decided to take a bike trail by myself. Midway through, one of the tires went empty. I got off the bike, and while trying to repair the tire, I saw a movement between the bushes and, suddenly, a boar appeared and started walking towards me ...
Animal	Numa viagem ao Ribatejo, fiquei alojado numa quinta. Nesse mesmo dia, houve uma largada de touros para inaugurar as festas da aldeia, sendo que um dos touros fugiu. No dia seguinte, quando estava a sair do alojamento sozinho(a) , deparei-me com o touro, que me fitava de frente…	On a trip to Ribatejo, I was lodged on a farm. That same day, there was a bull race to inaugurate the village festivities, and one of the bulls fled away. The next day, when I was leaving the accommodation alone, I came across the bull, facing me…

Animal	Num passeio na Serra da Arrábida encontrei uma gruta com uma bela vegetação. Decidi entrar e explorá-la sozinho(a). Depois de andar alguns metros dentro da gruta, começaram a aparecer imensas teias de aranha penduradas no teto. Foi então que senti que alguma coisa me tocava na cabeça…	On a walk in the Serra da Arrábida, I found a cave with beautiful vegetation. I decided to go in and explore it by myself. After walking a few meters inside the cave, huge cobwebs hanging from the ceiling began to appear. Then, I felt that something was touching my head ...
Animal	O ano passado viajei para o Havai para surfar sozinho(a). Durante uma tarde em que estava no mar à espera de uma boa onda, avistei uma forma ao longe, que se assemelhava a uma barbatana de tubarão e que vinha na minha direção…	Last year I traveled to Hawaii to surf alone. During an afternoon, when I was at sea waiting for a good wave, I saw a shape in the distance, which resembled a shark fin and was coming towards me ...
Animal	Um circo chegou à aldeia e preparava-se para apresentar o primeiro espetáculo, para o qual eu já tinha comprado bilhetes. Quando estava à porta a preparar-me para entrar sozinho(a), gerou-se um burburinho e um dos trabalhadores do circo anunciou, recorrendo a um megafone, que um leão tinha fugido da jaula e se dirigia para a entrada do circo…	A circus arrived in the village and prepared to present the first show, for which I had already bought tickets. When I was at the door preparing to enter alone, a buzz was generated, and one of the circus workers announced, using a megaphone, that a lion had escaped from the cage and was going to the entrance to the circus ...
Animal	Inscrevi-me num retiro espiritual publicitado na internet. Fiquei alojado numa cabana de madeira sozinho(a), entre riachos e montanhas. Durante a noite, ouvi vários barulhos estranhos. Quando me levantei da cama, deparei-me com uma cobra que tentava entrar por baixo da porta…	I signed up for a spiritual retreat advertised on the internet. I was lodged in a wooden hut alone, between streams and mountains. During the night, I heard several strange noises. When I got out of bed, I came across a snake trying to get under the door ...
Animal	Num dia de sol, decidi fazer um piquenique no Campo Grande sozinho(a). Pousei o cesto da comida, estendi a toalha e sentei-me a observar a paisagem. De repente o cesto começou a abanar. Foi então que vi o que parecia ser uma cobra a entrar nele…	On a sunny day, I decided to have a picnic in Campo Grande alone. I put down the food basket, stretched out the towel, and sat watching the scenery. Suddenly the basket started to shake. That's when I saw what appeared to be a snake entering the basket...
Social	Já era tarde da noite e eu encontrava-me numa praça isolada sozinho(a) a caminhar em direção ao carro. De repente apercebi-me que caminhava atrás de mim um indivíduo com um objeto pontiagudo na mão…	It was late at night, and I found myself alone in an isolated square, walking towards the car. Suddenly I realized that an individual was walking behind me with a sharp object in his hand …
Social	De madrugada, após uma saída à noite, estava a pé pela rua sozinho(a). Reparei que havia um indivíduo uns metros à frente a encarar-me. Decidi virar numa rua à direita e ele começou a caminhar atrás de mim…	At dawn, after a night out, I was walking down the street alone. I noticed that there was an individual a few meters ahead, staring at me. I decided to turn into a street on the right, and he started walking behind me ...

Social	Um casal amigo regressou a Portugal e convidou-me para um jantar. Após o jantar, já tarde, desloquei-me a pé para casa sozinho(a). Estava bastante escuro e ainda faltavam uns 2 quilómetros para o meu destino. Na rua, à minha frente, surgiu um indivíduo com um aspeto duvidoso que me chamou…	A couple of friends returned to Portugal and invited me to dinner. After dinner, already late, I walked home by myself. It was quite dark, and my destination was still 2 kilometers away. In the street, in front of me, an individual with a dubious look appeared and called me…
Social	Após um dia de trabalho até tarde, desloquei-me ao local de estacionamento habitual sozinho(a). O caminho que normalmente fazia encontrava-se impedido, pelo que tive de optar por um alternativo. Já a meio caminho, percebi que me encontrava numa rua estreita onde tinham sido reportados vários assaltos no último mês…	After one day of work until late in the afternoon, I went to the usual parking spot alone. The path I usually took was blocked, so I had to choose an alternative. Halfway through, I realized that I was on a narrow street where several robberies had been reported in the last month ...
Social	Após um longo dia de trabalho, apanhei o autocarro noturno de regresso a casa. Quando entrei no autocarro sozinho(a), apercebi-me que alguém me observava. Desci na minha paragem e esse indivíduo saiu ao mesmo tempo que eu, seguindo-me. Trazia um objeto brilhante na mão…	After a long day at work, I took the night bus back home. When I got on the bus alone, I realized that someone was watching me. I got off at my stop, and this guy left at the same time, following me. He had a shiny object in his hand ...
Social	Quando regressava a casa sozinho(a), reparei que o autocarro estava anormalmente vazio. Na paragem a seguir entrou um indivíduo que se sentou no banco atrás de mim a ler o jornal. Repentinamente, senti algo pontiagudo a tocar-me nas costas…	When I was returning home by myself, I noticed that the bus was abnormally empty. At the following stop, an individual entered the bus, sitting on the bench behind me reading the newspaper. Suddenly, I felt something sharp touching my back ...
Social	Tarde da noite, após uma saída com uns amigos, ia a descer as ruas do Bairro Alto sozinho(a). Ao virar uma esquina, deparei-me com uma situação que parecia ser um assalto com arma branca. Parei sem saber o que fazer, até que o suposto assaltante começou a caminhar na minha direção…	Late at night, after going out with friends, I went down the Bairro Alto streets alone. When I turned a corner, I came across a situation that appeared to be a robbery with a knife. I stopped without knowing what to do until the alleged burglar started walking towards me ...
Social	No último semestre, houve um dia que fiquei a estudar até tarde na Universidade e só consegui apanhar o último metro de regresso a casa. Nessa noite o metro estava praticamente vazio, estando apenas lá eu e um indivíduo estranho que começou a aproximar-se com uma mão dentro do casaco…	In the last semester, there was a day that I was studying late at the university, and I only managed to catch the last train back home. That night the train was nearly empty. There was just me and a strange guy, who started approaching me with one of his hands inside the jacket ...
Social	Nas férias de verão decidi fazer campismo selvagem sozinho(a). Estava muito calor e decidi sair da tenda para encher o cantil no rio. De repente, ouvi um barulho entre os arbustos e vi fumo. Reparei num indivíduo que parecia estar a atear um incêndio. Quando ele me viu, correu na minha direção…	In the summer holidays, I decided to go wild camping alone. It was scorching, and I decided to leave the tent to fill the canteen in the river. Suddenly, I heard a noise between the bushes and saw smoke. I noticed an individual who seemed to be starting a fire. When he saw me, he started running towards me ...

Social	Precisava de umas férias, e como destino escolhi o Rio de Janeiro, apesar da taxa de violência alta. Num passeio pela cidade perdi-me numa rua movimentada e acabei por virar num local estranho e isolado onde fiquei sozinho(a). Quando dei por isso, estava a entrar numa favela, onde fui barrado(a) por um indivíduo armado que me começou a questionar sobre o motivo de estar ali…	I needed vacations, and as a destination, I chose Rio de Janeiro, despite the high violence rates. On a walk through the city, I got lost in a busy street and ended up turning into a strange and isolated place where I was alone. When I realized it, I was entering a favela, where I was stopped by an armed individual who started to question me about the reason for being there ...
Social	Após um dia de trabalho até tarde, desloquei-me ao local de estacionamento sozinho(a). Quando estava a entrar no carro, vi um vulto no reflexo do vidro que se movia rapidamente na minha direção…	After a late working day, I went to the parking place alone. When I was getting into the car, I saw a figure in the reflection of the glass moving quickly towards me ...
Social	Após uma sessão de cinema ia a atravessar uma passadeira sozinho(a), quando recebi uma mensagem no telemóvel. Um número que não conhecia tinha acabado de me enviar uma foto minha a atravessar a passadeira naquele preciso momento, acompanhada de uma ameaça…	After a movie session, I was alone going to cross the street in the crosswalk when I received a message on my cell phone. A number I didn't know had just sent me a picture of me crossing the street at that very moment, accompanied by a threatening message …

References

Adolphs, R., & Andler, D. (2018). Investigating Emotions as Functional States Distinct From Feelings. *Emotion Review*, *10*(3), 191–201. https://doi.org/10.1177/1754073918765662

Anwyl-Irvine, A. L., Massonnié, J., Flitton, A., Kirkham, N., & Evershed, J. K. (2020). Gorilla in our midst: An online behavioral experiment builder. *Behavior Research Methods*, *52*(1), 388–407. https://doi.org/10.3758/s13428-019-01237-x

Barash, D. P. (1972). Human Ethology: The Snack-Bar Security Syndrome. *Psychological Reports*, *31*(2), 577–578. https://doi.org/10.2466/pr0.1972.31.2.577

Barrett, L. F. (2006). Solving the emotion paradox: Categorization and the experience of emotion. In *Personality and Social Psychology Review* (Vol. 10, Issue 1, pp. 20–46). Pers Soc Psychol Rev. https://doi.org/10.1207/s15327957pspr1001_2

Beauchamp, G. (2015). *Animal vigilance : monitoring predators and competitors*. Academic Press.

Bertram, B. C. R. (1978). Living in groups: predator and prey. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural Ecology* (pp. 64–96). Blackwell Publishing Ltd.

Blumstein, D. T., Evans, C. S., & Daniel, J. C. (1999). An experimental study of behavioural group size effects in tammar wallabies, Macropus eugenii. *Animal Behaviour*, *58*(2), 351–360. https://doi.org/10.1006/anbe.1999.1156

Brysbaert, M. (2019). How Many Participants Do We Have to Include in Properly Powered Experiments? A Tutorial of Power Analysis with Reference Tables. *Journal of Cognition*, *2*(1), 1–38. https://doi.org/10.5334/joc.72

Cacioppo, J. T., Hawkley, L. C., Ernst, J. M., Burleson, M., Berntson, G. G., Nouriani, B., & Spiegel, D. (2006). Loneliness within a nomological net: An evolutionary perspective. *Journal of Research in Personality*, *40*(6), 1054–1085. https://doi.org/10.1016/j.jrp.2005.11.007

Caraco, T., Martindale, S., & Pulliam, H. R. (1980). Avian Time Budgets and Distance to Cover. *The Auk: Ornithological Advances*, *97*(4), 872–875. https://doi.org/10.1093/auk/97.4.872

Cuthbert, B. N., Lang, P. J., Strauss, C., Drobes, D., Patrick, C. J., & Bradley, M. M. (2003). The psychophysiology of anxiety disorder: Fear memory imagery. *Psychophysiology*, *40*(3), 407–422. https://doi.org/10.1111/1469-8986.00043

Dawkins, R. (1990). *The selfish gene*. Oxford university press.

Epley, S. W. (1974). Reduction of the behavioral effects of aversive stimulation by the presence of companions. *Psychological Bulletin*, *81*(5), 271–283. https://doi.org/10.1037/h0036389

Fordyce, J. A., & Agrawal, A. A. (2001). The role of plant trichomes and caterpillar group size on growth and defence of the pipevine swallowtail *Battus philenor*. *Journal of Animal Ecology*, *70*(6), 997–1005. https://doi.org/10.1046/j.0021-8790.2001.00568.x

Gallucci, M. (2019). *GAMLj: General analyses for linear models*. https://gamlj.github.io

Galton, F. (1871). Gregariousness in cattle and in men. *Macmillan's Magazine, 23*(136), 353–357.

Gomes, N., & Semin, G. R. (2020). Mapping human vigilance: The influence of conspecifics. *Evolution and Human Behavior*, *41*(1), 69–75. https://doi.org/10.1016/j.evolhumbehav.2019.10.002

Gosselin-ildari, A. D., & Koenig, A. (2012). The Effects of Group Size and Reproductive Status on Vigilance in Captive Callithrix jacchus. *American Journal of Primatology*, *74*(7), 613–621. https://doi.org/10.1002/ajp.22013

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology, 31*(2), 295–311. https://doi.org/10.1016/0022-5193(71)90189-5

Hawkley, L. C., & Cacioppo, J. T. (2010). Loneliness matters: A theoretical and empirical review of consequences and mechanisms. *Annals of Behavioral Medicine*, *40*(2), 218–227. https://doi.org/10.1007/s12160-010-9210-8

Hawlena, D., & Schmitz, O. J. (2010). Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *American Naturalist*, *176*(5), 537–556. https://doi.org/10.1086/656495

Hornstein, E. A., & Eisenberger, N. I. (2018). A Social Safety Net: Developing a Model of Social-Support Figures as Prepared Safety Stimuli. *Current Directions in Psychological Science*, *27*(1), 25–31. https://doi.org/10.1177/0963721417729036

Hornstein, E. A., Fanselow, M. S., & Eisenberger, N. I. (2016). A Safe Haven: Investigating Social-Support Figures as Prepared Safety Stimuli. *Psychological Science*, *27*(8), 1051–1060. https://doi.org/10.1177/0956797616646580

Hornstein, E. A., Haltom, K. E. B., Shirole, K., & Eisenberger, N. I. (2018). A Unique Safety Signal: Social-Support Figures Enhance Rather Than Protect From Fear Extinction.

Clinical Psychological Science, *6*(3), 407–415. https://doi.org/10.1177/2167702617743002

Jacobs, W. J., & LoLordo, V. M. (1977). The sensory basis of avoidance responding in the rat. Relative dominance of auditory or visual warning signals and safety signals. *Learning and Motivation*, *8*(4), 448–466. https://doi.org/10.1016/0023-9690(77)90045-5

Kameda, T., & Tamura, R. (2007). “To eat or not to be eaten?” Collective risk-monitoring in groups. *Journal of Experimental Social Psychology*, *43*(2), 168–179. https://doi.org/10.1016/j.jesp.2006.02.003

Kikusui, T., Winslow, J. T., & Mori, Y. (2006). Social buffering: Relief from stress and anxiety. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*(1476), 2215–2228. https://doi.org/10.1098/rstb.2006.1941

Kiyokawa, Y., Takeuchi, Y., & Mori, Y. (2007). Two types of social buffering differentially mitigate conditioned fear responses. *European Journal of Neuroscience*, *26*(12), 3606–3613. https://doi.org/10.1111/j.1460-9568.2007.05969.x

Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, *49*(1), 11–20. https://doi.org/10.1016/0003-3472(95)80149-9

Mayer, E. (1974). Behavior programs and evolutionary strategies. *American Scientist*, *62*(6), 650–670.

Mayer, J. D., Allen, J. P., & Beauregard, K. (1995). Mood inductions for four specific moods: A procedure employing guided imagery vignettes with music. *Journal of Mental Imagery*, *19*(1–2), 151–159.

Michelena, P., Pillot, M. H., Henrion, C., Toulet, S., Boissy, A., & Bon, R. (2012). Group size elicits specific physiological response in herbivores. *Biology Letters*, *8*(4), 537–539. https://doi.org/10.1098/rsbl.2012.0197

Muris, P., Mayer, B., Van Eijk, S., & Van Dongen, M. (2008). “i’m not really afraid of Osama Bin Laden!” fear of terrorism in dutch children. *Journal of Child and Family Studies*, *17*(5), 706–713. https://doi.org/10.1007/s10826-007-9185-7

Reuman, L., Jacoby, R. J., Fabricant, L. E., Herring, B., & Abramowitz, J. S. (2015). Uncertainty as an anxiety cue at high and low levels of threat. *Journal of Behavior Therapy and Experimental Psychiatry*, *47*, 111–119. https://doi.org/10.1016/j.jbtep.2014.12.002

Rieucau, G., Morand-Ferron, J., & Giraldeau, L. A. (2010). Group size effect in nutmeg mannikin: Between-individuals behavioral differences but same plasticity. *Behavioral*

Ecology, *21*(4), 684–689. https://doi.org/10.1093/beheco/arq039

Seligman, M. E. P. (1971). Phobias and preparedness. *Behavior Therapy*, *2*(3), 307–320. https://doi.org/10.1016/S0005-7894(71)80064-3

Siedlecka, E., & Denson, T. F. (2019). Experimental Methods for Inducing Basic Emotions: A Qualitative Review. *Emotion Review*, *11*(1), 87–97. https://doi.org/10.1177/1754073917749016

The jamovi project. (2019). *jamovi* (version 1.0). https://www.jamovi.org

Thorsteinsson, E. B., & James, J. E. (1999). A meta-analysis of the effects of experimental manipulations of social support during laboratory stress. *Psychology and Health*, *14*(5), 869–886. https://doi.org/10.1080/08870449908407353

Vrana, S. R., & Lang, P. J. (1990). Fear Imagery and the Startle-Probe Reflex. *Journal of Abnormal Psychology*, *99*(2), 189–197. https://doi.org/10.1037/0021-843X.99.2.189

Wawra, M. (1988). Vigilance Patterns in Humans. *Behaviour*, *107*(1–2), 61–71. https://doi.org/10.1163/156853988X00197

West, B. T. (2009). Analyzing longitudinal data with the linear mixed models procedure in SPSS. *Evaluation and the Health Professions*, *32*(3), 207–228. https://doi.org/10.1177/0163278709338554

Wilson, D. S. (2007). *Evolution for everyone: How Darwin’s theory can change the way we think about our lives*. Delta.

Wirtz, P., & Wawra, M. (1986). Vigilance and Group Size in Homo sapiens. *Ethology*, *71*(4), 283–286. https://doi.org/10.1111/j.1439-0310.1986.tb00592.x

Zhang, X., Yu, H. W., & Barrett, L. F. (2014). How does this make you feel? A comparison of four affect induction procedures. *Frontiers in Psychology*, *5*(JUL), 689. https://doi.org/10.3389/fpsyg.2014.00689

Chapter IV:

In pursuit of collaborative and cooperative group effects on human vigilance

Pre-registered in the Open Science Framework: http://osf.io/ 27z56

Abstract

Recent research has shown that, as with other social species, the mere presence of conspecifics shapes humans' vigilance behavior. Arguably, the presence of conspecifics can represent an increase in safety, automatically reducing attentional resources (i.e. time) allocated to vigilance. However, animal studies have also shown that this phenomenon may be modulated by the group context. For instance, in adverse group contexts (e.g., highly competitive environments) the presence of conspecifics can no longer be perceived as a safety signal (i.e. group members competing for scarce resources), enhancing vigilance. On the other hand, a cooperative context can represent a signal of increased safety, reducing vigilance, and increasing the resources allocated to intake activities (e.g., foraging). However, little is known about how different group contexts shape human vigilance and, consequently, their threat detection efficiency. The present study (N= 67) examined how a competitive or a cooperative context (vs. a mere presence condition) shapes human vigilance strategies and threat detection in human beings. We relied on a paradigm that simulates a “foraging under threat” situation in the lab, along with an eye-tracker, to examine the attention allocation. The results showed that perceiving conspecifics as competitors or cooperators (vs. a mere presence condition) neither modulated vigilance behavior nor threat detection capacity. These results, together with earlier research, suggest that the role of competitive and cooperative contexts in shaping individuals’ vigilance strategies depends on the interaction and observation of the behavior of other conspecifics.

Keywords

Vigilance; Co-presence; Competition; Cooperation; Threat-detection; Eye-tracking

Introduction

In order to maximize survival chances, animal species (human beings included) developed strategies to efficiently trade-off their attentional resources between intake activities (i.e., foraging) and monitoring their surroundings for signals of threat (i.e. vigilance; see Beauchamp, 2015). Uncovering the variables that modulate such trade-off represents an important step to understand threat detection mechanisms (e.g., Kameda & Tamura, 2007; Öhman & Mineka, 2001). However, little is known about vigilance behavior in the human species. The few existing studies indicate that, as in other social animals (e.g., birds and mammals; Bertram, 1980; van Schaik et al., 1983), humans' vigilance behavior, namely threat detection can be modulated by the presence of conspecifics. The mere presence of conspecifics (compared to their absence) reduces the attentional resources allocated to vigilance and enhances intake activities (e.g., Gomes & Semin, 2020).

Nevertheless, the presence of conspecifics may modulate vigilance behavior in different ways as a function of the dynamics of the group context. In other words, distinct group properties may trigger distinct vigilance strategies. To understand how conspecifics shape individual vigilance strategies and threat detection it is important to understand how different group contexts drive vigilance behavior. In the study reported in this chapter, we attempted to go beyond the simple presence condition (i.e. mere presence) by leading participants to perceive two confederates as either competitors or cooperators (versus a mere presence condition). We anticipate the present study's findings already, as the moderation of the group dynamics by the cooperation and competition mindsets did not affect vigilance strategies or detection capacities. The absence of significant differences led us to a speculative discussion of the possible reasons behind the lack of group context effects in this study as well as to a set of considerations for future studies. Below, we first introduce the animal and human findings that have led the research reported here, followed next with a brief description of the results we were expecting.

As mentioned already, animal research on detecting threat and foraging revealed that the presence of conspecifics reduces in general vigilance and enhances intake activities (see Beauchamp, 2015). Arguably, individuals can rely on others as additional threat detection sources (mutual warning, e.g., Caraco et al., 1980; Galton, 1871; Lima, 1995) and/or as secondary targets for approaching predators (risk dilution, e.g., Bertram, 1978). Thus, group situations appear to be perceived as safer than individual situations, allowing individuals to relax vigilant states (Beauchamp, 2015). In fact, this was confirmed for a wide range of species, including some invertebrates (e.g., Fordyce & Agrawal, 2001), birds (e.g., Beauchamp &

Livoreil, 1997; Radford & Ridley, 2007), mammals (e.g., Blumstein et al., 1999), and even primates (e.g., Gosselin-ildari & Koenig, 2012; van Schaik et al., 1983).

Unfortunately, vigilance research has rarely focused on human subjects. The few studies that exist seem to generalize the findings from animal research to human beings. As in the case of other species, humans seem to display vigilance behavior (e.g., Barash, 1972; Wawra, 1988; Wirtz & Wawra, 1986) when facing a trade-off between intake activities and danger monitoring (Gomes & Semin, 2020; Kameda & Tamura, 2007). Interestingly, the resources allocated to vigilance (e.g., time) increase proportionally as the threat risk increases (e.g., higher costs in failing to detect threat stimuli or more frequent threat stimuli encounter; Beauchamp, 2020; Kameda & Tamura, 2007), supporting the relationship between vigilance and threat detection in our species (but see Dunbar et al., 2002). Moreover, as we have shown recently, the mere presence (vs. absence) of conspecifics modulates the aforementioned trade-off between foraging and vigilance (Gomes & Semin, 2020). In the mere presence of individuals, participants spent less time being vigilant, reducing the likelihood of detecting threatening changes and increasing their resources allocated to intake activities. As we argued (Gomes & Semin, 2020), the mere presence condition, may have been automatically perceived as safer compared to the alone condition (see also chapter III), reducing participants' alertness to danger, and consequently, the time spent being vigilant.

Nevertheless, in natural environments, the presence of conspecifics is not always perceived as a signal of safety. Animal research has been highlighting that, for instance, in highly competitive contexts, the presence of conspecifics can be treated as a signal of danger, resulting in a vigilance enhancement (see Treves, 2000). For instance, in bird species, higher vigilance levels in males appear to be not only related to the presence of predators but also to the presence of competitors (Guillemain et al., 2003; Portugal & Guillemain, 2011). This is also found in some primate species, where the presence of non-familiar or non-kin conspecifics (representing higher threat levels; see Gaynor & Cords, 2012; Kutsukake, 2006) increases the risk of attacks related to food, enhancing individuals' vigilance (e.g., Barbosa, 2002; Blumstein & Daniel, 2002; Cameron & Du Toit, 2005; Hirsch, 2002; Teichroeb & Sicotte, 2012). Thus, it is possible to speculate that in an adverse group context (e.g., competitive contexts), the presence of conspecifics is no longer a signal of safety that leads to an increase in vigilance. This means that, in other animal species, the group context plays an important role in modulating vigilance behavior. However, in the case of human beings, little is known about how different group contexts modulate the trade-off between intake activities and vigilance. This constituted the chief goal of the present study, namely to explore the effects of different group interdependencies (i.e., cooperative and competitive group contexts versus mere presence) on human vigilance strategies and consequently on threat detection capacity. To examine the trade-off between vigilance and foraging across the referred three group interdependencies, we employed a “foraging-vigilance” task developed in our lab (see Gomes & Semin, 2020). This task consists of a laboratory simulation of foraging under threat risk. Specifically, participants received small monetary rewards for solving a central letter discrimination task - foraging simulation. However, failing to detect changes occurring in their peripheral visual field resulted in strong monetary punishments - threat simulation (for similar threat manipulations see, for instance, Kameda & Tamura, 2007). This task was paired with an eye-tracker, allowing to examine participants’ attentional resource allocation. Moreover, to obtain an objective measure of the participants’ alertness during the experiment, their skin conductance level (SCL) was also recorded (see Raskin, 1973).

Considering the previously summarized research, we were expecting that perceiving conspecifics as competitors (i.e. an adverse group context) would mitigate the safety increment triggered by the mere presence of conspecifics. In turn, this would result in an increment of participants alertness (i.e. higher SCL; compared to the mere presence condition) and consequently in more time invested in vigilance (i.e. more time spent scanning the peripheral locations where a change can occur) at the detriment of foraging activity (i.e. a lower number of corrected identified target letters as well as more missed responses). On the other side, perceiving conspecifics as cooperators (i.e. a favorable group context) would reduce participants' alertness (i.e. lower SCL; compared to the mere presence condition) by increasing the safety feeling triggered by the presence of conspecifics. This would reduce vigilance levels (i.e. less time spent scanning the peripheral locations where a change can occur) and increase foraging (i.e. more corrected identified target letters as well as fewer miss responses). Additionally, as observed in previous studies (Gomes & Semin, 2020), we also hypothesized that a higher vigilance level would correspond to higher efficacy in detected threatening changes. Consequently, participants in the competition condition (compared to the mere presence condition) would detect a higher number of threatening changes. In turn, participants in the cooperation condition (compared to the mere presence condition) would detect a lower number of threatening changes. However, as we report after detailing the methodology and the results, these hypotheses were not confirmed. Finally, we provide a discussion about the possible reasons behind the lack of group context effects as well as a set of methodological considerations for future research aiming to explore these phenomena.

Method

Participants

Seventy-two Portuguese university students (ISPA - Instituto Universitário, Portugal) gave their informed consent and participated in the experiment. Five participants were excluded from the final sample, 2 due to psychological disorders, and the other 3 for not following the experimental instructions. The final sample consisted of 67 participants (19 men) between the ages of 18 and 29 (*M* = 20.01 years; *SD* = 2.03). All the participants did not have psychiatric or neurological disorders, no psychiatric medication intake, and had normal or corrected to normal eyesight. Participants were randomly assigned to one of the three experimental conditions: 25 performed the experiment in the mere presence condition (5 men; aged between 18 and 22, *M* = 19.48 years; *SD* = 1.19), 22 took part in the competition condition (8 men; aged between 18 and 29, *M* = 20.27 years; *SD* = 2.47), and the remaining 20 participated in the cooperation condition (6 men; aged between 18 and 28, *M* = 20.40 years; *SD* = 2.28).

The minimum required sample size was estimated, á priori, based on a power analysis (using G-Power 3.1.9.3; Faul et al., 2007). Considering a one-way MANOVA, and based on a *Pillai's Trace* = .177 (obtained from a previous study from our LAB, examining the effects of being in a group in human vigilance behavior; Gomes & Semin, 2020), an $\alpha = .05$, and a power = .8, results revealed that a minimum of 54 subjects (i.e., 18 per group condition) would be required.

Foraging-vigilance task

The task (Gomes & Semin, 2020) was designed to provide a simulation of foraging under a threat risk scenario, which represents the ideal evolutionary context to study the trade-off between foraging and vigilance behavior (see Beauchamp, 2015). Across 50 trials, participants were instructed to perform two simultaneous tasks. In the center of the screen, they were presented with several 3 by 4 letter matrices in which they had to identify, using a standard keyboard, one of two target letters (q or p). Each matrix lasted on the screen a maximum of 1.5 seconds or until an answer was given, being then immediately replaced by a new one. Participants were asked to find as many target letters as possible per trial. For each target letter correctly identified, 0.02€ were added to the participant's final reward - foraging simulation. At the same time, eight circular Gabor patches (2.25 visual degrees of diameter) were displayed around the letter matrices, equidistantly from the center of the screen 8 visual degrees (i.e. located in the participant's near peripheral visual field). In 40% of the trials (20 trials; randomly selected), one of these Gabor patches became gradually narrowed (to a third of its original size) across 4 seconds. This change occurred randomly between 2 seconds after the start of the trial and 4 seconds before its end. Participants had to signal that a change was occurring, pressing an escape key (i.e., the SPACE key), as fast as possible once they notice it. If they did not press the escape key, they received a feedback message informing that 0.50€ were removed from the accumulated reward - threat simulation. When a change was correctly signaled - and in order to control for spurious change detections - it immediately disappeared from the screen, and the participant was asked to identify, using the mouse, the location of the change (i.e., which Gabor patch became narrowed during the trial). Each trial ended after 20 seconds or when a change occurred.

In this task, to avoid losing money from their final reward (i.e., threat simulation) participants have to increase their vigilance level (i.e., spending more time per trial with their gaze focused on the peripheral Gabor patches). However, a vigilance increment results in a lower number of correctly identified target letters, and consequently, a lower amount of accumulated money (i.e., a foraging sacrifice). Hence, this task is creating the referred trade-off between foraging and vigilance.

Design and manipulation

The present study had a 3 between-subjects group design: mere presence vs. competition vs. cooperation. In all the group conditions participants performed the experiment in a room together with two confederates (1 female and 1 male), who were solving the same task on two independent screens.

Each group condition had a different set of initial instructions. (a) In the co-presence condition participants were told that 3 participants were recruited at a time to collect as much data as possible. Their tasks were identical and the rewards they received would be independent; (b) In the competition condition, participants were not allowed to interact with each other, and that they would receive the final reward only if they performed better compared to the other participants (confederates). Finally (c) in the cooperation condition, participants were introduced to the confederates at the beginning of the experiment and were told that they formed a team. They were led to believe that their reward would be contingent on the performance of the team and that they would be paid at end of the experiment with an amount of money corresponding to the average value achieved by the group. It is important to note that the words “competition” and “cooperation” were never used during the instructions.

Participants were blind to the study’s goal and manipulation and were randomly assigned to the different group conditions.

Equipment

To restrict head movements and to ensure a viewing distance of 55 cm, participants were instructed to place their chins in a chin and forehead rest.

In order to record participants’ eyes movement, we relied on an Eyelink 1000 plus eye tracker (SR Research), with a sampling rate of 1000 Hz. The calibration of the eye-tracker was performed using a standard 5-point procedure. At the beginning of each trial, a drift correction procedure was used, to ensure that the participants' gaze started in the center of the screen.

Furthermore, to record skin conductance level (SCL), palmar electrodes were applied to the left hand of the participants (Dawson et al., 2016). The SCL signal was collected using a BioNex chassis, powered by BioLab software (version 3.2.0; MindWare Technologies, Gahanna, OH). The signal was continuously recorded during the entire experiment.

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

Responses were collected using a standard keyboard and mouse.

Procedure

The experimental sessions started after the participants gave their informed consent. First, they filled out a demographic questionnaire (e.g., age, gender, psychological disorders history). Then the SCL palmar electrodes were then placed, and the participants received instructions regarding the foraging vigilance task. Specifically, they were first told that, in addition to the 5€ (or course credit) for their participation, they could win up to 5€ more, which depended on their performance on the “vigilance-foraging” task. They then received a specific set of group instructions depending on their condition (see design and manipulation section). In all group conditions, participants were informed about the value of the monetary rewards and punishments during the task.

After 15 practice trials, participants performed the main task, which consisted of 50 trials with a mandatory break in the middle of the task. In order to collect SCL baseline signals, a fixation cross remained on the screen for 1 min before starting the main task, and after the mandatory break.

Finally, participants filled out manipulation check questions about the effectiveness of the group manipulation. They were asked about their subjective feeling of competition and collaboration (i.e., *"Did you feel that you were competing/cooperating with the other people in the room?"*). All answers were obtained with visual analog scales (ranging from 0–100, i.e. *'nothing at all'* to *'very much'*),

At the end of the experiment, the rewards were calculated and were paid accordingly. This calculation was performed using a custom-made R script which only showed the amount of money that needs to be given to the participant.

All the procedures conformed to the Declaration of Helsinki and were approved by the host institution's ethics committee.

Data Preparation

Regarding the ocular movement, data were visually inspected first in order to correct for possible calibration problems. This correction procedure consisted of manually adjusting all fixations and saccades in trials where a clear calibration problem was identified. In total, 4.39 % of the trials were corrected. The mean percentage of time per trail spent scanning the peripheral targets (i.e., vigilance time) was then computed. Following earlier research (i.e. Gomes & Semin, 2020), only trials where no change occurred (i.e., 30 no-change trials) were used to compute vigilance time because these are the trials with a fixed duration. Change trials had random durations, depending on when a change occurred, and so including these trials in the analysis of vigilance time would create a confound.

Concerning the foraging activity (i.e., participants' performance on the central letter discrimination task), the mean number of correctly identified target letters, as well as the mean number of misses per trial were computed. Once again, only no-change trials were considered.

The efficacy in detecting and avoiding threatening changes was a measure as the percentage of correctly detected changes, and also the mean reaction time in pressing the escape key.

Lastly, SCL was computed in 2 distinct moments: at the beginning of the main task and after the mandatory break. To begin with, the SCL signal was averaged in 6 1-minute intervals. The first interval, collected 1 min before starting each block, served as a baseline. The remain

5 intervals constituted the target signal. The target signal was baseline corrected by subtracting for each 1-minute interval the mean activity of the corresponding baseline.

All variables were then checked for outliers using a 2.5 median absolute deviation criterion (Leys et al., 2013). Values identified as outliers (< 15 % in all variables) were altered to be one unit above or below the next extreme score on that variable (see Field, 2014).

Statistical analysis

First, in order to verify whether our group manipulation induced a 'competition' or a 'cooperation' subjective feeling in the participants, two separate one-way ANOVAs were performed (one for the competition and another for the collaboration subjective feelings). Post-hoc comparisons were performed using the Bonferroni correction procedure.

To explore if the different group conditions triggered distinct alertness states (i.e. SCL), a mixed factorial design ANOVA was conducted employing the group condition (i.e., co-presence vs. competition vs. cooperation) as the between-subjects' factor, and the experimental block (at the beginning of the main task vs. after the mandatory break), as well as the time interval (5 1-min intervals after starting/restarting the task) as within-subjects' factor.

Finally, we examined possible differences between group conditions in vigilance behavior and threat detection efficacy using two separate one-way MANOVAs. Regarding vigilance behavior, we used the group condition (mere presence vs. competition vs. cooperation) as the between-subjects factor, and the vigilance time, the number of correctly identified target letters, as well as the number of misses as dependent variables. Concerning the efficacy in detecting and avoiding threatening changes, the same between-subjects factor (i.e., the group condition) was used, but, as dependent variables, we entered the percentage of detected changes and the reaction time in pressing the escape key. Moreover, to report on the degree of support for a possible effect or null effect (e.g., Faulkenberry, 2018) we examined each dependent variable using separate one-way Bayesian ANOVAs. Non-informative priors were used (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).

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

Results

First of all, we examined whether confederates triggered a competition feeling in the competition condition and cooperation feeling in the cooperation condition. Regarding the competition measure, the one-way ANOVA revealed a main effect of group condition [F(2, 64)= 15.45, p< .001, ηp2= .33]. Post hoc tests showed that participants in the competition condition (M= 62.13; SD= 33.80) reported to feel more that they were competing with the confederates than participants in the mere presence (M= 21.13; SD= 30.96; p< .001; *95% CI* [19.54; 62.02]) and cooperation (M= 15.30; SD= 24.82; p< .001; *95% CI* [24.38; 69.29]) conditions. No significant differences were revealed between mere presence and cooperation conditions (p= 1.000; 95% CI [-15.75; 27.85]). A main effect of group condition [F(2, 64)= 11.30, p< .001, ηp^2= .26] was also found on the cooperation measure. Post hoc tests showed that in the cooperation condition (M= 53.53; SD= 25.37), participants reported to feel an higher cooperation feeling than participants in the mere presence (M= 20.66; SD= 24.65; p< .001; *95% CI* [15.40; 50.35]) and in the competition condition (M= 25.82; SD= 22.80; p= .001; *95% CI* [9.71; 45.71]). No significant differences were revealed between competition and mere presence conditions (p= 1.000; *95% CI* [-11.87; 22.19]). Hence, these results suggested that a competitive or a cooperative mindset was induced in the competition and cooperation conditions (respectively), supporting the group context manipulation.

Concerning participants SCL (i.e. alertness level), contrary to our predictions, no significant main effect of group condition [F(1, 62)= 1.02, p= .37, ηp^2= .03], no two-way interaction between group condition and experimental block [F(2, 62)= .06, p= .943, ηp^2= .00], no two-way interaction between group condition per time interval [F(8, 248)= 1.10, p= .367, ηp^2= .03], neither a three-way interaction between group condition, experimental block and time interval [F(8, 248)= .61, p= .768, ηp^2= .02] were revealed. These results suggest that the different group conditions did not modulate participants' alertness level. Although not relevant for the effects aimed to address in this study, we observed a main effect of the experimental block [F(1, 62)= 16.71, p< .001, ηp^2= .21], and a main effect of the time interval [F(4, 248)= 11.40, p< .001, ηp^2= .16] in the SCL. No significant interaction between the experimental block and time interval [F(4, 248)= .46, p= .366, ηp^2= .01] were observed. In short, these observed effects are related with a general decrement (across conditions) of participants' SCL over time, which is a widely observed phenomenon in studies involving SCL (see Dawson et al., 2016).

Finally, and also contrary to the hypothesized, the one-way MANOVA exploring vigilance behavior did not reveal a significant main effect of group condition (*Pillai's Trace*= .09; F(6, 126)= .94, p= .472, ηp^2= .04), indicating that there were no significant differences between mere presence, competition, and cooperation conditions regarding vigilance strategy. (see Figure 1). Bayesian ANOVAs confirm this data pattern showing moderate evidence in favor of the null hypothesis for the vigilance time (BF_{01}= 4.90 ± 3.0%) and for the number of misses (BF_{01}= 5.32 ± 3.0%). For the number of correctly identified target letters, a Bayesian ANOVA revealed the existence of only anecdotal evidence in favor of the null hypothesis (BF_{01}= 2.65 ± 3.0%).

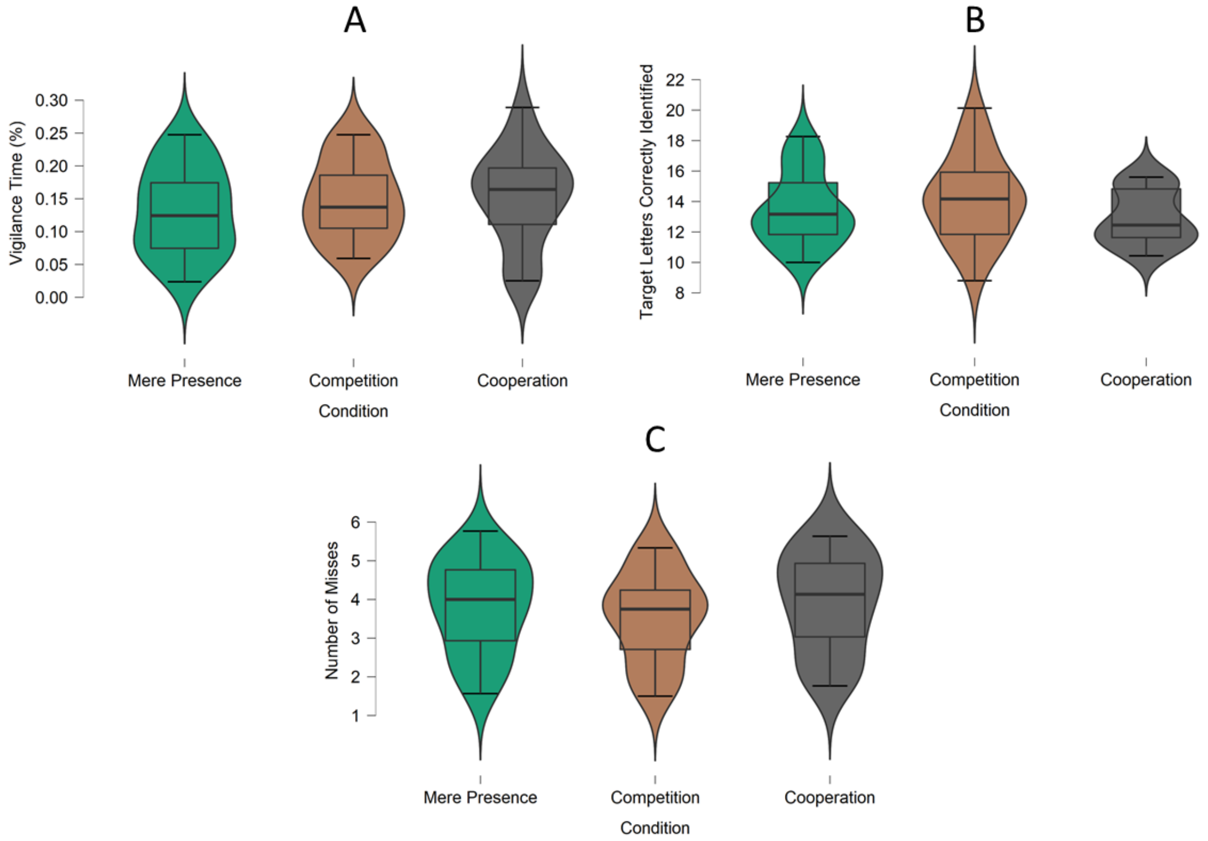

Figure 1: (A) Mean percentage of time spent scanning the peripheral targets; **(B)** Mean number of correctly identified letters per trial; **(C)** Mean number of misses per trial. No significant differences between group conditions were revealed for all the dependent variables.

Regarding threat detection, again contrary to what we have hypothesized, the one-way MANOVA revealed no main effect of group condition (*Pillai's Trace*= .06; *F*(4, 128)= .94, *p*= .443, ηp^2= .03). As for vigilance behavior, this suggests that there are no statistically significant differences between group conditions in the capacity to detect and avoid threatening stimuli (see Figure 2). Bayesian ANOVAs confirmed this data pattern, revealing that for both dependent variables there is moderate evidence in favor of the null hypothesis (percentage of detected changes: BF_{01}= 4.68 ± 3.0%; reaction time in pressing the escape key: 4.78 ± 3.0%).

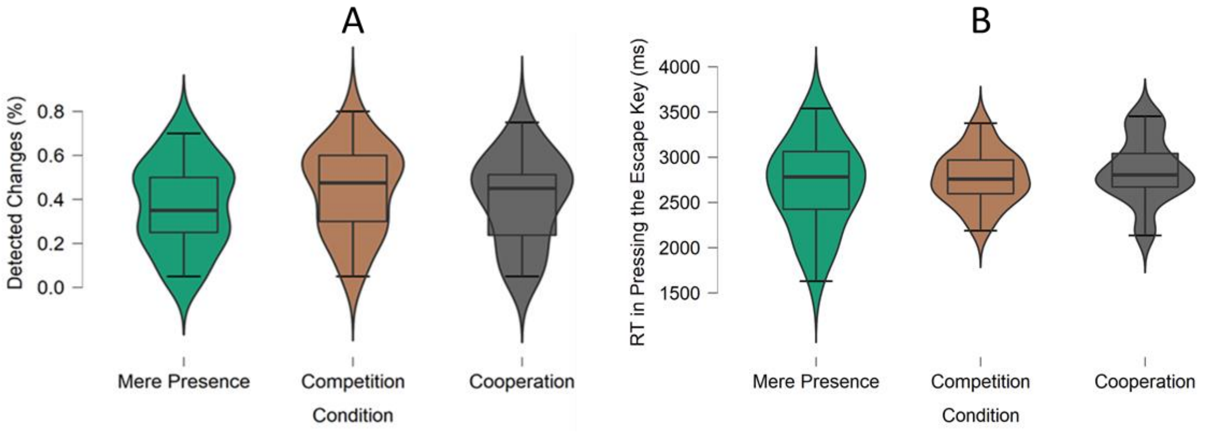

Figure 2: (A) Percentage of detected changes per group condition; **(B)** Mean reaction time (in milliseconds) in pressing the escape key. No significant differences between group conditions were revealed for both dependent variables.

Discussion

The study reported here was designed to investigate the potential modulatory effect of distinct group interdependencies (i.e. competition or cooperation contexts) on human vigilance strategies and threat detection capacity. Specifically, we aimed to examine whether the presence of conspecifics as competitors or cooperators would modulate vigilance and threat detection differently than a mere presence condition. To achieve our goal, we employed a "foraging-vigilance task". This task provides a simulation of "foraging under threat" scenario and represents an optimal context for studying the attentional trade-off between intake activities and vigilance focused on risk monitoring (see Beauchamp, 2015, 2020; Gomes & Semin, 2020). An eye-tracker was used, allowing a careful examination of participants' attention allocation.

The results confirmed that our manipulations were effective in creating either a competition or a cooperation context. Indeed, participants in the competition condition reported feeling a higher 'competition feeling' than participants in the mere presence and cooperation conditions. Participants in the cooperation condition reported a higher 'cooperation feeling' than participants in the other conditions. Although participants did feel that they were cooperating or competing with the confederates during the "foraging-vigilance" task, this seems to have had no impact on their risk-monitoring (compared to the mere presence condition). Indeed, contrary to what we had predicted, the different group conditions did not modulate participants' alertness state (i.e. SCL data) or vigilance strategies, which was assessed using the trade-off between the mean percentage of vigilance time as recorded with the eye-tracker, and the foraging activity represented by the mean number of hits and misses per trial in the letter discrimination task. Congruently, no differences were also observed in the capacity to detect and avoid threatening events. In other words, vigilance behavior and threat detection proved to be identical across all 3 group conditions.

Hence, a question that remains is why being either in a cooperative or competitive mindset did not result in distinct vigilance strategies compared to the mere presence condition. An immediate and tempting answer could be that distinct group interdependencies may have no direct influence on individuals' vigilance behavior. That is, vigilance might be modulated by the presence of conspecifics in a basic way, regardless of what conspecifics represent. However, as we will further explore, this answer is neither congruent with the previous animal (e.g., Portugal & Guillemain, 2011; Teichroeb & Sicotte, 2012) and few human findings (e.g., Kameda & Tamura, 2007; Kuroda & Kameda, 2019), nor can be concluded without further research considering distinct group aspects and context manipulations. In the following, although in a purely speculative manner, some alternative explanations and considerations for future research are provided.

A relevant aspect to consider is that perhaps, the group context manipulation was not successful in increasing or decreasing (respectively) the perceived threat risk and consequently modulate vigilance strategies. As already mentioned in the introductory section, animal research has shown that the threat risk (e.g., Creel et al., 2014), and consequently the individuals' stress level (e.g., assessed through the levels of stress hormones, such as cortisol; Hawlena & Schmitz, 2010; but see Tkaczynski et al., 2014), are directly correlated with the attentional resources invested in vigilance. Arguably, the presence of conspecifics, by representing a signal of increased safety (i.e. the perceived threat risk is reduced; see chapter III), results in less attentional resources invested in vigilance (see Beauchamp, 2015; Gomes & Semin, 2020). In the present study, our main hypothesis was that different presence conditions (i.e. adverse vs. favorable contexts) would distinctly modulate the perceived threat risk, resulting in distinct vigilance strategies. However, this was not verified. Thus, we speculate that in our study, the manipulation of competition and cooperation employed did not increase or decrease the perceived threat risk to an extent that would modulate vigilance and threat detection distinctively from the mere presence condition. In other words, the manipulation used to induce a competition or a cooperation context might not have led participants to perceive the presence of competitors (i.e. adverse context) or cooperators (i.e. favorable context) as a signal of increased/decreased threat probability (compared to the mere presence condition). Consequently, our manipulation did not change the participants' alertness, modulating neither their vigilance strategies nor threat detection efficacy.

Perhaps the role of competition and cooperation contexts governing individuals' vigilance strategies depends on the group dynamics and on online information gathering about conspecifics' behavior - which was not allowed in the present experiment. In contrast to previous studies (Kameda & Tamura, 2007; Kuroda & Kameda, 2019), we did not focus on exploring how group dynamics shape vigilance (e.g., producer-scrounger games; Giraldeau & Caraco, 2000) or how individuals change their vigilance strategies as a function of conspecifics' vigilance rates (e.g., Sirot, 2006). We aimed at a more basic phenomenon: to understand whether simply being in a competitive or cooperative mindset was enough to modulate the safety increment triggered by the mere presence of conspecifics, and consequently shape individuals' vigilance strategies. To this end, participants' had no online access to information about the other conspecifics behavior, and it did not directly affect their performance during the task (e.g., a cooperator detecting a threat event did not preclude the participant to be directly affected by one of such events). Competition and cooperation were manipulated here just by leading participants to believe that their final reward would depend on better individual performance compared to the others in the room (i.e., competition condition) or on a good performance of the group in general (i.e. cooperation condition).

Nevertheless, maybe competition and cooperation contexts only reveal their role in driving individuals' risk monitoring when group dynamics and online information about others' behavior are allowed. In fact, these variables seem to play an important role in natural competitive and cooperative contexts. For instance, the presence of competitors in nature represents a direct danger that may affect survival (e.g., aggression) or well-being (e.g., competition for food). In such situations where conspecifics are no longer representing a signal of safety, their behavior, as well as the dynamics between competitors constitute important vigilance modulators. For instance, animal research has shown that in competitive environments involving aggressive conspecifics, the presence of competitors and their proximity increases individual vigilance (Teichroeb & Sicotte, 2012). In contrast, in competitive contexts where food availability is at stake, the presence of competitors can result in lower levels of vigilance due to the high investment in foraging (e.g., Bednekoff & Lima, 2004). The same is true when cooperation contexts are considered. In this case, the presence of conspecifics provides joint efforts to avoid danger, increasing safety. However, this safety increment, as also shown in studies with humans (Kameda & Tamura, 2007; Kuroda & Kameda, 2019), is associated with different group dynamics that shape individual risk monitoring strategies. In fact, humans seem to adjust their vigilance strategies either using others as a source of vigilance while foraging continuously (producer-scrounger situation) or relying on conspecifics’ vigilance behavior as a statistical cue to infer the situated risk level and consequently the necessary amount of resources to invest in vigilance (i.e. herding behavior Kameda & Tamura, 2007). Moreover, humans seem also to be able to establish, just by observing others' behavior, tacit coordination of vigilance (i.e. cooperation), which allows some individuals to invest in intake activities, while others take care of vigilance (Kuroda & Kameda, 2019). Hence, group dynamics and the observation of others’ behavior are apparently an important piece for vigilance regulation in cooperative and competitive contexts. However, in our experiment, group dynamics and the use of others' behavior as a cue to adjust individual vigilance strategies were not allowed. Thus, although participants consciously perceived the confederates as competitors or cooperators, they may have not represented an online source of decreased or increased safety. That is, during the “foraging-vigilance” task: (a) the competitors’ behavior neither constituted a direct threat to the participants nor could it represent direct competition for the available resources (i.e. confederates foraging activity did not reduce the availability of potential resources to the participant); (b) the behavior of the cooperators did not directly increase participants’ safety (i.e. they did not constitute an additional threat detection source), and could not be coordinated with the participants’ behavior to allow them to forage while the others were vigilant. In such a way, competition and cooperation conditions have triggered in participants similar risk monitoring mechanisms as in the mere presence condition.

Having said that, it becomes clear that further research employing different designs and manipulations is needed to unravel the role of competitive and cooperative contexts shaping human vigilance behavior. From the previous discussion, it is possible to conclude that allowing participants to interact and have online access to the conspecifics’ performance on the task may be of high importance to observe the effects of cooperation and competition contexts on vigilance (e.g. Kameda & Tamura, 2007). Thus, in practical terms, instead of independent tasks (i.e. each participant solves his/her task, without affecting or being affected by the conspecifics behavior) and confederates simulating the presence of conspecifics, future research shall consider dynamical experiments. Limited foraging resources, simultaneous threatening events chasing all members, the possibility of conspecifics constituting a source of danger, and having groups of real participants cooperating or competing constitute some important features that would aid to create ecological simulations of cooperative and competitive contexts. Concretely, using the “foraging-vigilance” task as an example, future research can induce competition by introducing a ‘race’ for the available resources. That is, identifying a letter correctly would remove the opportunity of the other conspecifics to identify this same letter, precluding them from receiving the associated reward. Moreover, in a competition condition, besides random threatening events, participants should also need to be aware of “attacks” from conspecifics. This can be created by introducing the opportunity to attempt to steal the others’ accumulated resources, which can be avoided by the target participant being vigilant and pressing an ‘escape key’. On the other hand, in a cooperation condition, the accumulated money from foraging should be common to all the group members, and a group member detecting a threat event should give the opportunity to the group to avoid it. Moreover, to increase the cooperation feeling, participants can be led to believe that they need to cooperate not only to increase their final reward but also to win an extra prize for being better than other groups participating in the same experiment (intergroup competition seems to enhance intragroup cooperation; e.g., Puurtinen & Mappes, 2009). In both conditions, all participants should be aware of the others’ accumulated money and vigilance behavior. In an experiment with such characteristics, competition conditions will represent a context where conspecifics are no longer a signal of increased safety, also representing a threat source. On the other hand, a cooperation condition manipulated in this way will decrease threat-risk with conspecifics acting as additional threat detectors, and their vigilance behavior constituting a cue to individuals to regulate their own performance. In such a way, employing these ‘ecological’ competition and cooperation conditions will allow exploring whether these contexts contribute differentially to regulate human beings' vigilance behavior than a mere presence condition.

In sum, the present study pointed out that perceiving conspecifics as competitors or cooperators does not modulate individuals’ vigilance strategies differently than a mere presence condition. Together with previous research, the obtained results suggest that the potential role of competitive and cooperative contexts depends on the interaction and observation of the others’ behavior. Contrary to the effects of the conspecifics’ mere presence on vigilance strategies, which seems to be a more basic phenomenon triggered automatically, possible effects of competition and cooperation contexts on vigilance seem to involve more complex cognitive processing that depends on online information gathering. Future research is required to uncover the real effects of different group interdependencies on humans’ vigilance.

References

Barash, D. P. (1972). Human Ethology: The Snack-Bar Security Syndrome. *Psychological Reports*, *31*(2), 577–578. https://doi.org/10.2466/pr0.1972.31.2.577

Barbosa, A. (2002). Does vigilance always covary negatively with group size? Effects of foraging strategy. *Acta Ethologica*, *5*(1), 51–55. https://doi.org/10.1007/s10211-002-0059-0

Beauchamp, G. (2015). *Animal vigilance : monitoring predators and competitors*. Academic Press.

Beauchamp, G. (2020). Predator attack patterns influence vigilance in a virtual experiment. *Behavioral Ecology and Sociobiology*, *74*(4). https://doi.org/10.1007/s00265-020-02833-0

Beauchamp, G., & Livoreil, B. (1997). The effect of group size on vigilance and feeding rate in spice finches (Lonchura punctulata) . *Canadian Journal of Zoology*, *75*(9), 1526–1531. https://doi.org/10.1139/z97-776

Bednekoff, P. A., & Lima, S. L. (2004). Risk allocation and competition in foraging groups: reversed effects of competition if group size varies under risk of predation. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1547), 1491–1496. https://doi.org/10.1098/rspb.2004.2739

Bertram, B. C. R. (1978). Living in groups: predator and prey. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural Ecology* (pp. 64–96). Blackwell Publishing Ltd.

Bertram, B. C. R. (1980). Vigilance and group size in ostriches. *Animal Behaviour*, *28*(1), 278–286. https://doi.org/10.1016/S0003-3472(80)80030-3

Blumstein, D. T., & Daniel, J. C. (2002). Isolation from mammalian predators differentially affects two congeners. *Behavioral Ecology*, *13*(5), 657–663. https://doi.org/10.1093/beheco/13.5.657

Blumstein, D. T., Evans, C. S., & Daniel, J. C. (1999). An experimental study of behavioural group size effects in tammar wallabies, Macropus eugenii. *Animal Behaviour*, *58*(2), 351–360. https://doi.org/10.1006/anbe.1999.1156

Cameron, E. Z., & Du Toit, J. T. (2005). Social influences on vigilance behaviour in giraffes, Giraffa camelopardalis. *Animal Behaviour*, *69*(6), 1337–1344. https://doi.org/10.1016/j.anbehav.2004.08.015

Caraco, T., Martindale, S., & Pulliam, H. R. (1980). Avian flocking in the presence of a predator. *Nature*, *285*(5764), 400–401. https://doi.org/10.1038/285400a0

Creel, S., Schuette, P., & Christianson, D. (2014). Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology*, *25*(4), 773–784. https://doi.org/10.1093/beheco/aru050

Dawson, M. E., Schell, A. M., & Filion, D. L. (2016). The Electrodermal System. In *Handbook of Psychophysiology* (pp. 217–243). Cambridge University Press. https://doi.org/10.1017/9781107415782.010

Dunbar, R. I. M., Cornah, L., Daly, F. J., & Bowyer, K. M. (2002). Vigilance in human groups: A test of alternative hypotheses. *Behaviour*, *139*(5), 695–711. https://doi.org/10.1163/15685390260136771

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*(2), 175–191. https://doi.org/10.3758/BF03193146

Faulkenberry, T. J. (2018). Computing Bayes factors to measure evidence from experiments: An extension of the BIC approximation. *Biometrical Letters*, *55*(1), 31–43. https://doi.org/10.2478/bile-2018-0003

Field, A. (2014). Discovering Statistics Using SPSS, Second Edition. In *SAGE Publication*. https://doi.org/10.1111/j.1365-2648.2007.04270_1.x

Fordyce, J. A., & Agrawal, A. A. (2001). The role of plant trichomes and caterpillar group size on growth and defence of the pipevine swallowtail *Battus philenor*. *Journal of Animal Ecology*, *70*(6), 997–1005. https://doi.org/10.1046/j.0021-8790.2001.00568.x

Galton, F. (1871). Gregariousness in cattle and in men. *Macmillan's Magazine*, *23*(136), 353–357.

Gaynor, K. M., & Cords, M. (2012). Antipredator and social monitoring functions of vigilance behaviour in blue monkeys. *Animal Behaviour*, *84*(3), 531–537. https://doi.org/10.1016/j.anbehav.2012.06.003

Giraldeau, L.-A., & Caraco, T. (2000). *Social Foraging Theory*. Princeton University Press.

Gomes, N., & Semin, G. R. (2020). Mapping human vigilance: The influence of conspecifics. *Evolution and Human Behavior*, *41*(1), 69–75. https://doi.org/10.1016/j.evolhumbehav.2019.10.002

Gosselin-ildari, A. D., & Koenig, A. (2012). The Effects of Group Size and Reproductive Status on Vigilance in Captive Callithrix jacchus. *American Journal of Primatology*, *74*(7), 613–621. https://doi.org/10.1002/ajp.22013

Guillemain, M., Caldow, R. W. G., Hodder, K. H., & Goss-Custard, J. D. (2003). Increased vigilance of paired males in sexually dimorphic species: Distinguishing between alternative explanations in wintering Eurasian wigeon. *Behavioral Ecology*, *14*(5), 724–729. https://doi.org/10.1093/beheco/arg060

Hawlena, D., & Schmitz, O. J. (2010). Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *American Naturalist*, *176*(5), 537–556. https://doi.org/10.1086/656495

Hirsch, B. T. (2002). Social monitoring and vigilance behavior in brown capuchin monkeys (Cebus apella). *Behavioral Ecology and Sociobiology*, *52*(6), 458–464. https://doi.org/10.1007/s00265-002-0536-5

JASP Team. (2020). *JASP* (0.13.1). https://jasp-stats.org/

Kameda, T., & Tamura, R. (2007). "To eat or not to be eaten?" Collective risk-monitoring in groups. *Journal of Experimental Social Psychology*, *43*(2), 168–179. https://doi.org/10.1016/j.jesp.2006.02.003

Kuroda, K., & Kameda, T. (2019). You watch my back, I'll watch yours: Emergence of collective risk monitoring through tacit coordination in human social foraging. *Evolution and Human Behavior*, *40*(5), 427–435. https://doi.org/10.1016/J.EVOLHUMBEHAV.2019.05.004

Kutsukake, N. (2006). The Context and Quality of Social Relationships Affect Vigilance Behaviour in Wild Chimpanzees. *Ethology*, *112*(6), 581–591. https://doi.org/10.1111/j.1439-0310.2006.01200.x

Lee, M. D., & Wagenmakers, E. J. (2013). *Bayesian cognitive modeling: A practical course*. Cambridge University Press.

Leys, C., Ley, C., Klein, O., Bernard, P., & Licata, L. (2013). Detecting outliers: Do not use standard deviation around the mean, use absolute deviation around the median. *Journal of Experimental Social Psychology*, *49*(4), 764–766. https://doi.org/10.1016/j.jesp.2013.03.013

Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, *49*(1), 11–20. https://doi.org/10.1016/0003-3472(95)80149-9

Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, *108*(3), 483–522. https://doi.org/10.1037/0033-295X.108.3.483

Portugal, S. J., & Guillemain, M. (2011). Vigilance patterns of wintering Eurasian Wigeon: Female benefits from male low-cost behaviour. *Journal of Ornithology*, *152*(3), 661–668. https://doi.org/10.1007/s10336-010-0641-6

Puurtinen, M., & Mappes, T. (2009). Between-group competition and human cooperation. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1655), 355–360. https://doi.org/10.1098/rspb.2008.1060

Radford, A. N., & Ridley, A. R. (2007). Individuals in foraging groups may use vocal cues when assessing their need for anti-predator vigilance. *Biology Letters*, *3*(3), 249–252. https://doi.org/10.1098/rsbl.2007.0110

Raskin, D. C. (1973). Attention and Arousal. In W. F. Prokasy & D. C. Raskin (Eds.), *Electrodermal Activity in Psychological Research* (pp. 125–156). Academic Press.

Sirot, E. (2006). Social information, antipredatory vigilance and flight in bird flocks. *Animal Behaviour*, *72*(2), 373–382. https://doi.org/10.1016/j.anbehav.2005.10.028

Teichroeb, J. A., & Sicotte, P. (2012). Cost-free vigilance during feeding in folivorous primates? Examining the effect of predation risk, scramble competition, and infanticide threat on vigilance in ursine colobus monkeys (Colobus vellerosus). *Behavioral Ecology and Sociobiology*, *66*(3), 453–466. https://doi.org/10.1007/s00265-011-1292-1

Tkaczynski, P., MacLarnon, A., & Ross, C. (2014). Associations between spatial position, stress and anxiety in forest baboons Papio anubis. *Behavioural Processes*, *108*, 1–6. https://doi.org/10.1016/j.beproc.2014.08.006

Treves, A. (2000). Theory and method in studies of vigilance and aggregation. *Animal Behaviour*, *60*(6), 711–722. https://doi.org/10.1006/anbe.2000.1528

van Schaik, C. P., van Noordwijk, M. A., de Boer, R. J., & den Tonkelaar, I. (1983). The effect of group size on time budgets and social behaviour in wild long-tailed macaques (Macaca fascicularis). *Behavioral Ecology and Sociobiology*, *13*(3), 173–181. https://doi.org/10.1007/BF00299920

Wawra, M. (1988). Vigilance Patterns in Humans. *Behaviour*, *107*(1–2), 61–71. https://doi.org/10.1163/156853988X00197

Wirtz, P., & Wawra, M. (1986). Vigilance and Group Size in Homo sapiens. *Ethology*, *71*(4), 283–286. https://doi.org/10.1111/j.1439-0310.1986.tb00592.x

Chapter V:

The Function of Fear Chemosignals: Preparing for Danger

Chapter based on:

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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). 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.

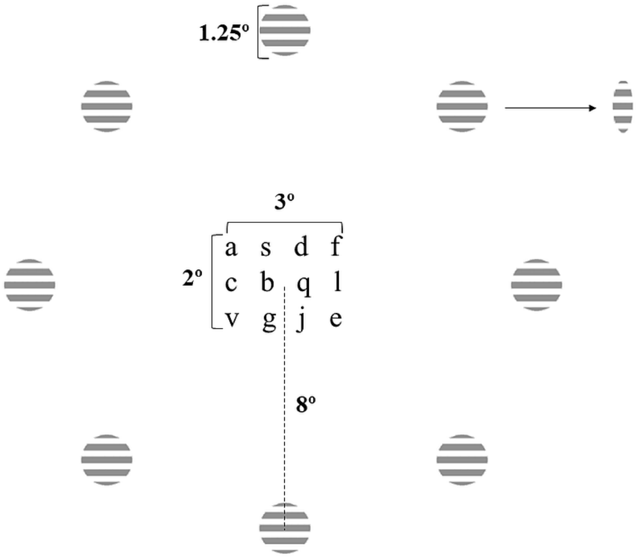

Figure 1: Example of a letter matrix surrounded by 8 Gabor patches. The arrow illustrates a possible change in one of the 8 Gabor patches (i.e., its width being gradually reduced to about a third of its original size). The dimensions of the different elements are specified in visual degrees.

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.

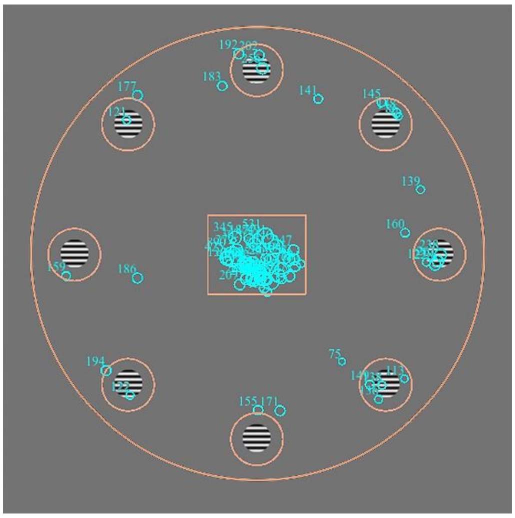

Figure 2: An example of a representative trial as viewed in the software used to extract and analyze the eye-tracker data (i.e., DataViewer; SR Research). The small blue circles represent each fixation of the participant (the blue numbers are the duration of each fixation in milliseconds). The elements 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.

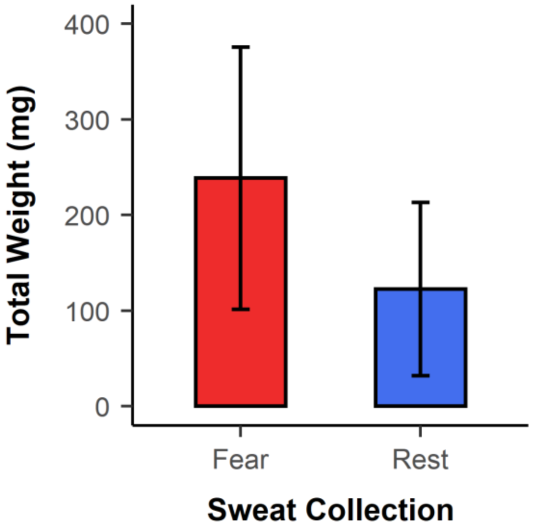

Figure 3: Mean sweat production, in milligrams, per sweat collection. Error bars represent 95% within-subject confidence intervals.

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).

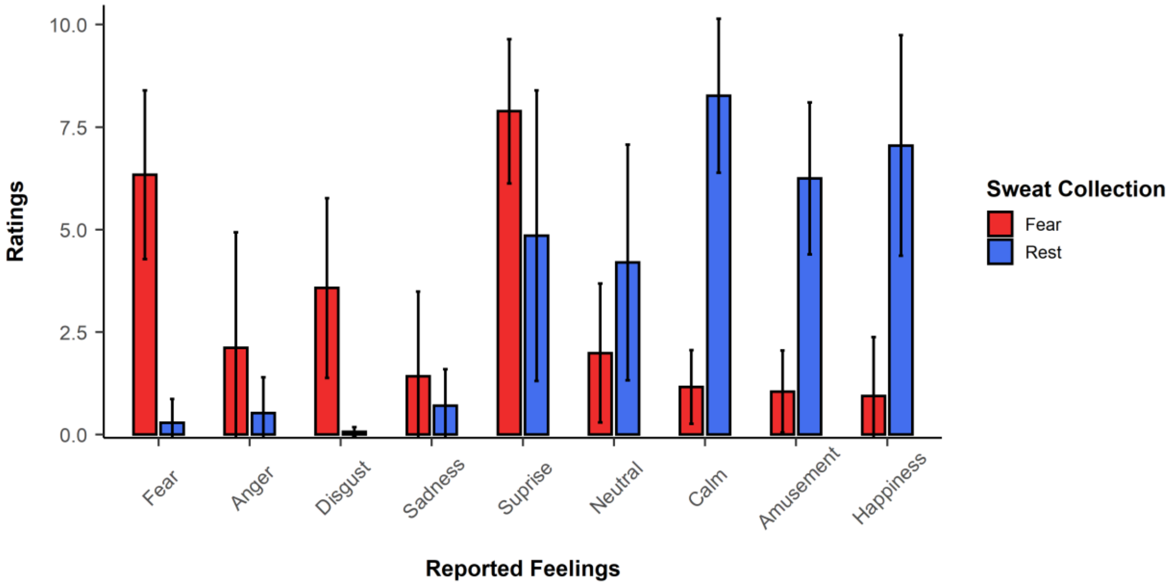

Figure 4: Mean reported feelings by sweat donors, per sweat collection. Error bars represent 95% within-subject confidence intervals.

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, $\eta^2 p$= .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.

	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)

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 ± 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).

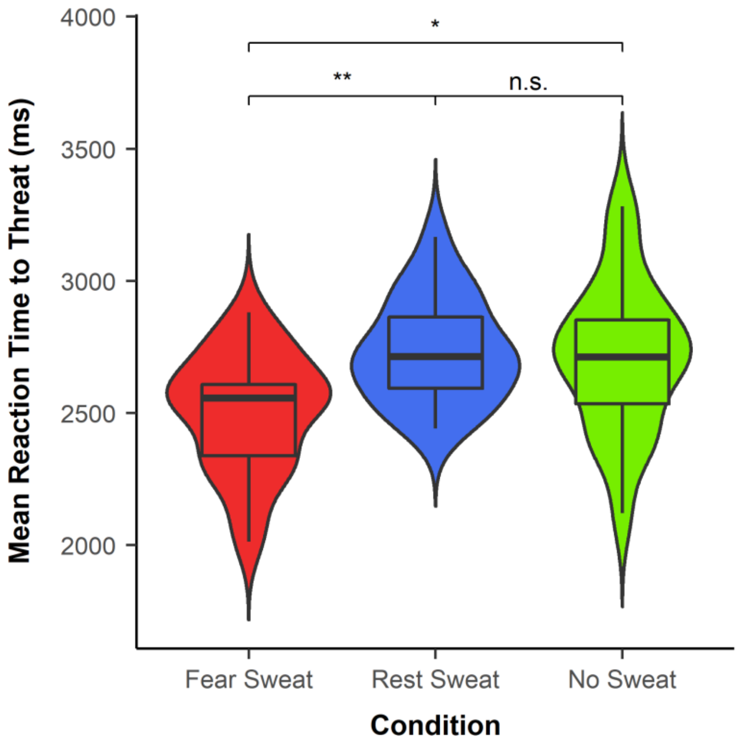

Figure 5: Mean reaction time (in milliseconds) in pressing the escape key. Participants in the fear condition pressed the escape key significantly faster than participants in the rest and no-sweat conditions. No statistically significant differences were observed between the rest and no-sweat conditions.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

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

	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)

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.

References

Bannerman, R. L., Milders, M., de Gelder, B., & Sahraie, A. (2009). Orienting to threat: faster localization of fearful facial expressions and body postures revealed by saccadic eye movements. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1662), 1635–1641. https://doi.org/10.1098/rspb.2008.1744

Barash, D. P. (1972). Human Ethology: The Snack-Bar Security Syndrome. *Psychological Reports*, *31*(2), 577–578. https://doi.org/10.2466/pr0.1972.31.2.577

Beauchamp, G. (2015). *Animal vigilance : monitoring predators and competitors*. Academic Press.

Bertram, B. C. R. (1978). Living in groups: predator and prey. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural Ecology* (pp. 64–96). Blackwell Publishing Ltd.

Botvinick, M., Nystrom, L. E., Fissell, K., Carter, C. S., & Cohen, J. D. (1999). Conflict monitoring versus selection for-action in anterior cingulate cortex. *Nature*, *402*(6758), 179–181. https://doi.org/10.1038/46035

Brown, G. E., Godin, J. G. J., & Pedersen, J. (1999). Fin-flicking behaviour: A visual antipredator alarm signal in a characin fish, Hemigrammus erythrozonus. *Animal Behaviour*, *58*(3), 469–475. https://doi.org/10.1006/anbe.1999.1173

Caraco, T., Martindale, S., & Pulliam, H. R. (1980). Avian Time Budgets and Distance to Cover. *The Auk: Ornithological Advances*, *97*(4), 872–875. https://doi.org/10.1093/auk/97.4.872

Cato, M. A., Crosson, B., Gökçay, D., Soltysik, D., Wierenga, C., Gopinath, K., Himes, N., Belanger, H., Bauer, R. M., Fischler, I. S., Gonzalez-Rothi, L., & Briggs, R. W. (2004). Processing Words with Emotional Connotation: An fMRI Study of Time Course and Laterality in Rostral Frontal and Retrosplenial Cortices. *Journal of Cognitive Neuroscience*, *16*(2), 167–177. https://doi.org/10.1162/089892904322984481

Creel, S., Schuette, P., & Christianson, D. (2014). Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology*, *25*(4), 773–784. https://doi.org/10.1093/beheco/aru050

De Gelder, B. (2006). Towards the neurobiology of emotional body language. In *Nature Reviews Neuroscience* (Vol. 7, Issue 3, pp. 242–249). https://doi.org/10.1038/nrn1872

de Groot, J. H. B., Semin, G. R., & Smeets, M. A. M. (2014). I can see, hear, and smell your fear: comparing olfactory and audiovisual media in fear communication. *Journal of*

Experimental Psychology. General, *143*(2), 825–834. https://doi.org/10.1037/a0033731

de Groot, J. H. B., & Smeets, M. A. M. (2017). Human fear chemosignaling: Evidence from a meta-analysis. *Chemical Senses*, *42*(8), 663–673. https://doi.org/10.1093/chemse/bjx049

de Groot, J. H. B., Smeets, M. A. M., Kaldewaij, A., Duijndam, M. J. a, & Semin, G. R. (2012). Chemosignals communicate human emotions. *Psychological Science*, *23*(11), 1417–1424. https://doi.org/10.1177/0956797612445317

de Groot, J. H. B., Smeets, M. A. M., Rowson, M. J., Bulsing, P. J., Blonk, C. G., Wilkinson, J. E., & Semin, G. R. (2015). A Sniff of Happiness. *Psychological Science*, *26*(6), 684–700. https://doi.org/10.1177/0956797614566318

de Groot, J. H. B., van Houtum, L. A. E. M., Gortemaker, I., Ye, Y., Chen, W., Zhou, W., & Smeets, M. A. M. (2018). Beyond the west: Chemosignaling of emotions transcends ethno-cultural boundaries. *Psychoneuroendocrinology*, *98*, 177–185. https://doi.org/10.1016/j.psyneuen.2018.08.005

Dolan, R. J., Morris, J. S., & de Gelder, B. (2001). Crossmodal binding of fear in voice and face. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(17), 10006–10010. https://doi.org/10.1073/pnas.171288598

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*(2), 175–191. https://doi.org/10.3758/BF03193146

Faulkenberry, T. J. (2018). Computing Bayes factors to measure evidence from experiments: An extension of the BIC approximation. *Biometrical Letters*, *55*(1), 31–43. https://doi.org/10.2478/bile-2018-0003

Field, A. (2014). Discovering Statistics Using SPSS, Second Edition. In *SAGE Publication*. https://doi.org/10.1111/j.1365-2648.2007.04270_1.x

Giardino, J., Gonzalez, A., Steiner, M., & Fleming, A. S. (2008). Effects of motherhood on physiological and subjective responses to infant cries in teenage mothers: A comparison with non-mothers and adult mothers. *Hormones and Behavior*, *53*(1), 149–158. https://doi.org/10.1016/j.yhbeh.2007.09.010

Gomes, N., & Semin, G. R. (2020). Mapping human vigilance: The influence of conspecifics. *Evolution and Human Behavior*, *41*(1), 69–75. https://doi.org/10.1016/j.evolhumbehav.2019.10.002

Gomes, N., Silva, F., & Semin, G. R. (2020). The Lasting Smell of Emotions: The Effects of

Reutilizing Fear Sweat Samples. *Behavior Research Methods*, 1–14. https://doi.org/10.3758/s13428-020-01412-5

Hawlena, D., & Schmitz, O. J. (2010). Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *American Naturalist*, *176*(5), 537–556. https://doi.org/10.1086/656495

Hoogland, J. L. (1979). The effect of colony size on individual alertness of prairie dogs (Sciuridae: Cynomys spp.). *Animal Behaviour*, *27*(PART 2), 394–407. https://doi.org/10.1016/0003-3472(79)90174-X

Hornung, J., Noack, H., Kogler, L., & Derntl, B. (2019). Exploring the fMRI based neural correlates of the dot probe task and its modulation by sex and body odor. *Psychoneuroendocrinology*, *99*, 87–96. https://doi.org/10.1016/j.psyneuen.2018.08.036

JASP Team. (2020). *JASP* (0.13.1). https://jasp-stats.org/

Kameda, T., & Tamura, R. (2007). “To eat or not to be eaten?” Collective risk-monitoring in groups. *Journal of Experimental Social Psychology*, *43*(2), 168–179. https://doi.org/10.1016/j.jesp.2006.02.003

Kamiloğlu, R. G., Smeets, M. A. M., de Groot, J. H. B., & Semin, G. R. (2018). Fear odor facilitates the detection of fear expressions over other negative expressions. *Chemical Senses*, *43*(6), 419–426. https://doi.org/10.1093/chemse/bjy029

Kikusui, T., Takigami, S., Takeuchi, Y., & Mori, Y. (2001). Alarm pheromone enhances stress-induced hyperthermia in rats. *Physiology and Behavior*, *72*(1–2), 45–50. https://doi.org/10.1016/S0031-9384(00)00370-X

LeDoux, J. E. (1996). *The emotional brain : the mysterious underpinnings of emotional life*. Simon & Schuster.

Lee, M. D., & Wagenmakers, E. J. (2013). *Bayesian cognitive modeling: A practical course*. Cambridge University Press.

Leys, C., Ley, C., Klein, O., Bernard, P., & Licata, L. (2013). Detecting outliers: Do not use standard deviation around the mean, use absolute deviation around the median. *Journal of Experimental Social Psychology*, *49*(4), 764–766. https://doi.org/10.1016/j.jesp.2013.03.013

Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, *49*(1), 11–20. https://doi.org/10.1016/0003-3472(95)80149-9

Lötsch, J., Ultsch, A., & Hummel, T. (2016). How many and which odor identification items are needed to establish normal olfactory function? *Chemical Senses*, *41*(4), 339–344. https://doi.org/10.1093/chemse/bjw006

Löw, A., Lang, P. J., Smith, J. C., & Bradley, M. M. (2008). Both predator and prey: Emotional arousal in threat and reward. *Psychological Science*, *19*(9), 865–873. https://doi.org/10.1111/j.1467-9280.2008.02170.x

Lundström, J. N., & Olsson, M. J. (2010). Functional neuronal processing of human body odors. *Vitamins and Hormones*, *83*(C), 1–23. https://doi.org/10.1016/S0083-6729(10)83001-8

Martín, J., Luque-Larena, J. J., & López, P. (2006). Collective detection in escape responses of temporary groups of Iberian green frogs. *Behavioral Ecology*, *17*(2), 222–226. https://doi.org/10.1093/beheco/arj024

Martins, Y., Preti, G., Crabtree, C. R., Runyan, T., Vainius, A. A., & Wysocki, C. J. (2005). Preference for human body odors is influenced by gender and sexual orientation. *Psychological Science*, *16*(9), 694–701. https://doi.org/10.1111/j.1467-9280.2005.01598.x

Mogg, K., Garner, M., & Bradley, B. P. (2007). Anxiety and orienting of gaze to angry and fearful faces. *Biological Psychology*, *76*(3), 163–169. https://doi.org/10.1016/j.biopsycho.2007.07.005

Morris, J. S., Ohman, A., & Dolan, R. J. (1999). A subcortical pathway to the right amygdala mediating “unseen” fear. *Proceedings of the National Academy of Sciences*, *96*(4), 1680–1685. https://doi.org/10.1073/pnas.96.4.1680

Mujica-Parodi, L. R., Strey, H. H., Frederick, B., Savoy, R., Cox, D., Botanov, Y., Tolkunov, D., Rubin, D., & Weber, J. (2009). Chemosensory cues to conspecific emotional stress activate amygdala in humans. *PLoS ONE*, *4*(7). https://doi.org/10.1371/journal.pone.0006415

Nabergoj, D., Janeš, D., Fatur, K., Glavač, N. K., & Kreft, S. (2020). Influence of the Human Menstrual Cycle on the Perception of Musks and Substances Responsible for Body Odour. *Journal of Evolutionary Biochemistry and Physiology*, *56*(6), 565–576. https://doi.org/10.1134/s0022093020060095

Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, *108*(3), 483–522. https://doi.org/10.1037/0033-295X.108.3.483

Parma, V., Gordon, A. R., Cinzia, C., Cavazzana, A., Lundström, J. N., & Olsson, M. J. (2017). Processing of Human Body Odors. In A. Buettner (Ed.), *Springer Handbook of Odor* (pp. 963–986). Springer.

Parma, V., Tirindelli, R., Bisazza, A., Massaccesi, S., & Castiello, U. (2012). Subliminally Perceived Odours Modulate Female Intrasexual Competition: An Eye Movement Study. *PLoS ONE*, *7*(2), e30645. https://doi.org/10.1371/journal.pone.0030645

Pourtois, G., Grandjean, D., Sander, D., & Vuilleumier, P. (2004). Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cerebral Cortex*, *14*(6), 619–633. https://doi.org/10.1093/cercor/bhh023

Prehn-Kristensen, A., Wiesner, C., Bergmann, T. O., Wolff, S., Jansen, O., Mehdorn, H. M., Ferstl, R., & Pause, B. M. (2009). Induction of empathy by the smell of anxiety. *PLoS ONE*, *4*(6), e5987. https://doi.org/10.1371/journal.pone.0005987

Prehn, A., Ohrt, A., Sojka, B., Ferstl, R., & Pause, B. M. (2006). Chemosensory anxiety signals augment the startle reflex in humans. *Neuroscience Letters*, *394*(2), 127–130. https://doi.org/10.1016/j.neulet.2005.10.012

Randall, J. A. (2001). Evolution and function of drumming as communication in mammals'. *American Zoologist*, *41*(5), 1143–1156. https://doi.org/10.1093/icb/41.5.1143

Rocha, M., Parma, V., Lundström, J. N., & Soares, S. C. (2018). Anxiety Body Odors as Context for Dynamic Faces: Categorization and Psychophysiological Biases. *Perception*, *47*(10–11), 1054–1069. https://doi.org/10.1177/0301006618797227

Rubin, D., Botanov, Y., Hajcak, G., & Mujica-Parodi, L. R. (2012). Second-hand stress: inhalation of stress sweat enhances neural response to neutral faces. *Social Cognitive and Affective Neuroscience*, *7*(2), 208–212. https://doi.org/10.1093/scan/nsq097

Schlund, M. W., & Cataldo, M. F. (2010). Amygdala involvement in human avoidance, escape and approach behavior. *NeuroImage*, *53*(2), 769–776. https://doi.org/10.1016/j.neuroimage.2010.06.058

Silva, F., Gomes, N., Korb, S., & Semin, G. R. (2020). Not All Emotions Are Equal: Fear Chemosignals Lower Awareness Thresholds Only for Fearful Faces. *Chemical Senses*, *45*(7), 601–608. https://doi.org/10.1093/chemse/bjaa047

Stienen, B. M. C., & de Gelder, B. (2011). Fear Modulates Visual Awareness Similarly for Facial and Bodily Expressions. *Frontiers in Human Neuroscience*, *5*. https://doi.org/10.3389/fnhum.2011.00132

Susskind, J. M., Lee, D. H., Cusi, A., Feiman, R., Grabski, W., & Anderson, A. K. (2008). Expressing fear enhances sensory acquisition. *Nature Neuroscience*, *11*(7), 843–850. https://doi.org/10.1038/nn.2138

Tipples, J. (2006). Fear and fearfulness potentiate automatic orienting to eye gaze. *Cognition and Emotion*, *20*(2), 309–320. https://doi.org/10.1080/02699930500405550

Tkaczynski, P., MacLarnon, A., & Ross, C. (2014). Associations between spatial position, stress and anxiety in forest baboons Papio anubis. *Behavioural Processes*, *108*, 1–6. https://doi.org/10.1016/j.beproc.2014.08.006

van Schaik, C. P., van Noordwijk, M. A., de Boer, R. J., & den Tonkelaar, I. (1983). The effect of group size on time budgets and social behaviour in wild long-tailed macaques (Macaca fascicularis). *Behavioral Ecology and Sociobiology*, *13*(3), 173–181. https://doi.org/10.1007/BF00299920

Voellmy, I. K., Goncalves, I. B., Barrette, M. F., Monfort, S. L., & Manser, M. B. (2014). Mean fecal glucocorticoid metabolites are associated with vigilance, whereas immediate cortisol levels better reflect acute anti-predator responses in meerkats. *Hormones and Behavior*, *66*(5), 759–765. https://doi.org/10.1016/j.yhbeh.2014.08.008

Wawra, M. (1988). Vigilance Patterns in Humans. *Behaviour*, *107*(1–2), 61–71. https://doi.org/10.1163/156853988X00197

Wirtz, P., & Wawra, M. (1986). Vigilance and Group Size in Homo sapiens. *Ethology*, *71*(4), 283–286. https://doi.org/10.1111/j.1439-0310.1986.tb00592.x

Wudarczyk, O. A., Kohn, N., Bergs, R., Goerlich, K. S., Gur, R. E., Turetsky, B., Schneider, F., & Habel, U. (2016). Chemosensory anxiety cues enhance the perception of fearful faces – An fMRI study. *NeuroImage*, *143*, 214–222. https://doi.org/10.1016/j.neuroimage.2016.09.002

Zhou, W., & Chen, D. (2009). Fear-related chemosignals modulate recognition of fear in ambiguous facial expressions. *Psychological Science*, *20*(2), 177–183. https://doi.org/10.1111/j.1467-9280.2009.02263.x

Chapter VI:

The Lasting Smell of Emotions: The Effects of Reutilizing Fear Sweat Samples

Chapter based on:

Gomes, N., Silva, F., & Semin, G. R. (2020). The Lasting Smell of Emotions: The Effects of Reutilizing Fear Sweat Samples. *Behavior Research Methods,* 1–14. https://doi.org/10.3758/s13428-020-01412-5.

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Abstract

A growing body of research has shown that human apocrine sweat carries information about the emotional state of its donor. Exposure to sweat produced in a fear-inducing context, triggers in its receivers a simulacrum of this emotional state, as evidenced by increased *medial frontalis* and *corrugator supercilii* (facial electromyography; fEMG) activity – two facial muscles involved in the display of fear facial expressions. However, despite the increased interest in the effects of emotional sweat, little is known about the proprieties of these chemical sweat samples. The goal of this study was to examine if a second application of the same sweat sample would yield reliable results. Specifically, we assessed whether sweat samples collected, from Portuguese males (N = 8) in fear (vs. neutral) inducing contexts, produce similar fEMG activations (i.e., in the *medial frontalis* and *corrugator supercilii*) in female receivers (N = 60) across two independent applications (the first with Dutch and the second with Portuguese receivers). Our findings showed that exposure to fear (vs. neutral) sweat resulted in higher activation of both muscles compared to neutral odors, revealing a similar data pattern across both applications underlining the feasibility of re-using emotional sweat samples. The implications of these findings for properties of these sweat volatiles are discussed.

Keywords

Human olfaction; Body Odors; Fear; Fear Sweat; Re-use; Facial EMG

Introduction

Compared to other senses, such as vision or hearing, human olfaction has been largely neglected. This started to change in the late 1970s (e.g., Russell, 1976). The interest of the scientific community in human sense of smell has been growing since then. One of the research fields in this area that has experienced more development over the last few years is the study of the social communicative function of human body odors (i.e., chemosignals; Semin & de Groot, 2013). However, while human chemosignals, as the medium carrying a wealth of information is receiving increasing attention, the carrier itself, sweat, is relatively neglected. An important question with considerable practical and theoretical relevance is how long sweat retains its message carrying function. In other words, how many times can the same sweat sample be used? To answer this question, we first provide a brief overview of the communicative function of human chemosignals leading to the main focus of our research: how durable are the message carrying properties of emotional body odor samples?

The accumulating research on the effects of human chemosignals on recipients has revealed that these volatiles carry a wide range of information. For instance, human chemosignals have been demonstrated to convey information about age (Mitro et al., 2012), gender (Penn et al., 2007), health status (Olsson et al., 2014), familiarity (e.g., Lundström et al., 2008), reproductive state (Stern & McClintock, 1998), genetic relatedness (Porter, 1998), as well as affective states (e.g., Chen et al., 2006). Indeed, in the case of affective states recent studies have shown that chemosignals induced during emotional states lead to a simulacrum of the donor's emotional state (e.g., fear and happiness; de Groot et al., 2015). Moreover, they modulate a wide range of behavioral responses including mimicry of the donor's facial expression (see de Groot et al., 2017). For instance, the exposure to fear chemosignals results in the activation of the *medial frontalis* and *corrugator supercilii* (de Groot et al., 2014), facial muscles associated with the expression of fear (see Fridlund & Cacioppo, 1986).

While the field of the communicative function of human odors that are produced while experiencing emotional states has grown considerably, there remain many challenges about how to handle sweat samples (e.g., Parma et al., 2017). One of these is addressed by controlling the bodily conditions to reduce variability between donors as much as possible while producing sweat samples. These involve restrictions on, for instance, daily habits of donors (dietary, hygienic and social restriction; e.g., Havlíček & Lenochova, 2006). The medium by which the odors are collected is another item (e.g., t-shirts or pads; Roberts et al., 2005). Similarly, the length of the sampling process (i.e., duration of the collection; Havlíček et al., 2006) and how the sample is stored (e.g., the time that the samples spent in a freezer; see Lenochova et al.,

2009) are issues that have been addressed. These are all crucial factors that can affect the final odor sample, and ascertaining all aforementioned constraints is an expensive process, both in terms of the time and monetary costs involved.

A common practice is to use a sweat sample only once. In other words, once a sweat sample has been used for a specific participant, that sample is normally not used again. The assumption driving this is that the properties of the volatiles responsible for whatever effect is being examined might be reduced or have dissipated. Few studies have directly examined this question. In a paper assessing the effects of freezing plain sweat samples, Lenochova and colleagues (2009) explored how repeated thawing cycles influence the perceived intensity, pleasantness, attractiveness, and masculinity of axillar sweat samples. The authors reported only a significant increment of sweat intensity from the first to the second thawing cycle. Nonetheless, the aforementioned study did not rely on emotional sweat samples and their conclusions are only based on subjective indicators (e.g., perceived intensity). In another study, de Groot and colleagues (2020), using a photo-ionization detector, quantified the volatile molecules in fear and neutral sweat samples, across a first and a second application. The authors showed that the re-used sweat released less volatiles when compared to its first use. However, despite the lower number of volatile molecules emitted, the authors did not examine the effects of the second-used sweat samples in communicating emotional information to their receivers. Thus, the information we have regarding the effectiveness of using an emotional sweat sample after it has been used once is sparse. The question that remains open is whether a second application of an emotional sweat sample with the same parameters of its first use manifests the same results in its receivers as it does the first time it is used.

If a second use of the same sweat sample produces similar results, then this would offer a wide range of advantages aside from scales of economy regarding the costs of collecting sweat samples. Obviously, this would reduce costs and time, by a second use of the same samples. Additionally, this would also encourage replications by, for instance, other researchers who could be given access to the sweat samples used in an experiment.

Equally important to these advantages is the type of information one would be able to glean about the nature of the volatiles involved in the transmission of emotional information. It is known that high volatile molecules disperse faster and travel longer distances, with the clear advantage of carrying their ‘message’ to different locations, however, for shorter time periods. In contrast, low volatile molecules do not travel long distances. The information they carry remains for longer time periods at the place of their emission. Consequently, the message they carry remains close to their location of emission, even when the sender is no longer there (e.g., Pause, 2017; Pause et al., 1997). Consequently, one may surmise that if the second use of the odor samples does not give rise to the same cognitive, behavioral or psychophysiological reactions, then it is very likely that the message contained in the chemosignals is carried by high volatile molecules. However, if their effects are comparable to those obtained in their first use, then one could infer that the message is likely transmitted through low volatile molecules.

The current study's main goal was to examine whether the sweat samples collected in fear inducing and neutral contexts produce the same (or different) psychophysiological responses in a second application. To answer this question, we used the same sweat samples twice. The aim was to examine if the facial electromyography (fEMG) effects obtained the first time would be reproduced in the second use of the sweat samples. Following previous research (e.g., de Groot et al., 2014), we expected that the exposure to fear sweat (compared to neutral sweat) triggers a stronger activation of the *medial frontalis* and *corrugator supercilii*, at least in the first application of the sweat samples. Moreover, if re-using emotional sweat samples is a viable approach, then the fEMG activation patterns would be comparable across both applications of the sweat samples. Notably, the question regarding the re-use of fear sweat samples was of an exploratory nature, relying on no strong à priori hypotheses regarding the outcome of the results.

Method

Sweat Donors

Participants

Eight Caucasian Portuguese males aged between 21 and 35 (M_{Age} = 27.5 years; *SD* = 4.87) gave their informed consent and participated on a voluntary basis in two sweat collection sessions (fear and neutral-inducing sessions), each were separated by a week's interval. Participants were heterosexual, nonsmokers, not under any medication at the time of the collection and did not have any reported psychological or neurological disorders. Following previous guidelines regarding sweat collection (e.g., de Groot et al., 2015), only males were included as sweat donors because of their larger and more active apocrine glands than females (Zhou & Chen, 2009). Moreover, only heterosexual males were included as sweat donors because only female participants were recruited as sweat receivers (please see the sweat receivers' section) and females seem to evaluate homosexual and heterosexual male sweat differently (Martins et al., 2005).

All the procedures for the sweat collection were approved by the host institution ethics committee and were conducted in accordance with the standards of the American Psychological Association and the guidelines of the Declaration of Helsinki.

Materials

Emotion induction film clips. In order to induce a fearful state or an unemotional (which we label from here on as 'neutral') state necessary for the sweat collection sessions, we selected, on the basis of a pilot study (N = 38), a set of short clips retrieved from horror movies (fearful condition) and several nature/animal-related documentaries plus nature sceneries (unemotional condition which we label as 'neutral') (for more information about the source of the film clips, see appendix A). The results obtained in the pilot study revealed that participants exposed to the fearful clips (N = 20) reported (using a 0-10 visual analogue scale with the scale ends anchored as not at all [0] and very much [10]) to have experienced significatively more fear (M = 6.63; SD = 3.62) than participants exposed to the neutral clips (N = *18*; M = 1.03; SD = 1.70) [t(27.60) = 6.21; p < .001]. In line with this, participants exposed to the neutral clips also reported feeling significantly more neutral (M = 6.06; SD = 3.32) than participants exposed to the fear-inducing clips (M = 2.00; SD = 2.31) [t(36) = 4.42; p < .001].

Self-report questionnaires. Similar to the procedure employed by de Groot and colleagues (2015), sweat donors were asked to report - on 0 - 10 separated visual analogue scales - to what extent they felt angry, fearful, happy, sad, disgusted, neutral, surprised, calm, and amused during the sweat collection session.

Sweat production calculation. Sweat was collected using absorbent non-woven pads (70% viscose, 30% polyester; Wells, Sonae SA, Portugal). To determine the amount of sweat produced in each session, the pads were weighted using a *Precisa* scale (model: *BJ 100M*), with .001g precision. The sweat production was calculated by subtracting the weight of the pads after the sweat collection from the weight of the pad before the sweat collection session.

Procedure

As in previous studies (e.g., de Groot et al., 2015; Kamiloğlu et al., 2018; Zhou & Chen, 2009), participants were instructed to follow a strict set of instructions 48 hours prior to both sweat collection sessions (i.e., fear-inducing and neutral session). This was done to prevent possible sources of odor contamination. In the two days that preceded each sweat collection, participants were instructed to shave their armpits and were not allowed to consume alcohol, have sexual intercourse, consume odorous food (e.g., garlic, chili, pepper, onion), practice excessive exercise, sleep in the same bed as their partner or pet, and also from using any type of perfume or perfumed deodorants. Participants received fragrance-free personal care products (i.e., soap, shampoo, and deodorant), and were only allowed to use these as their personal care products during those two days. On the collection day, participants were not allowed to wear any personal care products, even the deodorant that we provided them. Moreover, two hours before each sweat collection, participants were instructed not to eat or drink anything other than water.

Immediately before the sweat collection took place, participants were instructed to rinse their armpits and dry them with paper towels. Then the experimenter, wearing latex gloves and using hypoallergenic tape, attached the pads to the participants' armpits. Before entering the collection room, participants were given a sterilized t-shirt and sweater which they had to wear during the collection. The temperature inside the collection room was kept between 23 and 25ºC.

Participants were then exposed to one of the two emotion induction film sets (i.e., fear or neutral). Each session lasted approximately 30-minutes. As in de Groot and colleagues (2015), film clips were presented from the least to the most intense to create a gradual buildup of emotional experience. At the end of each session, participants rated their feelings using separate 0-10 visual analog scales. Pads were then removed and frozen at -80ºC, separately in Ambar vials.

Fear inducing and neutral sweat collections were separated with a week's interval. After completing the two collections, participants were debriefed and received monetary compensation.

Statistical Analysis

Possible differences in room temperature and sweat production across the two sweat collection sessions (fear-inducing and neutral conditions) were examined using separated paired samples Student's t-tests.

As for the self-reported affect, and because the data did not present a normal distribution, separated non-parametric Wilcoxon tests were conducted to examine possible differences in these variables, across conditions.

The analyses were conducted using the IBM SPSS statistics (version 25.0; IBM Corp).

Sweat Receivers

Participants

Sixty-four female university students gave their informed consent and participated in the experiment on a voluntary basis. Four participants were excluded from the experiment due to psychiatric disorders, revealing ethnic backgrounds other than Caucasian, and a software error that resulted in a loss of the data. Thus, 30 participants from Utrecht University (the Netherlands), aged between 19 and 34 years (M_{Age} = 23.20 years; SD = 3.11), took part in the first sweat-sample use, and 30 participants from ISPA – Instituto Universitário (Portugal), aged between 19 and 35 years (M_{Age} = 23.93 years; SD = 5.32), were in the second use sweat-sample experiment. All participants were right-handed, Caucasian, nonsmokers, who reported no psychiatric or neurological disorders, no respiratory disease, and no illness, cold, or allergy. Moreover, participants were screened for severe olfactory impairments (i.e., anosmia). All participants appeared not to suffer from anosmia since they were able to clearly identify three odors: cinnamon, fish odor, and banana (see Lötsch et al., 2016).

Only females were recruited due to their higher sensitivity towards emotional signals and a better sense of smell compared to men (see de Groot et al., 2015; Zhou & Chen, 2009). Moreover, research has shown that women perceive male sweat differently as a function of both the donors' and their own sexual orientation (Martins et al., 2005). Therefore, only heterosexual women were included as sweat receivers.

Both the first and the second sweat-sample studies were approved by the host institutions ethics committees (Utrecht university and ISPA, respectively), and were conducted in accordance with American Psychological Association standards and the guidelines of the Declaration of Helsinki.

Design

The present study employed a 2 sweat conditions (fear vs. neutral; within-subjects factor) per 2 sweat applications (first vs. second use; between-subjects factor) design. Sweat conditions were presented in a counterbalanced order, and neither the participants nor the experimenter were aware of the conditions (i.e., double-blind experiment). Moreover, the first and second sweat application were separated by approximately a year's interval.

Materials and Measures

Composition of Sweat Stimuli. As in previous studies (e.g., de Groot et al., 2015; Kamiloğlu et al., 2018), in order to reduce the effects of interindividual variability in sweat production, pad pieces of four sweat donors were combined to create a "super-donor". While still frozen, each pad obtained from the sweat donors' armpits was cut into 8 equal parts. Using a randomization script, each final 'super-donor' sample consisted of four pad pieces (2 from the left and 2 from the right armpits), coming from 4 distinct sweat donors. Each sweat receiver was exposed to the same combination of sweat donors across the 2 sweat conditions. The 'super-donor' samples were prepared and coded by an independent researcher. Thus, the experimenter was completely blind to the sweat conditions during the experiment.

Facial Electromyography (fEMG). Ag-AgCl EMG electrodes were bipolarly applied to the left *corrugator supercilii* and *medial frontalis*, two muscles involved in displaying fearful facial expressions (see Fridlund & Cacioppo, 1986). Only the facial left side was monitored because it seems to display stronger affective reactions (compared to the right facial side) in right-handed participants (see Dimberg & Petterson, 2000). The goal of the fEMG responses was to compare the activity of the two muscles across the two sweat conditions, in the two sweat applications.

EMG signal was collected using a Bionex 8-channel chassis, powered by the Biolab (first sweat application: version: 3.0.0; second sweat application: version 3.2.0; MindWare Technologies, Gahanna, OH). During the data collection, the signal was online filtered using a 20-200Hz bandpass filter. Before analyzing the data, the fEMG signal was also rectified and smoothed with a 20 Hz low-pass filter using the software EMG Analysis (for both sweat applications version 3.1.5; MindWare Technologies, Gahanna, OH).

Handedness Questionnaire. In order to control for possible effects of handedness on EMG data (see Dimberg & Petterson, 2000), as well as to confirm that all participants were, in fact, right-handed, a handedness questionnaire (see Williams, 1986) was used.

Sweat Ratings. Participants were asked to rate, in a counterbalanced order, the hedonic value (pleasantness) and intensity of the sweat samples that they were exposed to during the experiment on 7 points Likert scales. The scale ends were anchored with 'very weak' (1) and 'very strong' (7) in the case of intensity, and with 'very unpleasant' (1) and 'very pleasant' (7) in the case of pleasantness.

Sweat discrimination. Participants performed a two-alternative forced-choice reminder task (de Groot et al., 2014) to evaluate their ability to discriminate between sweat sample conditions (fear and neutral) that were used in the experiment.

Procedure

The procedure was replicated for the two odor uses, with the odor being conserved from the first to the second use at -80ºC in amber vials. The sweat samples were transported from Portugal to the Netherlands, and then back to Portugal in dry ice. The first and the second sweat application were separated by a year interval (see figure 1 for a general flowchart of the procedure). Moreover, all data collection sessions were conducted by female experimenters to avoid mood changes in the female participants that the presence of a male experimenter could induce (see Jacob et al., 2001).

Each data collection session began by thawing the sweat samples an hour and half prior to the start of the experiment. After entering the lab, participants were briefly given instructions about the experiment and the task, plus the fEMG devices, that would be used. Then, participants were instructed to fill in a socio-demographic questionnaire with some personal information. The experimenter began by cleaning the skin on the left side of the participant’s face and applying fEMG electrodes on the *medial frontalis* and *corrugator supercilii* muscles. Following the fEMG setup, participants were then given instructions via a computerized task, as those used in Kamiloğlu and colleagues (2018). This was for replication purposes and the collected data were unrelated to the goal of the present study, being our main focus the fEMG activity. Next, participants filled out a handedness questionnaire while the experimenter put the first vial (containing either a fear or a neutral sweat sample in a counterbalanced order) in a vial holder (flexible claw). Then participants were instructed to place their head on a chin rest, and the vial holder was adjusted such that the vial with the sweat sample was 2 cm below the participant’s nostrils. After a brief practice phase that allowed participant to get familiar with the task, and before starting the experimental task, the participants’ nostrils were closed with a nose clip and they were told to direct their gaze at the fixation cross on the screen. The vial with the sweat samples was opened and immediately after starting the experimental task, the experimenter also removed the nose clip. The experiment began with a fixation cross that remained on the screen for 5 seconds and then the computerized task proceeded. When the first block was completed, the experimenter changed the vial and placed the second one containing either a fear or a neutral-related sweat sample (counterbalanced). After a mandatory break of 5 minutes, the procedure for the experimental task was repeated for the remaining odor condition.

At the end of the task (two blocks), fEMG electrodes were removed, and the participants were asked to rate the hedonic value (pleasantness) and intensity of the sweat samples. Then participants’ absence of severe olfactory impairments (Lötsch et al., 2016) and their capacity to discriminate between sweat conditions were assessed. At the end of the experimental procedure, participants were debriefed about the study’s main goals and received a monetary compensation.

Each data collection session lasted 60 minutes - 15 minutes of facial preparation and fEMG electrodes placement, and 40 minutes of experiment with a mandatory 5-minute pause between sweat conditions. Each vial remained opened for 20 minutes.

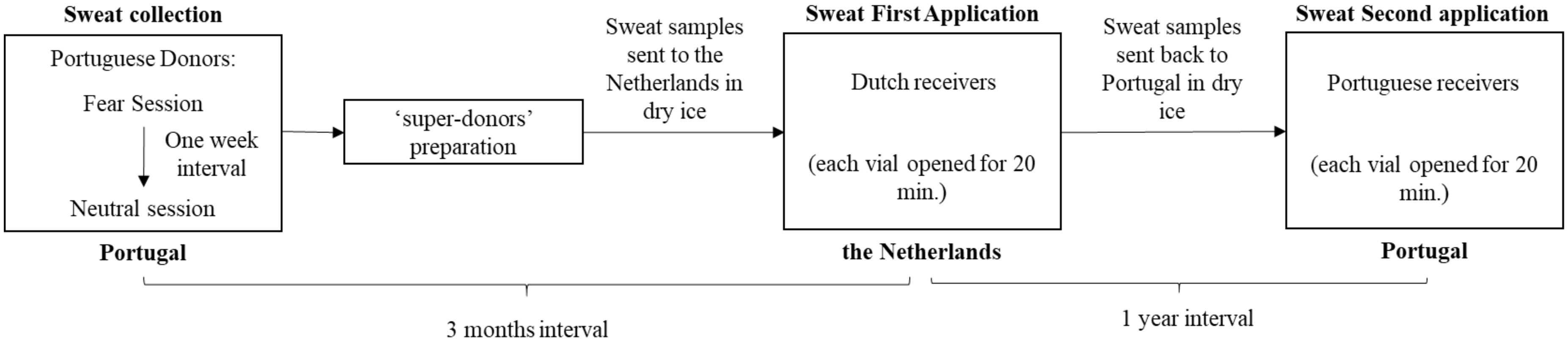

Figure 1: Flowchart of the general experimental procedure, from the sweat collection to the first and then the second sweat application. The respective time intervals between the different phases, as well as the countries where they occurred, are identified.

Data Preparation

Although the fEMG signal was continuously collected during the experiment, only the first 4.6 seconds after the sweat exposure were extracted and analyzed. Firstly, the fEMG data were checked for artifacts in intervals of 50ms. For each participant, each muscle and odor condition, values higher than 2.5 median absolute deviation (MAD) units (Leys et al., 2013) were marked as artifacts. Then, using participants' facial video recordings, the identified artifacts were visually inspected to ensure that they were associated with a non-odor related movement (e.g., sneezing). If such was observed, then these artifacts were removed from the signal, otherwise, they remained untouched. Missing data removed due to artifacts were linearly interpolated, using the R package '*Zoo*' (Zeileis & Grothendieck, 2005) (for information regarding the mean percentage of interpolated data per participant, see Appendix B).

Following earlier studies (e.g., Kamiloğlu et al., 2018), fEMG data were then averaged in 200ms intervals: the first 3 intervals (600 ms) constituted the baseline (since the typical first sniff starts at around 400ms; see Kamiloğlu et al., 2018; Sela & Sobel, 2010); the remaining 20 intervals (4 seconds) constituted the target signal. In sum, the first 600 ms of collected signal represented the baseline period and the next 4 second the test period. As in previous studies (e.g., Kamiloğlu et al., 2018), prior to the analysis, fEMG data were screened for outliers (within variable, i.e., the 23 200ms intervals), defined as values exceeding (below or above) 2.5 median absolute deviation (MAD) units (Leys et al., 2013). Participants with percentages of outlier data above 75% were excluded from the final analysis [(number of excluded participants in the sweat first use: fear condition *medial frontalis* = 1; fear condition *corrugator supercilii* = 3; neutral condition *medial frontalis* = 2; neutral condition *corrugator supercilii* = 3); (number of excluded participants in the sweat second use: fear condition *medial frontalis* = 4; fear condition *corrugator supercilii* = 2; neutral condition *medial frontalis* = 4; neutral condition *corrugator supercilii* = 2)]. As in previous studies (e.g., Kamiloğlu et al., 2018), missing data due to outlier-based removal were altered to be one unit above the next extreme score on that variable (see Field, 2013) (for more information regarding the mean percentage of altered data per participant, see Appendix C).

fEMG data analysis was based on baseline-corrected data, obtained by subtracting from each 200ms segment the mean activity of the corresponding muscle's baseline.

Statistical Analysis

Regarding the fEMG data[1], our aim was to examine whether exposure to fear sweat samples (compared to neutral sweat samples) induces higher activity in the facial muscles involved in fearful facial expressions (i.e., *the medial frontalis* and the *corrugator supercilii*), in both the first and second use of the same sweat samples. Thus – after a visual inspection of the residual plots that did not reveal any severe violation of the homoscedasticity or normality assumptions – two separate linear mix models (LMM; one for each muscle) were conducted including the subjects ID as a clustering factor, the muscle activation as the dependent variable, linear and quadratic time (i.e., 20 200ms time intervals) as continuous independent variables, and the sweat application (1st vs. 2nd use; between subjects) and the sweat condition (i.e., fear vs. neutral sweat samples; within-subjects) as predictors to the model. In order to estimate the linear trend of time and to ease the parameter interpretation, the variable time was centered. As fixed effects in the model, we consider the sweat use, the sweat condition, the linear and quadratic time, as well as their 2-way and 3-way interactions. The quadratic effect of time was considered because: (a) a visual inspection suggested that a quadratic trend provided a better fit to the data pattern, which had also been seen in earlier studies (see for instance, Kamiloğlu et al., 2018 figure 3); (b) a combination of linear and quadratic effects of time allows to uncover not only the general increment of the muscles activation over time (i.e., the linear effect), but also the pattern of this increment (i.e., the quadratic effect). As the quadratic effect of time proved to be significant (for both the *medial frontalis* and *corrugator supercilii*), it was retained in the models.

As random effects, we considered random intercepts per subject, as well as by subject random slopes for the sweat condition, linear time, and their interaction. Following Little and colleagues (2000), any parameter with variance greater than 0 was left as random. Moreover, the model was estimated using restricted maximum likelihood, and a Satterthwaite approximation of the degrees of freedom was considered (see West, 2009). The LMM analyses were performed using the GAMLj module (Gallucci, 2019) implemented with the jamovi software (The jamovi project, 2019).

To examine possible differences in the perceived hedonic value (pleasantness) and intensity of the sweat samples, two separate (one for the intensity and the other for the

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[1] Regarding the fEMG activity, we changed the pre-registered analysis plan. Instead of the planned repeated measures ANOVAs, we decided to use linear mixed models, which have been demonstrably advantageous in analysing physiological data (e.g., Wolfinger, 1997). These advantages include, for instance, the possibility to treat time as a continuous variable, add a quadratic description of non-linear changes over time, and also to deal with individual variability across time (see Krueger & Tian, 2004).

pleasantness), mixed 2x2 ANOVAs factorial design were conducted. Sweat condition (fear vs. neutral sweat) was entered as the within-subjects factor and sweat application (first vs. second use) was entered as the between-subjects factor. Finally, one-sample Wilcoxon signed-rank tests were used to evaluate whether the participants were able to discriminate between sweat conditions. These analyses were conducted using the IBM SPSS statistics (version 25.0; IBM Corp).

Results

Sweat Donors

Concerning the self-reported questionnaires, the non-parametric Wilcoxon signed-ranks test revealed that participants reported, as expected, more fear (*N = 8*; *Z* = -2.37; *p* =.016) in the fear condition (*Mdn* = 3.60; *IQR* = 2.15 – 5.2) than in neutral condition (*Mdn* = .05; *IQR* = .00 – 0.35). Regarding calmness, more calmness (*N = 8*; *Z* = -2.37; *p* =.016) was reported in the neutral condition (*Mdn* = 9.60; *IQR* = 7.25 – 10.00) than the fear condition (*Mdn* = 3.65; *IQR* = 1.85 – 4.68), pointing to a successful emotional manipulation during the sweat collection sessions. Furthermore, the results showed statistically significant differences in reported happiness (*N = 8*; *Z* = -2.20; *p* =.031), with more happiness reported in the neutral condition (*Mdn* = 6.35; *IQR* = 4.98 – 7.98) than in the fear condition (*Mdn* = 5.50; *IQR* = 3.93 – 6.75). Surprisingly, no statistically significant differences were observed in the reported neutral affect between the fear (*Mdn* = 4.85; *IQR* = 4.10 – 5.13) and the neutral (*Mdn* = 5.00; *IQR* = 4.63 – 5.20) conditions (*N = 8*; *Z* = -.28; *p* = .811). Moreover, no statistically significant differences were observed between conditions in the reported anger (*N = 8*; *Z* = -.73; *p* = .625), disgust (*N = 8*; *Z* = -1.75; *p* = .130), sadness (*N = 8*; *Z* = -1.38; *p* = .203), surprise (*N = 8*; *Z* = -1.02; *p* =.359), and amusement (*N = 8*; *Z* = -1.01; *p* =.380). Figure 2 provides an overview of the self-reported affect.

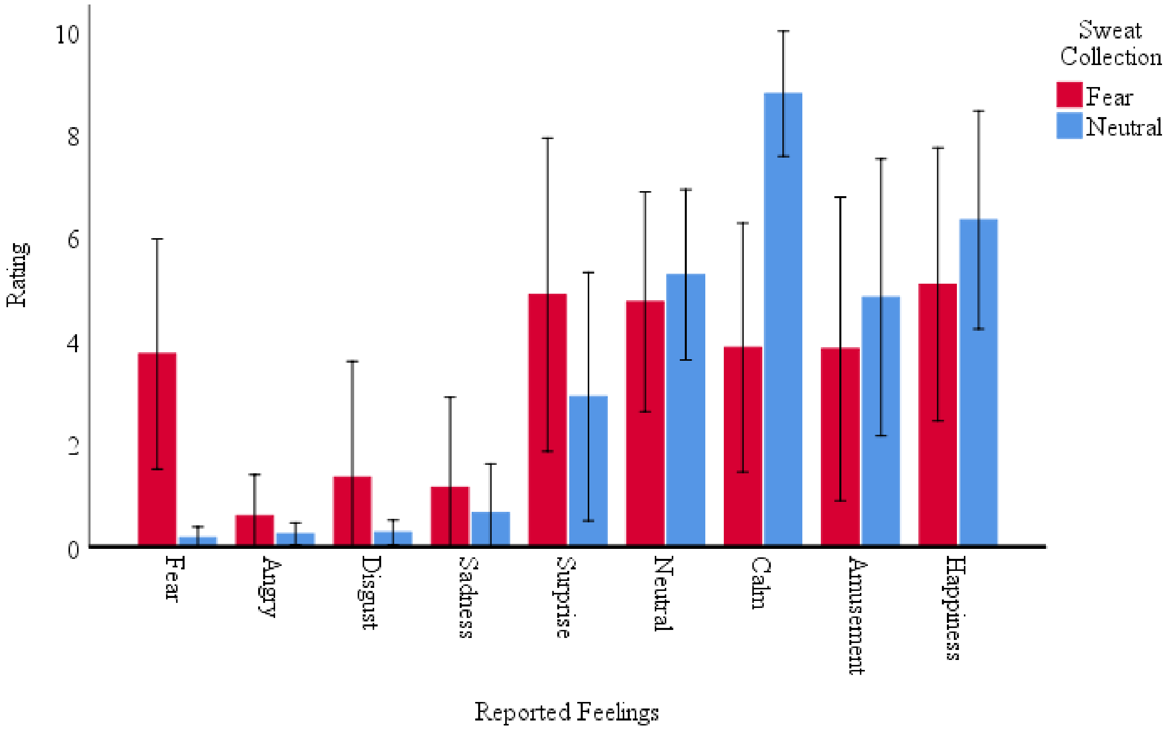

Figure 2: Mean reported feelings by sweat donors, per sweat collection. Error bars represent 95% within- subjects confidence intervals.

Regarding the sweat production, a paired samples Student’s t-test evidenced that participants in the fear condition (*M* = .06g; *SD* = .05) produced significatively more sweat [*t*(7) = 2.56; *p* = .038] than in the neutral condition (*M* = .01g; *SD* = .01) (see figure 3), suggesting that the emotional manipulation influenced participant’s sweat production. Additionally, considering the room temperature (in Celsius), a paired samples Student’s t-test revealed no statistically significant differences [t(7) = 1.16; p = .285] between the fear (*M* = 24.05; *SD* = .76) and the neutral conditions (*M* = 24.13; *SD* = .64), ruling out the role of temperature in the differences observed in the sweat production.

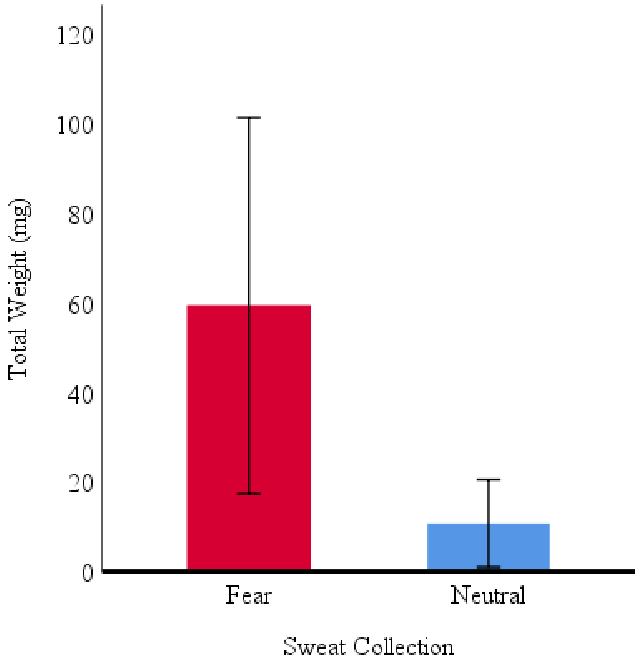

Figure 3: Mean sweat production, in milligrams, per sweat collection. Error bars represent 95% within-subjects confidence intervals.

Taken together, the results obtained from the sweat donors (*N* = 8) suggest a successful emotion manipulation during sweat collection. Although the subjective fear ratings, in the fear condition, are low, not exceeding the rating of neutral emotion, calmness, surprise, amusement, and happiness (as can be seen in figure 2), the fear rating remains significantly higher than the fear ratings for the neutral condition. Additionally, the differences observed in sweat production – an objective measure – shows that the emotional manipulation modulated participants perspiration. In line with previous research (see de Groot et al., 2015) more sweat was produced during the fear than neutral condition. The observed low fear rating might be explained by a social desirability. Due to cultural factors men tend to report lower levels of fear (e.g., Spiegler & Liebert, 1970). However, as no social desirability measure was used, no strong conclusions can be made.

Sweat Receivers

fEMG

Medial frontalis muscle. The LMM analysis ($R^2_{marginal} = .05$; $R^2_{conditional} = .60$) revealed a significant main effect of the sweat condition (*B* = -.07; *F*(1, 60.9) = 4.89; *p* = .031; *95% CI* [-.131; -.008]), suggesting that, overall, the fear sweat (*M* = .13μV; *SE* = .03) activates the *medial frontalis* muscle more than the neutral sweat ($M = .06\mu V$; $SE = .03$). Moreover, a significant interaction between the sweat condition with linear time was also revealed ($B = -.01$; $F(1, 53.3) = 4.24$; $p = .044$; *95% CI* [-.012; $-2.88*10^{-4}$]), indicating that the activation of the medial frontalis diverges between sweat conditions over time for the two sweat applications (see figure 4). These results are in accordance with previous studies (e.g., de Groot et al., 2012, 2014, 2015; Kamiloğlu et al., 2018), showing that the exposure to sweat produced under fear states results in a higher activation (compared with the exposure to neutral sweat) of *medial frontalis* - one of the facial muscles involved in the fear facial expression (see Fridlund & Cacioppo, 1986).

Notably, the LMM showed no main effect of sweat application ($B = .03$; $F(1, 57.7) = .34$; $p = .560$; *95% CI* [-.065; .121]), no interaction between sweat application and sweat condition ($B = .03$; $F(1, 60.9) = .30$; $p = .583$; *95% CI* [-.088; .158]), no interaction between sweat application, sweat condition, and linear time ($B = 4.64*10^{-3}$; $F(1, 53.3) = .65$; $p = .425$; *95% CI* [-.007; .016])], and no interaction between sweat application, sweat condition and quadratic time ($B = -4.72*10^{-4}$; $F(1, 1948.4) = .74$; $p = .390$; *95% CI* [-.002; $6.05*10^{-4}$]). These results indicate that there are no significant differences between the first and second use of the sweat samples, pointing to the reliability of re-using sweat samples, at least a second time[2].

Additionally, although not relevant to test our hypothesis, there was also a significant main effect of linear ($B = 4.91*10^{-3}$; $F(1, 53.9) = 7.23$; $p = .010$; *95% CI* [.001; .008]) and quadratic time ($B = -6.37*10^{-4}$; $F(1, 1948.4) = 21.51$; $p < .001$; *95% CI* [$-9.06*10^{-4}$; $-3.68*10^{-4}$]), and also significant interaction of sweat application per linear time ($B = .01$; $F(1, 53.9) = 12.41$; $p < .001$; *95% CI* [.006; .020]). Moreover, there was no interaction between sweat application and quadratic time ($B = 5.23*10^{-4}$; $F(1, 1948.4) = 3.62$; $p = .057$; *95% CI* [$-1.59*10^{-}$

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[2] To further support the observed non-significant differences between sweat applications, a log-likelihood ratio test (LRT) comparing the reported model with a model without the 3-way interactions was conducted, and the variance explained by each model was inspected ($R^2_{Conditional}$). The LRT revealed that no significant differences between the two models [$X^2(2) = 1.41$, $p = .495$], and the $R^2_{Conditional}$ for the two models were the same: .60. Hence, the variance explained by the two 3-way interactions is apparently very small, providing further evidence - beyond the already reported p-values – for the absence of differences between sweat applications.

^{5}; .001]), and no interaction between sweat condition and quadratic time (B = -2.25*10^{-4}; F(1, 1948.4) = .67; p = .412; *95% CI* [-7.64*10^{-4}; 3.13*10^{-4}]).

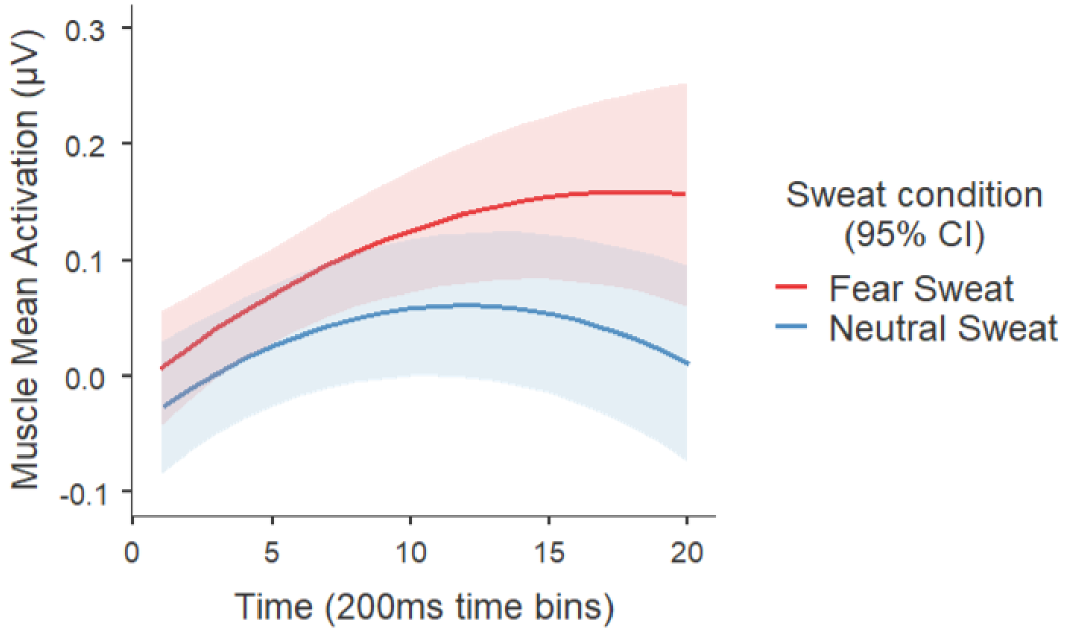

Figure 4: Mean activation of the *medial frontalis in microvolts (µV),* per sweat condition, across sweat applications. Each time point represents a 200ms time bin. The shaded area represents 95 % confidence intervals.

Corrugator supercilii muscle. The LMM analysis ($R^2_{marginal}$ = .15; $R^2_{conditional}$ = .78) revealed a significant main effect of the sweat condition (B = -.30; F(1, 55.7) = 10.23; p = .002; *95% CI* [-.484; -.116]), with an overall stronger activation of this muscle when participants were exposed to fear (M = .49µV; SE = .09) than to neutral sweat (M = .19µV; SE = .05). Furthermore, a significant interaction between sweat condition and linear time was also found (B = -.02; F(1, 54.7) = 6.45; p = .014; *95% CI* [-.034; -.004]), suggesting that the activation of the *corrugator supercilii* diverges between sweat conditions, over time, across sweat applications (see figure 5). Once again, and in accordance with previous studies (e.g., de Groot et al., 2014; Kamiloğlu et al., 2018), these results showed that the exposure to fear sweat (compared to the exposure to neutral sweat) results in a stronger activation of the *corrugator supercilii* – another muscle related with the facial expression of fear (see Fridlund & Cacioppo, 1986).

Moreover, although a significant main effect of sweat application was revealed (B = .40; F(1, 57.2) = 13.13; p < .001; *95% CI* [.182; .609]), there was neither a significant interaction between sweat condition and sweat application (B = -.37; F(1, 55.7) = 3.97; p = .051; *95% CI*

[-.742; -.006]), nor a significant interaction between sweat application, sweat condition, and linear time (*B* = $1.07*10^{-3}$; *F*(1, 54.7) = .01; *p* = .943; *95% CI* [-.028; .030]). These results seems to indicate that, even though the two sweat applications had different overall activations [first use: *M* = .14µV; *SE* = .08; second use: *M* = .54µV; *SE* = .08], the linear data trend did not differ across the two sweat use conditions, suggesting, once again, that it is reliable to use sweat samples a second time[3]. However, a significant interaction between sweat application, sweat condition, and quadratic time was showed (*B* = $3.56*10^{-3}$; *F*(1, 1976) = 12.57; *p* < .001; *95% CI* [.002; .006]), indicating that the quadratic data trend may vary between sweat applications (see figure 4). Possible explanations for the observed differences in the corrugator activity between sweat applications are explored in the discussion section.

Furthermore, and again not directed towards our hypotheses, we observed a significant main effect of linear (*B* = .02; *F*(1, 56.4) = 20.76; *p* < .001; *95% CI* [.013; .033]) and quadratic time (*B* = $-9.90*10^{-4}$; *F*(1, 1976) = 15.53; *p* < .001; *95% CI* [-.001; -4.98e-4]), and also significant interactions between sweat condition and quadratic time (*B* = $1.55*10^{-3}$; *F*(1, 1976) = 9.48; *p* = .002; *95% CI* [$5.63*10^{-4}$; .003]), sweat application and linear time (*B* = .03; *F*(1, 56.4) = 11.66; *p* < .001; *95% CI* [.015; .054]), and sweat application and quadratic time (*B* = -$1.23*10^{-3}$; *F*(1, 1976) = 6.01; *p* = .014; *95% CI* [-.002; $-2.47*10^{-4}$]).

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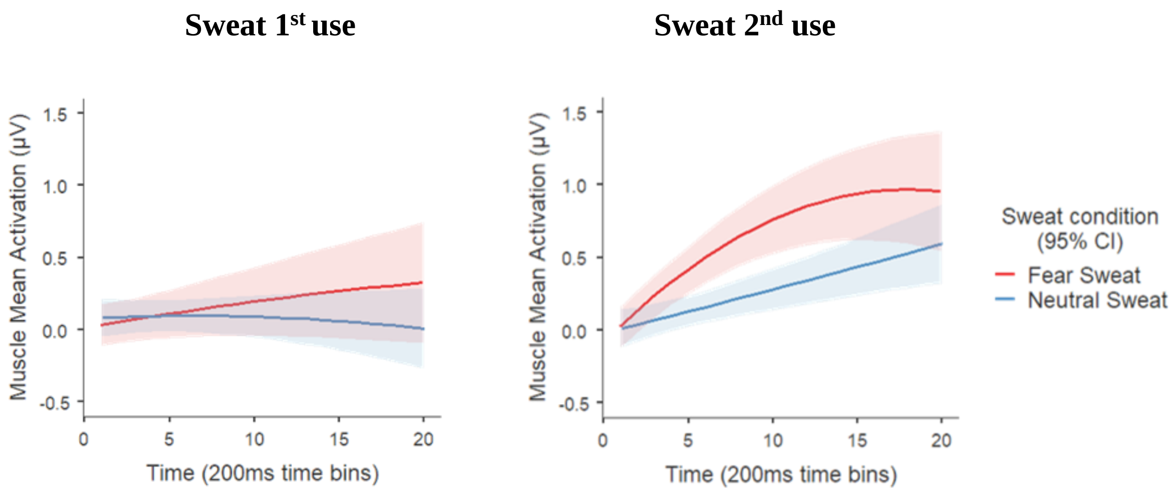
[3] Once again, to further support the observed non-significant differences between sweat applications, a log-likelihood ratio test (LRT) comparing the reported model with a model without the non-significant 3-way interaction was conducted, and the variance explained by each model were inspected ($R^2_{Conditional}$). The LRT test revealed no significant differences between the models with and without the 3-way interaction [$X^2(1)$ =.006, *p* = .938]. Moreover, the $R^2_{Conditional}$ for the two models was the same: .78. Hence, the variance explained by the 3-way interaction seems to be very small, providing further evidence for the absence of differences between sweat applications regarding the linear effect of time.


Sweat 1st use

Sweat 2nd use

Figure 5: Mean activation of the *corrugator supercilii in microvolts (µV)*, per sweat condition and sweat application. Each time point represents a 200ms time bin. The shaded area represents 95 % confidence intervals.

Sweat ratings

Concerning the perceived intensity of sweat, results showed no significant main effect for the sweat condition [*F*(1, 58) = .87; *p* = .354], no significant main effect for sweat use condition [*F*(1, 58) = 3.60; *p* = .063], and also no interaction between sweat condition and sweat use [*F*(1, 58) = .02; *p* = .877]. In sum, these results indicate that, participants did not perceive a difference in sweat intensity across sweat conditions or sweat administration.

Similarly, regarding perceived pleasantness the results revealed no significant main effect of the sweat condition [*F*(1, 58) = .04; *p* = .842], and no significant interaction between the sweat application and the sweat condition [*F*(1, 58) = .64; *p* = .427]. However, a main effect of the sweat application [*F*(1, 58) = 17.63; *p* = .018] was found, with the sweat samples - regardless the sweat condition - were rated as more pleasant in the second (*M* = 4.32; *SE* = .22) compared to the first use (*M* = 3.55; *SE* = .22). Thus, these results show that no difference in pleasantness was consciously perceived between sweat conditions in both sweat use conditions. However, from the first to the second use the perceived pleasantness seems to have increased (see table 1).

Table 1: Means and standard deviations (in parenthesis) of the subjective ratings of the sweat stimuli

	Fear Sweat				Neutral Sweat			
	First Application		Second Application		First Application		Second Application	
Subjective ratings of stimuli								
Intensity (1 = very weak to 7 = very strong)	2.90	(1.30)	2.37	(1.67)	2.73	(1.46)	2.13	(1.22)
Pleasantness (1 = very unpleasant to 7 = very pleasant)	3.60	(1.30)	4.23	(1.50)	3.50	(1.11)	4.40	(1.57)

Moreover, when both intensity and pleasantness were entered to the two separate LMMs as control covariates, the interpretation of the results remained the same. Table 2 provides an overview of the principal main effects and interactions after entering the aforementioned covariates in the model.

Table 2: Principal main effects and interactions after entering the intensity and pleasantness as covariates in the LMMs

	Medial Frontalis			Corrugator Supercilii		
	B	***F***	***p***	***B***	***F***	***p***
Effect						
Sweat Application	.02	.14	.707	.42	14.60	< .001
Sweat Condition	-.07	5.26	.025	-.30	10.04	.003
Sweat Condition*Time	-.01	4.28	.043	-.02	6.40	.014
Sweat Application*Sweat Condition	.03	.25	.618	-.37	3.93	.052
Sweat Application*Sweat Condition*Time	$4.62*10^{-3}$	.64	.428	$7.74*10^{-4}$	$2.68*10^{-3}$	.959
Sweat Application*Sweat Condition*Time²	$-4.72*10^{-4}$	.74	.391	$3.56*10^{-3}$	12.57	< .001

Sweat discrimination

Regarding the first sweat use, a one-sample Wilcoxon signed-rank test revealed that participants were successful in discriminating both the neutral (from the fear) sweat when this was presented as reference sweat (*median under the null hypothesis* = .50; $N = 30$; $Z = 2.67$, $p = .008$), and the fear (from the neutral) sweat when fear sweat was presented as reference (*median under the null hypothesis* = .50; $N = 30$; $Z = 2.00$, $p = .046$).

As far as the second sweat application is concerned, the results also evidenced that participants were able to discriminate the neutral (from the fear) sweat sample (when presented as reference)(*median under the null hypothesis* = .50; $N = 30$; $Z= 2.67$, $p = .008$), but not the fear (from the neutral) sweat sample (when this sample was presented as reference) (*median under the null hypothesis* = .50; $N = 30$; $Z = .89$, $p = .371$).

Discussion

The aim of the research reported in this paper was to test whether sweat samples (i.e., fear and neutral) obtained from donors can be reliably used on two separate occasions. We compared psychophysiological responses (i.e., fEMG) obtained across two administrations of the same odors (fear vs neutral) with a year's interval. The results of the study showed that, in both the first and the second administration of the sweat samples, the exposure to fear sweat (compared to neutral sweat) triggered a significantly higher activation of the facial muscles involved in the fear facial expression (i.e., the *medial frontalis* and the *corrugator supercilii*; Fridlund & Cacioppo, 1986). Furthermore, the perceived intensity and pleasantness between the sweat samples revealed no differences within each of the two applications of the sweat samples, ruling out the possibility that either dimension could have contributed to the observed distinct fEMG activation patterns between the fear and neutral sweat conditions (e.g., Kamiloğlu et al., 2018). This set of results show that it is reliable to re-use sweat samples collected in emotion contexts, at least a second time.

The conclusions presented here have a number of relevant implications for research on human chemosignals produced under emotional conditions. Being able to use the same sweat sample twice: (1) reduces the amount of sweat required to run a study; (2) reduces expenses; (3) facilitates possible replication studies (even across labs); (4) allows researchers to conduct studies with larger sample sizes, thus limiting potential criticisms of sample sizes used in research with chemosignals (for a similar argument see Lenochova et al., 2009).

The robustness of re-using sweat samples becomes even more remarkable when one considers that the sweat samples were collected from Portuguese donors and then sent to the Netherlands where they were first used. In this case, the receivers were Dutch. The sweat samples were then sent back to Portugal, where they remained frozen at -80 ºC for a year before the second application of the sweat took place. This time, however, the receivers were Portuguese (see methods section). The second application produced comparable fEMG findings suggesting that the emotional information carriers in the sweat were not lost, despite a year's interval between the two applications.

The only difference between the first and second applications was observed in the case of the *corrugator supercilii* activity. There was an overall stronger muscle activation in the second compared to the first sweat application, along with a distinct quadratic time data trend. Thus, although the data pattern was similar, some differences were observed between the two applications. It is difficult to interpret this difference, since there are multiple possible contributors to the observed difference between the two applications. The equipment was identical in both studies. A speculative account can be that the difference between the first and second applications may have resulted from potential cultural differences between sweat donors and receivers. It is hypothetically possible that the Portuguese frown more in general and the sweat sample, therefore, leads to a stronger *corrugator supercilii* response in the Portuguese sample than the Dutch sample. It is possible that the sweat from Portuguese donors may be more familiar to Portuguese than to Dutch receivers, which might have increased the pleasantness ratings of the sweat (for a relation between repeatedly exposure to odor and increased pleasantness see Delplanque et al., 2009), and also the *corrugator supercilii* activity. But this remains mere speculation. On the other hand, and considering that the sweat samples (regardless the sweat condition) were rated as more pleasant in the second compared to the first application, it is also possible that the reuse of the samples, their shipping, and/or the one-year storage may have changed some of the chemical properties of the samples. Consequently, these possible changes may have induced the stronger *corrugator supercilii* activation observed in their second application. Hence, it is important to note that we are not claiming that our results show that the chemical composition of the sweat samples remained unchanged between applications. Instead, our argument is that, despite possible chemical changes in the sweat samples, the chemicals responsible for the fear signal were preserved across applications.

The findings of our research provide also some cues about the properties of the emotional sweat samples. To date, few attempts have been made to unravel the chemical properties of human sweat (e.g., Penn et al., 2007; Smeets et al., 2020). Consequently, what we know about sweat volatiles that carry emotional information is limited. In a recent study, de Groot and Colleagues (2020) evidenced that fear sweat emits a higher quantity of volatiles than neutral sweat. However, the quantity of volatiles emitted significantly decayed in a second application of the same sweat samples (see de Groot et al., 2020). The data from the aforementioned study, together with our results, seems to suggest that, although the quantity of volatiles is reduced in a second application of the same sweat samples, the chemical compounds communicating fear information were preserved. Moreover, as we already mentioned in the introduction, high volatile molecules are known to spread faster than low volatile molecules, conveying their information to distant locations. In contrast, low volatile molecules remain at the same location for longer periods of time, retaining their 'message' (see Pause, 2017; Pause et al., 1997). The fact that the two emotional sweat sample applications induced the same psychophysiological reactions across time (one year) and location (Utrecht and Lisbon) indicates that the volatiles preserved the relevant information. This suggests that low volatile molecules are the more likely carriers of the emotional information. It is then hypothetically possible that the decrease in the quantity of volatiles' from a first to a second application of the same sweat samples, observed by de Groot and colleagues (2020), has been related with high volatile molecules – which are likely to be the first ones dissipating. The molecules that remained from the first to the second sweat application – i.e., the low volatile compounds – may have continued to carry the fear-related information to their receivers, resulting in the comparable fEMG activation patterns observed in our study.

Nevertheless, it is important not to forget that de Groot et al. (2020) quantified the sweat volatiles that were released by a continuous flow olfactometer, which is inherently different from the sweat delivery method used in our study - sweat was sampled with pads which were then put in vials and presented to receiver participants. It is, therefore, possible that the different delivery methodologies have affected the outcome of the studies – the continuous airflow in the olfactometer, in de Groot et al (2020), could have diluted the sweat stimulus to a greater extent (compared with the delivery method used in our study), reducing the quantity of volatiles available in the second application. Further research is required to assess whether our findings generalize to alternative delivery methods (e.g., an olfactometer; Lundström et al., 2010).

A final consideration that might prove relevant and perhaps limit the scope of our conclusions is that our senders and receivers were males and females respectively. Although this procedure is common to most studies(e.g., de Groot et al., 2012, 2014, 2015; Kamiloğlu et al., 2018), it is nonetheless a variable that requires addressing.

Lastly, Smeets and colleagues (2020) recently took the first step in uncovering the chemical fingerprint of fear sweat. In their work, the authors showed that the fear and the neutral sweat have distinct chemical signatures, providing a list of candidate chemical classes associated with emotional sweat. Considering our results, together with the findings from de Groot et al (2020), future chemical analyses could benefit from using sweat after it has been used once – compounds that are not strictly necessary to communicate fear through olfaction may dissipate in a first application of the sweat samples, reducing the noise in chemical analyses using second application sweat samples.

In conclusion, we have been able to show that re-using fear (and neutral) sweat samples is feasible as they induce similar fEMG activity in their receivers across a first and second application. To our knowledge, this is the first study that approaches this issue which aside from practical implications for future research with human chemosignals, raises potentially interesting questions regarding the chemical properties of emotion-inducing human odors. Are the carriers of emotion-related information in human odors high or low volatiles? The tentative direction our research suggests is that low volatiles carry emotion relevant information.

Appendix A. Information about the source of the selected film clips

For the fear-inducing condition, the clips were selected from the following terror films: *The Nun* (04 min 54 s), *Mamma* (07 min 40 s), *Sinister* (02 min 07 s), *The Descent* (02 min 41 s), *The Grudge* (02 min 10 s), *REC 1* (02 min 53 s), *Insidious* (04 min 55 s), and *A Tale of Two Sisters* (07 min 30 s).

Regarding the neutral condition, the clips were part of the documentaries *Solar eclipse* (02 min 37 s), *The Secret Life of Birds* (04 min 25 s), *The Transit of Venus* (03 min 02 s), *Equator: Battle for the light* (02 min 12 s), *Do we need the moon?* (02 min 09 s), *Discovery decade* (01 min 42 s), *Portugal Earth* (03 min 08 s), *Wooly mammoth* (03 min 36 s), and nature sceneries retrieved from YouTube (11min 40 s).

Appendix B. Mean percentage of interpolated data per participant

Sweat first use: fear condition *medial frontalis* = 4.07%; fear condition *corrugator supercilii* = 6.83%; neutral condition *medial frontalis* = 6.27%; neutral condition *corrugator supercilii* = 6.37%.

Sweat second use: fear condition *medial frontalis* = 4.02%; fear condition *corrugator supercilii* = 6.01%; neutral condition *medial frontalis* = 4.96%; neutral condition *corrugator supercilii* = 6.38%.

Appendix C. Mean percentage of altered outlier data per participant

Sweat first use: fear condition *medial frontalis* = 10.34%; fear condition *corrugator supercilii* = 3.56%; neutral condition *medial frontalis* = 9.14%; neutral condition *corrugator supercilii* = 5.19%.

Sweat second use: fear condition *medial frontalis* = 11.71%; fear condition *corrugator supercilii* = 11.18%; neutral condition *medial frontalis* = 7.86%; neutral condition *corrugator supercilii* = 9.63%.

References

Chen, D., Katdare, A., & Lucas, N. (2006). Chemosignals of fear enhance cognitive performance in humans. *Chemical Senses*, *31*(5), 415–423. https://doi.org/10.1093/chemse/bjj046

de Groot, J. H. B., Kirk, P. A., & Gottfried, J. A. (2020). Encoding fear intensity in human sweat. *Philosophical Transactions B*, *20190271*. https://doi.org/http://dx.doi.org/10.1098/rstb.2019.0271

de Groot, J. H. B., Semin, G. R., & Smeets, M. A. M. (2014). I can see, hear, and smell your fear: comparing olfactory and audiovisual media in fear communication. *Journal of Experimental Psychology. General*, *143*(2), 825–834. https://doi.org/10.1037/a0033731

de Groot, J. H. B., Semin, G. R., & Smeets, M. A. M. (2017). On the Communicative Function of Body Odors: A Theoretical Integration and Review. *Perspectives on Psychological Science*, *12*(2), 306–324. https://doi.org/10.1177/1745691616676599

de Groot, J. H. B., Smeets, M. A. M., Kaldewaij, A., Duijndam, M. J. a, & Semin, G. R. (2012). Chemosignals communicate human emotions. *Psychological Science*, *23*(11), 1417–1424. https://doi.org/10.1177/0956797612445317

de Groot, J. H. B., Smeets, M. A. M., Rowson, M. J., Bulsing, P. J., Blonk, C. G., Wilkinson, J. E., & Semin, G. R. (2015). A Sniff of Happiness. *Psychological Science*, *26*(6), 684–700. https://doi.org/10.1177/0956797614566318

Delplanque, S., Grandjean, D., Chrea, C., Coppin, G., Aymard, L., Cayeux, I., Margot, C., Velazco, M. I., Sander, D., & Scherer, K. R. (2009). Sequential Unfolding of Novelty and Pleasantness Appraisals of Odors: Evidence From Facial Electromyography and Autonomic Reactions. *Emotion*, *9*(3), 316–328. https://doi.org/10.1037/a0015369

Dimberg, U., & Petterson, M. (2000). Facial reactions to happy and angry facial expressions: Evidence for right hemisphere dominance. *Psychophysiology*, *37*(5), 693–696. https://doi.org/10.1017/S0048577200990759

Field, A. (2013). Discovering Statistics using IBM SPSS Statistics. *Discovering Statistics Using IBM SPSS Statistics*, 297–321. https://doi.org/10.1016/B978-012691360-6/50012-4

Fridlund, A. J., & Cacioppo, J. T. (1986). Guidelines for Human Electromyographic Research. *Psychophysiology*, *23*(5), 567–589. https://doi.org/10.1111/j.1469-8986.1986.tb00676.x

Gallucci, M. (2019). *GAMLj: General analyses for linear models*. https://gamlj.github.io

Havlíček, J., Dvořáková, R., Bartoš, L., & Flegr, J. (2006). Non-advertized does not mean concealed: Body odour changes across the human menstrual cycle. *Ethology*, *112*(1), 81–90. https://doi.org/10.1111/j.1439-0310.2006.01125.x

Havlíček, J., & Lenochova, P. (2006). The Effect of Meat Consumption on Body Odor Attractiveness. *Chemical Senses*, *31*(8), 747–752. https://doi.org/10.1093/chemse/bjl017

Jacob, S., Hayreh, D. J. S., & McClintock, M. K. (2001). Context-dependent effects of steroid chemosignals on human physiology and mood. *Physiology and Behavior*, *74*(1–2), 15–27. https://doi.org/10.1016/S0031-9384(01)00537-6

Kamiloğlu, R. G., Smeets, M. A. M., de Groot, J. H. B., & Semin, G. R. (2018). Fear odor facilitates the detection of fear expressions over other negative expressions. *Chemical Senses*, *43*(6), 419–426. https://doi.org/10.1093/chemse/bjy029

Krueger, C., & Tian, L. (2004). A comparison of the general linear mixed model and repeated measures ANOVA using a dataset with multiple missing data points. *Biological Research for Nursing*, *6*(2), 151–157. https://doi.org/10.1177/1099800404267682

Lenochova, P., Roberts, S. C., & Havlíček, J. (2009). Methods of human body odor sampling: The effect of freezing. *Chemical Senses*, *34*(2), 127–138. https://doi.org/10.1093/chemse/bjn067

Leys, C., Ley, C., Klein, O., Bernard, P., & Licata, L. (2013). Detecting outliers: Do not use standard deviation around the mean, use absolute deviation around the median. *Journal of Experimental Social Psychology*, *49*(4), 764–766. https://doi.org/10.1016/j.jesp.2013.03.013

Littell, R. C., Pendergast, J., & Natarajan, R. (2000). Modelling covariance structure in the analysis of repeated measures data. *Statistics in Medicine*, *19*(13), 1793–1819. https://doi.org/10.1002/1097-0258(20000715)19:13<1793::AID-SIM482>3.0.CO;2-Q

Lötsch, J., Ultsch, A., & Hummel, T. (2016). How many and which odor identification items are needed to establish normal olfactory function? *Chemical Senses*, *41*(4), 339–344. https://doi.org/10.1093/chemse/bjw006

Lundström, J. N., Boyle, J. A., Zatorre, R. J., & Jones-Gotman, M. (2008). Functional neuronal processing of body odors differs from that of similar common odors. *Cerebral Cortex*, *18*(6), 1466–1474. https://doi.org/10.1093/cercor/bhm178

Lundström, J. N., Gordon, A. R., Alden, E. C., Boesveldt, S., & Albrecht, J. (2010). Methods for building an inexpensive computer-controlled olfactometer for temporally-precise experiments. *International Journal of Psychophysiology*, *78*(2), 179–189. https://doi.org/10.1016/j.ijpsycho.2010.07.007

Martins, Y., Preti, G., Crabtree, C. R., Runyan, T., Vainius, A. A., & Wysocki, C. J. (2005). Preference for human body odors is influenced by gender and sexual orientation. *Psychological Science*, *16*(9), 694–701. https://doi.org/10.1111/j.1467-9280.2005.01598.x

Mitro, S., Gordon, A. R., Olsson, M. J., & Lundström, J. N. (2012). The smell of age: Perception and discrimination of body odors of different ages. *PLoS ONE*, *7*(5). https://doi.org/10.1371/journal.pone.0038110

Olsson, M. J., Lundström, J. N., Kimball, B. A., Gordon, A. R., Karshikoff, B., Hosseini, N., Sorjonen, K., Olgart Höglund, C., Solares, C., Soop, A., Axelsson, J., & Lekander, M. (2014). The Scent of Disease: Human Body Odor Contains an Early Chemosensory Cue of Sickness. *Psychological Science*, *25*(3), 817–823. https://doi.org/10.1177/0956797613515681

Parma, V., Gordon, A. R., Cinzia, C., Cavazzana, A., Lundström, J. N., & Olsson, M. J. (2017). Processing of Human Body Odors. In A. Buettner (Ed.), *Springer Handbook of Odor* (pp. 963–986). Springer.

Pause, B. M. (2017). Human Chemosensory Communication. In A. Buettner (Ed.), *Springer Handbook of Odor* (pp. 987–1010). Springer.

Pause, B. M., Haberkorn, K., Eggert, F., Müller-Ruchholtz, W., Bestmann, H. J., & Ferstl, R. (1997). Fractionation and bioassay of human odor types. *Physiology & Behavior*, *61*(6), 957–961. https://doi.org/10.1016/s0031-9384(97)00013-9

Penn, D. J., Oberzaucher, E., Grammer, K., Fischer, G., Soini, H. A., Wiesler, D., Novotny, M. V., Dixon, S. J., Xu, Y., & Brereton, R. G. (2007). Individual and gender fingerprints in human body odour. *Journal of the Royal Society Interface*, *4*(13), 331–340. https://doi.org/10.1098/rsif.2006.0182

Porter, R. H. (1998). Olfaction and human kin recognition. *Genetica*, *104*(3), 259–263. https://doi.org/10.1023/A:1026404319384

Roberts, S. C., Gosling, L. M., Spector, T. D., Miller, P., Penn, D. J., & Petrie, M. (2005). Body odor similarity in noncohabiting twins. *Chemical Senses*, *30*(8), 651–656. https://doi.org/10.1093/chemse/bji058

Russell, M. J. (1976). Human olfactory communication. *Nature*, *260*(5551), 520–522.

https://doi.org/10.1038/260520a0

Sela, L., & Sobel, N. (2010). Human olfaction: A constant state of change-blindness. In *Experimental Brain Research* (Vol. 205, Issue 1, pp. 13–29). Springer Verlag. https://doi.org/10.1007/s00221-010-2348-6

Semin, G. R., & de Groot, J. H. B. (2013). The chemical bases of human sociality. *Trends in Cognitive Sciences*, *17*(9), 427–429. https://doi.org/10.1016/j.tics.2013.05.008

Smeets, M. A. M., Rosing, E. A. E., Jacobs, D. M., van Velzen, E., Koek, J. H., Blonk, C., Gortemaker, I., Eidhof, M. B., Markovitch, B., de Groot, J. H. B., & Semin, G. R. (2020). Chemical fingerprints of emotional body odor. *Metabolites*, *10*(3). https://doi.org/10.3390/metabo10030084

Spiegler, M. D., & Liebert, R. M. (1970). Some correlates of self-reported fear. *Psychological Reports*, *26*(3), 691–695. https://doi.org/10.2466/pr0.1970.26.3.691

Stern, K., & McClintock, M. K. (1998). Regulation of ovulation by human pheromones. *Nature*, *392*(6672), 177–179. https://doi.org/10.1038/32408

The jamovi project. (2019). *jamovi* (version 1.0). https://www.jamovi.org

West, B. T. (2009). Analyzing longitudinal data with the linear mixed models procedure in SPSS. *Evaluation and the Health Professions*, *32*(3), 207–228. https://doi.org/10.1177/0163278709338554

Williams, S. M. (1986). Factor Analysis of the Edinburgh Handedness Inventory. *Cortex*, *22*(2), 325–326. https://doi.org/10.1016/S0010-9452(86)80058-2

Wolfinger, R. D. (1997). An example of using mixed models and PROC MIXED for longitudinal data. *Journal of Biopharmaceutical Statistics*, *7*(4), 481–500. https://doi.org/10.1080/10543409708835203

Zeileis, A., & Grothendieck, G. (2005). Zoo: S3 infrastructure for regular and irregular time series. *Journal of Statistical Software*, *14*. https://doi.org/10.18637/jss.v014.i06

Zhou, W., & Chen, D. (2009). Fear-related chemosignals modulate recognition of fear in ambiguous facial expressions. *Psychological Science*, *20*(2), 177–183. https://doi.org/10.1111/j.1467-9280.2009.02263.x

Chapter VII:

General Discussion

Avoiding threat sources is an adaptive process of considerable relevance for the species. Hence, several species have developed strategies to efficiently monitor the surrounding environment looking for danger (i.e. vigilance) without compromising other survival-relevant activities (e.g., foraging for food, mate-seeking) (see Beauchamp, 2015). Humans are no exception, being continuously exposed to individual and collective threats (e.g., Reason, 1997) and in need of a proper attentional balance between vigilance and other relevant activities (e.g., Kameda & Tamura, 2007). Inspired by vigilance research in social animal species (e.g., Pulliam, 1973) and recent research on danger communication through chemosignals (i.e. fear-related chemosignals; de Groot et al., 2017), the present thesis aimed to bring further insights into the regulation of this attentional trade-off in human beings.

Within this broader topic, I present 5 studies exploring how conspecifics directly (i.e. through their presence) or indirectly (i.e. by releasing sensory cues signaling danger) modulate individual vigilance strategies and threat detection. In the following, we start by giving a brief summary of the results obtained in each study. Then, across 3 sections, a discussion is provided about how these findings are related to each another and their added value to social psychology and threat detection research. The first section is dedicated to the role of conspecifics' presence in modulating vigilance strategies and threat detection (chapters II to IV). This charts out the relation between our results and the animal models described in the literature (see Beauchamp, 2015), and their relationship with other social phenomena (e.g., social buffering; Bratec et al., 2020; Hornstein & Eisenberger, 2018; Hostinar et al., 2014; Kikusui et al., 2006). The second section is focused on how fear-related chemosignals prepare their receivers to deal with dangerous stimuli (chapters V and VI). The results (particularly the ones described in chapter V) are integrated with a very recent model proposed by us (Semin & Gomes, under review) regarding the function of chemosignal driven emotion-related information. In the third section, some limitations of the studies reported in this thesis and new directions for future research are covered. To conclude, possible practical implications of our findings and a set of final remarks are provided.

Summary of main findings

The first study (chapter II) was designed to investigate whether human beings use similar vigilance strategies as other social species. Specifically, we examined the role of the mere presence of conspecifics (vs. an alone condition) in modulating vigilance and how it relates to the detection and avoidance of threatening events. To achieve our goal, we developed and employed an innovative paradigm representing a foraging under a threat risk situation (i.e., the *"foraging-vigilance task"*). This paradigm was planned to have a laboratory simulation of the evolutionary trade-off between risk-monitoring and other survival-relevant activities. According to several authors, this represents the ideal context to study vigilance because it stimulates the natural conditions where this defense behavior seems to have evolved (see Beauchamp, 2015). Using a state-of-the-art eye-tracking device, we confirmed that human beings display vigilance behavior, which has a threat detection function in situations of imminent danger (but see Dunbar et al., 2002). Remarkably, as in the case of other social animals, the presence of conspecifics strongly modulates the adaptive trade-off between risk-monitoring and intake-activities in human beings (see also Wirtz & Wawra, 1986). Our results clearly showed that in the mere presence of conspecifics (compared to the alone condition) participants allocated more attentional resources to foraging and reduced the time dedicated to vigilance. Consequently, the likelihood of detecting peripheral threatening events was reduced.

The second study (chapter III) assessed if the presence of conspecifics (vs. an alone condition) reduces the perceived threat in ambiguous dangerous situations. This increased safety given by the presence of conspecifics has been hypothesized in animal research as one of the precursors of vigilance reduction in group conditions. Our aim was to understand whether this mechanism was also present in human beings. In an online study, we asked participants to envision themselves (either alone, in the company of 2 friends, or in the presence of 2 strangers) in several dangerous situations. Participants rated how threatened they would feel and how likely it was that they would be harmed in each of the scenarios. As hypothesized by early theories of animal gregariousness (e.g., Galton, 1871; Hamilton, 1971) and vigilance studies (e.g., Barash, 1972; Caraco et al., 1980a), our results showed that when participants envisioned themselves in the presence of conspecifics (compared to an alone condition) perceived threat was reduced. Arguably, these data support the hypothesis that conspecifics' mere presence reduces the attentional resources allocated to vigilance by increasing the safety feeling, thus reducing individuals' alertness level. Moreover, envisioning themselves in the presence of 2 friends or 2 non-threatening strangers did not produce significant differences. This data suggests that regarding threat appraisals, the simple presence of conspecifics increases safety feelings, irrespective of whether participants had a social connection to the target individual or not.

The study in chapter IV aimed to go one step further and explore whether different group contexts (i.e., competitive and cooperative contexts vs. mere presence) shape vigilance strategies distinctively. In this experiment, we used the "foraging-vigilance task" with different sets of instructions leading participants to believe that they were competing or cooperating with others (confederates) in the same room (compared with the mere presence condition). The results showed that perceiving conspecifics as competitors or cooperators neither modulated vigilance nor threat detection and was not different from the mere presence condition either. These data suggest that perceiving conspecifics as competitors or cooperators is not sufficient to increase/decrease individuals' alertness and consequently modulate vigilance. It is possible to speculate, together with earlier research (e.g., Kameda & Tamura, 2007; Kuroda & Kameda, 2019), that competitive and cooperative contexts may play a role in governing individuals' vigilance strategies only when conspecifics interact with them, using the behavior of others as a cue to tune their own.

In chapter V, we turned to the effects of fear-related chemosignals on vigilance and threat detection. Specifically, in this chapter, we reported an experiment exploring whether the exposure to fear-related chemosignals (vs. rest chemosignals and a clean air condition) modulates vigilance and threat detection during the "foraging-vigilance task". Our results indicated that exposure to fear-related chemosignals had no impact on the individuals' vigilance strategies but triggered faster reactions to avoid imminently threatening events. Notably, these results suggest that exposure to fear-related chemosignals does not increase participants' alertness and consequently their vigilance levels. Instead, the exposure to these danger-related olfactory cues triggers an unconscious readiness state, preparing participants to detect and avoid potentially dangerous events.

Finally, chapter VI reports a methodological study examining the reliability of using the same fear-related chemosignal samples a second time. Using facial EMG, we replicated previous findings (e.g., de Groot et al., 2014a) showing that the exposure to fear-related chemosignals (compared to rest chemosignals) produces stronger activation of the facial muscles involved in facial fear expressions (i.e. the *medial frontalis* and the *corrugator supercilii*; see Fridlund & Cacioppo, 1986). Moreover, this effect was similar across 2 applications of the same sweat samples. These results indicate that samples of fear-related chemosignals can be re-used, reducing the monetary and time cost of research employing chemosignals. Notably, these findings also allow us to speculate about the properties of the molecules carrying the "fear-related information" in the chemosignal. The fact that the chemical information remains functional from a first to a second use of the same samples suggests that the molecules involved in carrying the "fear information" are low volatile molecules that stay in the place where they were released for extended periods of time (e.g., Pause et al., 1997).

Vigilance and threat detection: The modulatory effects of the presence of conspecifics

Altogether, the findings reported in chapters II to IV bring the notion that the presence of non-threatening conspecifics automatically reduces participants' perceived threat-risk and the attentional investment in vigilance (relative to alone conditions). Consequently, individuals can focus to a greater extent on other survival-relevant activities (e.g., intake or rewarding activities as in the case of our experiments). Moreover, the time allocated to vigilance predicted the percentage of avoided threat-related events. The higher the attentional resources allocated to vigilance, the higher the detection of peripheral changes, suggesting that in threatening contexts, humans' vigilance behavior still serves threat avoidance purposes (but see Dunbar et al., 2002). Remarkably, this set of findings, aside from being in line with previous observational studies with human beings (Barash, 1972; Wawra, 1988; Wirtz & Wawra, 1986), strongly converges with the extensive animal behavior literature on vigilance (see Beauchamp, 2015). Being in a group reduces the individuals' alertness state (e.g., lower cortisol levels in sheep living in larger groups; Michelena et al., 2012), leading them to invest less attentional resources (e.g., time) in risk-monitoring (Blumstein et al., 1999; e.g., Fordyce & Agrawal, 2001; Gosselin-ildari & Koenig, 2012; Rieucau et al., 2010).

To understand the convergence between animal and human findings, one may hypothesize a possible common evolutionary pressure shaping the effects of conspecific's presence on threat appraisals and risk-monitoring strategies. As aforementioned, to survive and prosper, animal species had to develop strategies that allow them to efficiently monitor danger (i.e. vigilance) without sacrificing other survival-relevant activities to an extent that impairs their well-being and reproduction. Group living might have been the answer to this evolutionary challenge (e.g., Wilson, 2007). As suggested by several prominent theories (see Galton, 1871; Hamilton, 1971; Williams, 1966), gregariousness probably owes its origins to survival reasons because living in a group strongly increases individuals' safety. As discussed several times in this thesis, the presence of conspecifics is thought to reduce individuals' odds of being harmed by an incoming threat. In fact, group situations seem to increase individuals' survival chances, because conspecifics can provide sensory cues signaling the imminence of dangerous events (i.e. *"many-eyes effect"* and *"mutual warning"*; e.g., Caraco et al., 1980b; Galton, 1871) or act as additional targets for threat stimuli (i.e. *"risk dilution"*; e.g., Bertram, 1978; Hamilton, 1971; Williams, 1966). Additionally, increased safety allows engagement in activities other than vigilance such as foraging, mate searching, or nurturing, increasing individuals' fitness and chances of offspring production.

Considering what was mentioned in the previous paragraph, it is possible to speculate how gregariousness became an innate characteristic of animal species known nowadays as social. Considering a "Baldwin approach"[1] to evolution (e.g., Baldwin, 1896; Heyes et al., 2020; Simpson, 1953), the constant pressure exerted by threat encounters (e.g., predators) may have led the phylogenetic ancestors of diverse species, through trial and error (i.e. learning), to stay close to conspecifics seeking for safety and become social. As a result, this initially learned behavior increased individuals' survival chances, and further potentiated the transmission of their genetic information to future generations. Thus, any type of genetic variation that facilitates gregarious behavior increasing a sense of safety would have been favored by natural selection. As a consequence, these features might have been marked in species' genetics. In other words, any mutation that had facilitated and automatized gregarious behavior reducing the need for environmental inputs to gather in herds should have been kept by evolution. This way, an automatic drive to gather in herds, and consequently feeling safer in group contexts, may have become an innate characteristic of gregarious species, being marked in their genotype (for a similar argument regarding fear leaning, see Heyes et al., 2020).

This defense mechanism and its automatization have obvious advantages, especially if one considers animal species like our own. Humans are rather limited in speed and strength compared to other deadly animals (e.g., snakes; see Isbell, 2006, 2009). In fact, the strong evolutionary pressure exerted in species with a physically weak constitution (i.e. humans) is thought to be the precursor of not only gregariousness but also the development of strong social networks, allowing human beings to think, cooperate, and work together to defend themselves (see for instance Cacioppo et al., 2006; Wilson, 2007). Thus, considering that living in a group provided increased safety for our evolutionary dominance and that this advantageous adaptation is likely marked in the species' genetics, it is not surprising that the importance of sociality still holds nowadays in our species. Even in modern societies considered individualistic, sociality is still so crucial for our daily lives that 80% of the awake-time is spent in the presence of other conspecifics (Hawkley & Cacioppo, 2010; e.g., Kahneman et al., 2004). Human beings continue to feel safer when conspecifics are present (compared to when they are alone, chapter III), despite numerous modern mechanisms that ensure our safety. The presence of others is

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[1] Proposed by James M. Baldwin more than 130 years ago, the Baldwin effect (Baldwin, 1896) describes a hypothetical process in which ontogenetic responses acquired through learning gain a genetic base. In other words, individuals can find potential solutions to cope with environmental challenges more efficiently through learning than through random genetic variation. Once a solution is found, it can aid the sustain of the adaptive genetic phenotype the sufficient amount of time for it become genetically assimilated or *"Baldwinised"* (Heyes et al., 2020).

still reassuring, reducing attention to sources of danger and increasing intake activities (chapter II).

In fact, the importance of conspecifics in shaping our daily life, particularly in dealing with threatening events, was already proposed by earlier psychological research. The effects of the presence of conspecifics seem to go beyond modulating threat appraisals (chapter III) and risk-monitoring (chapter II), also impacting the stress response of already “harmed” individuals (see Beckes & Coan, 2011; Coan & Sbarra, 2015). Research in several social animal species (e.g., Hennessy, 1984, 1986; Vogt et al., 1981) including human beings (e.g., Kirschbaum et al., 1995; Taylor et al., 2008) on a phenomenon termed “social buffering” indicates that the presence of conspecifics with a social connection to the “harmed” individual (e.g., friends, romantic partner, relatives) mitigates the psychological, physiological and hormonal responses associated with stress[2] (e.g., Epley, 1974; Hornstein & Eisenberger, 2018; Hostinar et al., 2014; Kikusui et al., 2006). For instance, this line of research has shown that the presence of conspecifics reduces the individuals’ stress hormones secretion (i.e. cortisol; Kirschbaum et al., 1995) and impacts their cardiovascular, blood pressure, and skin conductance responses in laboratory-induced stress situations (e.g., Gerin et al., 1995; Thorsteinsson & James, 1999). Moreover, the presence of conspecifics seems to mitigate pain experiences reducing the stress response triggered by them (e.g., Eisenberger et al., 2011; Younger et al., 2010). This appears to be true also for fear learning[3] (i.e. conditioning through electrical shocks). Conspecifics with a social connection with the “harmed” individuals reduce their fear acquisition and enhanced fear extinction (Hornstein et al., 2016, 2018). In fact, conspecifics are apparently so relevant in dealing with stress (e.g., threat-related events), that being in harmful situations seems to foster the establishment of social connections between human beings (Friedman, 1981; Zucker et al., 1968).

Interestingly, it is thought that the presence of conspecifics buffers stress responses because it is processed as a safety cue (see Hostinar et al., 2014). Analogous to what we have argued above regarding reduced threat appraisals and vigilance in group contexts, it has been hypothesized in social buffering research that the presence of conspecifics may trigger a *“preparedness for safety”* (Hornstein & Eisenberger, 2018; Jacobs & LoLordo, 1977). That is, by potentially providing increased resources to deal with a stressful event (i.e. help), the presence of conspecifics automatically increases the harmed individual’s perceived safety,

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[2] Defined here as *“a real or interpreted threat to physiological or psychological integrity of an individual that results in psychological and/or behavioral responses”* (McEwen, 2000, p. 508).

[3] Which is an emotional state that, considering a functional perspective (Adolphs & Andler, 2018; Öhman & Mineka, 2001), has the role of preparing mind and body to cope with threat stimuli.

downregulating the brain activity associated with stress feelings, and buffering the stress response (Bratec et al., 2020). In fact, this mechanism may have critical survival advantages by reducing the damaging effects of stress on health (McEwen, 2008; Miller et al., 2011). Hence, due to its survival benefits, some authors have defended that the mechanisms associated with social buffering (as we argued above for threat appraisals and vigilance) may have been selected by evolution and hardwired in our genetic makeup and neural system (e.g., Carter, 1998, 2003).

Compared to phenomena we have explored in the current thesis (i.e. vigilance and threat appraisals), a distinct aspect of social buffering is the fact that the presence of conspecifics with no social connection to the harmed individual (i.e. strangers) have reduced or no impact on stress responses. In other words, in our studies, the presence of strangers (i.e. confederates) reduced the attentional resources allocated by participants to risk-monitoring (compared to an alone condition; chapter II), and no difference was observed between individuals envisioning themselves in the presence of 2 strangers or 2 friends regarding threat appraisals (for a discussion of the limitations of this type of study see chapter III). However, in the case of the research examining social buffering, a social connection between the harmed individual and the present conspecifics seems to be crucial in buffering the stress response (see Krahé et al., 2013). Although speculatively, this distinct role of the presence of strangers reducing vigilance (chapter II) and threat appraisals (chapter III) but having no impact on the stress response of a "harmed" individual might be explained, as we argued below, by the different nature of the processes examined in our studies when compared with the research on social buffering.

Contrary to social buffering research, our studies did not focus on the role of the presence of conspecifics in dealing with threatening events that have already occurred (i.e. threat coping). Instead, what we examined was how threatened individuals felt in situations where a threatening event could occur (i.e. threat appraisals; chapter III) and the attentional resources devoted to detected and avoid it (i.e. vigilance; chapter II). In other words, we examined 2 preventive processes that take place before a threatening event actually affects the individual. Arguably, such as briefly discussed in chapter III, in these cases, the presence of conspecifics regardless of their social connection to the target individual (see also chapter IV) may always be construed as lowering the likelihood of being harmed by a possible threatening event. Vigilance research on social animal species (Beauchamp, 2015) suggest that this happens because the presence of conspecifics can act as additional threat detectors (i.e. *"many-eyes effect"* and *"collective detection"*; e.g., Caraco et al., 1980b; Galton, 1871) or as alternative targets for incoming danger (i.e. "risk-dilution"; e.g., Bertram, 1978; Hamilton, 1971; Williams, 1966). Consequently, when a threatening event is still just a probability, the presence of conspecifics, even if strangers, always reduces the individual threat-risk. As noted by Beckes and Coan (2011, pp. 978–979) in their *"Social Baseline Theory"*, *"…risk distribution does not imply familiarity or relational partnerships. It is simply a numbers game, where group size changes risk exposure…"*.

However, once a threatening event occurs and a given individual is affected, being in the presence of conspecifics with a social connection or in the presence of strangers may make a difference in terms of safety and helping resources (associated with the social buffering phenomenon). If there is no social connection between the harmed individual and the conspecifics in the surrounding environment, cooperating to defend or helping others may not be the immediate choices. Decades of social (for a review see Smith et al., 2015, Chapter 14) and evolutionary (e.g., Axelrod & Hamilton, 1981) research on prosocial behavior (e.g., altruism, cooperation), has shown that human beings still need to be somehow motivated to help even when others need help and social norms suggest that a given individual should be helped. Among others, a crucial variable motivating the decision to help is the existence of a social connection between the conspecifics and the harmed individual (e.g., being friends). The role of social connections in emerging help (e.g., altruistic behavior) between conspecifics was firstly noted by several prominent evolutionists decades ago (e.g., Darwin, 1871; Hamilton, 1964; Williams, 1966), and there is no doubt nowadays that people are more likely to help a friend or a relative than a stranger (Curry & Dunbar, 2013). In fact, even a small social connection between individuals appears to be crucial to turning a mere bystander into a likely helper (Solomon et al., 1981). This seems to be especially true in threat-related scenarios, with some research showing striking similarities in brain responses to threats directed at the self and at friends, but not at strangers (Beckes et al., 2013). Hence, once a threatening event affects a given individual, being in the presence of conspecifics with whom the individual has a social connection or in the presence of strangers may be critical for the probability of being helped (see also Beckes & Coan, 2011). In other words, friends are more likely to provide help than strangers when an individual is harmed, reducing the consequences of, for instance, a threat encounter.

Having said that, one could argue that the distinct role of the presence of strangers in modulating threat appraisals and vigilance (chapters II-IV) or the stress response of an already harmed individual (social buffering research) may be related to their distinct contribution in diluting risk (as in the case of our studies) or in providing help to others (associated with social buffering). That is, the presence of strangers is enough to reduce threat appraisals and the attentional resources devoted to vigilance because it dilutes the individuals' risk, representing a lower probability of getting harmed. However, their presence does not buffer the stress responses of harmed individuals because they do not represent increased resources or help in dealing with a threatening situation. Please note that this is not to say that the presence of, for instance, friends would not have even a greater impact in reducing vigilance when compared to the presence of stranger confederates. Such comparison was not performed in our studies assessing vigilance behavior, precluding us from going beyond speculation without supporting research.

In fact, this distinction between the role of strangers in diluting risk or providing coping resources highlights the added value of the results obtained in the current thesis for the literature in threat detection and social psychology. Our data together with previous literature suggests that, to study how conspecifics shape individuals' risk monitoring and coping, one should consider the temporal events sequence (i.e. if a threatening event is just a probability or already occurred) as its interaction with the involving social context. That is, strangers may be important in reducing threat probability, but they have little or no effect if being affected by the dangerous stimuli is a certainty. This important distinction for understanding humans' risk monitoring and threat coping in social contexts constitutes an interesting avenue for future studies on this research field (see also Beckes & Coan, 2011; Coan & Sbarra, 2015).

Fear-related chemosignals: a tool for collective detection in human beings[4]

Such as already mentioned in the previous section, one of the mechanisms hypothesized as being behind the increased safety provided by the presence of conspecifics is *"collective detection"* or *"mutual warning"* (e.g., Galton, 1871; Lima, 1990; see also Beauchamp, 2015). This mechanism highlights that an important feature of the presence of conspecifics in dealing with possible threat encounters is the capacity to "communicate" danger-related information between the species' members. That is, in a group context, once an individual notices the presence of a dangerous stimulus, he/she can then emit or release diverse sensory cues. In turn, these cues, when perceived by other conspecifics, can alert/prepare them to detect and deal with possible threatening situations. Interestingly, years of psychology research have pointed to a similar mechanism in humans, with diverse sensory cues playing a role in this information transfer. Some examples are facial expressions (e.g., Pourtois et al., 2004), body postures (e.g., Stienen & de Gelder, 2011), and even prosody related to fear emotional states (e.g., Dolan et

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[4] A part of this section is based on the model reported in: Semin., G. R., & Gomes, N. (under review). Human Emotion Chemosignals: A Functional Activation-Articulation Model.

al., 2001). As shown in several studies, these cues increase alertness or preparedness enhancing the capacity to detect and react to threat-related stimuli (e.g., Gallup et al., 2014; Rigoulot & Pell, 2012; Stienen et al., 2011). In the studies reported in chapters V and VI, we investigated whether fear-related chemosignals (see de Groot et al., 2017; de Groot & Smeets, 2017) serve the same function in humans. Specifically, our focus was to explore how exposure to these danger-related olfactory cues modulates risk-monitoring strategies (i.e. vigilance) and threat detection efficacy in our species.

As studies with social animal species show (see Kikusui et al., 2001; Kiyokawa et al., 2006), the results reported in chapter V and VI indicate that fear-related chemosignals constitute relevant mutual warning-like cues for human beings. More specifically, in chapter VI, we replicated previous research on this very recent field (de Groot et al., 2012, 2014a, 2015), showing that the exposure to these sensory cues activates in receivers the facial muscles (i.e. *corrugator supercilii* and *medial frontalis*) involved in displaying fear facial expressions. Arguably, these muscles' activation expands the visual field, increases the inhalation volume, and speeds up ocular movement (Susskind et al., 2008). This increased sensory acquisition is thought to allow receivers to explore and gather information about the surrounding environment more efficiently, which may be highly advantageous when a threatening event is about to occur. Furthermore, in the study reported in chapter V, we went further with evidence that exposure to fear-related chemosignals has an effective advantage for receivers in coping with threatening events. The exposure to these olfactory cues carrying threat-related information did not modulate participants' vigilance strategies during the *"foraging-vigilance task"* but triggered what we referred to as a preparedness/readiness state. Participants exposed to the fear-related chemosignals evidenced faster avoidance reactions to threatening events than those who did not receive the threat-related olfactory signal.

In fact, findings supporting similar preparedness/readiness states can be found in several previous studies employing not only fear but also other chemosignals sampled during distinct increased alertness states such as anxiety or high-stress situations. For instance, besides the aforementioned results showing that fear chemosignals activate facial muscles associated with fear facial expressions (e.g., de Groot et al., 2014a), research employing anxiety-related chemosignals evidenced that the exposure to this olfactory stimulus facilitates withdrawal behaviors (e.g., increasing the amplitude of the startle reflex Prehn et al., 2006) and modulates cardiac activity in congruence with a stress response (Rocha et al., 2018). Moreover, previous research went beyond peripherical physiological measures and behavioral findings showing that the exposure to anxiety chemosignals activates in the human brain a complex network

(Prehn-Kristensen et al., 2009). This involves, among others, areas previously associated with attentional control (i.e. anterior cingulated cortex; e.g., Botvinick et al., 1999) and emotional regulation and action (i.e. posterior cingulated cortex; e.g., Cato et al., 2004). Research using chemosignals collected during high-stress situations adds to the previous findings showing the activation of the amygdala in response to this specific olfactory stimulus (Mujica-Parodi et al., 2009), which is a brain structure deeply associated with threat processing (e.g., LeDoux, 1996; Morris et al., 1996). From our perspective, the research summarized earlier seems not only to indicate that alertness-related chemosignals are processed as threat-related information but also to confirm that they prepare receivers, by modulating their attention and sensory acquisition, to detect signals that may indicate the imminence of a dangerous event.

Notably, Rubin and colleagues (2012), in an interesting EEG study employing high-stress chemosignals, provided further insights that can aid to solve the characteristics of this hypothetical preparedness state. Their results showed that exposure to sweat collected during high-stress situations resulted in heightened attentional activity (i.e. heightened late positive potentials) to both human faces displaying threat signals (angry faces) and neutral facial expressions. Following the authors' reasoning, this data pattern suggests that exposure to alertness-related chemosignals triggers an increased attentiveness state. Remarkably, this enhanced attentiveness was verified not only to danger-related information (i.e. angry faces) but also to neutral visual stimuli (faces) that in the absence of these chemosignals would not require such attention allocation. In other words, alertness-related chemosignals increased participants' attentiveness, enhancing the processing of visual cues that were otherwise not relevant (see Rubin et al., 2012). These results, together with the increased sensory acquisition revealed by de Groot and colleagues (2012) and partially replicated by us in chapter VI (i.e. increased activation of the facial muscles involved in expressing fear), indicate that the preparedness state triggered by alertness-related chemosignals increases the receivers' capacity to explore and gather information of their surroundings. This increased attentiveness may not be necessarily specific to danger-related information but enhancing processing in general. Danger-specific or not, this enhanced processing will ultimately aid receivers in identifying in their surroundings cues that can mean threat faster, thus being advantageous for the individual's survival. In fact, such a mechanism fits well with the data reported in chapter V. Although speculative, it is possible to argue that exposure to fear chemosignals might have triggered a similar preparedness/readiness state in the participants characterized by high attentiveness. Consequently, this allowed them to identify the slight changes displayed in the peripheral Gabor patches faster than participants who did not receive the olfactory warning signal (i.e. participants exposed to rest chemosignals or clean air).

If alertness-related chemosignals constitute an important warning signal involving survival advantages for human beings, then an important issue is the temporal characteristics of this information-transfer. Olfactory stimuli seem to take longer to be processed compared to stimuli from other sensory modalities, such as vision or audition, (Wetter et al., 2004). For instance, some research suggests that, while visual stimuli take approximately 200ms from their perceptual onset to their first cognitive processing, olfactory stimuli seem to need roughly double as long (e.g., Olofsson et al., 2008; Pause & Krauel, 2000). One may argue that this delayed processing speaks against the advantage of olfaction signaling. This is especially critical when results as the ones reported in chapter V (evidencing reaction time advantages in avoiding threat stimuli of only approximately 200ms) are considered. Taking into account the slower processing associated with this sensory modality, what would be the advantage of communicating warning information through chemosignals? The answer to this question may become clearer when one considers the singular characteristics of chemosignals (and olfaction) as a vehicle to transfer information. Chemosignals are constituted by several volatile molecules that, individually or together, carry information from a sender to a receiver. Because volatiles spread in the air, this type of information transfer can then overcome environmental factors that may impair other sensorial modalities (for a similar argument see Lundström & Olsson, 2010). For instance, visual barriers, light conditions, and noisy environments can significatively impact the transfer of information through vision or audition, but olfaction can still remain functional when these other senses are blocked. Importantly, this is not to say that communication through chemosignals is not affected by environmental factors. In fact, windy environments or extreme temperatures may change the volatility of chemical compounds and affect the transfer of chemosensory information. However, considering the relevance of warning-related information, olfaction finds its relevance in complementing other sensorial modalities when these are impaired or not fully functional.

It is also possible that, instead of communicating warning signals rapidly, alertness-related chemosignals have the advantage of being long-lasting compared to other sensory modalities. In contrast to visual or auditory warning information that is processed very rapidly but also disappears rapidly, chemosignals seem to remain longer in the environment. For instance, there is some evidence in other social species (e.g., coral reef fishes and mice) that olfactory warning cues remain functional for periods up to 30 min after their release (e.g., Bind et al., 2013; Chivers et al., 2013). One could therefore argue that chemosignals do not constitute fast-warning signals to alert conspecifics for an immediate threat. However, they may provide a longer-lasting message signaling that the environment is potentially dangerous. In turn, by triggering a preparedness state categorized by higher attentiveness, the exposure to olfactory warning cues may allow receivers to explore that location more efficiently, detecting quickly further signals of danger. Hence, assuming that the function of chemosignals may not be to signal an immediate threat, the slower processing of olfactory stimuli in the brain may not be critical to their warning function.

Notably, the argument advanced in the previous paragraph converges with what was suggested in chapter VI regarding the volatility of the chemicals involved in carrying the warning message. It is known that high volatile molecules disperse faster and travel longer distances but remain functional for shorter periods. In contrast, low volatile molecules remain for longer periods in the same location where they were released, keeping the information that they carry in the same location, even when their sender is no longer there (Pause, 2017; Pause et al., 1997). By showing that sweat samples remain functional in transmitting their warning message across two distinct applications of approximately 20 min each, we suggested that the molecules carrying fear-related information may be low volatiles (see chapter VI). Interestingly, this low volatility hypothesis supports the role of chemosignals as long-lasting information carriers. In other words, olfactory cues may remain in the place where they were released for longer periods signaling that a conspecific recently faced a stressful situation there. However, it is important to note that research on fear-related chemosignals' chemical properties is still in its infancy (Smeets et al., 2020), and further chemical research is needed to confirm this hypothesis.

Another important aspect that deserves to be discussed is the fact that the exposure to fear-related chemosignals did not modulate vigilance strategies (see chapter V). Contrary to what we have hypothesized, receiving an olfactory warning signal did not lead participants to overtly allocate more attentional resources to risk-monitoring. This absence of effects on vigilance may be explained by several characteristics of both the governing of vigilance behavior in social species and the communication of emotional-related information through chemosignals. As mentioned earlier, vigilance is defined as an alertness state that governs threat-monitoring. That is, as a danger avoidance mechanism, vigilance increases as threat-risk increases (and consequently stress-levels) (Beauchamp, 2015). This is supported, for instance, by vigilance research in animal species showing that the levels of stress hormones are directly correlated with the attentional resources allocated to vigilance (e.g., cortisol and norepinephrine; Hawlena & Schmitz, 2010; but see Tkaczynski et al., 2014; Voellmy et al., 2014). Hence, it is possible to argue that, in the study reported in chapter V, the exposure to fear-related chemosignals (compared to rest chemosignals and a clean air condition) did not modulate vigilance because it did not increase participants' alertness and perceived threat-risk. This is supported by the absence of differences in the participants' self-reported stress levels between the different chemosignal conditions. Fear chemosignals did not trigger in participants' a threat-related state (i.e. a fear-like emotional reaction categorized by increased alertness), but only modulated their receivers' behavior in a more basic way: preparing them (possibly by increasing attentiveness) to process and consequently avoid potential harmful events faster.

From our point of view, these results challenge the prominent idea in the literature that the communication of emotion-related information through chemosignals is associated with an emotional contagion phenomenon (Hatfield et al., 1993), inducing a "simulacrum" of the senders' emotional state (de Groot et al., 2012, 2015; Semin & de Groot, 2013). If this was the case, our receivers should have experienced a fear-like emotional state categorized by increased alertness and stress levels (Öhman & Mineka, 2001), which would have resulted in increased attentional resources allocated to vigilance. However, this was not verified. In fact, the obtained data pattern seems to fit better with the hypotheses suggested in a recent model proposed by us (Semin & Gomes, under review). As we summarize below, this functional activation-articulation model of human emotion chemosignaling posits that instead of a "transfer of emotion", emotional chemosignals may just trigger a preparedness or readiness state in their receivers categorized by several physiological, cognitive, and behavioral changes. In turn, this readiness state can lead to a goal attainment behavior (i.e. articulation), and consequently to an emotional experience, only if the ecology in which the receiver is interfaces with the state of readiness (Semin & Gomes, under review).

Senders (e.g., sweat donors) experiencing different emotional states release chemosignals with distinct chemical compositions (Smeets et al., 2020). In turn, these emotion-related chemosignals trigger, in receivers, particular patterns of neural activity (e.g., Prehn-Kristensen et al., 2009; Zheng et al., 2018) and psychophysiological changes (e.g., de Groot et al., 2012; Prehn et al., 2006) that are congruent with the emotional state of the sender but do not constitute an emotional experience *stricto sensu*. For instance, and as already mentioned in this section, the exposure to alertness-related chemosignals (i.e. sweat sample during fear, anxiety, or high-stress inducing contexts) leads receivers to an increased sensory acquisition (e.g., de Groot et al., 2012) and attentiveness (e.g., Rubin et al., 2012), facilitating also withdraw behaviors (Prehn et al., 2006). This hypothetically prepares receivers to search for threat signals and facilitate a possible threat avoidance reaction. On the other hand, when receivers are exposed to disgust-related chemosignals (i.e. sweat sampled during disgust-inducing context), they seem to go into a sensory rejection state. This is categorized by the activation of facial muscles associated with disgust facial expressions (i.e. *levator labii*; de Groot et al., 2012) that decreases sniff magnitude and eye aperture at the service of avoiding noxious stimuli (Susskind et al., 2008). Exposure to these specific chemosignals seems to also facilitate food healthiness judgments (Zheng et al., 2018), contributing to increased discrimination of possible harmful intakes.

However, these activation and behavioral patterns do not constitute an emotional experience as vivid as that undergone by the sender during the sweat sampling. Receivers display in fact systematic but imperceptible and subtle changes that are recorded by highly sensitive devices, but none of these can be considered a signal of an "emotional" experience (LeDoux, 2014a). In other words, none of the receivers of the aforementioned studies (including ours) evidenced feeling afraid or disgusted during exposure to different chemosignals as the sweat donors reported to be during the sweat sampling. To reach a "naked-eye" observable emotional reaction, receivers must be in a context where these preparatory states are functional. For instance, the readiness state induced by fear chemosignals increases sensory acquisition, but only if during this state the receiver identifies a threat (e.g., a snake), a diverse set of bodily functions gets activated, leading to a visually manifest reaction and a fear emotional experience. On the other hand, if there is no match between the readiness state and the ecology, this articulation does not take place, and no behavioral/emotional changes are observed or even perceived by the receiver.

This argument follows the reasoning of some theorists in the emotion research field. One example is Joseph E. LeDoux (LeDoux, 2014a, 2014b, 2015) and his work describing the role of emotion-related processes in the detection and avoidance of threat stimuli. The readiness state triggered by emotion-related chemosignals and its neural and psychophysiological changes can be seen, in the light of our model, analogously to *"... innate circuits that control responses to significant stimuli (like stimuli related to danger, maintaining energy supplies and fluid balance, and reproduction)"* (LeDoux, 2014b, p. 319), which *"did not evolve to make emotions but to give organisms behavioral tools to stay alive"* (LeDoux, 2014b, p. 319). Emotional experiences, on the other side, are *"...product(s) of cognitive processes."* (LeDoux, 2014b, p. 319). They are thought to be constructed, being this construction highly variable and individual, since it integrates, for instance, previous personal experiences (e.g., Barrett, 2017). In short, one thing is the precognitive preparatory state that aids in coping with several harmful situations, another is an emotional experience that can occur or not in parallel, depending on the match with surrounding ecology and individual characteristics. Before this match between the information contained in the chemosignal and congruent contextual cues, we argue, only a pre-cognitive readiness state is achieved, which will not reach an emotional experience until it matches with the surrounding environment (see Semin & Gomes, under review).

Therefore, back to the results reported in chapter V, as no fear emotional state (involving high stress and an increment of alertness levels) was achieved during the exposure to fear chemosignals, no increment in the attentional resources allocated to vigilance was observed. However, the preparatory state induced by the fear chemosignals, namely the increased attentiveness, allowed participants to detect and react faster to the peripheral threat-related changes. In sum, we argue that danger-related olfactory cues play their role in humans' mutual warning, not by increasing individuals' alertness and the attentional investment in danger monitoring, but by leading receivers to a precognitive state of increased attentiveness allowing them to identify threat signals more efficiently.

Limitations and future directions

Throughout the current thesis, we have been highlighting some limitations of each of the reported studies and suggesting future research to overcome them. In this section, some of these constraints are recapped and briefly discussed in the context of the main message emerging from this set of studies. Additionally, general limitations of the current thesis as well as suggestions for further research are also advanced.

In what concerns the research dedicated to exploring the role of conspecifics' presence in governing individuals' vigilance strategies and threat detection, a general constraint of these 3 first studies, when compared to animal models, is the relation found with group size and vigilance (i.e. the *"group size effect"*; e.g., Beauchamp, 2008). That is, although our studies were inspired by the animal literature suggesting that the attentional resources devoted to vigilance are inversely correlated with the number of present conspecifics, our presence conditions were always constituted by 3 individuals (the participant and 2 confederates). Therefore, whether a "*group size effect"* can be observed in human beings influencing the trade-off between intake activities and threat monitoring remains unknown. Future research using a similar paradigm (i.e. the "foraging-vigilance task") but manipulating the number of conspecifics in the surroundings is needed to fully understand the heuristic value of animal models for humans' risk-monitoring. In fact, examining the impact of a *"group size effect"* in our own species constitutes a necessary step to unravel the social moderators of risk-monitoring and threat detection.

Another important point that deserves further attention is the relation between the perceived risk of threat and the attentional investment in vigilance. This potential relation suggested by animal research (e.g., Michelena et al., 2012) was inferred for humans in the present thesis using independent studies with distinct participants and data collection methods. In other words, after observing a vigilance decrease in human beings in the presence of conspecifics (chapter II), we examined and showed that the presence of conspecifics induces a feeling of increased safety (i.e. reduced threat risk; chapter III). We argued then that, as observed in animal studies, this increased safety would justify the relaxed vigilance in group contexts. However, this relation was not demonstrated yet in a single laboratory study employing the same set of participants and directly associating their perceived risk and alertness levels with the investment in risk-monitoring. Our plan was to establish this relation in a final study that the world pandemic situation (i.e. COVID 19) precluded us to run (see chapter I). Hence, this remains unexamined and is an important issue for future research. Specifically, further studies using the "foraging-vigilance task", should consider employing measures of both the participants' perceived threat-risk (e.g., assessed as in chapter III) and alertness state (e.g., skin conductance levels; see Raskin, 1973), examining the relation of these measures with the time allocated to vigilance.

Turning to the conclusions drawn from the studies involving olfactory warning cues, a point that deserves to be discussed concerns the null effects of fear chemosignals in modulating vigilance (chapter V). It is important to note here that the research reported in chapter V constitutes a first step in exploring how fear-related chemosignals modulate vigilance and threat-detection. Consequently, the dependent variable used to assess vigilance (i.e. the % of time allocated to risk-monitoring) constitutes just one among several possible measures that can be used to examine risk-monitoring strategies (e.g., scan duration and frequency; see Beauchamp, 2015). Thus, the conclusions that were taken from the fact that the exposure to fear chemosignals did not directly impact vigilance, should be interpreted with caution. Future studies designed to use distinct vigilance measures are needed to strengthen the confidence in our findings.

Additionally, studies involving fear-related chemosignals were conducted under strict protocols, that although in congruence with the common practices in the field, may diminish the ecological validity of our findings. Following previous research using emotion-related chemosignals (e.g., de Groot et al., 2012, 2014b; Zhou & Chen, 2009), to avoid sweat contamination, sweat donors were asked, in our experiments, to follow dietary and habit restrictions in the days before, and not to wear any personal care products (e.g., deodorant) on the sweat collection day. However, these restrictions do not mimic ecological contexts where the transfer of information through chemosignals may occur. For instance, in societies like ours, people wear personal care products and, in general, adopt habits that reduce the intensity of their body odors (i.e. *"...societies that have become deodorized and desensitized to odours"*; Roberts et al., 2020, p. 3). Hence, it would be very interesting not only for future research on fear-related chemosignals as a warning cue but also for the entire field of emotion-related chemosignals that future studies assess the effect of these olfactory stimuli when collected without such strict protocols. In fact, without studies involving sweat collected under more ecological conditions, it is hard to predict the real impact of olfactory warning mechanisms in contemporary contexts.

In the same vein, and again following the common practices in the field, sweat donors in our experiments were always men because of their large and more active apocrine glands compared to women (Doty, 1981). On the other hand, receivers were always women due to their higher sensitivity towards emotional signals and a better sense of smell compared to men (Brand & Millot, 2001; Brody & Hall, 2000). Hence, additional research exploring whether these effects are independent of participants' sex may be valuable to understand the real extension of the observed phenomena.

To conclude this section, an important limitation for this thesis's message is the absence of a final study exploring the concomitant effects of the 2 major phenomena examined here. That is, a study assessing the impact of fear chemosignals, the presence of conspecifics, and their combined effects on vigilance and threat-detection. Assuming the relevance of these factors in ecological contexts, it is plausible to think that the exposure to olfactory danger cues may occur in the presence of conspecifics. So, on the one hand, from the receivers' perspective, there is a sensory cue preparing them to deal with a possible dangerous stimulus, but on the other hand, they are in the presence of conspecifics which automatically represent increased safety. Olfactory danger cues and the presence of conspecifics are likely to exert effects in opposite directions (while one increases attentiveness, the other reduces vigilance). Understanding how this "dilemma" is processed and solved by our species would provide an integrative perspective regarding the social modulators of risk-monitoring and threat detection. Even at a more fundamental level, research on emotion-related information transfer through olfaction was only conducted in individual scenarios. Therefore, the question remains whether the presence of conspecifics may modulate the phenomena described in the literature. In fact, as mentioned in chapter I, an experiment with these characteristics was part of our original research plan but the world pandemic situation led us to postpone this final study, not including it in the current thesis.

Potential practical implications

As already mentioned, despite all mechanisms in modern societies aiming to increase individual and collective safety, there are still several risks threatening our daily lives. Hence, insufficient risk-monitoring can result in severe damage to human beings across the most varied contexts (Reason, 1997; Slovic, 1987, 1999). As a social species that spends approximately 80% of the awake time in the presence of others (Kahneman et al., 2004), understanding how conspecifics modulate individuals' risk-monitoring strategies represents an important step in developing and improving mechanisms designed to increase safety. It is precisely here, I argue, that the practical value of this thesis emerges. Of course, as a fundamental research project giving the first steps on this research field, the obtained results do not provide immediate practical applications but may pave the way for future translational research with potentially considerable impact on the way our societies think about danger monitoring. Below, I provide some illustrative examples of contexts where efficient risk monitoring is crucial, speculating how our results could influence practical research aiming to improve it.

An interesting example of a context where the early detection of signals indicating that a prejudicial event is occurring or may occur in a close future is in financial markets. As illustrated by Kameda & Tamura (Kameda & Tamura, 2007), there are examples where the actions of a single trader, that remained unnoticed by entire teams of accounts and auditors, led to the loss of tens of millions of pounds. Another example where timely detection of signals indicating danger is crucial is in air traffic control (Blachman & Proschan, 1959). A failure of a team member can result in the loss of several hundred lives. This also applies to internal security forces that monitor cues indicating a possible terrorist attack, or even health organizations tracking new potentially deadly diseases. In all of these contexts, early detection of danger is crucial to avoid dramatic consequences for the individual and the collective. Back to the results reported in this thesis, they suggest that individuals in group situations tend to automatically feel safer, which arguably reduces the attentional investment in danger monitoring. Thus, we ask: Would it be better in terms of risk-monitoring if individuals working in aforementioned contexts performed their functions in separated cubicles instead of open spaces or in the presence of an entire team? Or is it the case that contrary to the results we obtained, the presence of conspecifics has no implications in these practical contexts? These are paramount questions for future translational research with critical practical implications for our societies, that I believe our results may inspire.

The reported research regarding fear-related chemosignals and the general attentiveness that they seem to induce can also be relevant in improving risk-monitoring in practical situations. For instance, although in their very beginning, there are considerable efforts to synthesize emotional body odors and to examine whether receivers are susceptible to the relevant effects triggered by these artificial compounds (some of this research is being conducted by a consortium in which our lab is taking part). In the hypothetical scenario that this research yields relevant results and proves that synthetic fear-related chemosignals can increase receivers' attentiveness, these stimuli can be used as a way to automatically improve risk-detection in the aforementioned critical contexts. However, this will certainly involve years of fundamental and translational research and a considerable number of ethical considerations before being considered a viable option. Our results represent just a small piece of this enormous puzzle, but as a fundamental research project, it is my hope that they contribute to this long way.

Final Remarks

The present work provides further insights into how conspecifics directly (i.e. through their presence) or indirectly (i.e. through fear-related chemosignals) shape humans' risk-monitoring and threat-detection.

In a nutshell, our findings showed that, as in other social species, human beings perceive an increased safety when others are present. Arguably, this is behind the vigilance reduction and greater investment in other survival-relevant activities when in the presence of conspecifics. These findings were obtained for the first-time using gaze movement data in a laboratory environment simulating threat. Additionally, our results also add to previous literature in related social phenomena (e.g., social support). They show that contrary to what is observed in threat-coping (i.e. social buffering), in what concerns threat appraisals and risk-monitoring, the simple presence of stranger conspecifics (i.e., with no social connection to the target individual) seems to be enough to increase safety feelings and to reduce vigilance.

Moreover, our data also indicates that olfaction has a role in transmitting warning information between human beings. Interestingly, this was not evidenced in shaping vigilance strategies but in preparing receivers to quickly detect and avoid threat-related events. This can be interpreted as an indicator that the exposure to fear-related chemosignals does not increase receivers’ alertness state or triggers in them a fear-like emotional state. Instead, the exposure to these olfactory warning cues leads receivers to a pre-cognitive preparedness state only observable when the environmental conditions match the information carried by the volatile molecules. Noteworthy, it is also possible to speculate from our data that the molecules carrying the fear-related information are low volatiles that may work as a long-lasting warning message.

Altogether, these results have taken few but important steps to understand the social moderators of risk-monitoring and threat detection in human beings, highlighting the heuristic value of animal behavioral models to study these phenomena in our own species.

References

Adolphs, R., & Andler, D. (2018). Investigating Emotions as Functional States Distinct From Feelings. *Emotion Review*, *10*(3), 191–201. https://doi.org/10.1177/1754073918765662

Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. In *Science*. https://doi.org/10.1126/science.7466396

Baldwin, J. M. (1896). A New Factor in Evolution. *The American Naturalist*. https://doi.org/10.1086/276408

Barash, D. P. (1972). Human Ethology: The Snack-Bar Security Syndrome. *Psychological Reports*, *31*(2), 577–578. https://doi.org/10.2466/pr0.1972.31.2.577

Barrett, L. F. (2017). How emotions are made: The secret life of the brain. In *How emotions are made: The secret life of the brain.*

Beauchamp, G. (2008). What is the magnitude of the group-size effect on vigilance? *Behavioral Ecology*, *19*(6), 1361–1368. https://doi.org/10.1093/beheco/arn096

Beauchamp, G. (2015). *Animal vigilance : monitoring predators and competitors*. Academic Press.

Beckes, L., & Coan, J. A. (2011). Social baseline theory: The role of social proximity in emotion and economy of action. *Social and Personality Psychology Compass*, *5*(12), 976–988. https://doi.org/10.1111/j.1751-9004.2011.00400.x

Beckes, L., Coan, J. A., & Hasselmo, K. (2013). Familiarity promotes the blurring of self and other in the neural representation of threat. *Social Cognitive and Affective Neuroscience*, *8*(6), 670–677. https://doi.org/10.1093/scan/nss046

Bertram, B. C. R. (1978). Living in groups: predator and prey. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural Ecology* (pp. 64–96). Blackwell Publishing Ltd.

Bind, R. H., Minney, S. M., Rosenfeld, S., & Hallock, R. M. (2013). The role of pheromonal responses in rodent behavior: Future directions for the development of laboratory protocols. *Journal of the American Association for Laboratory Animal Science*, *52*(2), 124–129.

Blachman, N., & Proschan, F. (1959). Optimum Search for Objects Having Unknown Arrival Times. *Operations Research*, *7*(5), 625–638. https://doi.org/10.1287/opre.7.5.625

Blumstein, D. T., Evans, C. S., & Daniel, J. C. (1999). An experimental study of behavioural group size effects in tammar wallabies, Macropus eugenii. *Animal Behaviour*, *58*(2), 351–

360. https://doi.org/10.1006/anbe.1999.1156

Botvinick, M., Nystrom, L. E., Fissell, K., Carter, C. S., & Cohen, J. D. (1999). Conflict monitoring versus selection for-action in anterior cingulate cortex. *Nature, 402*(6758), 179–181. https://doi.org/10.1038/46035

Brand, G., & Millot, J. L. (2001). Sex differences in human olfaction: Between evidence and enigma. *Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology*, *54*(3), 259–270. https://doi.org/10.1080/02724990143000045

Bratec, S. M., Bertram, T., Starke, G., Brandl, F., Xie, X., & Sorg, C. (2020). Your presence soothes me: a neural process model of aversive emotion regulation via social buffering. *Social Cognitive and Affective Neuroscience, 15*(5), 561–570. https://doi.org/10.1093/scan/nsaa068

Brody, L. R., & Hall, J. A. (2000). Gender, emotion, and expression. In M. Lewis & J. Haviland-Jones (Eds.), *Handbook of emotions* (2nd ed., pp. 338–349). Guilford Press.

Cacioppo, J. T., Hawkley, L. C., Ernst, J. M., Burleson, M., Berntson, G. G., Nouriani, B., & Spiegel, D. (2006). Loneliness within a nomological net: An evolutionary perspective. *Journal of Research in Personality, 40*(6), 1054–1085. https://doi.org/10.1016/j.jrp.2005.11.007

Caraco, T., Martindale, S., & Pulliam, H. R. (1980a). Avian flocking in the presence of a predator. *Nature, 285*(5764), 400–401. https://doi.org/10.1038/285400a0

Caraco, T., Martindale, S., & Pulliam, H. R. (1980b). Avian Time Budgets and Distance to Cover. *The Auk: Ornithological Advances, 97*(4), 872–875. https://doi.org/10.1093/auk/97.4.872

Carter, S. C. (2003). Developmental consequences of oxytocin. *Physiology and Behavior, 79*(3), 383–397. https://doi.org/10.1016/S0031-9384(03)00151-3

Carter, S. C. (1998). Neuroendocrine perspectives on social attachment and love. *Psychoneuroendocrinology, 23*(8), 779–818. https://doi.org/10.1016/S0306-4530(98)00055-9

Cato, M. A., Crosson, B., Gökçay, D., Soltysik, D., Wierenga, C., Gopinath, K., Himes, N., Belanger, H., Bauer, R. M., Fischler, I. S., Gonzalez-Rothi, L., & Briggs, R. W. (2004). Processing Words with Emotional Connotation: An fMRI Study of Time Course and Laterality in Rostral Frontal and Retrosplenial Cortices. *Journal of Cognitive Neuroscience, 16*(2), 167–177. https://doi.org/10.1162/089892904322984481

Chivers, D. P., Dixson, D. L., White, J. R., McCormick, M. I., & Ferrari, M. C. O. (2013). Degradation of chemical alarm cues and assessment of risk throughout the day. *Ecology and Evolution*, *3*(11), 3925–3934. https://doi.org/10.1002/ece3.760

Coan, J. A., & Sbarra, D. A. (2015). Social Baseline Theory. *Current Opinion in Psychology*, *1*, 87–91. https://doi.org/10.1016/j.copsyc.2014.12.021

Curry, O., & Dunbar, R. I. M. (2013). Do Birds of a Feather Flock Together?: The Relationship between Similarity and Altruism in Social Networks. *Human Nature*, *24*(3), 336–347. https://doi.org/10.1007/s12110-013-9174-z

Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex*. Murray Press. https://doi.org/10.1038/011305a0

de Groot, J. H. B., Semin, G. R., & Smeets, M. A. M. (2014a). I can see, hear, and smell your fear: comparing olfactory and audiovisual media in fear communication. *Journal of Experimental Psychology. General*, *143*(2), 825–834. https://doi.org/10.1037/a0033731

de Groot, J. H. B., Semin, G. R., & Smeets, M. A. M. (2014b). Chemical communication of fear: A case of male-female asymmetry. *Journal of Experimental Psychology: General*, *143*(4), 1515–1525. https://doi.org/10.1037/a0035950

de Groot, J. H. B., Semin, G. R., & Smeets, M. A. M. (2017). On the Communicative Function of Body Odors: A Theoretical Integration and Review. *Perspectives on Psychological Science*, *12*(2), 306–324. https://doi.org/10.1177/1745691616676599

de Groot, J. H. B., & Smeets, M. A. M. (2017). Human fear chemosignaling: Evidence from a meta-analysis. *Chemical Senses*, *42*(8), 663–673. https://doi.org/10.1093/chemse/bjx049

de Groot, J. H. B., Smeets, M. A. M., Kaldewaij, A., Duijndam, M. J. a, & Semin, G. R. (2012). Chemosignals communicate human emotions. *Psychological Science*, *23*(11), 1417–1424. https://doi.org/10.1177/0956797612445317

de Groot, J. H. B., Smeets, M. A. M., Rowson, M. J., Bulsing, P. J., Blonk, C. G., Wilkinson, J. E., & Semin, G. R. (2015). A Sniff of Happiness. *Psychological Science*, *26*(6), 684–700. https://doi.org/10.1177/0956797614566318

Dolan, R. J., Morris, J. S., & de Gelder, B. (2001). Crossmodal binding of fear in voice and face. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(17), 10006–10010. https://doi.org/10.1073/pnas.171288598

Doty, R. L. (1981). Olfactory communication in humans. *Chemical Senses*, *6*(4), 351–376. https://doi.org/10.1093/chemse/6.4.351

Dunbar, R. I. M., Cornah, L., Daly, F. J., & Bowyer, K. M. (2002). Vigilance in human groups: A test of alternative hypotheses. *Behaviour, 139*(5), 695–711. https://doi.org/10.1163/15685390260136771

Eisenberger, N. I., Master, S. L., Inagaki, T. K., Taylor, S. E., Shirinyan, D., Lieberman, M. D., & Naliboff, B. D. (2011). Attachment figures activate a safety signal-related neural region and reduce pain experience. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(28), 11721–11726. https://doi.org/10.1073/pnas.1108239108

Epley, S. W. (1974). Reduction of the behavioral effects of aversive stimulation by the presence of companions. *Psychological Bulletin, 81*(5), 271–283. https://doi.org/10.1037/h0036389

Fordyce, J. A., & Agrawal, A. A. (2001). The role of plant trichomes and caterpillar group size on growth and defence of the pipevine swallowtail *Battus philenor*. *Journal of Animal Ecology*, *70*(6), 997–1005. https://doi.org/10.1046/j.0021-8790.2001.00568.x

Fridlund, A. J., & Cacioppo, J. T. (1986). Guidelines for Human Electromyographic Research. *Psychophysiology*, *23*(5), 567–589. https://doi.org/10.1111/j.1469-8986.1986.tb00676.x

Friedman, L. (1981). How affiliation affects stress in fear and anxiety situations. *Journal of Personality and Social Psychology*, *40*(6), 1102–1117. https://doi.org/10.1037//0022-3514.40.6.1102

Gallup, A. C., Chong, A., Kacelnik, A., Krebs, J. R., & Couzin, I. D. (2014). The influence of emotional facial expressions on gaze-following in grouped and solitary pedestrians. *Scientific Reports, 4*(1), 1–4. https://doi.org/10.1038/srep05794

Galton, F. (1871). Gregariousness in cattle and in men. *Macmillan's Magazine*, *23*(136), 353–357.

Gerin, W., Milner, D., Chawla, S., & Pickering, T. G. (1995). Social support as a moderator of cardiovascular reactivity in women: A test of the direct effects and buffering hypotheses. *Psychosomatic Medicine, 57*(1), 16–22. https://doi.org/10.1097/00006842-199501000-00003

Gosselin-ildari, A. D., & Koenig, A. (2012). The Effects of Group Size and Reproductive Status on Vigilance in Captive Callithrix jacchus. *American Journal of Primatology*, *74*(7), 613–621. https://doi.org/10.1002/ajp.22013

Hamilton, W. D. (1964). The genetical evolution of social behavior. II. *Journal of Theoretical Biology*, *7*, 17–52. https://doi.org/10.4324/9780203790427-5

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, *31*(2), 295–311. https://doi.org/10.1016/0022-5193(71)90189-5

Hatfield, E., Cacioppo, J. T., & Rapson, R. L. (1993). Emotional Contagion. *Current Directions in Psychological Science*, *2*(3), 96–100. https://doi.org/10.1111/1467-8721.ep10770953

Hawkley, L. C., & Cacioppo, J. T. (2010). Loneliness matters: A theoretical and empirical review of consequences and mechanisms. *Annals of Behavioral Medicine*, *40*(2), 218–227. https://doi.org/10.1007/s12160-010-9210-8

Hawlena, D., & Schmitz, O. J. (2010). Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *American Naturalist*, *176*(5), 537–556. https://doi.org/10.1086/656495

Hennessy, M. B. (1984). Presence of companion moderates arousal of monkeys with restricted social experience. *Physiology and Behavior*, *33*(5), 693–698. https://doi.org/10.1016/0031-9384(84)90033-7

Hennessy, M. B. (1986). Effects of social partners on pituitary-adrenal activity during novelty exposure in adult female squirrel monkeys. *Physiology and Behavior*, *38*(6), 803–807. https://doi.org/10.1016/0031-9384(86)90046-6

Heyes, C., Chater, N., & Dwyer, D. M. (2020). Sinking In: The Peripheral Baldwinisation of Human Cognition. In *Trends in Cognitive Sciences* (Vol. 24, Issue 11, pp. 884–899). Elsevier Ltd. https://doi.org/10.1016/j.tics.2020.08.006

Hornstein, E. A., & Eisenberger, N. I. (2018). A Social Safety Net: Developing a Model of Social-Support Figures as Prepared Safety Stimuli. *Current Directions in Psychological Science*, *27*(1), 25–31. https://doi.org/10.1177/0963721417729036

Hornstein, E. A., Fanselow, M. S., & Eisenberger, N. I. (2016). A Safe Haven: Investigating Social-Support Figures as Prepared Safety Stimuli. *Psychological Science*, *27*(8), 1051–1060. https://doi.org/10.1177/0956797616646580

Hornstein, E. A., Haltom, K. E. B., Shirole, K., & Eisenberger, N. I. (2018). A Unique Safety Signal: Social-Support Figures Enhance Rather Than Protect From Fear Extinction. *Clinical Psychological Science*, *6*(3), 407–415. https://doi.org/10.1177/2167702617743002

Hostinar, C. E., Sullivan, R. M., & Gunnar, M. R. (2014). Psychobiological mechanisms underlying the social buffering of the hypothalamic-pituitary-adrenocortical axis: A review of animal models and human studies across development. *Psychological Bulletin*, *140*(1), 256–282. https://doi.org/10.1037/a0032671

Isbell, L. A. (2006). Snakes as agents of evolutionary change in primate brains. *Journal of Human Evolution*, *51*(1), 1–35. https://doi.org/10.1016/j.jhevol.2005.12.012

Isbell, L. A. (2009). *The fruit, the tree, and the serpent : why we see so well*. Harvard University Press.

Jacobs, W. J., & LoLordo, V. M. (1977). The sensory basis of avoidance responding in the rat. Relative dominance of auditory or visual warning signals and safety signals. *Learning and Motivation*, *8*(4), 448–466. https://doi.org/10.1016/0023-9690(77)90045-5

Kahneman, D., Krueger, A. B., Schkade, D. A., Schwarz, N., & Stone, A. A. (2004). A survey method for characterizing daily life experience: The day reconstruction method. *Science*, *306*(5702), 1776–1780. https://doi.org/10.1126/science.1103572

Kameda, T., & Tamura, R. (2007). “To eat or not to be eaten?” Collective risk-monitoring in groups. *Journal of Experimental Social Psychology*, *43*(2), 168–179. https://doi.org/10.1016/j.jesp.2006.02.003

Kikusui, T., Takigami, S., Takeuchi, Y., & Mori, Y. (2001). Alarm pheromone enhances stress-induced hyperthermia in rats. *Physiology and Behavior*, *72*(1–2), 45–50. https://doi.org/10.1016/S0031-9384(00)00370-X

Kikusui, T., Winslow, J. T., & Mori, Y. (2006). Social buffering: Relief from stress and anxiety. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*(1476), 2215–2228. https://doi.org/10.1098/rstb.2006.1941

Kirschbaum, C., Klauer, T., Filipp, S.-H., & Hellhammer, D. H. (1995). Sex-Specific Effects of Social Support on Cortisol and Subje... : Psychosomatic Medicine. *Psychosomatic Medicine*, *57*(1), 23–31. https://journals.lww.com/psychosomaticmedicine/Abstract/1995/01000/Sex_Specific_Effects_of_Social_Support_on_Cortisol.4.aspx

Kiyokawa, Y., Shimozuru, M., Kikusui, T., Takeuchi, Y., & Mori, Y. (2006). Alarm pheromone increases defensive and risk assessment behaviors in male rats. *Physiology and Behavior*, *87*(2), 383–387. https://doi.org/10.1016/j.physbeh.2005.11.003

Krahé, C., Springer, A., Weinman, J. A., & Fotopoulou, A. (2013). The social modulation of pain: Others as predictive signals of salience - a systematic review. In *Frontiers in Human Neuroscience* (Vol. 7, Issue JUL). Frontiers Media S. A. https://doi.org/10.3389/fnhum.2013.00386

Kuroda, K., & Kameda, T. (2019). You watch my back, I'll watch yours: Emergence of collective risk monitoring through tacit coordination in human social foraging. *Evolution and Human Behavior*, *40*(5), 427–435. https://doi.org/10.1016/J.EVOLHUMBEHAV.2019.05.004

LeDoux, J. E. (1996). *The emotional brain : the mysterious underpinnings of emotional life*. Simon & Schuster.

LeDoux, J. E. (2014a). Coming to terms with fear. *Proceedings of the National Academy of Sciences*, *111*(8), 2871–2878. https://doi.org/10.1073/PNAS.1400335111

LeDoux, J. E. (2014b). Comment: What's basic about the brain mechanisms of emotion? *Emotion Review*, *6*(4), 318–320. https://doi.org/10.1177/1754073914534506

LeDoux, J. E. (2015). *Anxious : using the brain to understand and treat fear and anxiety* (1st ed.). Penguin Books.

Lima, S. L. (1990). The influence of models on the interpretation of vigilance. In M. Bekoff & D. Jamieson (Eds.), *Interpretation and Explanation in the Study of Animal Behavior: Vol. 2. Explanation, Evolution and Adaptation.* (pp. 246–267). Westview Press.

Lundström, J. N., & Olsson, M. J. (2010). Functional neuronal processing of human body odors. *Vitamins and Hormones*, *83*(C), 1–23. https://doi.org/10.1016/S0083-6729(10)83001-8

McEwen, B. S. (2000). Stress, definition and concepts of. In G. Fink (Ed.), *Encyclopedia of stress* (pp. 508–509). Academic Press.

McEwen, B. S. (2008). Central effects of stress hormones in health and disease: Understanding the protective and damaging effects of stress and stress mediators. In *European Journal of Pharmacology* (Vol. 583, Issues 2–3, pp. 174–185). NIH Public Access. https://doi.org/10.1016/j.ejphar.2007.11.071

Michelena, P., Pillot, M. H., Henrion, C., Toulet, S., Boissy, A., & Bon, R. (2012). Group size elicits specific physiological response in herbivores. *Biology Letters*, *8*(4), 537–539. https://doi.org/10.1098/rsbl.2012.0197

Miller, G. E., Chen, E., & Parker, K. J. (2011). Psychological Stress in Childhood and Susceptibility to the Chronic Diseases of Aging: Moving Toward a Model of Behavioral and Biological Mechanisms. *Psychological Bulletin*, *137*(6), 959–997. https://doi.org/10.1037/a0024768

Morris, J. S., Frith, C. D., Perrett, D. I., Rowland, D., Young, A. W., Calder, A. J., & Dolan, R. J. (1996). A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature*, *383*(6603), 812–815. https://doi.org/10.1038/383812a0

Mujica-Parodi, L. R., Strey, H. H., Frederick, B., Savoy, R., Cox, D., Botanov, Y., Tolkunov, D., Rubin, D., & Weber, J. (2009). Chemosensory cues to conspecific emotional stress activate amygdala in humans. *PLoS ONE*, *4*(7). https://doi.org/10.1371/journal.pone.0006415

Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, *108*(3), 483–522. https://doi.org/10.1037/0033-295X.108.3.483

Olofsson, J. K., Ericsson, E., & Nordin, S. (2008). Comparison of chemosensory, auditory and visual event-related potential amplitudes: Cognition and Neurosciences. *Scandinavian Journal of Psychology*, *49*(3), 231–237. https://doi.org/10.1111/j.1467-9450.2008.00647.x

Pause, B. M. (2017). Human Chemosensory Communication. In A. Buettner (Ed.), *Springer Handbook of Odor* (pp. 987–1010). Springer.

Pause, B. M., Haberkorn, K., Eggert, F., Müller-Ruchholtz, W., Bestmann, H. J., & Ferstl, R. (1997). Fractionation and bioassay of human odor types. *Physiology and Behavior*, *61*(6), 957–961. https://doi.org/10.1016/S0031-9384(97)00013-9

Pause, B. M., & Krauel, K. (2000). Chemosensory event-related potentials (CSERP) as a key to the psychology of odors. *International Journal of Psychophysiology*, *36*(2), 105–122. https://doi.org/10.1016/S0167-8760(99)00105-1

Pourtois, G., Grandjean, D., Sander, D., & Vuilleumier, P. (2004). Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cerebral Cortex*, *14*(6), 619–633. https://doi.org/10.1093/cercor/bhh023

Prehn-Kristensen, A., Wiesner, C., Bergmann, T. O., Wolff, S., Jansen, O., Mehdorn, H. M., Ferstl, R., & Pause, B. M. (2009). Induction of empathy by the smell of anxiety. *PLoS ONE*, *4*(6), e5987. https://doi.org/10.1371/journal.pone.0005987

Prehn, A., Ohrt, A., Sojka, B., Ferstl, R., & Pause, B. M. (2006). Chemosensory anxiety signals augment the startle reflex in humans. *Neuroscience Letters*, *394*(2), 127–130. https://doi.org/10.1016/j.neulet.2005.10.012

Pulliam, H. R. (1973). On the advantages of flocking. In *Journal of Theoretical Biology* (Vol. 38, Issue 2, pp. 419–422). J Theor Biol. https://doi.org/10.1016/0022-5193(73)90184-7

Raskin, D. C. (1973). Attention and Arousal. In W. F. Prokasy & D. C. Raskin (Eds.), *Electrodermal Activity in Psychological Research* (pp. 125–156). Academic Press.

Reason, J. T. (1997). *Managing the Risks of Organizational Accidents*. Ashgate. https://doi.org/10.4324/9781315543543

Rieucau, G., Morand-Ferron, J., & Giraldeau, L. A. (2010). Group size effect in nutmeg mannikin: Between-individuals behavioral differences but same plasticity. *Behavioral Ecology*, *21*(4), 684–689. https://doi.org/10.1093/beheco/arq039

Rigoulot, S., & Pell, M. D. (2012). Seeing emotion with your ears: Emotional prosody implicitly guides visual attention to faces. *PLoS ONE*, *7*(1), 30740. https://doi.org/10.1371/journal.pone.0030740

Roberts, S. C., Havlíček, J., & Schaal, B. (2020). Human olfactory communication: current challenges and future prospects. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1800), 20190258. https://doi.org/10.1098/rstb.2019.0258

Rocha, M., Parma, V., Lundström, J. N., & Soares, S. C. (2018). Anxiety Body Odors as Context for Dynamic Faces: Categorization and Psychophysiological Biases. *Perception*, *47*(10–11), 1054–1069. https://doi.org/10.1177/0301006618797227

Rubin, D., Botanov, Y., Hajcak, G., & Mujica-Parodi, L. R. (2012). Second-hand stress: inhalation of stress sweat enhances neural response to neutral faces. *Social Cognitive and Affective Neuroscience*, *7*(2), 208–212. https://doi.org/10.1093/scan/nsq097

Semin, G. R., & de Groot, J. H. B. (2013). The chemical bases of human sociality. *Trends in Cognitive Sciences*, *17*(9), 427–429. https://doi.org/10.1016/j.tics.2013.05.008

Simpson, G. G. (1953). The Baldwin Effect. *Evolution*, *7*(2), 110. https://doi.org/10.2307/2405746

Slovic, P. (1987). Perception of risk. *Science*, *236*(4799), 280–285. https://doi.org/10.1126/science.3563507

Slovic, P. (1999). Trust, emotion, sex, politics, and science: Surveying the risk- assessment battlefield. *Risk Analysis*, *19*(4), 689–701. https://doi.org/10.1023/A:1007041821623

Smeets, M. A. M., Rosing, E. A. E., Jacobs, D. M., van Velzen, E., Koek, J. H., Blonk, C., Gortemaker, I., Eidhof, M. B., Markovitch, B., de Groot, J. H. B., & Semin, G. R. (2020). Chemical fingerprints of emotional body odor. *Metabolites*, *10*(3). https://doi.org/10.3390/metabo10030084

Smith, E. R., Mackie, D. M., & Claypool, H. M. (2015). *Social Psychology* (Fourth).

Psychology Press.

Solomon, H., Solomon, L. Z., Arnone, M. M., Maur, B. J., Reda, R. M., & Roth, E. O. (1981). Anonymity and helping. *Journal of Social Psychology*, *113*(1), 37–43. https://doi.org/10.1080/00224545.1981.9924347

Stienen, B. M. C., & de Gelder, B. (2011). Fear Modulates Visual Awareness Similarly for Facial and Bodily Expressions. *Frontiers in Human Neuroscience*, *5*. https://doi.org/10.3389/fnhum.2011.00132

Stienen, B. M. C., Tanaka, A., & de Gelder, B. (2011). Emotional Voice and Emotional Body Postures Influence Each Other Independently of Visual Awareness. *PLoS ONE*, *6*(10), e25517. https://doi.org/10.1371/journal.pone.0025517

Susskind, J. M., Lee, D. H., Cusi, A., Feiman, R., Grabski, W., & Anderson, A. K. (2008). Expressing fear enhances sensory acquisition. *Nature Neuroscience*, *11*(7), 843–850. https://doi.org/10.1038/nn.2138

Taylor, S. E., Burklund, L. J., Eisenberger, N. I., Lehman, B. J., Hilmert, C. J., & Lieberman, M. D. (2008). Neural Bases of Moderation of Cortisol Stress Responses by Psychosocial Resources. *Journal of Personality and Social Psychology*, *95*(1), 197–211. https://doi.org/10.1037/0022-3514.95.1.197

Thorsteinsson, E. B., & James, J. E. (1999). A meta-analysis of the effects of experimental manipulations of social support during laboratory stress. *Psychology and Health*, *14*(5), 869–886. https://doi.org/10.1080/08870449908407353

Tkaczynski, P., MacLarnon, A., & Ross, C. (2014). Associations between spatial position, stress and anxiety in forest baboons Papio anubis. *Behavioural Processes*, *108*, 1–6. https://doi.org/10.1016/j.beproc.2014.08.006

Voellmy, I. K., Goncalves, I. B., Barrette, M. F., Monfort, S. L., & Manser, M. B. (2014). Mean fecal glucocorticoid metabolites are associated with vigilance, whereas immediate cortisol levels better reflect acute anti-predator responses in meerkats. *Hormones and Behavior*, *66*(5), 759–765. https://doi.org/10.1016/j.yhbeh.2014.08.008

Vogt, J. L., Coe, C. L., & Levine, S. (1981). Behavioral and adrenocorticoid responsiveness of squirrel monkeys to a live snake: Is flight necessarily stressful? *Behavioral and Neural Biology*, *32*(4), 391–405. https://doi.org/10.1016/S0163-1047(81)90826-8

Wawra, M. (1988). Vigilance Patterns in Humans. *Behaviour*, *107*(1–2), 61–71. https://doi.org/10.1163/156853988X00197

Wetter, S., Polich, J., & Murphy, C. (2004). Olfactory, auditory, and visual ERPs from single trials: No evidence for habituation. *International Journal of Psychophysiology*, *54*(3), 263–272. https://doi.org/10.1016/j.ijpsycho.2004.04.008

Williams, G. C. (1966). *Adaptations and Natural Selection*. Princeton University Press.

Wilson, D. S. (2007). *Evolution for everyone: How Darwin's theory can change the way we think about our lives*. Delta.

Wirtz, P., & Wawra, M. (1986). Vigilance and Group Size in Homo sapiens. *Ethology*, *71*(4), 283–286. https://doi.org/10.1111/j.1439-0310.1986.tb00592.x

Younger, J., Aron, A., Parke, S., Chatterjee, N., & Mackey, S. (2010). Viewing Pictures of a Romantic Partner Reduces Experimental Pain: Involvement of Neural Reward Systems. *PLoS ONE*, *5*(10), e13309. https://doi.org/10.1371/journal.pone.0013309

Zheng, Y., You, Y., Farias, A. R., Simon, J., Semin, G. R., Smeets, M. A. M., & Li, W. (2018). Human chemosignals of disgust facilitate food judgment. *Scientific Reports*, *8*(1), 1–10. https://doi.org/10.1038/s41598-018-35132-w

Zhou, W., & Chen, D. (2009). Fear-related chemosignals modulate recognition of fear in ambiguous facial expressions. *Psychological Science*, *20*(2), 177–183. https://doi.org/10.1111/j.1467-9280.2009.02263.x

Zucker, R. A., Manosevitz, M., & Lanyon, R. I. (1968). Birth order, anxiety, and affiliation during a crisis. *Journal of Personality and Social Psychology*, *8*(4 PART 1), 354–359. https://doi.org/10.1037/h0025574