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Social cognition under threat anxiety-inducing contexts

Morgan Beurenaut

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THÈSE DE DOCTORAT
DE L'UNIVERSITÉ PSL

Préparée à L'Ecole Normale Supérieure de Paris

**SOCIAL COGNITION UNDER THREAT ANXIETY
INDUCING CONTEXTS**

Soutenue par

Morgan BEAURENAUT

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I would like to thank the jury members for having agreed to review my work.

“To survive, you have to care about yourself first. It doesn’t mean that you don’t care for others, but you have to survive first.”

Jean Decety

“For each solution, its new problem”

Ozeray & Bearenaut featuring Matlab

FOREWORD

During the gap-year following my master's degree, I have joined Julie Grèzes from the Laboratory of Cognitive and Computational Neurosciences (LNC², PSL Research University) in her Social Group. In June 2017, we applied to the Brain, Cognition, and Behavior (ED3C) doctoral school funding to obtain a Ph.D. scholarship.

Formerly, Julie Grèzes and Guillaume Dezeache had obtained a CNRS funding from a call-for-project entitled 'CNRS Recherche Attentats'. Its purpose was to offer financial support to investigate impacts of attacks on society. They led the project 'One for all? Individual and collective reactions to threat during Paris' attack', an interview-type study aiming at better defining the typology of behaviors arising under deadly situations as well as their underlying motivations. They showed that survivors of the Bataclan attacks often reported having set up social strategies under threat, but it seemed that this maintenance of sociality could be due to different motivations depending on the costs and benefits of the different supportive actions.

If this study brought encouraging results to defend that, contrary to popular belief, social cognition seems to be working under threat, several limitations remain. First, interviews took place *a posteriori* and then, some elements of the subjective reports could have been modified. So, the validity of these data can be debate. In addition, this type of study informs us of the kind of actions observed under threat, but it does not depict the cognitive mechanisms involved in their planning.

To resolve this question, we designed the 'Social Cognition Under Threat Anxiety-Inducing Contexts' Ph.D. project, which investigated how the 'sense of being threatened' modifies important cognitive mechanisms involved during human social interactions. Our research therefore focuses on the essential question of how danger transforms sociality, that is, how threat endangers the relationship to one another. We assumed that, if social cognition is maintained under threat, anxiety should either maintain or enhance the perception of social signals conveyed by our fellow human beings as well as the integration of others in our action plans. Conversely, these mechanisms should be shut down if sociality is interrupted under threat. Depending on whether the maintenance of social cognition represents an advantage for survival or not, both results could be observed. To test our hypothesis, we first validated a paradigm that creates threat anxiety-inducing context in the lab. We investigated how it impacts action co-representation and perception of social cues conveyed by human faces, while modifying the relevance of the interaction or the social meaning of the transmitted cues.

Ultimately, this project was designed to study the way the perception of danger in a laboratory-controlled context modifies (how and why) social cognition, both at the perception and action levels.

The theoretical part of this thesis will first introduce the well-studied stimuli called the threatening signals. Then, two points of view will be faced: while, in neuroscience, theoretical models about human defensive reactions only take into account individual reaction, field studies in social psychology often report supportive behavior under threat. To match the results coming from these two extremely different domains, we will discuss how social mechanisms usually measured at lab can explain the variability of social and asocial behavior described by research in social psychology. The experimental part will present 3 studies: (i) the validation of the threat-of-scream paradigm to create threat context in the lab and the impact of this procedure (ii) on action co-representation and (iii) on perception of fear emotional displays. To conclude, the general discussion will summarize the main findings of this Ph.D. thesis. Also, I will try to build a theoretical bridge between neuroscience and social psychology by using my cognitive psychology approach to investigate collective reaction under threat.

“While neuroscientists assume that the perception of threat triggers the development and the emergence of self-preservative responses, it was known from more than 50 years in sociology departments that people are actually very supporting and prosocial in that contexts. So, there is a need for interdisciplinarity in this regard” – Guillaume Dezechache, Collective Emotions conference (Paris, 2016). Even if this need is at the origin of my incredible Ph.D project, these last three years have been a really massive challenge because it involves mastering the literature coming from different fields in order to build relevant connections between them. It was particularly difficult to equally distribute the time that I was spending in my appropriation of each field. Finally, I noticed that tracking all these researches was impossible. I needed time to understand that my project alone would not be enough to create convincing bridges between neuroscience, psychology and social science and to provide a perfect framework from all the articles I had read. However, I hope that my effort to put the results acquired in the lab into perspective with the huge framework of collective reactions in deadly contexts will be considered praiseworthy, even if it surely raises many questions and even debates.

THEORETICAL BACKGROUND

CHAPTER 1

HUMAN REACTIONS UNDER THREAT: ARE THEY PREDICTABLE?

An explosion, a tornado, an attack: as diverse as they may be, each of these situations represents a threat (also called stressor) to an individual's homeostasis. It is then necessary to quickly set up an adapted response to restore the balance. When human beings are faced to a threatening situation, they are surrounded by different kinds of source of information (Haghani, Sarvi, Shahhoseini, & Boltes, 2016). Being able to detect threats and relevant safety cues, as well as initiating efficient defensive responses is essential for the individual's survival (Davidson, Maxwell, & Shackman, 2004; Öhman, 2009; Öhman & Mineka, 2001, Blanchard et al., 2008). This relation between action, perception and threat is central in this thesis.

In this first chapter, I will define what stressors are, describe what responses they induce, and the factors influencing the type of responses. Ultimately, I will ask if we can predict human behavior under threat.

1-Threat: a stimulus inducing motivation to survive

How human brain processes threatening stimuli is one of the most studied topics in neuroscience, as it is relevant for understanding our individual reaction to danger as well as the emergence of anxiety disorders. Threat can be defined as “a statement of an intention to inflict pain, injury, damage, or other hostile action on someone” (Oxford's English dictionaries). Thus, threat is a future-oriented stimulus which is associated with the potential for harm (Scholtz, 2000). It is consequently negatively appraised and responsible for the induction of negative affective emotions as it represents a negative outcome for our well-being, and potentially, our survival. Danger is so much a part of individuals' life that our cognition system is thought to have evolved in response to threat pressures (Ledoux & Daw, 2018; Mobbs, Hagan, Dalgleish, Silston, & Prévost, 2015; Taborsky et al., 2020). Indeed, research on the defensive circuits engaged when organisms are exposed to threatening stimuli suggest they have been shaped through evolution to efficiently favor survival (Öhman, 1993; Öhman & Mineka, 2001), as neural circuits are particularly well conserved across mammals (In rats: Canteras, 2002; In mice: Martinez, Carvalho-Netto, Amaral, Nunes-de-Souza, & Canteras, 2008; In humans: Mobbs et al., 2007). This suggests the existence of a homology of individual defensive reaction across mammals. Across phylogeny, qualitatively different reactions to threat have been selected to enable individuals to avoid a large variety of dangers in their environment (Bolles, 1970; Fanselow & Lester, 1988).

More precisely, it has been proposed that, when exposed to threat, a Central Fear Generator composed of cortical and subcortical brain regions triggers an emotion episode which is composed of (Fanselow & Pennington, 2018): (i) internal autonomic physiological modulations to prepare the body to react (heart rate & respiration (Cannon, 1915; Carrive, 2000; Garfinkel & Critchley, 2016; Lang, Davis, & Öhman, 2000), glycogenolysis (Nirupama, Rajaraman, & Yajurvedi, 2018), pupil dilatation (Van Steenbergen, Band, & Hommel, 2011), (ii) defensive motor actions (Davis, 1992; Fendt & Fanselow, 1999; Perusini & Fanselow, 2015) and (iii) a subjective reportable experience in humans (Panksepp, 1998, 2011). Darwin (Darwin, 1872) argued that emotion episodes play a key role under threat as they prompt improvement of the perception of information inside the surrounding environment and as they interact with motor processes. Aversive emotion stimuli such as snakes, spiders or angry faces are perceptually prioritized (Öhman, 2009): they orient saccadic movements faster and yield more accurate detection than control or non-aversive emotion stimuli (Calvo, Averó, & Lundqvist, 2006; Eastwood, Smilek, & Merikle, 2001; Fox, Griggs, & Mouchlianitis, 2007; Öhman, Flykt, & Esteves, 2001). In addition, threat-related stimuli are known to enhance contrast (Phelps, Ling, & Carrasco, 2006), low spatial-frequency sensitivity (Bocanegra & Zeelenberg, 2009) and search efficiency for task-relevant objects (Becker, 2009). The possibility of being harmed is associated with hypervigilance mechanism (Kastner-Dorn, Andreatta, Pauli, & Wieser, 2018). Moreover, it has been proposed that emotional threatening stimuli generate motivational tendency, i.e. a state of readiness to act (Bradley, Codispoti, Cuthbert, & Lang, 2001; Meaux, El Zein, Mennella, Wyart, & Grèzes, 2020; Mennella, Vilarem, & Grèzes, 2020; Vilarem, Armony, & Grèzes, 2019). To conclude, under threat, the ultimate goal motivating our actions is to survive and the body is consequently prepared for it.

2-Taxonomy of possible defensive reactions under threat

However, to achieve the goal ‘survive’¹, organisms can respond to danger in a various ways as threat contexts are really diverse and can be highly complex (Mobbs, Headley, Ding, & Dayan, 2020). Defensive behaviors are highly selected reactions which increase the survival rate of those who carry out them in an appropriate way (Blanchard & Blanchard, 2008). Defensive reactions are strongly modulated by features of both the threat stimulus and the context in which it is encountered. Several theoretical models have described factors influencing our actions and cognitive processes under threat (i.e., Blanchard & Blanchard, 2008; Fanselow & Lester, 1988; Roelofs, 2017). Studies investigating

¹ Describing the goal of an endangered individual depends on the level of analysis under examination. At the evolutionary level of analysis, cognition has been shaped to survive and reproduce. At the proximal scale of analysis, the goal is to restore homeostasis by avoiding new stressors (i.e. being harmed) and by reaching safety (to ensure well-being). The proximate mechanisms make the fulfilment of the evolutionary function possible. Both levels of analysis can be used to explain our behaviors under threat.

the defensive circuits in non-human species provide evidence for the identification of at least 5 relatively well-defined prototypes of defensive behavior and the contexts in which they take place. Decisions under threat would depend on 5 dimensions intrinsic to threat situations: distance to the danger, threat intensity, ambiguity about the source of the danger, the possibility to escape or to hide. These characteristics would favour 5 different strategies (Blanchard, 1997): freezing, flight, risk assessment, defensive threat (i.e., vocalization, body-posture) and defensive attack. Combinations between these environmental factors and strategies are summarized in **Figure 1-1**, which illustrates the main theoretical models explaining the variability of defensive behaviors. For example, ambiguity is associated with a state of anxiety resulting in assessment and appraisal behaviors, the existence of an emergency exit favors flight behaviors, while proximity to danger without the possibility of escaping or hiding induces a state of fear characterized by defensive threat or attack reactions.

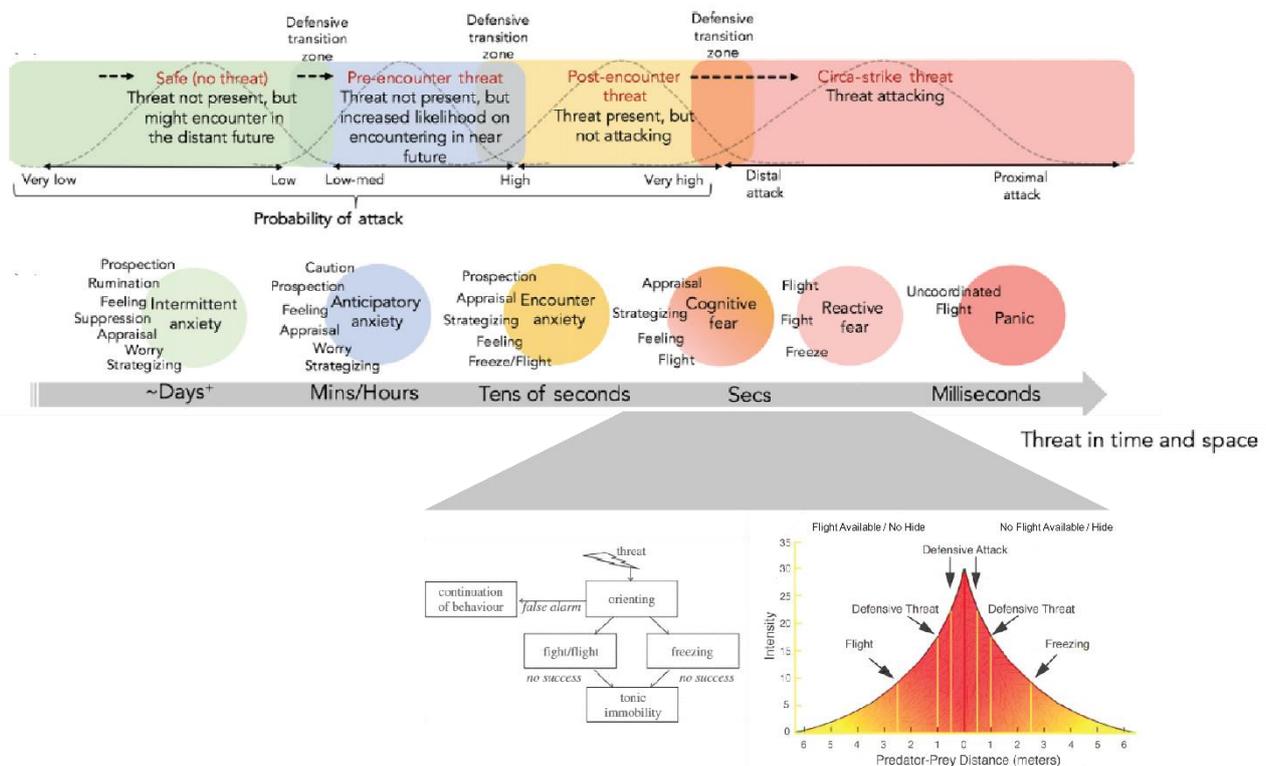


Figure 1-1. Schematic representation of defensive reaction depending of the threat dimension. (Top) The threat imminence continuum running from high- to low-imminence threats. (Middle) A hypothetical model of the different behaviors, cognitions, and emotions depending temporal and space distance to threat continuum. (Bottom). This continuum is influenced by other dimensions which favor particular defensive reactions. Adapted from Blanchard and Blanchard (2008); Mobbs et al. (2020) and Roelofs, (2017).

One of the questions raised by these studies is the following: do these models also predict human reactions to dangers? In order to investigate the congruencies that exist between defensive systems in non-human animal species and humans, Blanchard et al. (Blanchard, Hynd, Minke, Minemoto, & Blanchard, 2001) created 12 scenarios that vary according to the 5 dimensions mentioned above. These scenarios were evaluated by hundreds of participants on the characteristics representing the threat

described (magnitude of threat, escapability, effective distance to the threat, clear dangerousness or presence of a place of concealment) and on the most appropriate strategy to adopt (hide, freeze, run away, threaten to scream or call for help, yell/scream/call for help, threaten to attack, attack/struggle, check out/approach/investigate, look for a weapon, beg/plead for mercy/negotiate). Authors correlated participants' self-reported defensive behaviors and parameters of each scenario (see **Table 1-1**).

<ol style="list-style-type: none"> (1) You are walking alone in an isolated but familiar area when a menacing stranger suddenly jumps out of the bushes to attack you (2) You are alone in an elevator late at night. As it stops and the doors open, a menacing stranger rushes in to attack you, blocking the door (3) You are alone in a car on your way home. While stopped at a traffic signal, an angry stranger begins banging on your car window and yelling threatening things at you (4) Driving along a two-lane road, you see in your rearview mirror that a car is dangerously tailgating you. They cannot pass and begin honking their horn aggressively at you while continuing to follow too closely (5) It is past midnight and you are walking through an unfamiliar part of town. As you round a corner, you accidentally run into a man. He becomes angry and shoves you (6) You and someone you do not really know that well are standing around and talking in an empty parking lot. The acquaintance begins to shove and push you. You are unsure whether s/he (same sex as you,) is serious or just kidding around (7) You are outside in a park area at night when you see a menacing stranger with a knife about 30 ft. away directly approaching you. It is obvious the person is planning to attack you (8) You are alone as you exit an empty campus building late one night. Just as you get outside, you feel a hand grab your arm (9) You are sleeping in bed during the night, but suddenly wake up thinking you have heard a suspicious noise. It is dark and you are alone (10) You are alone at home one night about to go to bed when the phone rings. You answer it, and there is an unfamiliar voice on the other end. It tells you that they are right outside of your house and hangs up (11) Coming home one day, you find an unexpected shoebox-sized package waiting for you by the mailbox. As you sit down to open it, you notice a faint ticking sound that appears to come from inside the package (12) Alone at home one night, you have settled down to read a book when you hear some movement right outside of your window. You cannot see anything, but when you listen more closely, it sounds like people whispering 						
Rating	Behavior					
	Attack	Run	Freeze	Risk Assess	Scream	Hide
Dangerousness	0.475	0.464	0.308	-0.825*	0.381	-0.212
Inescapability	0.762*	-.101	0.432	-0.516	0.158	-0.435
Distant (far)	-0.592*	0.398	-0.628*	-0.017	0.487	0.653*
Not ambiguous	0.525	0.504	0.324	-0.892*	0.128	-0.175
Conceal/Protect	-0.7674*	-0.023	-0.030	0.408	-0.0313	0.598*

Table 1-1. The threat scenario questionnaire created by Blanchard et al. (2001) and the correlation results between parameters of scenario and behavior chosen.

Most of the predictions derived from the animal literature were confirmed in this study. First, ambiguity correlates positively with the risk assessment rate, and attacking behavior correlates positively with proximity to the target and with the inescapability of the scenario. Second, hiding behaviors correlate positively with the conceal/protect scores. However, one result does not meet hypotheses from the animal literature: escaping behavior should correlate negatively with the inescapability of the scenario (which is not the case here). The authors argue that this lack of correlation

can be explained by the ambiguity factor, which would prevail over the inescapability factor. In order to verify this hypothesis, they carried out a post-doc analysis of the same correlations between scenarios in which the source of the danger is very ambiguous and scenarios in which it is not. As predicted, they observed a positive correlation in the less ambiguous scenarios. All these results suggest that the same patterns of defensive strategies identified in studies on non-human animals occur also in humans.

Besides, these results have been replicated over three studies in three different countries: Brazil (Shuhama, Del-Ben, Loureiro, & Graeff, 2008), USA (Harrison, Ahn, & Adolphs, 2015) and UK (Perkins & Corr, 2006), suggesting that these results are robust but also not very sensitive to cultural variations. Based on their collected data, Harrison et al. (Harrison et al., 2015) created a data-driven decision tree predicting subjects' choice of defensive responses to threat scenarios depending on the deterministic factors of each scenario. This decision tree was able to correctly predict the most popular response for all scenarios and performed five times better than chance at predicting individual participants' responses. All these studies suggest that our theoretical models of understanding human behavior in threat situations appear to be valid since they are able to predict a large part of our behavior in a wide variety of situations (see **Figure 1-2**).

But in that case, how can the unexplained variability be determined? A first and a simplest answer is inter-individual variability. Obviously, we are not all acting the same way. For example, Perkins and Corr (Perkins & Corr, 2006) investigated which traits (such as anxiety) influenced our defensive strategies. To do so, they categorized strategies along two axes: intensity of the defensive reaction (weak to strong) and trajectory direction of the action (away from or towards the threat). To illustrate, attacking behavior is a high-intensity threat-directed behavior, risk-assessment is also a threat-directed but a low-intensity behavior. Also, freezing is described as neutral because no action is done, and the individual remains at the same distance from threat, whereas flight is an action directed away from the threat (it takes us away from it). The authors then showed that trait anxiety favors low-intensity approach behavior and that punishment sensitivity scores (measured using the BIS scale of the BIS/BAS questionnaire created by Carver & White (Carver & White, 1994)) were positively correlated with the probability of avoiding threat. Another explanation would be that the models proposed by Blanchard, Fanselow or Roelofs lack one or more situational factors to explain the set of behaviors observed in threat contexts.

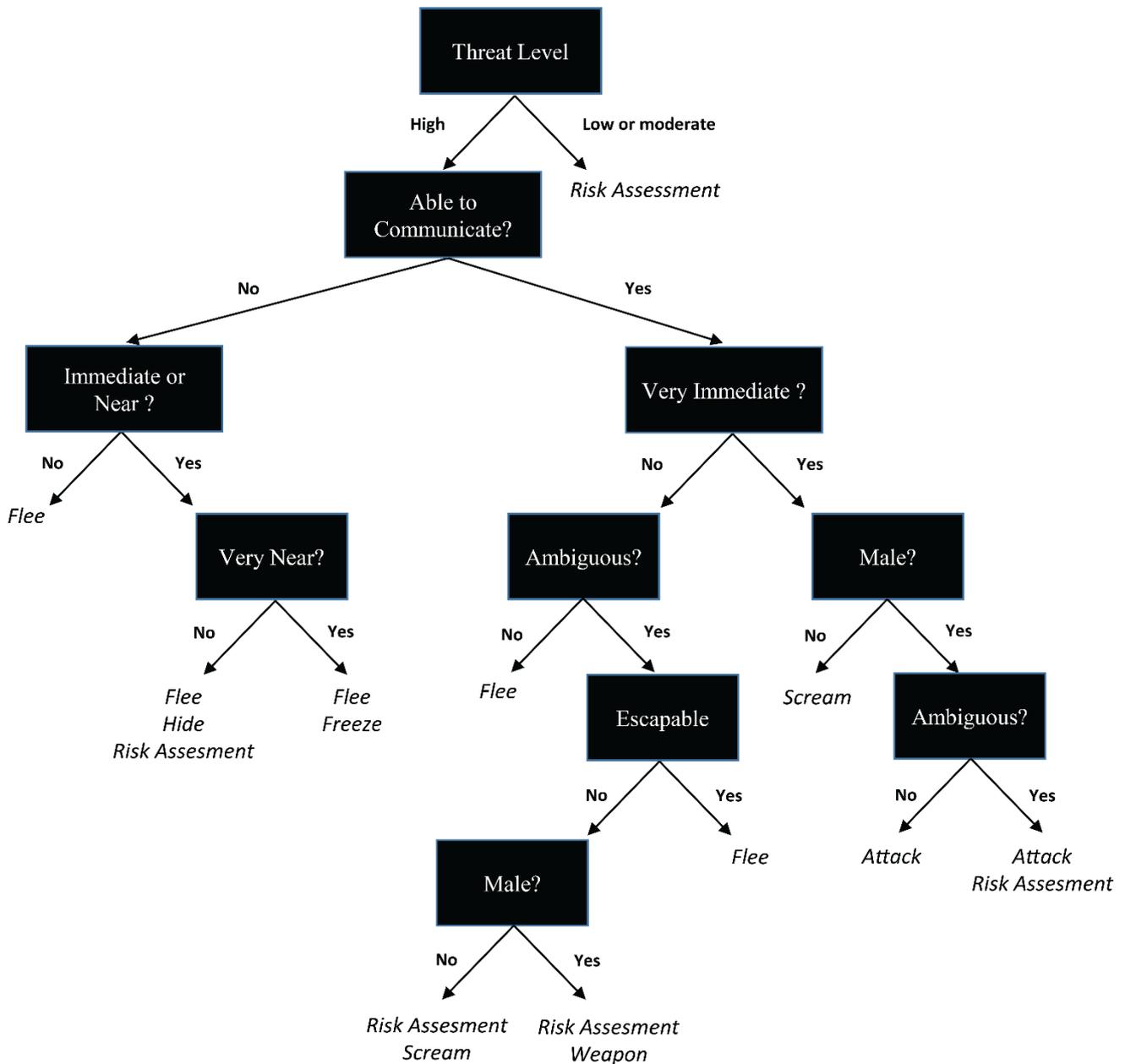


Figure 1-2. Decision Tree for Defensive Behaviors to Threatening Scenarios. Decision tree predicting the defensive behavior chosen by the majority of subjects based on intrinsic characteristics of the threat scenario

3-Danger can be a social experience

Critically, exposure to threat are almost always social episodes. Indeed, it turns out that shouting/asking for help is the most defensive response given in some scenarios: according to the participants, seeking assistance and/or collaboration seems to be the appropriate response in certain situations. Furthermore, it is interesting to note that in Harrison et al. (Harrison et al., 2015), a negative correlation of -0.8 is observed between the amount of help perceived by participants in the scenarios and the probability of freezing (correlation which is not discussed by the authors). This result suggests that individuals would be more active in the presence of another human-being. However, this correlational analysis does not allow us to identify which type of behaviors the presence of other human

fellows would favor. One reason could be that the possibility of receiving assistance is extremely implicit in the scenarios' description, which prevents from clearly identifying a dominant strategy in contexts where social support is available.

While evolution has played an important role in the selection of our response to threatening stimuli, it has also shaped our cognition, generation after generation, so that problem solving can be carried out in groups. If cognition and threat have co-evolved together and if cognition and cooperation have also co-evolved together, it seems relevant to think that cognition, cooperation and threat are intimately linked, and that cooperation plays a major role in response to threat situations. Of interest, tend-and-befriend theoretical model originally developed by Taylor et al. (Taylor et al., 2000) seems particularly in line with these assumptions. This evolutionary model describes two types of behavior exhibited by organisms in response to threat: protection of offspring (tending) and seeking out their social group for mutual defense (befriending). These strategies represent behavioral sequences selected by natural selection as efficient to increase probability of survival. Under threat, tending behavior such as protecting offspring while blending into the environment reduce probability to be located by the source of threat (e.g., predators). By contrast, befriending behaviors enhance grouping which is associated with numerous benefits inside the social group to maximize protection. In his book 'Antipredator Defenses in birds and Mammals', Tom Caro (Caro, 2005) reports benefits of the collective reaction organization in threatening situations. Firstly, working in a group allows the distribution of vigilance, reducing the cost of vigilance provided by each individual, and allows individuals to alert one another (using alarm calls) about the presence of a threat. Then, by being part of a group, not only the probability of being captured decreases (e.g., if the predator only captures one individual, the probability of being caught is $1/n$, with n being the size of the group) but also, individuals can set up collective attacks (i.e., mobbing). Finally, it has been observed in corvids (Emery, Seed, Von Bayern, & Clayton, 2007; Fraser & Bugnyar, 2010), elephants (Plotnik & de Waal, 2014), canids (Cools, Van Hout, & Nelissen, 2008; Palagi & Cordoni, 2009), rats (Burkett et al., 2016) and great apes (Clay & de Waal, 2013; De Waal & Yoshihara, 1983) that consoling behavior is oriented towards individuals in distress, suggesting that empathic mechanisms take place following collective exposure to threat. Thus, so-called tend-and-befriend defensive reactions appear to be a particularly relevant strategies when individuals collectively face danger.

Surprisingly, in studies of human defensive systems, the presence of social partners is not considered, while humans are a hyper-social species (Dunbar, 2007; Dunbar, 2012; Hill & Dunbar, 2003). Two main reasons can be found. The first one is technical: the investigation of cognitive mechanisms is much simpler in social isolation than in a group, because it would mean being able to accommodate

several participants and to measure their behavior/(neuro)physiological state at the same time. Moreover, the experimental context would be more unpredictable in presence of several participants but also less controlled (more confounding factors and variability in the data). The second reason is that believing our reactions to be selfish and highly self-preservative in threatening situations is a common thought (Dezecache, 2015). This popular belief posits that, in situations of collective danger, individuals would panic, i.e. they would be subject to an "acute fear reaction, marked by a loss of self-control followed by irrational and anti-social flight behavior" (Quarantelli, 1954). It would manifest as a feeling of instinctive, irrational and uncontrollable fear that could propagate from one individual to another, making their actions reckless and selfish (Alexander, 2007; Drury, Novelli, & Stott, 2013). In real life, this would lead to a competition for the few escape routes, each individual behaving in order to maximize his or her own chances of escape, even if it results in deadly trampling and jeopardizing the survival of other members of the group to one's own benefit (Brown, 1954).

This representation of selfish behavior in response to danger is extremely rooted in people's mind (Wester, 2011). In a study in which 354 American subjects were questioned about their beliefs about people's reactions in emergency contexts (Wenger, 1975), 83% shared this opinion, despite the fact that they had personally never faced a situation of collective danger (79% of them). These results were recently replicated with a French sample (Le Montr er, 2020), supporting that panic is also quite prevalent in citizens' representation of crowds in emergency situations. More surprisingly, this idea of panic is also particularly robust even for people dealing with emergency situations (firemen, security guards and policemen) but in a lesser way than in general population (Drury et al., 2013; Nogami, 2018). This false belief most likely impacts the way in which sociality has been considered an explanatory factor for our behavior in situations of danger: indeed, if the social link is considered broken during threatening situations, then the investigation of collective reactions is meaningless.

Yet, among social science studies that have collected and analyzed reports from individuals who actually experienced emergency situations, individual and collective behaviors described in such contexts depict a very different vision: there is in fact a relative absence of collective panic, and a prevalence of pro-social behavior over self-preservative ones (Dezecache, 2015; Drury, 2018; Drury, Cocking, & Reicher, 2009a). The number of examples based on the disaster literature illustrating the maintenance of social bonds is very large and is still growing. The most common witnessed behaviors are helping (i.e. to give help) and cooperation (i.e. mutual support). Chertkoff and Kushigian (Chertkoff & Kushigian, 1999) identified that the evacuation of the World Trade Center during the 1993 bombing was calm, and people provided support to one another, despite the darkness, smoke and uncertainty. Same results were obtained in Proulx and Fahy's study (Fahy & Proulx, 2005) of the

September 11 attacks. Even though people were conscious of the high level of danger (85% most of the participants had moderate or full knowledge of what had happened), people perceived others as reacting calmly and helping each other (found in 46% of the reports). In the context of the London bombings of July 7th of 2005 (Drury, Cocking, & Reicher, 2009b), there was also substantial evidence that sociality was preserved (see **Figure 1-3**): survivors reported witnessing (and receiving) help, and many reported providing assistance, including reassuring people, sharing water, physically supporting them during evacuation, checking on others, and even tying tourniquets. Only a small number described personally selfish behaviors (such as pushing others). Similarly, a survey of survivors of Typhoon Haiyan (Philippines) in December 2013 revealed signs of solidarity, especially between individuals who did not know each other (Bartolucci & Magni, 2017).

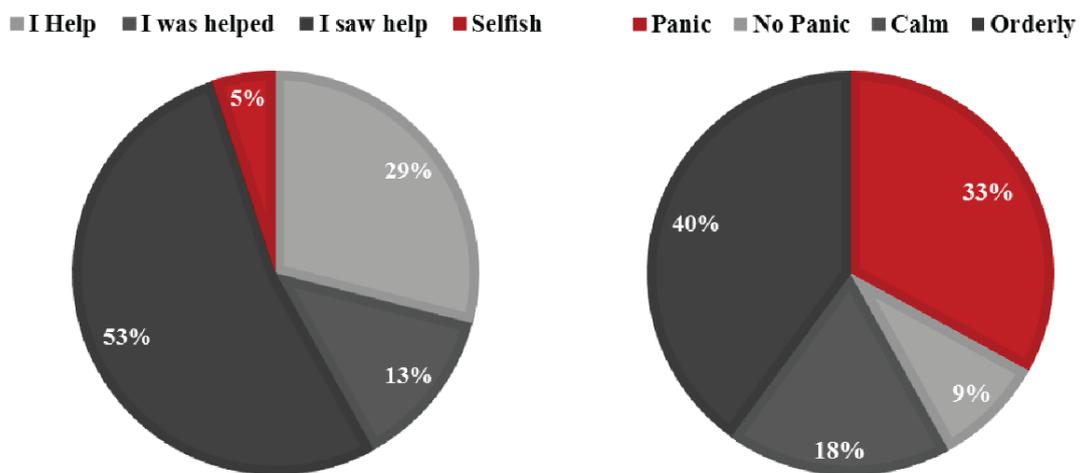


Figure 1-3. Adapted from Drury et al. (2009): coding of people’s experiences, perceptions, behaviors, and feelings during the London bombing attacks reported in newspapers and personal archive accounts

It is important to note that in these situations where the danger is brief, the sense of life-threatening danger is much more long-lasting: after explosions, there is no way of knowing whether a new explosion is coming and whether we need to prepare for a new danger. Thus, the prevalence of cooperative behavior in these disasters does not seem to be explained by the fact that survivors have judged their decision to help to be risk-free (Drury, Cocking, & Reicher, 2009b, 2009a). Moreover, studies reporting many individualistic behaviors are strongly criticized. For example, in the 1903 Iroquois theater fires, where nearly 600 people died, and in the Cocoanut Grove Theater fire in 1942, where nearly 500 people died, it has been claimed that deaths were mainly due to the flight behavior of the crowd. In reality, it turned out that the emergency exits were not adapted and that the number of people present was higher than the maximum authorized (Chertkoff & Kushigian, 1999). As a result, this does not directly foretell a lack of cooperation among crowd members. In fact, it seems that our social cognition is still working under threat (i.e., not interrupted). Besides, our behavior is marked by

the prevalence of supportive behavior. To understand the human reactions under threat, it still remains necessary to investigate factors and motives responsible for maintaining collective actions when we are exposed to danger.

4-Why would sociality be maintained in a situation of danger?

In his 2015 review, Dezechache reports three reasons why sociality would be maintained in a situation of danger. The first one is that social norms (Aguirre, Torres, Gill, & Lawrence Hotchkiss, 2011; Donald & Canter, 1992) would survive in a dangerous situation. The literature reports many cases where "women and children first" or the protection of the elderly have influenced the actions of individuals during disasters. During the sinking of the Titanic, the lifeboats were mainly occupied by women and children (Frey, Savage, & Torgler, 2010). Similarly, during the Beverly Hills Supper Club fire (Johnson, 1988), many newspapers reported that young people were helping the elderly to escape from the facility. These social norms limited competitive behavior and even encouraged social support and pro-social behavior towards the weaker ones. Nevertheless, it would seem that when the probability of survival decreases very rapidly, social norms no longer stand: survival drives can overcome the respect of social norms (Frey et al., 2010). The second reason is proposed by Mawson (Mawson, 2005, 2017) who describes that what drives our behavior in threatening situations is the need for affiliation. When we face a threat, we seek for familiar cues rather than the exit, because the presence of familiar others is responsible for social buffering (i.e., their presence reduces the physiological, endocrinological and subjective response to stress). This affiliation tendency explains why people were shown to turn toward loved ones (even if it means putting oneself in danger) and tend to form clusters of familiar individuals before starting to leave, which is against a primary "fight or flight" reaction under threat. Nevertheless, this theory does not explain the set of prosocial behaviors oriented toward strangers. Finally, the third reason, defended by Drury and colleagues (see Drury, 2018 for a review), argues that sharing a danger together is responsible for creating a shared social identity between victims through experiencing altogether a common fate. As an example, during the London bombing attacks (Drury, Cocking, & Reicher, 2009b), survivors reported their experience using words as "unity", "together", "similarity", "affinity", "part of a group" or "teamness". Of interest, respondents who described experiencing unity also described helping others. Sense of shared or common fate appears to enhance mutually supportive behaviors between crowd members.

In addition, a fourth reason can be raised. Once again, if we place ourselves in a motivational framework, the goal leading our action in a threatening situation is to survive as the functioning of our organism (including its cognitive system) has been shaped by natural selection to reproduce. Then, it is necessary to monitor and overcome obstacles representing a cost for our survival. The majority of

neuroscience research has largely focused on the processing of threat cue. Nevertheless, the environment surrounding us is made up of many elements that can help us maximizing our survival. For example, whether they perceive a weapon or a hiding place, individuals may differ in their preference to fight, flee or freeze. If in some situations, monitoring threat is more instrumental for survival (i.e. use to achieve the goal), sometimes monitoring safety signals, such as potential weapons or escape routes, can be more relevant for reaching safety (Vogt, Koster, & De Houwer, 2017). But what if others were a relevant resource for survival? Befriending behaviors (in reference to tend-and-befriend model, Taylor, 2006; Taylor et al., 2000) in animal seems to be quite relevant to reduce probability of being hurt under threat, anxiety and individual cost in defensive actions (Caro, 2005). It is very likely that mechanisms allowing for tend-and-befriend defensive reactions have been selected by evolution (Taylor & Master, 2011). Consequently, we believe that conspecifics can bring safety, in a similar way to the carrying of a weapon or the proximity of a hiding place. This assumption is in line with Rofé's utility affiliative theory (Rofé, 1984), whereby affiliative tendencies depend on the perceived or anticipated cost-benefit ratio of being with another to one's own ability to cope with anxiety. Hence, the greater the probability being with another will help coping with anxiety (by either eliminating or decreasing the source of danger or by providing social support), the stronger the tendency to affiliate. Altogether, it suggests that the brain appraises the value of all cues available in the surrounding environment, in particular the social ones, to choose the better strategies based on a cost-benefit ratio. If one wants to fully predict defensive reaction under threat, it is fundamental to integrate sociality as a relevant factor. However, to understand the role of sociality in survival, it is necessary to understand whether and why social cognition is working under threat and clearly identify the benefits of the different social strategies that can take place.

Two studies led by Dezechache et al. support this theoretical position. In a first study (Dezechache, Grèzes, & Dahl, 2017), the authors took advantage of a series of photographs freely accessible online, of visitors participating to a haunted house attraction. Among spontaneous reactions, two salient behaviors were particularly frequent in this picture: hiding behind as well as gripping another person. While the role of hiding is clearly to protect oneself, the motives of gripping is more ambiguous. This affiliative reaction can be underlain by two opposite functions: gripping could be either produced to protect oneself, or as a way to protect others. To investigate the motivational correlates of affiliative behaviors in dangerous situation, authors quantified the proportion of gripping and notably mutual gripping depending of the size of the groups, the composition of groups and the distance of members to the source of threat (see **Figure 1-4**). They observed that gripping is a common phenomenon as it has been observed 75% of the time suggesting that one of the primary reactions to danger can be

finding a social partner. However, as group size increased, the number of mutual gripping (i.e. reciprocal protection) decreased, suggesting that gripping behavior most probably reflects a self-preservative motivation. Coherently, they outlined two findings: they first observed the nearest the individuals are from the source of threat, the less they received social support. In addition, they noticed that juveniles are the age-class who received the least of reciprocal protection. Altogether, these results suggested that affiliation can be supported by instrumental motives as social contacts were toward people with the more resources to help.

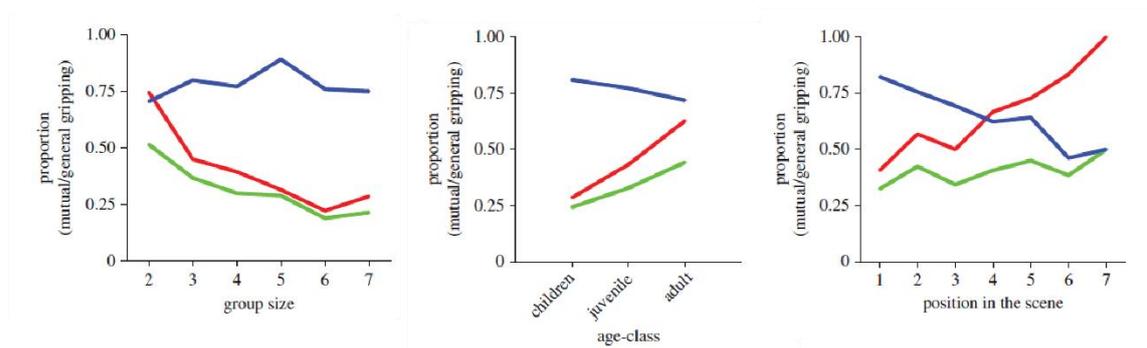


Figure 1-4. (Top) Example of photographs redrawn (note that real photographs were used by the authors for coding; they can be found at: <https://www.flickr.com/photos/nightmaresfearfactory>). Grasping, mutual grasping, hiding and absence of contact were observable on pictures. (Bottom part) Results from the study: Proportion of gripping (blue line), mutual gripping (green line) and ratio of gripping being mutual (red line) relative to (left) group size, (middle) age-class and (right) position in the scene.

In a second study, Dezechache et al. (Dezechache et al., 2020) conducted an interview-based investigation in order to better identify the nature and determinants of social actions under threat. To do so, thirty-two survivors of the Paris attacks at ‘Le Bataclan’ (on the evening of 13-11-2015 in Paris, France) were interviewed through a series of questions on their spontaneous reaction, their behavior toward others and their communication with people inside and outside the Bataclan. Interviews were segmented into 426 social episodes, with 290 of them describing supportive behaviors toward others, and 121 of them reporting detrimental actions to others. To infer why social cognition was still present during the attacks, the authors examined the situational factors associated with a higher probability of socially supportive behaviors among hostages. Participants reported less supported action in context

where an escape road was available and when the probability to be injured increased (see **Figure 1-5**). The proportion of supportive action decreasing can be the outcome of a cost-benefit ratio in favor of escape or hiding. Conversely, authors reported a positive relationship between the feeling of being under the same common fate and the probability of acting together. It suggests that, as Drury and al. (Drury, 2018) proposed, the sense of sharing a same social identity promotes positive in-group actions. In addition, authors noticed that the supportive action could be underlain by different types of motivation. Actions could be described as individualistic (when the welfare of an agent is the only thing being relevant, and the welfare of others being ignored), cooperative (the welfare of the agent and others are both relevant) and altruistic tendencies (the welfare of the others is the only thing considered). Identification of motivations under socially supportive action revealed that 6.5 % of them were described as individualistic, 40.5% were instances of cooperation, and 53% were classified as altruistic.

To conclude, socially supportive action strategies seem therefore really frequent but they depend on two conditions: first, there are no other potentially beneficial options (such as fleeing or hiding) and second, a minimal sense of safety has to be met. In addition, supportive actions seem to reflect a variety of psychological incentives. The investigation of the possible action planned under threat, in particular social ones, should be performed by considering their associated payoff structures. Based on their results, we proposed several assumptions. First, we posit that perception of danger boosts people's perception and investment in supportive action opportunities, insofar as those are likely to offer immediate emotional or physical comfort. Consequently, supportive behavior is not a 'by-default option' as this type of action is preferred only when safety cannot be met by other actions (i.e. escape not possible and the danger is away) and can be underlain by a spectrum of possible incentives.

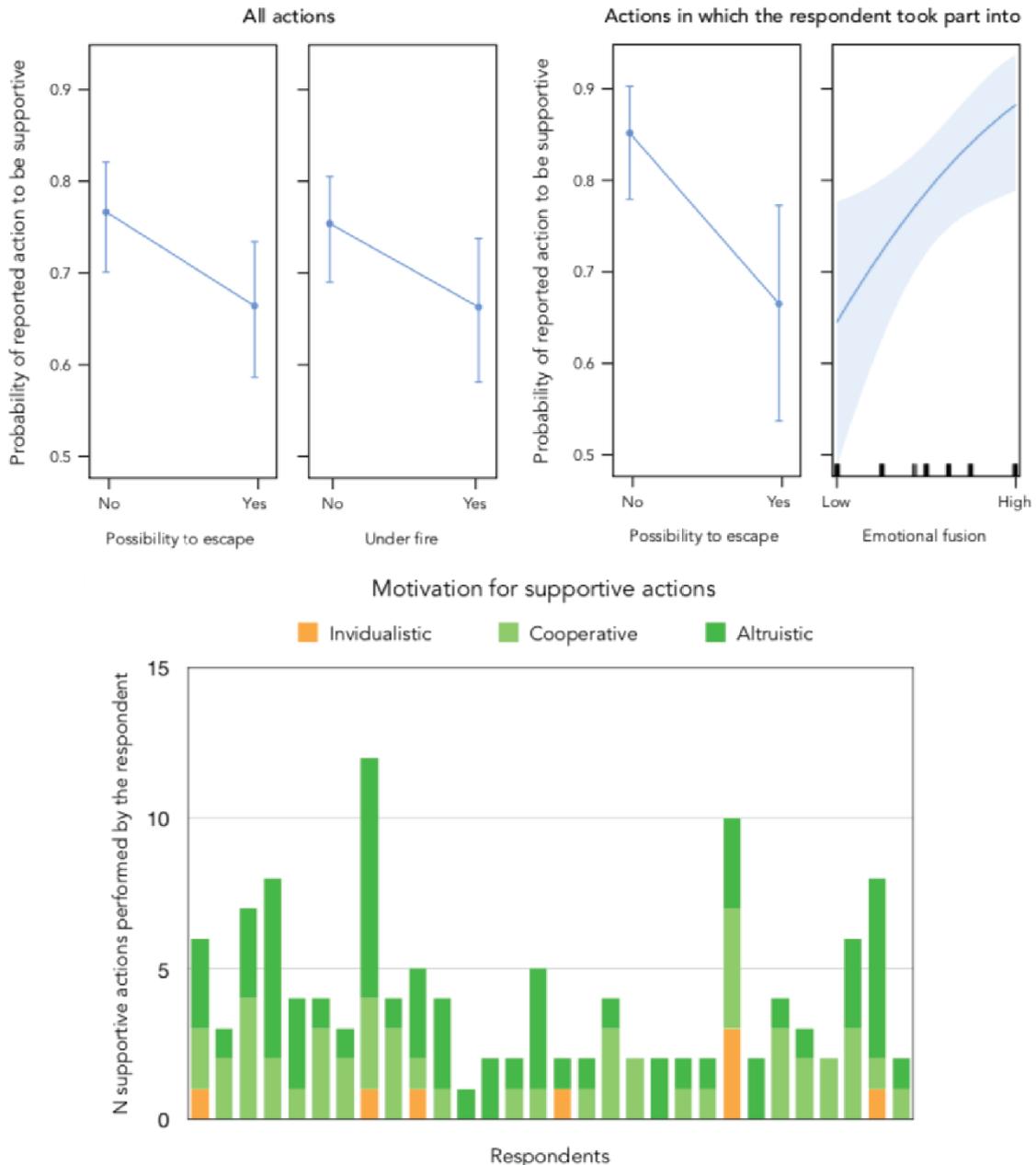


Figure 1-5. Distribution of supportive and non-supportive actions during Paris Attacks (based on Dezechache et al. 2020). (Top-Left) Effect of contextual factors on the occurrence of supportive behavior under threat for all narrated episodes (regardless of who was the agent). Each plot represents the predicted probability of a reported action to be supportive as a function of the possibility to escape and the presence of immediate firing. (Top-Right) Effect of contextual factors on the participation to a supportive behavior under threat by the agent. The predicted probability of an action in which the agent took part to be supportive varies with the possibility to escape and the degree of emotional fusion of the agent with the other individuals involved. (Bottom). Psychological motivations underlying supportive actions for which the respondent was the agent.

5-Conclusion of the Chapter

Exposure to a threat requires to react effectively in order to satisfy a unique goal: proximally, to survive, and ultimately, to reproduce. Situations in which we feel threatened take extremely different forms: depending on its contextual variations, different reactions to threat have been shaped and

selected by evolution. Scientific progress in the understanding of defense circuits allow the construction of models establishing a taxonomy of different responses to threat. These models seem to be able of predicting an important part of behaviors initiated in a threat situation. A long-forgotten factor explaining a good part of the variability of our reactions (especially collective ones) in situations of danger could be the presence and availability of others. It is deeply rooted in the popular belief that our reactions are antisocial in situations of danger. However, social science studies based on interviews with survivors of natural disasters or terrorist attacks reveal that social bonds would be maintained or even strengthened under threat.

Of course, individualistic behaviors have been reported and are part of strategies set up when we feel threatened. Nevertheless, mutual assistance and social support is very frequent in survivors' narratives. Four explanations have been put forward to explain why social cognition would be maintained. The first three explanations suggest cooperation is in some way an indirect consequence of threat: (i) social norms pre-established before threat would be maintained, (ii) identity fusion would favor pro-social behaviors with people sharing the same fate and (iii) the need for affiliation would induce behaviors allowing the social link with familiar ones to be maintained. Conversely, the fourth approach (motivational/instrumental) highlights that collective actions are relevant solutions for survival, which consequently do not take place if the cost-benefit ratio is too small (e.g. under fire) or if there is a better strategy (e.g. if one can run away). Thus, whether one would adopt social or asocial strategies in a threat situation could be context-dependent and modulated by the cost-benefit ratio of an action at a given moment (with the presence of others being included in the computation of this trade-off calculation). It also means that self-preservative action can be both social (helping another person to progress through the crowd) and asocial (solitary flight). Therefore, it seems important to integrate this cost-benefit component in order to better understand how threat affects the cognitive mechanisms underlying our ability to integrate others in our decisions in a flexible manner.

To conclude, social cognition is maintained under threat and it should be part of the current models of defensive reaction under threat. However, some caveats should therefore be kept in mind when interpreting these results: respondents represent a small proportion of individuals who were exposed to sources of danger. Thus, they may not be representative of those who survived these events. In addition, some interviews took place days, months or even years after the events. Memory, social desirability and self-presentation biases may interfere during interviews. For example, in Dezechache et al.'s study on the Bataclan attacks, it is very likely that the quantity of individualistic supportive actions was underestimated and the altruistic one overestimated. There is still a lot of work to be done to understand the complexity of our behavior in threat situations, especially on this collective aspect.

In particular, derived from the results obtained by Dezecache and colleagues, we argue the perception of danger would transform social cognition (instead of breaking the social bond as it is generally thought). However, although these studies allow us to analyze qualitatively and quantitatively behaviors established in life-threatening contexts, we could not really identify potential modulations of the socio-cognitive functions that are important for social interactions. To understand whether there is indeed a “transformation of social cognition” by threat, it is necessary to momentarily abandon field research and get back to controlled laboratory experimentation. Lab experimentations allow us to investigate the cognitive mechanisms involved when integrating other human fellows, the signal they convey and their action, during an exposition to a threatening stimulus.

HOW DOES THREAT TRANSFORM SOCIAL COGNITION?

Understanding the cognitive functions involved in social interactions has gradually increased, but their study is still limited to classic everyday situations. Indeed, the number of studies investigating sociocognitive functions in situations such as danger is scarce. The present chapter aims at describing the literature that investigated the impact of threat on socio-cognitive mechanisms, and at drawing parallels with the theoretical position presented in the previous chapter. To our knowledge, there is no existing review of how the ‘sense of being threatened’ modulates social cognition. Building a state-of-art of how social cognition is transformed by threat is currently necessary to progress in our understanding of human reaction under threat.

1-How can we deepen our understanding of our reactions in threat situations in the field of cognitive psychology?

Surprisingly, if the question of sociality has been barely addressed in models of defensive reactions to threat, the question of being antisocial or prosocial is the core of many studies investigating the modulation of socio-cognitive functions by stress (Nickels, Kubicki, & Maestriperi, 2017; Steinbeis, Engert, Linz, & Singer, 2015). This literature very often opposes the two positions described in Chapter 1: the tend-and-befriend and the (freeze) flight-or-fight². It is hypothesized that, if stress favors tend-and-befriend strategies, social bonds should be maintained or even reinforced during dangerous situation. This type of strategy would then be reflected by an increase in the number of social decisions taken and in a significant involvement of the mechanisms essential to our daily interactions. The opposite would be expected in the case of so-called asocial strategies. To test this, these different studies needed effective experimental paradigms to approach the concept of threat.

1.1-Two main approaches to investigate threat

The two main approaches investigating threat are summed up in **Figure 2-1**. First, it is possible to create an artificial threat situation during which we can measure the online behavior of participants. We can control experimental factors that are expected to influence our decisions under threat. This is very difficult in the case of a real threat, since it is not possible to predict its arrival and its evolution.

² These studies are rooted in the traditional dichotomy between asocial and prosocial strategies, which assumes self-preservative actions to be necessarily asocial. However, in the previous chapter, we criticized this vocabulary by showing that social bond may be maintained in order to carry out instrumental collective actions (i.e. for my personal interest only). In this chapter, I will borrow the vocabulary of the studies I will quote, which can be confusing considering my conclusion of the previous chapter. Nevertheless, I will progressively pointing out that this vocabulary is not necessarily appropriate.

In practice, this type of studies is carried out either in virtual reality (the participant has to escape from a burning tunnel (Kinader, Ronchi, Gromer, et al., 2014), or from a station that has just been bombed (Drury, Cocking, Reicher, et al., 2009), or through evacuation drills (i.e. fire alarms in a theater, Nilsson & Johansson, 2009). Different factors can be manipulated by the experimenter to match dimensions of threat: ambiguity and level of threat, physical constraints impacting hiding or escaping reactions as well as the presence of other individuals (virtual avatars) which may then influence our action choices.

Alternatively, classical laboratory experiments using cognitive tasks can be used. These studies will then simulate a threat by exploiting some sub-components of a threat (negative emotional experience, impact on well-being, pain, which can induce a stress response, etc.) to transform them into experimental factors. The purpose is to associate these experimental factors with a task of interest allowing us to measure a behavior or a cognitive function. Experimental designs created to investigate threat are various and differed in a lot of parameters. First, the measurement of interest can be assessed simultaneously or after the exposition with the stressor. Then, dimensions of stressors are highly variable. As these factors can impact results and interpretation of the recorded data, I propose first to summarize the different simulations used in classical laboratory experiments.

1.2-Experimental designs of stress procedures used in classical laboratory experiments.

Stressor may be social, i.e. the acute stress state plays with the threat of reputation costs to the participants. There are at least two procedures used at this aim. First, the Trier Social Stress Test (TSST), in which participants must unexpectedly prepare a job interview in front of a panel of strangers followed by a set of mathematical exercises that are far too difficult to be passed (for review: Frisch, Häusser, & Mojzisch, 2015). This paradigm was created by Kirschbaum, Pirke & Hellhammer in 1993 (Kirschbaum, Pirke, Hellhammer, 1993) in order to induce a state of psychological and biological acute stress in participants in the laboratory. This stress episode is characterized by a cortisol peak from 20 to 45 minutes after the beginning of the procedure (through Hypothalamic-Pituitary-Adrenal (HPA) axis) and by the activation of the sympathetic system (increased heart rate, high skin conductance activity, alpha amylase saliva) throughout the procedure. Sympathetic system returns to its baseline immediately afterwards (Berger, Heinrichs, von Dawans, Way, & Chen, 2016; Margittai et al., 2015; Vinkers et al., 2013). Different versions have been implemented: a group version (TSST-G; Von Dawans, Kirschbaum, & Heinrichs, 2011) in which several participants are exposed to stressors at the same time in order to test participants simultaneously, an adapted version for children (TSST-C, Gilissen, Bakermans-Kranenburg, van IJzendoorn, & Linting, 2008) and a virtual reality

version (TSST-VR, Jönsson et al., 2010; Zimmer, Buttlar, Halbeisen, Walther, & Domes, 2019). Second, very similar to the TSST, the Montreal Imaging Stress Task (Dedovic et al., 2005) proposes to induce a state of stress by asking participants to solve arithmetic problems with a strong time pressure under the eye of the experimenter. For both procedures, the task of interest is performed after exposure to stressor and preferably when the cortisol level is at its peak level.

Stressor may also be physical in nature, i.e. a danger to participant's physical integrity. Two procedures are generally employed. The first is the Cold Pressor Test (CPT, Errico, Parsons, King, & Lovallo, 1993; Pascualy et al., 2000). This is an aversive paradigm in which participants' hands are dropped into cold water (from 0 to 4 degrees) for one to two minutes. Like the TSST, this procedure increases cortisol levels as well as sympathetic nervous system. However, physiological responses and subjective reports of perceived aversion appear to be less important for this paradigm than with the TSST (McRae et al., 2006). A social variant has been proposed, the Social Evaluative CPT (Schwabe, Haddad, & Schachinger, 2008; von Dawans, Trueg, Kirschbaum, Fischbacher, & Heinrichs, 2018), in which participants are warned that their facial expression would be filmed while they have to judge the water temperature with their hands. The addition of a psychosocial stressor amplifies the effect of CPT on cortisol levels. Again, the task of interest is performed after exposure to stressor.

The second procedure is the Threat-of-Shock paradigm: it is a technique for inducing prolonged stress (i.e., anxiety) with a within-subject design (for review: Oliver Joe Robinson, Vytal, Cornwell, & Grillon, 2013). It consists of dividing an experimental task into threat blocks, in which participants can receive an electric shock at any time, compared to safe blocks in which they do not. The unpredictable nature of this aversive stimulus is responsible for the induction of hypervigilance state (Balderston, Hale, et al., 2017). It manifests itself by a negative subjective experience (Bublitzky, Kavcıoğlu, Guerra, Doll, & Junghöfer, 2020; Garibbo, Aylward, & Robinson, 2019), accompanied by intrusive thoughts (Grillon et al., 2017; Grillon, Robinson, Mathur, & Ernst, 2016) and an increase activity in the sympathetic nervous system (startle reflex or SCL, i.e. Bradley, Zlata, & Lang, 2018) during threat blocks compared to the safe ones. To our knowledge, there is no evidence in favor of cortisol involvement in the response to sustained stress induced by electric shocks (Berghorst, Bogdan, Frank, & Pizzagalli, 2013; Maruyama et al., 2012). A possible explanation would be the alternation between the Threat and Safe blocks would prevent the stress axis from getting out of control. Nevertheless, CPT procedure (which is a shorter manipulation than the threat-of-shock) is enough to induce an HPA axis response. Future studies will need to clearly identify the implication or not of the HPA axis in the Threat-of-Shock paradigm.

Finally, some studies have attempted to induce a stress response in a more indirect way. First, it is possible to induce a negative emotional state in participants by displaying segments of film characterized as scary/anxiogenic (Stanković & Nešić, 2020) or by asking them to recall a very stressful event (Cataldo & Cohen, 2015). Some studies have also induced stress by using a pharmacological induction (Margittai, Van Wingerden, Schnitzler, Joëls, & Kalenscher, 2018; Schultebrasucks et al., 2016). An increase of both the HPA axis and the sympathetic nervous system activities can be achieved by using respectively an administration of hydrocortisol (cortisol) or α 2-adrenergic antagonist yohimbine which effects are then compared to a placebo. Finally, some authors use temporal pressure to investigate our reactions to danger (Rand, Greene, & Nowak, 2012). Although this method may appear to be far different from the others, the temporal pressure remains relevant for understanding our cognition under threat insofar as, in danger situations, the speed of decision-making can be decisive. Time pressure is one of the stressing factors in the TSST or MIST procedures.

1.3-Organization of the review ‘How does threat transform social cognition?’

These different paradigms have been used in various studies. In order to introduce this literature³, I have decided to create three subgroups, each of them will be detailed:

- 1- How social decision-making is impacted by exposure to a threat/stress: this part is going to detail whether individuals make prosocial or self-preservative choices **AFTER** being exposed to a stressor (measurement post-manipulation).
- 2- How sociocognitive mechanisms are modulated following exposure to a threat/stress event: this second part will specify how social cognition functions (i.e. emotional perception or self-other representation) are modified **AFTER** being exposed to a stressor (measurement post-manipulation).
- 3- How sociocognitive mechanisms are modulated under threatening contexts: this third part will describe how social cognition functions (i.e. emotional perception or self-other representation) are modified **DURING** exposition to a stressor (measurement during manipulation).

³ In this review, described articles reflect the literature accumulated during my Ph.D. There were no rules for article selection as it would have been expected for a review article submitted to a publication process. Over the last three years, I regularly conducted an electronic search in Google Scholar for publications from Bublatzky, Drury, Ernst, Grillon, Margittai, Robinson, Todd, Tomova & von Dawans. The selected articles needed to focus on stress/threat and social cognition or attention and motivation. Introduction and discussion of these articles were screened to find new relevant publications. This review is consequently non-exhaustive.

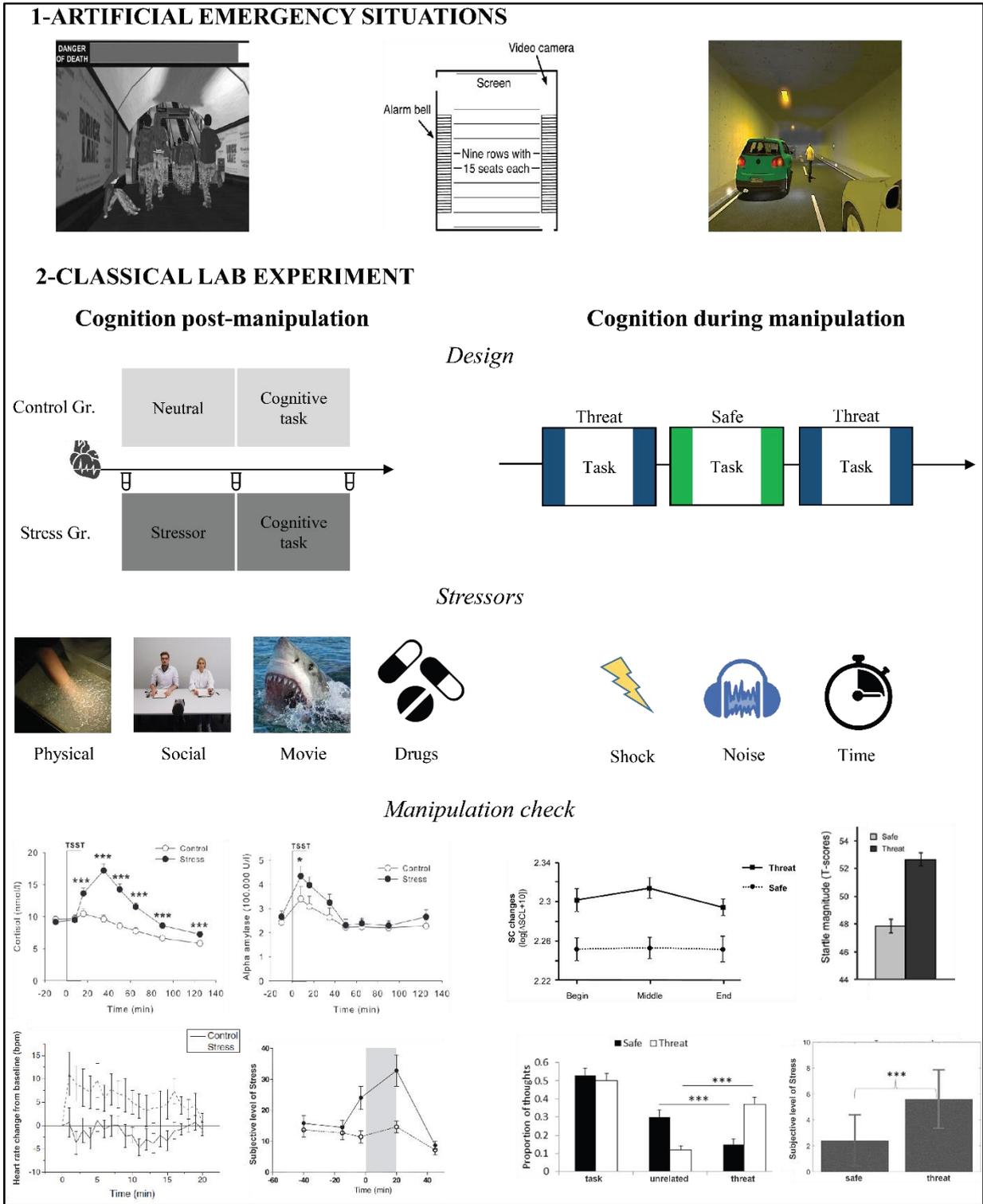


Figure 2-1. How experimentally investigate threat? Two possible ways: 1-Artificial emergency situation (evacuation of a train station, theater, tunnel...) can be created in real or virtual reality. 2-Classical lab experiment can be run. This one can be divided in two sub-categories: the ones investigating cognition post-stress induction and the ones investigating cognition during stress-induction. Each are associated with particular design (between or within subject), stressors or manipulation check (subjective, physiological or endocrinal). Figures are from: Berger et al. (2016); Bublatzky et al. (2013); Drury et al. (2009); Garibbo et al. (2019); Grillon et al. (2016); Kinatader et al. (2014); Margittai et al. (2015); Nilsson & Johansson (2008); Vinkers et al. (2013).

2-Social decision-making and stress

In order to understand whether stress favors affiliative tendencies (tend-and-befriend) or self-preservative tendencies (fight-or-flight), the operational hypothesis postulated by many authors is the following: after exposure to a stressor, our decisions can be (i) asocial by favoring our own benefits or (ii) social by favoring the benefits of others. In order to draw a portrait of the literature, results from 17 different studies were compared here. This is not exhaustive but it provides enough evidence to draw some conclusions about the relationship between stress and social decision-making.

Social decisions can be of very different types. These can be measured experimentally with specific economic games. One may decide to give one's trust (measured by the Trust Game) or to give it back to someone who has previously given it to us (Trustworthiness Game). One can choose to have moral decisions (Everyday Moral Decision Making) or to defend fairness (Ultimatum and Punishment Game). One can be altruistic by being generous (Dictator and Sharing Game) or by helping someone (Prosocial Risk-Taking Game). Finally, one can decide to establish cooperative (Public Good Game, Prisoner's Dilemma, Ultimatum Game and Social Discounting Task) or antisocial (Money Burning Game and Anti-social Risk-Taking Game) strategies. To understand how these decisions are modulated by threat, four types of stressors have been previously used: social, physical, time pressure and drugs. Results of these studies are summarized in **Table 2-1**.

2.1-Trust and Trustworthiness

Social trust can be defined as people's tendency to invest in social interactions in which their potential benefits are affected by others' behavior (Mell et al., 2020). Thus, social trust reflects the willingness of an individual to be vulnerable to others' actions and depends on individual's estimation of the probability that others will actually be trustworthy with them (Mayer, Davis, & Schoorman, 2006). Trust and trustworthiness attitudes can be assessed using the Trust game. In the Trust game (von Dawans, Fischbacher, Kirschbaum, Fehr, & Heinrichs, 2012), one player first decides to trust or not a second player by giving money to him or not, knowing that the money sent will be tripled by the experimenter. Then, the second player decides to be trustworthy or not by respectively sharing or keeping all the money for him. First, results show that trust and trustworthiness are diminished following exposure to a physical stressor (Potts, McCuddy, Jayan, & Porcelli, 2019; von Dawans et al., 2018). However, the presence of an additional social pressure (a socio-evaluative component) can counterbalance the effect of a physical stressor (two out of three studies: Potts et al., 2019; von Dawans et al., 2018). Exposure to social stress alone (von Dawans, Ditzen, Trueg, Fischbacher, & Heinrichs, 2019; von Dawans et al., 2012, 2018) promotes trust and trustworthiness attitudes (three out of four

studies): it is quite interesting to note that a decrease was only observed in the unique study in which only one participant in the room was in an acute stress (Steinbeis et al., 2015). These results suggest that sharing a stressful situation (i.e. being stress together) could influence our prosociality (insofar as trust and trustworthiness attitudes are concerned).

2.2-General Altruism

General altruism is defined as individual temperament that support behaviors bringing advantages to others, even if it results in disadvantage for yourself. To assess it, studies in decision-making usually used the dictator (Kahneman, Knetsch, & Thaler, 1986) or the sharing games (von Dawans et al., 2012): they consist in deciding if you want to share an amount of money or not with someone else. Importantly, the receiver cannot impact the decision outcome by rejecting the proposition and cancelling the gain for both players: this is why it is supposed to assess altruism. In addition, altruism can be assessed by quantifying the amount of risky behavior undertaken for other (while no benefit is associated with this risk-taking, Nickels et al., 2017). Results show that exposure to a social stressor (monetary) increase sharing behavior with a second virtual player (Nickels et al., 2017; von Dawans et al., 2019, 2012), while it decreases when participants had to share with a charity (Vinkers et al., 2013). Of note, one study reports no effect of the social stressor on general altruism (Steinbeis et al., 2015). A possible explanation would be that in the case of the charity organization, the recipient is more abstract and the consequence on the reputation as well. Also, stressed participants report more often they would rescue someone in need after reading hypothetical scenarios, even if it is a risky decision to them (Nickels et al., 2017). In contrast, CPT-induced stress reduces sharing behavior (von Dawans et al., 2018). Again, this effect seems to be inhibited when the physical stressor is combined with social stress. To conclude, altruistic behavior can globally be reinforced when a social component is associated with a stressful context.

2.3-Maintenance of social norms

An interesting way of investigating how others is considered under threat is to see whether we respect the informal rules that drive and limit our behavior in society (acting in a moral and fair way or not). Concerning the maintenance of social norms, when examining the literature on moral dilemmas, studies brings contradictory results: following exposure to stress, one study reports a positive correlation between cortisol elevation and altruistic decisions (Singer et al., 2017) while another one shows a negative correlation (Starcke, Polzer, Wolf, & Brand, 2011). It is important to note that, the first study was conducted on a male population cohort while the second is gender balanced. These results are thus inconclusive regarding social norms.

Fairness can be quantified using the Ultimatum (Güth, Schmittberger, & Schwarze, 1982) and Punishment Games (von Dawans et al., 2012). In these games, one player receives an amount of money that he has to share with a second player. If the money is equally divided, the game is fair, and it is unfair otherwise. Importantly, the second player can reject the proposal and punish his partner for an unfair proposal. Proportion of proposal rejection can be used as proxy of sensitivity to fairness (Youssef, Bachew, Bissessar, Crockett, & Faber, 2018). Interestingly, neither study observed an increase in the number of rejections of unfair proposals. Conversely, it seems that stress (mostly social stress in the studies listed) decreases or maintained the rejection rate (Prasad et al., 2017; Steinbeis et al., 2015; Vinkers et al., 2013; von Dawans et al., 2019, 2012, 2018; Youssef et al., 2018). Overall, these results suggest that the willingness to expect fairness is possibly diminished by stress, with participants limiting costly punishments to maximize their gain. Indeed, in a stressful situation, any gain for oneself is good to take (rather an asocial/self-centered gain). Nevertheless, some authors have proposed an alternative interpretation to the reduction of the rejection rate: namely that it is preferable to maintain the link between the two players of these economic tasks, which would rather reflect tend-and-befriend tendencies (Youssef et al., 2018). Future studies should distinguish between these two totally plausible but antagonist explanations.

2.4-Antisocial or Cooperative Decision

Finally, few studies investigated antisocial behaviors and moreover they are not gender balanced. On one hand, male participants seem not to punish gratuitously under stress (Steinbeis et al., 2015), but on the other hand, they more often allow themselves to bet using others' gains (Bendahan et al., 2017). Concerning cooperative strategies, the literature is not convincing. Under time pressure, it seems that the amount of money invested for our social group increases (Rand et al., 2012). However, this factor does not seem to affect the amount distributed during a social discounting task (a sharing money decision task in which experimenters varied the social proximity of player #2, (Passarelli & Buchanan, 2020)). When this task is carried out after a TSST-G procedure, Margittai et al. showed an increase in generosity toward close others (Margittai et al., 2015). While this result was not replicated in a recent study using a TSST-G procedure (Passarelli & Buchanan, 2020), it was by pharmacological inducing a cortisol peak (Margittai, van Wingerden, Schnitzler, Joëls, & Kalenscher, 2018). Sample size and participants' gender may explain these different results. However, it is important to note that a decrease of sharing was never observed in these studies.

Interestingly, Margittai et al. (Margittai et al., 2018) investigated the implication of two stress neuromodulators, cortisol and noradrenaline, on social discounting. To do so, four groups of male

participants performed cooperative decisions after administration of placebo, hydrocortisol, α 2-adrenergic antagonist yohimbine or both substances, respectively. While hydrocortisone administration promoted prosocial tendencies towards close others (replicating results in Margittai, Strombach, Van Wingerden, et al., 2015), the combined pharmacological induction of the HPA axis and of the sympathetic nervous system cancelled out the effect of cortisol on prosociality. These results suggest that the sympathetic system promotes fight-or-flight tendencies while cortisol (HPA) fosters tend-and-befriends strategies. However, more evidence is needed to draw a clear association between stress responses and strategies.

Finally, it seems that women (compared to men) more often invest in cooperative strategies (assessed using the well-known prisoner's dilemma (Flood, Dresher, Tucker, & Device, 1950)) in stressful situations and share more money when unfair proposals can be punished (Nickels et al., 2017). These results seem inconsistent with the altruistic tendency induced by a social stressor observed in male participants. Two possible explanations can be provided for these results. First, most of the studies studying altruistic decisions employed a group stress procedure, which is not the case for studies on cooperation. Again, sharing a common stress could increase social tendencies. Second, in contrast to the dictator game paradigm, under the ultimatum paradigm, it is possible to be punished by refusing an offer. Risk is an important part of that decision and it could explain this difference if male participants become more risk-takers in social decision-making.

2.5-Conclusion: social decisions following stress exposure

In conclusion, many studies seem to show that exposure to a stressor with a social component would induce tend-and-befriend tendencies, tendencies which could be more frequent among women than men. Moreover, when stress induction is carried out in a social group, prosociality increases even more. The opposite effect is observed when physical stressors alone are used, but this effect seems to be inhibited if they are associated with a socio-evaluative threat. In many attacks or disasters, the stressful situation (i.e., risk of death) is shared by several people at the same time, who also are observing each other. As proposed by Drury (Drury, Cocking, & Reicher, 2009b) and Mawson (Mawson, 2005), sharing a common fate as well as reputation could mediate pro-sociality and strengthen mutual support and the preservation of social norms under threat. These laboratory results seem consistent with the interpretations detailed in the previous chapter.

Social Decision	Task details	References	Stressors	Effect
Trust	Trust Game	Steinbeis et al. 2015	TSST	Stress \blacktriangledown trust in men
		FeldmanHall et al. 2015 [◦]	CPT	Stress \blacktriangledown trust
		von Dawans et al. 2012	TSST-G	Stress \blacktriangleright trust in men
		von Dawans et al. 2019	TSST-G	Stress \blacktriangleright trust in women
		von Dawans et al. 2018	CPT, SECPT	SECPT \blacktriangleright - trust in men
	Potts et al. 2019 [◦]	CPT, SECPT 25 min or just before the task	No effect of type of stressor or latency	
	Trustworthiness Game	von Dawans et al. 2018	CPT, SECPT	Stress \blacktriangledown trust in men Physical Stress \blacktriangledown trustworthy decision in men Social stressors cancel the effect of physical stressors in men
von Dawans et al. 2012		TSST-G	Stress \blacktriangleright trustworthiness in men	
von Dawans et al. 2019			Stress \blacktriangleright trustworthiness in women	
Moral Decision	EMDM Task	Singer et al. 2017	TSST	Stress \blacktriangleright altruistic moral decision in men + Correlation between induced cortisol and altruism in men
		Starcke et al. 2010 [◦]		+ Correlation between induced cortisol and egoist decision
General Altruism	Dictator Game	Vinkers et al. 2013	TSST-G	Stress \blacktriangledown general altruism to charity in men
		Steinbeis et al. 2015		No effect in men
	Sharing Game	von Dawans et al. 2018	CPT, SECPT	Physical Stress \blacktriangledown sharing Social stressors cancel the effect of physical stressors
		von Dawans et al. 2012	TSST-G	Stress \blacktriangleright sharing in men
		von Dawans et al. 2019	TSST-G	Stress \blacktriangleright sharing in women
Prosocial Risk-Taking task	Nickels et al. 2017 [◦]	TSST	Stress \blacktriangleright prosocial risk	
Costly Punishment	Ultimatum Game	Steinbeis et al. 2015	TSST	Stress \blacktriangledown rejection of unfair proposition in men
		Youssef et al. 2018 [◦]		Stress \blacktriangledown rejection of unfair proposition in female, no change in male
		Prasad et al. 2017 [◦]		Stress \blacktriangledown rejection of unfair proposition in female, no change in male
		Nickels et al. 2017 [◦]		No effect
	Punishment Game	Vinkers et al. 2013	TSST-G 75 min or just before the task	Stress \blacktriangledown rejection of unfair proposition after 75 min in men
		von Dawans et al. 2018	CPT, SECPT	SECPT \blacktriangledown - punishment in men
		von Dawans et al. 2012	TSST-G	No effect in men
von Dawans et al. 2019		No effect in women		
Antisocial Decision	Anti-social Risk Game	Bendahan et al. 2017 [◦]	TSST-G	Stress \blacktriangleright egoist decision
	Money Burning Game	Steinbeis et al. 2015	TSST	No effect in men
Cooperation	Public Good Game	Rand et al. 2012 [◦]	Time pressure	Time pressure \blacktriangleright contribution
	Prisoner's Dilemma	Nickels et al. 2017 [◦]	TSST	Stress \blacktriangleright cooperation decision in female, \blacktriangledown in men
	Ultimatum Game	Nickels et al. 2017 [◦]		Stress \blacktriangleright sharing in women, \blacktriangledown in men
	Social Discounting Task	Margittai et al. 2018	pharmacological: CORT vs. NA	CORT \blacktriangleright generosity towards close other in men NA \blacktriangledown the effect of CORT in men
		Margittai et al. 2015	TSST-G 70 min or just before the task	Stress \blacktriangleright generosity towards close others directly after stress in men
		Passarellia et al. 2020 [◦]	TSST-G	No effect
Passarellia et al. 2020 [◦]	Time pressure	No effect		

Table 2-1. Effect of different stressors on several explicit Social Decisions reported in 17 articles on the impact of stress on social decision-making. Arrows indicates the direction of the effect (\blacktriangleright indicates an increase while \blacktriangledown indicates a decrease). ~ indicates a trend toward significance. [◦] indicates that experimenters recruited both male and female participants. TSST: Trier Social Stress Test; TSST-G: Trier Social Stress Test for Groups; SECPT: Socially Evaluated Cold Pressor Test; CPT: Cold Pressor Test; CORT: Neuromodulators Cortisol; NA: neuromodulators noradrenaline.

Moreover, the pharmacological study conducted by Margittai et al. (Margittai et al., 2018) cautiously proposes that the variability of results supporting either tend-and-befriend or fight-or-flight strategies

could be explained by different activation trade-offs between the two systems involved in response to a stressful context. Since these two systems are associated with different kinetics and are triggered by different stressors, the question of interest is not “Does stress promote prosocial or asocial behaviors?” anymore but rather “Which threat context favored this strategy and why?”: A theoretical framework that would more easily encompass contradictory results as they would no longer be perceived as false positive/negative (depending on one’s position) but as behavioral variations resulting from paradigmatic variations.

Furthermore, several limitations can be drawn. First, studies are mostly carried out between-subject designs, with a control group and a stressed group. These studies are generally gender unbalanced because of the interaction between cortisol and other hormones (Kirschbaum, Kudielka, Gaab, Schommer, & Hellhammer, 1999). Second, these studies focused on the modulation of outcomes resulting from social decisions. Then, as it has already been pointed out, both the asocial and the prosocial position can justify the same behavioral outcome (i.e., fairness). Finally, decision-making tasks are explicit prosocial measures that may be sensitive to demand effects.

3-Modulation of socio-cognitive functions following exposure to a stressor

How and which cognitive functions essential to our daily social interactions are impacted following exposure to a stressor? These functions are multiple: affiliation, representation and integration of others’ presence and action plans, the perception of signals conveyed by others, the encoding of social information around us, but also empathy. Their modulations can help us to understand the way we interact with others in threatening situations because they inform us about how we perceive our environment, especially our social environment, and how we prepare to act in it, with or without others. The next part will thus explore the relationship between social cognition and stressors. Once again, results are summarized in **Table 2-2**.

3.1-Affiliation with other

The idea that exposure to a social stressor promotes affiliation strategies is generally supported in the literature. This phenomenon of affiliation is first observable through measurement such as a higher desire for closeness after exposure to stressor (compared to a control group), reported by female participants thanks to a Likert scale (von Dawans et al., 2019). In addition, stressed female participants showed a preference for male faces expressing more affiliative facial features during attractiveness appraisal task (Ditzen, Palm-Fischbacher, Gossweiler, Stucky, & Ehlert, 2017). Furthermore, the level of cortisol induced following a TSST procedure correlates positively with the interpersonal proximity between two male participants who have together achieved a Fast Friend Procedure (an interview game

able to create quickly social bonds between strangers, (Berger et al., 2016)). However, one study (Deckers et al., 2015) revealed an effect in the opposite direction: the experimenter is evaluated negatively following a TSST procedure. One explanation can be that the experimenter is identified as one of the responsible factors for the participant's state of stress. Authors defend that this need for affiliation could easily be justified by the phenomenon of social buffering, which has been illustrated through various studies (Levine, Johnson, & Gonzalez, 1985). These show that the presence of others reduced physiological, endocrinological and subjective responses when exposed to a stressor, which support tend-and-befriend theories (for review: Frisch et al., 2015). However, other functions of affiliation have been proposed, such as helping to read one's own emotional state by emotional comparison when we are in uncertain/anxious situations (Kulik, Mahler, & Earnest, 1994; Schachter, 1959).

3.2-Perception of emotional displays

In order to interact with people, we need to process the social cues they convey. Of interest, the induction of a state of stress change the socio-emotional cue processing conveyed by facial expressions (Stanković & Nešić, 2020). Indeed, several studies suggest that emotional content is prioritized when we are stressed. The presentation of irrelevant emotional faces during a working memory task (Oei et al., 2012) negatively impacts response times in the stress condition and is associated with higher activations in brain regions involved in affective processes (right amygdala and inferior frontal gyrus) and lower activations in brain areas associated with executive functions (lateral parietal cortex, dorsolateral prefrontal cortex). In addition, Deckers et al. (Deckers et al., 2015) showed an increase of emotion categorization score after stress induction but without specifying whether there was an interaction with the type of emotions. One stimulus whose perception seems to particularly be improved after exposure to stress is the face of happiness: it appears to be able to capture attention during a dot-probe task (**see Figure 2-2**) and to be better categorized/detected (Barel & Cohen, 2018; Domes & Zimmer, 2019; von Dawans, Spenthof, Zimmer, & Domes, 2020). Following stress exposure, the amygdala also responds similarly to faces of fear, anger and joy (van Marle, Hermans, Qin, & Fernández, 2009). These results suggest that participants have a higher sensitivity to happy faces after exposure to a stress. However, using an approach-avoidance paradigm, Roelofs et al. (Roelofs, Elzinga, & Rotteveel, 2005) failed to maintain the well-known congruence effect between approach movement and positive emotions, which may potentially challenge this interpretation.

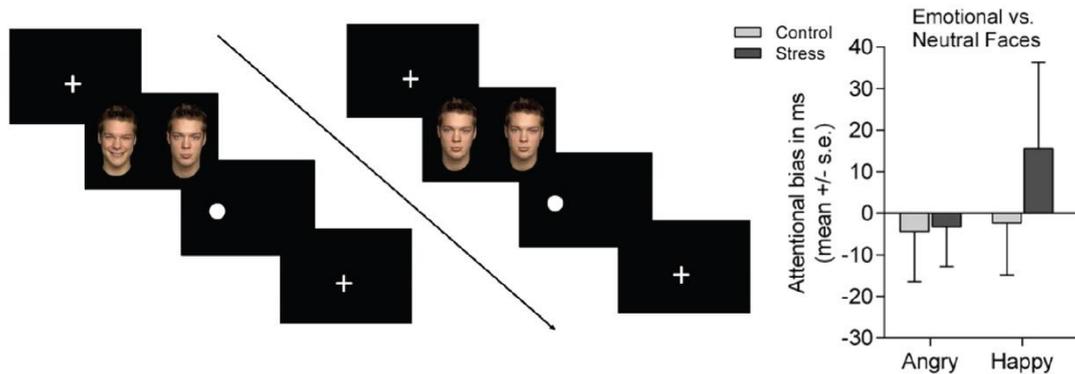


Figure 2-2. (Left) Facial dot-probe task paradigm (based on Hornung, Noack, Kogler, & Derntl, 2019). Emotional-neutral or neutral-neutral face pair is displayed to participant. Then, faces disappear and a dot probe is presented behind one of the faces. Participants were asked to indicate the dot position as quickly and accurately as possible. (Right) Results from Von Dawans et al. (2020). Attentional bias to happy and angry emotional displays. Positive values represent attentional preference.

Results about anger are less convincing. Some studies showed that angry faces are also better recognized and detected following stress compared to no stress condition (Barel & Cohen, 2018; Domes & Zimmer, 2019), suggesting that threatening signals are quickly spotted in stressful situations. However, these results have not always been replicated (von Dawans et al., 2020). As with the happy faces, Roelofs et al. (Roelofs et al., 2005) failed to show an association between avoidance movement and angry faces when subjects were stressed. Moreover, when angry faces are in competition with fearful faces, participants show a greater sensitivity for fearful faces (Chen, Schmitz, Domes, Tuschen-Caffier, & Heinrichs, 2014; Rabasco & Sheets, 2016). There are two possible explanations: first, fear signals convey an *ambiguous threat* (Adams & Kleck, 2005; Wieser & Keil, 2014) that needs to be decoded in order to be understood and located, making this signal a priority. Second, the fearful face signals a *distress social message* in addition to the presence of a danger in the environment (Hess, Blairy, & Kleck, 2000; Marsh, Adams, & Kleck, 2005; Nichols, 2001; Schenkel, 1967). If stress promotes affiliation, distress signals should be prioritized. In line with such proposal, when contrasting sad and happy faces, Schultebrucks et al. (Schultebrucks et al., 2016) revealed an attentional bias toward distress and/or negative-valence signals (sadness) only. Yet, expressions of distress, i.e. fear and sadness, were not found to be better recognized after stress (Barel & Cohen, 2018). To summarize, exposure to stress appear to enhance attention toward positive expressions which can be interpreted as a source of social support and toward distress displays for their affiliative component. These interpretations need to be confirmed by bringing supplementary (and more direct) evidence.

3.3-Empathetic processing

Another interesting way to investigate whether stress promotes affiliation is to look at processes of empathy. One position suggests that empathy is a multidimensional construct organized in two

components (Kerr-Gaffney, Harrison, & Tchanturia, 2019; Warrier et al., 2018). The first component is a cognitive one which can be defined as the ability to infer others' mental states (i.e. Theory of Mind, ToM). To assess it, participants are asked to guess the correct intention or mental states of characters in picture (using Reading the Mind in the Eyes Test (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001) or Multifaceted Empathy Test (Dziobek et al., 2008; Foell, Brislin, Drislane, Dziobek, & Patrick, 2018)) or movies (the Movie for the Assessment of Social Cognition Task, (Dziobek et al., 2006)). Stress does not appear to robustly reinforce the ToM (cognitive empathy) component: indeed, out of five studies, only one showed a positive correlation between stress-induced cortisol levels and ToM capacities (Smeets, Dziobek, & Wolf, 2009; Wingenfeld et al., 2014; Wolf et al., 2015). However, highest levels of ToM capacities (i.e. the depth of recursive beliefs: "I know you know that I know...") seem diminished under stress, suggesting that stress favors more intuitive reasoning (Leder, Häusser, & Mojzisch, 2013).

The second component is an emotional one which can be described as empathic concern (i.e. observer's emotional response to another person's emotional state). This component is increased by stress: participants more often felt the same emotional state they perceived in others (Wingenfeld et al., 2014; Wolf et al., 2015). While this emotional component indicates how individuals are affected by others' emotional states in stressful situations, it doesn't provide information regarding individuals' reactions toward others. Interestingly, Tomova et al. (Tomova et al., 2017) showed that, in a state of stress (compared to a normal situation), the activity of the "empathy for pain" network was more important when perceiving pain in others. Importantly here, the activity of this network mediate people's prosocial behavior in the ultimatum task following fMRI acquisition. This study elegantly demonstrated the modulation of a function by stress and its behavioral outcome.

Altogether, this suggests that cognitive empathy is performing and emotional empathy is boosted following exposure to stressors. It is likely that these empathic mechanisms drive our future cooperative choices.

3.4-Self-Other Balance

The complexity of human social life implies that we must be very skilled at perceiving, understanding and anticipating the behavior of others to perform efficient collective actions (Era, Aglioti, Mancusi, & Candidi, 2018; Sebanz, Bekkering, & Knoblich, 2006). Aligning self-cognition with that of others is called alter-centrism phenomenon and the investigation of alter-centric effects in stress situations is particularly relevant. Indeed, these effects can be used as a proxy as to which extent others influence our own cognitions, i.e. to which extent they are taken into consideration (Kampis & Southgate, 2020).

For example, alter-centrism can be assessed using the Visual-Perspective Taking task (VPT) developed by Samson et al. in 2010 (Samson, Apperly, Braithwaite, Andrews, & Bodley Scott, 2010). Participants observe a scene in which an avatar is located in a room and is looking at one wall of the room (See **Figure 2-3**). Red targets are displayed on the scene walls such that the participant and the avatar either see the same number of targets (congruent perception) or not (incongruent perception). Participants are asked to report either the number of points they saw themselves (first-VPT) or the number the avatar saw (third-VPT). Both an alter-centric bias, i.e. how the representation of visual information perceived by the avatar impacts participants' reports from a 1st-VPT, and an egocentric bias, i.e. how the representation of visual information that participant perceived impacts participants' reports from a 3rd-VPT, can be computed.

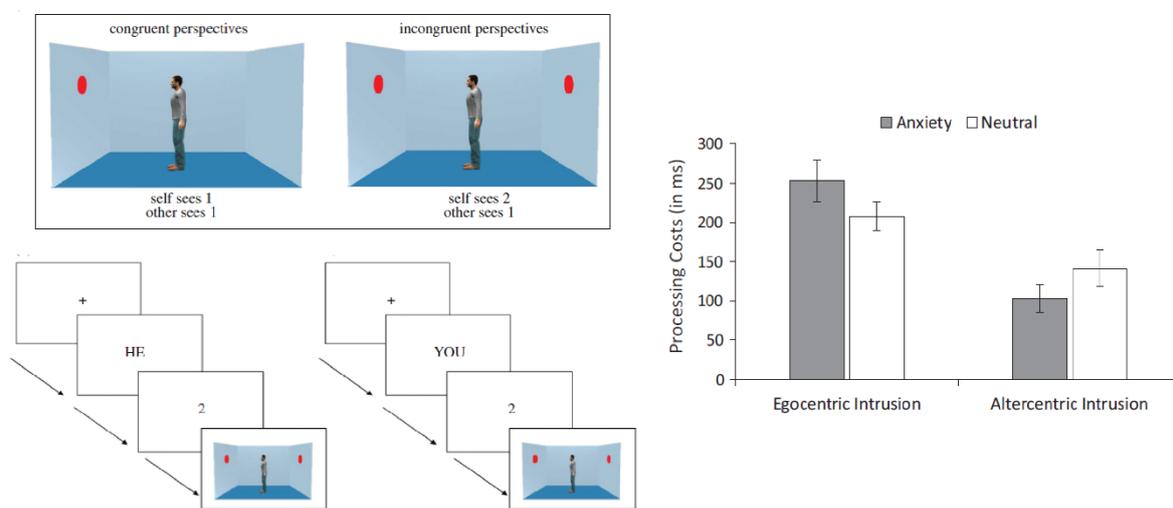


Figure 2-3. (Left) Experimental design of VPT task (from Wang, Tseng, Juan, Frisson, & Apperly, 2019). Examples of image display from the congruent/incongruent perception and temporal organization of a trial. Participants are noticed if they have to take a first (indicated by 'YOU') or third perspective (indicated by 'HE/SHE') to assess the number of perceived targets. Then, the computer proposes an answer followed by the scene. Depending of the imposed perspective taking, participants have to answer if the proposed answer was correct or not. (Right) Results from Todd and Simpson (2016). Anxiety increased egocentric intrusion during 3rd-VPT and decreased alter-centric bias during 1st-VPT.

Using VPT task, Todd and Simpson (Todd & Simpson, 2016) showed that stress induction by autobiographical recall of a stressful event increase participants' egocentric bias when assessing the visual perspective of others and decrease alter-centric interference when assessing participants' visual perspective. Anxiety decreases the integration of others' visual information. However, one potential confounding factor is related to the nature of the stressor which consists in autobiographical recall of a stressful event and most likely promotes self-centred processes.

Furthermore, the stress induced in Tomova et al. (Tomova, Von Dawans, Heinrichs, Silani, & Lamm, 2014) seems to modulate self-other alignment differently according to gender: while female participants' capacity for self-other distinction increased (i.e., self and others' representations are not

confounded), it decreases for men. The authors argue that women flexibly disambiguate their own person from that of others in stressful situations: thus, it allows them to engage in with precise social responses, while men react with increased self-centredness and less adaptive regulation. Nevertheless, this interpretation should be taken with caution: these effects are mainly measured by reaction times and could be explained either by a poor self-other distinction in men as proposed by the authors, or by an overrepresentation of information about others. In the same study, male participants showed a tendency to judge emotions of others using their own frame of reference, so it seems unlikely that the effects previously presented can be explained by an alter-centric bias. Future studies will need to confirm this explanation. With the same willingness to investigate how self and others representations are encoded after stress, Tomova et al. (Tomova, Saxe, Klöbl, Lanzenberger, & Lamm, 2020) recently compared self and others reward neural representations. Of interest, they showed that when stressed, participants better represent the amplitude of possible rewards when they play for others than when they play for themselves (higher activity in the dorsomedial prefrontal cortex and in the striatum), suggesting increased prosocial tendencies under threat.

Unfortunately, too few studies have been carried out and the number of confounding factors is too high to be conclusive on alter-centric cognition following stress. However, these results are really encouraging and alter-centric paradigms should be more often used to infer social orientation of participants.

3.5-Social Memory

Several studies have focused on how social information is encoded in memory following a stress event. If social information is important under threat, it can be assumed that individuals better consolidate social information in their memory when they are stressed because they are particularly salient and meaningful. However, the literature rather indicates that stress decreases the encoding of social information. Following a TSST procedure, participants showed a decrease in performance when learning name-face association (Takahashi et al., 2004) or biographical contents (Merz, Wolf, & Hennig, 2010). Both studies reveal that the higher the induced cortisol level, the lower the recovery score. Li et al. (Li, Weerda, Milde, Wolf, & Thiel, 2014) investigated whether faces were better encoded if they expressed an emotion. Participants were asked to recall 50 faces expressing fear and 50 neutral faces. Results showed that stress does not affect performance in an old-new task. However, hyperactivity of fronto-medial regions is observed when faces expressing fear presented in the encoding phase are displayed again (with a neutral expression) to participants during the retrieval

phase. The authors suggest a particular processing of emotional content as described above for the emotional-recognition tasks.

3.6-Conclusion: socio-cognitive mechanism modulations after stress exposure event

When participants are stressed, they seek for affiliation, in particular, so as to regulate their own emotional states. Socio-emotional information is associated with a particular processing, even if participants are not able to consciously report or remember it. Participants are particularly sensitive to expressions of joy that can be interpreted as sources of potential emotional support. They may also be sensitive to emotional expressions of fear and sadness, but the literature does not allow us to fully conclude whether this preference is explained by a more pronounced negative affective bias (or even a threat bias) and/or higher sensitivity to distress signals from others, which would indicate a stress-induced prosocial orientation. A maintained ToM and empathy processes may explain the cooperative social decisions presented in the previous section. Stress is also believed to promote social decisions by fostering a better neural representation of rewards when they are for others. However, due to confounding factors limiting interpretations, we cannot conclude whether stress favors egocentric bias or alter-centricity. Further research is needed in this area as it allows an efficient qualitative and quantitative approach to understand whether stress prompts individuals to orient their attention toward others or toward themselves. Overall, this second chapter suggests that social cognition can be maintained in stressful situations.

Nevertheless, several limitations can be raised in these studies. First of all, it is important to note that 23 out of the 28 studies induced a cortisol peak by using a purely social stressor. In the previous section, we observed that proportion of prosocial choices increased following social stressor while it decreases after physical stressors. Once again, these studies are mostly carried out between-subject designs and more often among men. Then, if some effects seem very robust, the function/motivation of these modulations of cognitive functions often remain unclear (such as for fearful face). Moreover, some effects seem to depend on the chosen experimental contrasts (i.e. Happy vs. Anger or Happy vs. Sad) which makes the interpretations complex. Finally, one of the major limitations for understanding the human behavior in situations of danger is that all these results describe the modulation of mechanism after exposure to stress and not during it. In order to investigate behaviors during a situation of danger as closely as possible, it is necessary to be able to modulate cognitive functions when participants feel threatened.

Mechanisms	Task details	References	Stressors	Effects
Affiliation	Fast Friend Paradigm	Berger et al. 2015	TSST-G	+ Correlation between induced cortisol and interpersonal closeness in men Stress ↗ wish for closeness in women
	VAS Closeness	von Dawans et al. 2019		
	Attractiveness	Ditzen et al. 2017	TSST	Stress ↗ preference for affiliative trait in women
	Social evaluation	Deckers et al. 2015 °		Stress ↗ negative evaluation of experimenter in women
	Social buffering	See Frisch et al. 2015 for review	TSST / TSST-G	Presence of others ↘ stress
Self-other Balance	Visual Perspective Taking (VPT)	Todd & Simpson 2016 °	Autobiographical recall	Anxiety ↗ egocentric bias, ↘ altercentric bias
	Wheel of Fortune Game	Tomova et al. 2020	Montreal Imaging Stress Task	Stress ↗ dissimilarity between neural patterns underlying high and low value for the other, not for self
	Perspective taking task	Tomova et al. 2014 ^o		Stress ↘ Self-Other distinction in men. ↗ in women
	Imitation-Inhibition task	Tomova et al. 2014 °		Stress ↗ automatic motor imitative tendencies in men. ↘ in women
	Emotional Egocentricity Task	Tomova et al. 2014 °		Stress ↗ emotional egocentricity in men. ↘ in women
Emotion Perception	Emotion Recognition Task	Barel & Cohen 2018 °	TSST	Stress ↗ emotion recognition of anger, happiness, surprise, and neutral. ↘ of fear and no effect on sadness and disgust.
		Deckers et al. 2015	TSST	Stress ↗ emotion recognition in women
	Ambiguous Categorization Task	Chen et al. 2014	TSST-C	Stress ↗ sensitivity to fearful (compared to anger) face in young boy
		Rabasco & Sheets 2016 °	TSST	Stress ↗ sensitivity to fearful (compared to anger) face in men. No effect in women
	Emotion Detection Task	Von Dawans et al. 2020	TSST-G	Stress ↗ sensitivity to happy faces, ↘ sensitivity to anger faces in men
		Domes & Zimmer et al. 2019	TSST-VR	Stress ↗ sensitivity and RT to detect happy and angry faces in men
	Facial Dot-Probe	Schultebrucks et al. 2016 °	pharmacological: MC	Stress ↗ attentional bias away of sad face. No effect for happy face
		Von Dawans et al. 2020	TSST-G	Stress ↗ attentional bias toward happy face in men.
	Emotional Distraction	Schultebrucks et al. 2016 °	pharmacological: MC	No effect
		Oie et al. 2012	TSST	Stress ↗ RT during working memory task in presence of emotional distractor. Stress ↗ ventral affective brain areas, ↘ dorsal executive areas
Dynamic Facial Expression Passive Task	Van Marle et al. 2009	Movie (Irreversible)	Stress ↗ amygdala responses to equally high levels for anger, fear and happy faces in women	
	Stanković & Nešić 2020	Movie (Shallow)	Stress ↗ left hemisphere dominance in emotional face perception	
Visual-Field Emotion Categorization	Roelofs et al. 2015	TSST	Stress cancelled congruency effect between Happy-Approach and Anger-Avoidance	
Social Memory	Face-name Associations	Takahashi et al. 2004	TSST	Stress ↘ social memory in men. - Correlation between induced cortisol and social memory
	Biographical Learning	Merz et al. 2010 °	TSST	Stress ↘ social memory. - Correlation between induced cortisol and social memory
	Face Recognition Memory paradigm	Li et al. 2014	TSST	Stress ↗ frontal and medial temporal brain activity for fearful faces recognition in men. No effect on old-new recognition accuracy
Empathy	Multifaceted Empathy Test	Wolf et al. 2015	TSST	Stress ↗ emotional empathy in men, no effect in cognitive empathy
		Wingenfeld et al. 2014	pharmacological: MC	Stress ↗ emotional empathy in women, no effect in cognitive empathy
	Reading the Mind in the Eyes Test	Smeets et al. 2009 °	TSST	No effect
		Movie for the Assessment of Social Cognition	Smeets et al. 2009 °	TSST
	Empathy for pain Task	Wingenfeld et al. 2014	pharmacological: MC	No effect in women
		Tomova et al. 2017	TSST	Stress ↗ empathy for pain network in men. Activation mediate sharing in the Ultimatum Game
Beauty Contest	Leder et al. 2013	TSST-G	Stress ↘ levels of strategic reasoning in men	

Table 2-2 - Effect of different stressors on several socio-cognitive mechanisms reported in 28 articles. Arrows indicate the direction of the effect (↗ indicates an increase, while ↘ indicates a decrease.). ° indicates that experimenters recruited both male and female participants. TSST: Trier Social Stress Test; TSST-G: Trier Social Stress Test for Groups; TSST-G: Trier Social Stress Test for Children; MC = mineralocorticoid.

4-Modulation of socio-cognitive functions under threat

As it was very well described by Robinson et al. in his 2013 review (Robinson, Vytal, Cornwell, & Grillon, 2013), the previously mentioned paradigms (TSST, MIST, CPT, pharmacological or the use of negative emotional content) are associated with a major experimental limitation in the investigation of our question. Exposure to stressors precedes the experimental task: it is therefore difficult to say whether the above-mentioned effects are due to the threat context itself or if they are related to recovery from stressors. In order to create a relevant parallel between results from cognitive psychology and the real-life behavior of individuals when they are in danger (a fire, an earthquake, an attack), it is necessary to use manipulations allowing us to study human cognition *when* threatened. Different techniques can be used to induce a “sense of being threatened”. Either the participant is placed in a situation mimicking reality thanks to virtual reality and evacuation drills. Alternatively, the feeling of being threatened/anxiety or urgency can be studied in a within-subject design, using respectively the Threat-of-Shock paradigm or time-pressure procedure while participants performed a task. Different cognitive mechanisms have already been investigated using these manipulations. Contrary to the two previous parts of this chapter, the literature is less focused on social cognition but much more on attentional, executive or motivational aspects. Nevertheless, these results can be informative as motivation (i.e., cost-benefit trade-off) is an important factor to explain social action under threat. Thus, such studies can be useful for the current debate between social or individualistic strategies and can be relevant for creating new experimental designs. We propose a review of the results of 39 studies which are listed in **Table 2-3**.

4.1-Supportive and affiliative behaviors under threat

Again, social strategies seem to be advantageous in threatening situations. Indeed, similarly to the studies using TSST, receiving a hand-holding from a partner during a ToS procedure reduces the subjective anxiety level as well as the activity in brain regions associated with vigilance, salience and self-control (Coan et al., 2017). Nevertheless, this effect was not observed when social support was provided by a stranger, and participants reported a negative experience. These results raised the following question: when under threat, is our social cognition only maintained for our socially close ones? Of interest, Drury et al. (Drury, Cocking, Reicher, et al., 2009) reported in a virtual reality study that the rate of helping behavior toward an avatar in danger correlated positively with the feeling of sharing the same social identity as them (potentially through the common fate they experienced in relation to the dangerous situation). Moreover, this result confirms their previous findings, using interviews (for review see Drury, 2018). Interestingly, inter-individual variability seems to be an important factor to consider when investigating social behaviors in threatening situations. For example,

Vieira et al. (Vieira, Pierzchajlo, & Mitchell, 2020) showed that the imminence of a danger increased rescue behaviors toward others and that this effect correlates with participants' empathic concern trait. Nevertheless, the risk of getting a shock reduced the prosocial behavior, which is very similar to the conclusions of the study carried out by Dezechache et al. on the Bataclan attacks (Dezechache et al., 2020). Similarly, Moussaïd & Trauernicht (Moussaïd & Trauernicht, 2016) showed that situations of danger associated with strong time pressure to act reinforced participants' "baseline" social strategies: prosocial individuals become even more prosocial and the reverse pattern was observed in the case of individualistic individuals. Overall, these studies revealed, although not systematically, that social bonds are maintained when we feel in danger, with individuals being able to provide social support and to collaborate together.

4.2-Social influence

Preserving social bonds may therefore be relevant to one's own survival under threat. This is especially true if others have information that we do not possess. Various studies have shown that our action choices during evacuation contexts seem to be impacted by those of others. Nilsson & Johansson (Nilsson & Johansson, 2009) showed, during a simulation of an evacuation in a theatre, that spectators tend to be socially influenced by others, especially when the danger origin is unspecified (by comparing the effect of an alarm sound which is unclear or uninformative to a clear vocal message). Also, Kinateder et al. (Kinateder, Ronchi, Gromer, et al., 2014) obtained similar results in a virtual reality paradigm in which participants tend to follow the same trajectory as an avatar when they have to evacuate a burning tunnel. Interestingly, the results of the study conducted by Moussaïd et al. (Moussaïd et al., 2016) in virtual reality seems to suggest that crowding effects, usually accompanied by pushing (connoted as asocial phenomena) could be due to a social influence phenomenon. In fact, trying to be close to others and the possible information they might have can be useful for our survival. Altogether, this amount of evidence suggests that sociality does not vanish under threat. On the contrary, others can be a source of information influencing our actions.

4.3-Perception of fearful faces

A social signal able to convey information that we do not possess is fearful face. Indeed, this signal informs us about the presence of a threat in the environment (Adams & Kleck, 2005; Wieser & Keil, 2014). Consistent with studies that have investigated the processing of this signal after the induction of a cortisol peak, it seems to be particularly privileged when we feel threatened. Repeatedly, studies replicated a negative emotional processing bias which manifests itself by: an attentional capture by fearful face (Lago et al., 2019; Robinson et al., 2016; Robinson, Letkiewicz, Overstreet, Ernst, &

Grillon, 2011), a bias to respond fear in emotional-categorization tasks (Bublitzky, Kavcioglu, et al., 2020), an increase of intensity appraisal of this emotion (Kavcioglu, Bublitzky, Pittig, & Alpers, 2019, see **Figure 2-4**), faster response times to identify a fearful face (Robinson, Charney, Overstreet, Vytal, & Grillon, 2012) and finally a positive correlation between the subjective arousal level of the participants induced by the Threat-of-Shock procedure and the tendency to categorize a surprised face as negative (Neta et al., 2017).

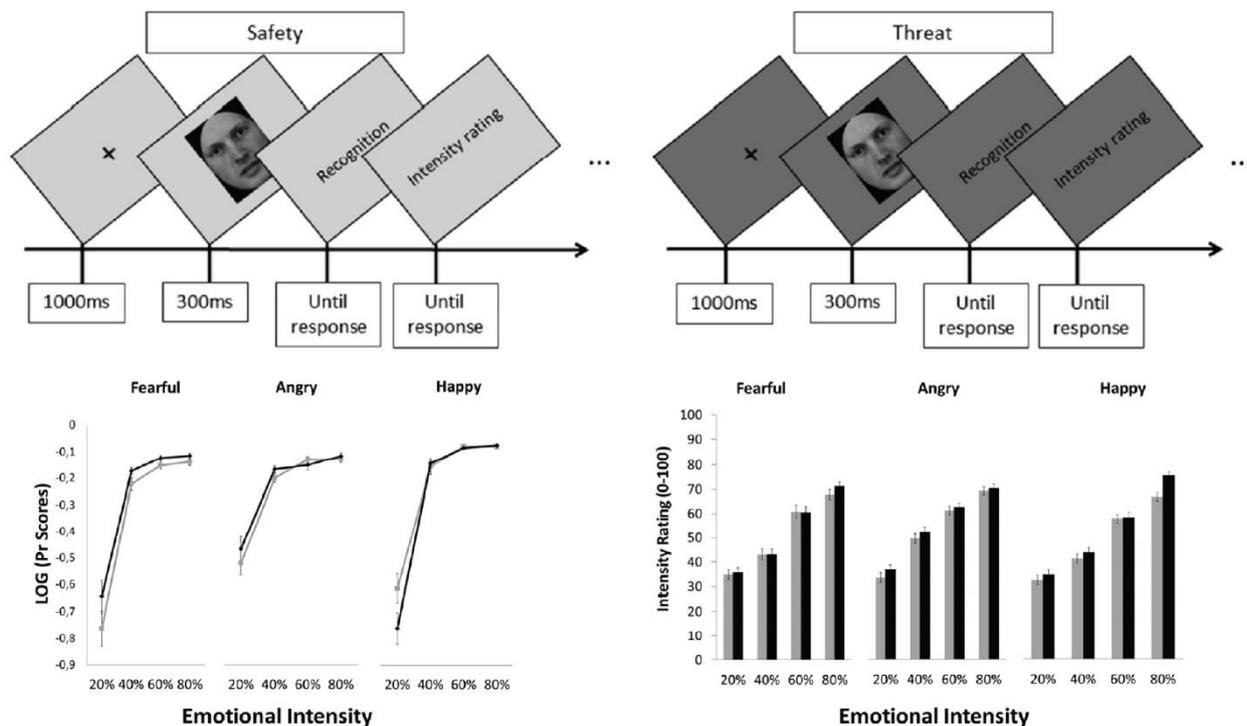


Figure 2-4. (Top) Experimental design used by Kavcioglu et al. (2019): Face pictures were presented during threat-of-shock or safe blocks. After viewing the face picture, participants had to categorize (neutral, angry, fearful, or happy) and rate the intensity of the facial emotional display. (Bottom-Left) Averaged recognition accuracy of participants. (Bottom-Right) Intensity rating of participants.

However, it remains unclear whether this bias is associated with threat information conveyed by fearful face or the distress signal it embodies ('I am scared, I need help') or both. On one hand, it has been observed that fearful face perception during Threat-of-Shock procedure is associated with an increase in the connectivity between the amygdala and the dmPFC (Robinson, Charney, Overstreet, & Grillon, 2012) involved in reasoning about thoughts and intentions of conspecifics (Wagner, Kelley, Haxby, & Heatherton, 2016). These results suggest that participants would be sensitive to the distress conveyed by this signal. Furthermore, "sense of being threatened" does not appear to impact on the categorization of anger (identify as an explicit threat, Kavcioglu et al., 2019). Conversely, Grillon et al. (Grillon & Charney, 2011) showed that reflex startle was potentiated during threat blocks when participants perceived fearful face. Fear is then interpreted as a potential threat when participants felt anxious, as it generates defensive mobilization. Furthermore, Vytal et al. (Vytal, Overstreet, Charney, Robinson,

& Grillon, 2014) observed that the feeling of being threatened favored the coupling of brain regions involved in mechanisms important for defensive responding (such as affective bias, appraising of threat, motor preparation and alertness). This implementation of defensive mobilization suggests that being under threat could favor the prioritization of the threat signal conveyed by fear. Future studies should clearly assess the implication of these two interpretations.

4.4-Perception of positive signals

Regarding the processing of positive signals (happy face/positive picture), contrary to the studies using the TSST procedure, results are not in favor of an increase in the sensitivity of positive stimuli. Through five studies, three studies report that the positive processing bias observed under safe blocks disappeared under threat ones (Neta et al., 2017; Robinson et al., 2016; Robinson et al., 2011) and two studies reported no impact of anxiety on positive bias (Aylward et al., 2017; Lago et al., 2019). It means that these studies robustly find no particular stress effect on perception of positive cues (happy face/positive picture). However, when participants felt threatened, they rated highly positive faces as more intense (Kavcioglu et al., 2019). In addition, the defensive reaction measured by the startle reflex decreases in the presence of positive stimuli (Bublitzky, Guerra, Pastor, Schupp, & Vila, 2013). Of interest, startle reflex is not modulated if the person threatening or conveying the presence of the threat (i.e. threat-of-shock is indicated by an avatar) is smiling (Bublitzky, Guerra, & Alpers, 2018; Bublitzky, Riemer, & Guerra, 2019). Based on these results, I would like to suggest that positive cues may impact our reactions if they are perceived as a potential social support. Furthermore, in a MEG study, Bublitzky et al. (Bublitzky et al., 2020) showed that the incongruous presentation of a positive face in a negative threat context is associated with late activity in the ventrolateral prefrontal cortex as well as the temporal pole. These clusters are associated with a time window more later than the cluster involved in threat processing. The authors argue that these clusters reflect in-depth processing of unexpected environmental conditions. Another possible interpretation is that, under threat, participants remain sensitive to positive information but process it later, after the processing of threat information. This interpretation could explain why the literature on cortisol found an increased positive bias while participants perform the task of interest when they are no longer exposed to stress. Again, this result can be totally in line with our assumptions: positive cue is relevant but safety first.

4.5-Self-other Balance

Concerning self-other distinction, to our knowledge, very few studies have investigated this phenomenon. Using the VPT presented before, Todd & Simpson (Simpson, Todd, & Simpson, 2018) showed that under time pressure, level-1 visual perspective-taking (i.e., what others see) is not

impacted, while level-2 visual perspective-taking (i.e., how they see things) is reduced. The authors suggest that level-2 calculations take longer and are not adapted to short response times. Reimer et al. (Reimer, Bublatzky, Trojan, & Alpers, 2015) proposed to investigate the plasticity of our body schema (an important component of the self) when we feel threatened. To do this, participants performed the well-known rubber hand (Botvinick & Cohen, 1998) illusion task during threat and safe blocks. The authors observed that, while markers of induced anxiety correlated positively with the subjective feeling that the plastic hand belongs to their own body, no effect was observed on proprioceptive drift, used as an objective measure of the modification of bodily-ownership. These two studies suggest for the moment that alter-centric cognition may be negatively impacted under time pressure, and that the self-representation appears to be not plastic under threat situation. However, too little studies have been done on this subject to conclude. To understand how others are processed in threatening situations, other mechanisms involving self-other balance need to be investigated. For example, other forms of co-representation (action or reasoning) or the modification of our peripersonal space, defined as a space of body defense (de Vignemont & Iannetti, 2015), should be future lines of research to pursue the debate of sociality under threat.

4.6-Social memory

Consistent with experiments using the TSST paradigm, a decrease in old-new performance was found when faces were encoded while participants felt threatened, compared to when they felt safe (Bolton & Robinson, 2017; Garibbo et al., 2019). However, Schellhaas and al. (Schellhaas, Arnold, Schmahl, & Bublatzky, 2020) showed that, while participants were not better to retrieve faces they encoded under threat, an MEG investigation of the neural signatures of encoding and retrieval processes revealed a sustained involvement of several clusters. First, under threat, early parieto-occipital and late fronto-central negative potentials were observed during encoding. Authors proposed that these clusters are associated with early attention directed toward motivationally relevant information. In addition, during recognition, they observed late centro- and parieto-occipital negativities when participants perceived faces which were encoded under threat. These clusters are known to be associated with perception and attention allocation. Altogether, it suggests that faces are relevant under threat even if participants are not able to recall their identities.

4.7-Value representation and attention: instrumental signals for goal-directed actions

When we are threatened, different action opportunities may arise in order to achieve the same general goal: to survive. For these goal-directed actions to be planned, it is necessary to represent the values of their associated outcomes. What happen to our representations of costs and benefits in situations of

danger? First of all, under threat, a hyper-activation of the striatum is observed (see **Figure 2-5**): it is of the same amplitude when participants perform a monetary experiment in the gain domain or in loss domain (Gorka, Fuchs, Grillon, & Ernst, 2018). Nevertheless, the striatum region appears to be especially sensitive to aversive errors of prediction, i.e. when bad prediction lead to a costly punishment (Robinson, Overstreet, Charney, Vytal, & Grillon, 2013). Under threat situations, a high priority is done to avoid aversive stimuli. Similarly, Bublatzky et al. (Bublatzky, Alpers, & Pittig, 2017) showed that, in a threat situation, participants refused high rewards if they were associated with a high probability of receiving a shock. However, in this task, participants did not actually receive any shock. Thus, over the time, participants tended to accept more high reward options (compared to the beginning of the experiment), probably because they understood that it was ultimately risk-free.

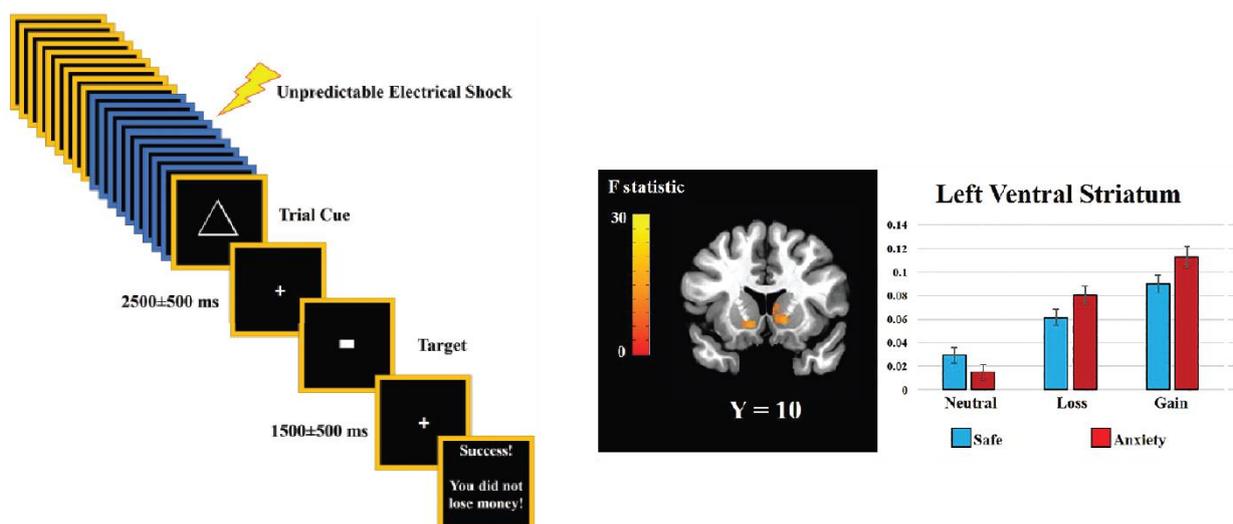


Figure 2-5. (Left) Experimental design used by Gorka et al. (2018): a geometric shape (Trial Cue) indicated the type of trial (i.e. gain, loss or neutral) was followed by a target. Participant task consisted on successfully pressing the button when the target was displayed. Feedback (i.e. success or failure and its monetary consequence) ended each trial. The task was performed under safe blocks (denoted here in yellow) and during threat-of-shocks blocks (denoted here in blue). (Right) Statistical parametric map of the condition (threat vs. safe) by trial type (neutral, gain, loss) interaction during the anticipation of the target within the bilateral Striatum. The extracted parameter estimates from the left Ventral Striatum were also provided here (Y axis values represent arbitrary units and the error bars represent ± 1 standard error).

Consistently, there is a strong literature supporting that threat signal is the priority. However, some argue that what drives our cognitive mechanisms is survival (Vogt et al., 2017). For example, if more relevant signals (i.e., maximizing the probability of survival) are presented, they should receive more attention even if they do not convey threat. Indeed, in context of danger, safety signals (i.e., increasing the probability of escaping an aversive stimulus) induced greater attentional capture than those conveying threat (Vogt et al., 2017). Since attention cannot be easily dissociated from motivational processes (Okon-Singer, Lichtenstein-Vidne, & Cohen, 2013; Pessoa & Adolphs, 2010; Vogt, De

Houwer, Crombez, & Van Damme, 2013; Vromen, Lipp, & Remington, 2015), it is oriented according to the cost/benefit ratio of the various cues present in the environment.

Attention mechanisms are essential in situations of danger. In the context of threat, neural activity as well as the global connectivity of the intraparietal sulcus, involved in attentional orientation, are increased (Balderston, Hale, et al., 2017). They would promote hypervigilance mechanisms allowing effective visual navigation in a changing environment where a fast action is required. These attentional capacities seem to depend on the possibility of escaping or not. When threat is unavoidable (L w, Weymar, & Hamm, 2015), it induces a phenomenon of attentional freezing which manifests itself physiologically by an increase in arousal (increase of SCR), an increase in defensive mobilization and by bradycardia (decrease in HR). These bodily modulations favor an efficient scanning of the external world. However, when it can be avoided, response-preparedness processes are involved, manifested by a decrease in the startle reflex and a drop of P3 component of the evoked brain potentials (used as a marker of attention). Several studies also showed that action inhibition mechanisms are particularly effective in threat situations (Grillon et al., 2017; Grillon, Robinson, Mathur, & Ernst, 2016; Torrisi et al., 2016). Authors suggest this inhibition to be in favor of freezing strategies under threat. Indeed, the performance of participants correlates positively with startle-reflex (Grillon et al., 2017) and is associated with hyperactivation of the frontoparietal network involved in attentional processes and problem solving (Torrisi et al., 2016). These results suggest that threat initially promotes attentional freezing mechanisms. Montoya et al. (Montoya, van Honk, Bos, & Terburg, 2015) suggest that one of the physiological mechanisms allowing to switch from an attentional and emotional regulation system to a readiness for action system would be cortisol induction. If this hypervigilance seems appropriate for survival, it remains unclear on which category of stimuli our attention stops and why.

The previous paragraphs suggest that our attention could be oriented toward both threat and safety signals. But since social-emotional signals can simultaneously convey affiliation or threat, the motivation behind this attentional capture remains to be identified. Lojowska et al. (Lojowska, Gladwin, Hermans, & Roelofs, 2015) observed that attentional freezing was correlated with a better perception of low-spatial frequencies. The perception of these low-frequencies would favor a fast processing of threat information contained in emotional expressions of fear and anger. Electroencephalographic investigation of face perception by participants who may be exposed to electric shocks or not (Bublitzky, Guerra, & Alpers, 2020) indicates that anxiety increases the neural signatures associated with threat appraisal and attention (P3, EPN and N170). Taken together, it again appears that human have unique processes for threat signal. However, no studies have investigated clearly the role of others in our chance of survival under threat. According to the tend-and-befriend

hypothesis and the assumptions derived from the results of Dezechache and al., our social partners may represent a source of help during danger. It is then very possible to imagine that they receive the same amount of attention in a context where this strategy has the best cost-benefit ratio.

4.8-Conclusion: socio-cognitive mechanism modulations under threat

To sum up this review of the literature on cognition under threat, the results seem to show first of all that the social bond can be maintained under threat: social support, social influence as well as sensitivity to faces, emotional expressions of fear and in some cases hedonic stimuli. Participants are vigilant to threat signals: threat elicits negative affective processing bias (which is consistent with an expected anticipation to danger/mobilization to defend themselves). One primary reaction to threat seems to be freezing to efficiently assess threat in the environment. This is in line with theoretical model of defensive reaction as risk assessment is a prototypic reaction. In addition, brain areas associated with value estimation become very sensitive to gains and losses but appear to be particularly involved in maximizing loss avoidance behaviors.

As certain contextual factors modulate the values' indices in our environment, some of these effects seem to vary according to certain parameters: the possibility of escaping or the risk of being injured modifies the attention given to signals conveying safety and impacts our affiliative strategy. Altogether, these results seem to stand with Decety's opinion: "To survive, you have to care about yourself first. It doesn't mean that you don't care for others, but you have to survive first" (Chicago news - 25/08/2020). However, some of these results are particularly difficult to be interpreted as the representation of the stimuli values displayed to participants is often inferred *a posteriori* by the authors and that some effects depend on neuroimaging results whose interpretations suffer from inverse inferences. The case of the fearful face, for example, which can convey distress and threat, leaves room for interpretations that may be antagonistic or even complementary. Consequently, the question "why social cognition is maintained under threat" still remains. Nevertheless, it seems that a cognitive approach is relevant to study collective behaviors facing a threat insofar as certain parallels can be established: for example, the association between risk and cooperation or social identification and cooperation which has been previously established in social science.

Mechanisms	Task details	References	Stressors	Effects
Emotion Perception	Emotion Categorization	Kavcioglu et al. 2019 °	Instructed TOS	Anxiety biased categorization of fearful, but not happy and anger facial expressions. Anxiety ↗ intensity of anger face as well as highly fearful and happy faces.
		Bublitzky et al. 2020 °	Instructed TOS	Anxiety biased categorization of fearful, but not happy facial expressions. Incongruence valence (e.g. happy/threat) and congruence (e.g. fear/threat) are processed by different networks.
		Robinson et al. 2012 °	TOS	Anxiety ↗ faster behavioral response to identify fearful faces. Anxiety ↗ positive DMPFC-amygdala connectivity during fearful faces processing.
Defense preparation	Reversal Learning Task (Safe/Threat vs. Happy/Anger)	Bublitzky et al. 2019 °	Instructed TOS	Happy and anger faces learned to signal threat, triggered similar physiological defense preparation while subjective reports were sensitive to valence of the cue. After the reversal of association, physiological activities were again insensitive to valence while subjective reports were modulated by valence.
		Bublitzky et al. 2018 °		Happy and anger faces learned to signal threat, triggered similar physiological defense in both instantiation and reversal block.
	Picture Viewing	Bublitzky et al. 2013 °		Startle reflex under anxiety is decreased by the presentation of hedonic picture.
	Emotion Categorization	Grillon & Charney 2011 °	TOS	Anxiety ↗ startle reflex transiently potentiated by fearful faces (compared to neutral faces).
	Fear-and-Escape Task	Motoya et al. 2015	Aversive noise + HC	Anxiety ↗ successful escape (% and RT). Cortisol ↘ fear-related midbrain activity during inescapable threat while ↗ activity in the frontal salience network (autonomic control, visceral perception and motivated action) when escape is possible.
Self-other Balance	Rubber Hand Illusion	Riemer et al. 2015 °	Instructed TOS	+ Correlation between anxiety markers and sense of ownership. No correlation with proprioceptive drift.
	Visual Perspective Taking (VPT)	Todd & Simpson 2018 °	Time pressure	Time pressure ↘ egocentric bias in Level 1 and 2 of VPT, ↘ altercentric bias in Level 2 of VPT.
Negative Bias	Affective Stroop Task	Lago et al. 2019 °	TOS	Anxiety ↘ Stroop-Effect for Negative pictures. No effect on neutral or positive.
		Robinson et al. 2011 °		Anxiety ↗ negative processing (higher accuracy for fearful face) and abolished a positive affective bias (happy face).
	Affective Sustained Attention to Response Task	Aylward et al. 2017 °		No emotion (fear vs. happy) x Anxiety interaction.
	Face-Shape Attention Control Task	Robinson et al. 2016 °		Anxiety ↗ 'affective bias-related' amygdala-dorsal medial frontal coupling during the processing of emotional faces. Anxiety ↗ coupling between the amygdala and a more rostral prefrontal region to overcome affective bias when attentional control is explicitly asked. These effects are more driven by positive cues.
	Valence Categorization	Neta et al. 2017 °		+ Correlation between emotional arousal elicited by TOS and the % of negative categorization of surprised facial cues. Anxiety abolishes positive bias.
	No-Task	Vytal et al. 2014 °		Anxiety ↗ + coupling between regions involved in defensive responding (affective bias, appraising threat, motor preparation or alertness), and decreased coupling between regions involved in emotional control and the default mode network.
Attention	Face Identity Threat Cueing task	Bublitzky et al. 2020 °	Instructed TOS	Anxiety ↗ motivated attention and affective appraisal flexibly of identity implicit and explicitly related to threat (ERP: P3, EPN and N170).
	Online Anxiety Ratings	Balderston et al. 2017 °	TOS	Anxiety ↗ neural activity and global brain connectivity of the intraparietal sulcus (IPS) involved in attention orienting.
	Passive or Active Threat Exposure	Low et al. 2015 °	TOS	Anxiety ↗ Attentive freezing (i.e. increase in SCR, fear bradycardia, startle reflex) when threat can't be avoided. Anxiety ↗ response preparation (↘ startle reflex, ↘ ERP-P3) when it can be avoided.
	Gabor Perception	Lojowska et al. 2015	TOS	Anxiety detection of Low Spatial Frequency information at the expense of High Spatial Frequency. This effect is correlated with fear bradycardia.

Inhibition	Go-Nogo	Grillon et al. 2017 °	TOS	Anxiety ↗ response inhibition. + Correlation between No-go accuracy and defensive reactivity. - Correlation between No-go accuracy and threat-related task-irrelevant thoughts.
	Sustained Attention to Response Task	Grillon et al. 2017 °		Anxiety ↗ response inhibition in participant with low attention control abilities. No effect in high group.
	Sustained Attention to Response Task	Torrissi et al. 2016 °		Anxiety ↗ response inhibition. Anxiety ↗ right frontoparietal attention network and the insula activity which ↓ after No-go error. Anxiety ↗ striatal activity (associated with inhibitory processing) during No-go trials
	Emotional Go-No-go	Cohen et al. 2016 °	Unpredictable noise	Anxiety ↓ cognitive control in young adults associated with a ↓ activity of lateral and medial prefrontal circuit.
Social Influence	Real Fire evacuation	Nilsson & Johansson 2009 °	Alarm vs. clear vocal message	Uncertainty about danger ↗ social influence. – Correlation between spatial distance between visitors and social influence.
	Evacuation Task tunnel fire	Kinatader et al. 2014 °	VR: smoke flow	Presence of others influences route choice.
	Mass Emergency Evacuation Task	Moussaïd et al. 2016 °	VR: low vs. high stress context	High stress ↗ physical collision between individual. Social Influence is mediated by crowdedness.
Social Support	Helping Decision Task	Vieira et al. 2020 °	TOS	Imminent Threat ↗ helping behavior. Risk ↓ helping behavior. + Correlation between empathic concern and helping behavior.
		Moussaïd & Trauernicht 2016 °	Time pressure and monetary punishment	No effect on risk-taking. Stress reinforces initial collaborative strategies of participants.
	Social Regulation	Coan et al. 2017 °	ToS	Under anxious context, handholding by familiar relational partners attenuates both subjective distress and activity in a network associated with salience, vigilance and regulatory self-control.
	Virtual Fire evacuation	Drury et al. 2009 °	VR: burning underground rail station	High-identification participants with avatar were more helpful and pushed less.
Social Memory	Old-New Task with Faces	Bolton & Robinson 2017 °	TOS	Anxiety ↓ the encoding of faces.
		Garibbo et al. 2019 °	Instructed TOS	Anxiety ↓ the encoding of faces.
		Schellhaas et al. 2020 °		No effect on recognition. Anxiety ↗ early parieto-occipital and late fronto-central negative potentials during encoding (associated with early perception processing tagging of motivationally relevant information). During recognition, late central and parieto-occipital negativities are ↗ for face encoding under anxiety (associated with perception and attention allocation).
Motivation	High-Risk Low-Safe Decision-Making Task	Bublitzky et al. 2017 °	Instructed TOS	Anxiety ↗ avoided high rewarded but threat-related option until they learned that shock is never delivered.
	Monetary Incentive Delay Task	Gorka et al. 2018 °	TOS	Anxiety ↗ ventral striatum and dorsal areas of occipital cortex activities to incentives (no difference of gain or loss) while ↓ ventral areas of occipital cortex.
	Framing effect	Robinson et al. 2015 °		No effect on choice but anxiety ↗ RT in gain domain.
	Temporal Discounting Task	Robinson et al. 2015 °		No effect.
	Attentional Cueing Paradigm	Vogt et al. 2016 °	Imminent Aversive noises	Anxiety ↗ attention to safety cues over threat ones when they decrease the probability to be harmed.
	“What’s in the box?”	Robinson et al. 2013		Anxiety ↗ significantly increases ventral striatum aversive (but not appetitive) prediction error signal.

Table 2-3 - Effect of “being under threat” on several socio-cognitive mechanisms reported in 34 articles on the literature. Arrows indicate the direction of the effect (↗ indicates an increase, while ↓ indicates a decrease). ° indicates that experimenters recruited both male and female participants. HC: Hydrocortisol; TOS: Threat-of-Shock; VR: Virtual Reality.

5-Conclusion of the Chapter

In this chapter, we established links between different laboratory studies investigating the relationship between cognition and threat in an attempt to infer which processes might occur when we are in danger

and why. Previous models classifying human defensive reactions showed that these were influenced by the distance from the danger, the time available to react, the probability of being injured and the possibility to escape. In light of this review, it would be legitimate and even necessary to add the presence of social partners in these models, since others have an important place in the cognitive processes that take place when one feels threatened. This review provides a start for defining what “transformation of social cognition by threat” means.

The number of studies remains low, especially in regard to the number of experimental factors manipulated (i.e. type of threat and cognitive function targeted). It is therefore complicated for the moment to establish a clear picture of the social cognition involvement in our behaviors under threat. The above review of the literature however brings some insights: social vs. physical stress, stressed alone vs. in group, cognition assessed after vs. under threat, threat vs. instrumental safety cue and so on. Overcoming this theoretical antagonism between asocial versus (pro)social reactions in a situation of danger was necessary to understand the function of social cognition under threat. At first glance, all these results taken separately seem to be contradictory and not convincing, but they represent meaningful experimental variations driving our defensive reactions. These are small jigsaw pieces from different literatures that we tried to put together to depict a more global scientific understanding of our social cognition under threat. This work is needed to move forward on more common bases.

In order to make progress in building this bridge between neuroscience and social psychology, it is necessary to keep accumulating empirical evidence that will allow us the construction of a more solid theoretical framework. So far, it has been shown that social cognition is sustained and that some mechanisms are still running in response to threat. Yet, we still need to clearly describe which ones and their roles. One possible approach is to try to understand what motivations underlie social strategies. In particular, Dezechache et al. (Dezechache, Grèzes, & Dahl, 2017; Dezechache et al., 2020) pointed out the need to clearly identify in which contexts others are taken into consideration (i.e. distance to danger, presence of escape road).

In conclusion, addressing the motivational component by finding the appropriate experimental factors would feed ongoing discussions. Lastly, and above all, almost all studies introduced previously explored social cognition in situations of danger only through tasks involving one participant. However, to tackle collective reactions under threat, it is then necessary to explore social cognition during joint tasks, involving more than one participant.

IMPACT OF ANXIETY-INDUCING CONTEXTS ON SOCIAL ACTION AND PERCEPTION

In previous chapters, we have described defensive reactions in threat situations, highlighting the value of investigating social cognition in this context. Indeed, field studies from social sciences have shown several times that sociality is maintained under threat. These studies then discussed why it was the case. One of the possible and particularly attractive reasons is to conceive that others would be a possible solution for an individual exposed to a stressor to restore his or her homeostasis. These solutions take a wide variety of forms, ranging from providing social support to reduce negative affect as well as physiological and endocrinological responses provoked by stress, but also through the organization of cooperative actions. To implement this type of strategies, it is necessary to perceive, to identify and to evaluate the relevant social resources existing in the environment but also to coordinate with other individuals. Also, these strategies seem to be implemented only if associated with a low cost-benefit ratio. Several laboratory studies investigating these functions seem to confirm some predictions from social psychology. First, exposure to a stressor or the feeling of being threatened does not interrupt social cognition: this would be expected if individuals panicked and became asocial under threat. If individuals keep monitoring the sources of threats and seem particularly sensitive to the possibility of a negative outcome, they are also particularly sensitive to rewards. Indeed, their attention is directed towards safety signals. In addition, they are generally seeking and sensitive to social signals, and sometimes they engage in seemingly pro-social strategies. All these results suggest that social cognition is modified rather than interrupted in threatening situations.

1-Summary of current gaps in our research questions

The function of the socio-cognitive mechanisms that may be in place when we feel threatened is often interpretative (not to say speculative) and sometimes even multiple and contradictory. One of the most striking examples identified in the previous chapter is the case of fearful face. This stimulus is a particularly interesting tool to understand our reactions in situations of danger because it is likely the most conveyed social signal in contexts such as the Bataclan attacks in Paris (13-11-2015). Our cognitive system, from perception to action, is especially sensitive to fearful faces (Koizumi, Mobbs, & Lau, 2016; Méndez-Bértolo et al., 2016; West, Al-Aidroos, Susskind, & Pratt, 2011). Indeed, the emotional expression of fear has two functions (supporting literature will be detailed in Chapter 6): the first one is to indicate the presence of danger to our social partners. Coupled with the direction of the gaze (i.e. averted gaze), it can also inform about the position of this danger. It is then a relevant social

signal in a context in which threat is still ambiguous for the one perceiving this signal. At the same time, fear emotional display conveys a demand for affiliation, it communicates vulnerability and could be interpreted as an invitation to cooperation in a threatening situation. This signal would be particularly salient when the person expressing this social message establishes gaze contact (i.e. direct gaze orientation). Several studies have investigated how perception of fear affects our cognition under threat but without controlling which of these two functions is responsible for the observed modulation. This leaves room for multiple and antagonistic interpretations such as "the priority being *my own* survival, clues indicating the position of danger are the most relevant" or "in a situation of threat, my primary reaction is affiliation because it is an effective solution to restore my homeostasis". Thus, as attending to the same social signal can be supported by very different motivations, Dezechache et al.'s opinion (social versus asocial taxonomy is not precise enough to be explanatory) needs to be developed and tested.

Moreover, "how threat transforms social cognition" problematic indirectly questions how others are included in our action choices in situations of danger. Indeed, in everyday social interactions, humans often need to coordinate their actions with those of others. Sharing perceptions and representations with others facilitate coordination. To do so, people appear to spontaneously compute another person's visual perspective (Samson et al., 2010) and to represent their actions (Sebanz, Knoblich, & Prinz, 2003). However, the literature about threatening context and alter-centric cognition is scarce. Yet, contextual modulations of shared perceptions and representations and their functional implications would be a very interesting tool, both qualitatively and quantitatively, to predict our strategies in situations of collective danger. In order to implement collective actions, it is necessary to align our mental representations with those of others (i.e., co-represent them): they should therefore be mandatory in the preparation of social strategies for survival, regardless of whether they are implemented for individual or collective benefits. Conversely, if collaboration is an action that is costly in a context, it should not be interesting to maintain these representations that are resource-consuming (Usal & Hohenberger, 2017). This could explain the stomping and pushing behaviors in some contexts as individuals have completely stopped representing others. Finally and importantly, no one has studied how threat impacts participants' performance in joint tasks (i.e., joint action or joint perception). However, these experimental designs are the closest/more ecological in order to understand collective actions.

2-Objective and research questions

The investigation of social cognition when feeling threatened must keep going in order to create a clearer theoretical framework to work. Thus, it will be necessary to understand which factors favor

one strategy over another. Previous chapters provide conceptual and methodological guidelines in regards to research on social cognition under threat. Following these directions, we believe that putting experimental factors in competition with each other in the same study, as Vogt et al. (Vogt et al., 2017) elegantly did when they presented both safety and danger signals, is an approach that can be effective in understanding the motivational balance underlying the orientation of our perception-action loop. This is the main objective of this thesis which materializes through the two previously introduced examples: co-representation and the perception of fear.

In fact, identifying whether one still includes others in his action plans when feeling threatened and under what conditions is crucial: (i) to understand which strategy set up and (ii) to challenge theoretical positions. For example, if we observe that co-representation mechanisms are completely shut down, this could lead us to question the subjective reports of disaster survivors reporting cooperation. Results from Dezechache et al. (Dezechache et al., 2020) suggest that perception of danger boosts people's perception and investment in supportive action opportunities. Indeed, these latter are likely to offer immediate emotional or physical comfort. To confirm this, co-representation should be influenced by the ability of my social partners around me to provide this comfort. Similarly, investigating simultaneously how the two messages conveyed by fearful face are processed (i.e., affiliation vs. danger) would be a possible proxy for inferring incentives influencing the motivational balance. Under threat, individual could stop processing social signals (i.e., such as perceiving fear from others, independently of gaze direction) which would likely be underlined by an asocial strategy. Conversely, threat could boost the processing of either social signals communicating the presence of danger (i.e., gaze with an averted gaze) to quickly locate its position (to maximize individuals' own survival) or signals communicating a request for affiliation (i.e., direct fearful face), which would be the result of a cooperative strategy.

Finally, considering how to induce a feeling of being threatened in an efficient way was central in this Ph.D. project. It was largely inspired by the analyses of the strategies put in place during the Bataclan attacks, in Paris (France), 13-11-2015. This was a situation in which victims were exposed to a source of danger for a prolonged period of time and in which reactions took place while they were still exposed to this danger. Consequently, the use of a paradigm such as the threat-of-shock paradigm would be particularly relevant because it is the most akin to a real situation. Nevertheless, several problems (detailed in Chapter 4) have led us to propose an alternative version of this paradigm. First, using electric shocks was not materially possible in our laboratory. Also, this technique requires inducing pain when searching for participant's nociceptive threshold, which we did not want. Another alternative, which has already been implemented (Patel, Stoodley, Pine, Grillon, & Ernst, 2017; Patel

et al., 2016), is to replace the shocks with distress screams that are aversive because of their social meaning (Arnal, Flinker, Kleinschmidt, Giraud, & Poeppel, 2015; Belin & Zatorre, 2015). The presentation of random distress screams should be enough to induce a state of sustained anxiety. Nevertheless, previous studies have presented screams at an intensity higher than 95dB, which again raised problems because they exceeded the danger thresholds for hearing (85dB). Moreover, based on the results of studies that employed threat-for-shock paradigms, it was difficult to ensure that this type of paradigm was able of inducing a stable (i.e. without habituation) state of anxiety over time, which is problematic when some measures require a lot of trials.

Thus, the research questions I explored in this dissertation assessed these three core issues/subjects:

1-Can we induce a prolonged feeling of being threatened by randomly delivering distress screams at low intensity (70dB)? Can this be used to study responses to ongoing threat in the lab? (**Chapter 4**)

2-What happens to my ability to co-represent under threat? Does it depend on the social context/resources of the individuals around me? (**Chapter 5**)

3-What message conveyed by fearful face is prioritized in a situation of threat? The presence of danger, the request for affiliation, neither or both? (**Chapter 6**)

Ultimately, we hope that the answers will provide some insights into why and how social cognition is transformed during threatening situation.

3-General Methodology

All studies in the present thesis involved both an anxiety-inducing procedure (threat-of-scream) and social cognition task (social Simon or fear-neutral categorization task). Within each task, the instrumentality (i.e. incentives) of social cues was manipulated by modulating either the social context where they were presented or by modifying their social meaning by combining them with a secondary cue. This section details the experimental design and the parameters implemented.

3.1-The Threat-of Scream Paradigm

To induce a ‘sense of being threat’, we used an acoustic version of the gold standard threat-of-shock paradigm (Robinson et al., 2013). It consists in repeatedly exposing participants to blocks during which they were at risk of hearing aversive screams at any time (Threat) versus blocks during which they were safe of screams (Safe). The type of block was indicated by color bands at each side of the screen (blue for threat blocks; green for safe blocks). Importantly, we controlled the screams to be below 70dB. Impressive amount of studies supports that unpredictability and uncontrollability are central

features of stressful experiences (De Berker et al., 2016). Based on that, to effectively induce anxiety, aversive stimuli had to be delivered in an unpredictable manner. During each threat block, six distress screams were delivered once (approximately 6% of the trials), randomly during the block (following a uniform distribution) at any time during trials. Screams were provided by Professor Jorge Armony, and had been previously validated (Fecteau, Armony, Joannette, & Belin, 2005): half of them were female voices and half of them were male voices. To check whether this manipulation was robust through time, we tested it twice during a one-hour experiment in which skin conductance level and subjective reports of anxiety were measured during each safe and threat blocks.

3.2-The Social Simon Task

A task developed to assess co-representation of action is the social version of the Simon task which has been developed by Sebanz et al. (Sebanz et al., 2003). During a Simon task, participants are exposed to two different colored stimuli presented either on the left or on the right of the computer screen. Each stimulus is associated with a left- and right-oriented key press, such that the colored cue can be spatially aligned with the corresponding key press (congruent trials) or not (incongruent trials). Stimulus location on the screen is completely task-irrelevant and participant should focus only on colors. This task can be performed in a categorization or in a go/no-go version (see **Figure 3-1**) depending on how many colored cues participants are responsible for (playing with one or two hand) or/and how many players took part in the task (playing alone or in pair). When participants performed the categorization task, we observed the so-called Simon Effect (SE), a positive difference in reaction times between congruent and incongruent trials. In incongruent trials, each spatial and color information activates an action plan and the two compete with each other, thus slowing down participant's responses to the cue. However, and of interest here, when the go/no-go version of the task is performed alone, the SE disappears (one action plan) while it reappears in the dyadic version. This alter-centric interference, better known as Social SE, may be regarded as an objective measure of self-other integration. This social effect is explained by an automatic co-representation of surrounding individuals' actions, as if the co-partner was the second hand (Dolk, Hommel, Prinz, & Liepelt, 2013; Sebanz et al., 2003; for a debate on the underlying mechanisms)

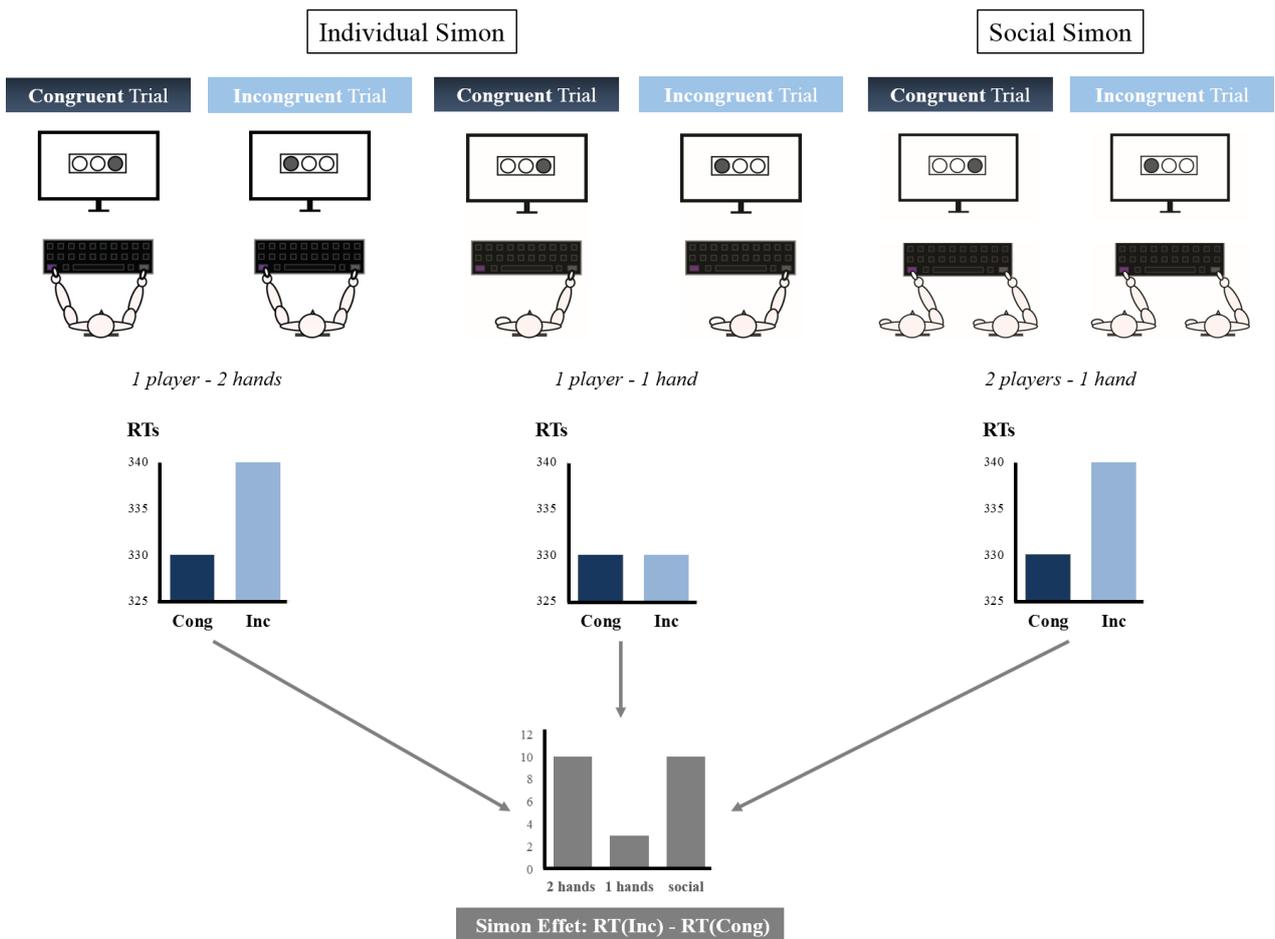


Figure 3-1. Explanation of the social Simon task and the social Simon effect.

In the haunted house study led by Dezechache et al. (Dezechache et al., 2017) social contacts toward individuals who were the closer from danger decrease probably because recruiting support from this individual was (i) highly risky as near of threat and (ii) slightly beneficial as the individual could not provide help. Inspired by these results, we manipulated the social value of the co-partners by creating two versions of the task. In the Common fate version, participants shared the same anxiety context (both are exposed to distress screams at the same time vs. both are totally safe), whereas in the Non-Common fate version, only one participant is under threat while the other is safe (with the roles being reversed in following blocks). Whether co-representation under threat depends on the safety of the second partner (an accessible social resource who can provide help) or not, it will help understanding the mechanism supporting the recruitment of self-preservative or mutual support.

3.3-Neutral-Fear Categorization task

To deepen our understanding of the social strategies undertaken during dangerous situations, a perception framework can be used. As action and perception systems are strongly interconnected (Decety & Grèzes, 1999; El Zein, Wyart, & Grèzes, 2015; Grossman et al., 2000), signals conveyed

by others are key piece of information able to influence our action choices. Thus, one possible approach to identify incentives of human social behaviors under threat is to study how social cues are processed. During this thesis, we investigated the communicative functions of one of the more meaningful cues in danger situation: fearful faces which simultaneously signal distress and danger. One secondary cue is gaze direction: averted gaze increases danger-related signal conveyed by fearful faces while direct gaze may be associated with a need-for-help. Looking at how fearful faces and gaze direction combinations are processed under threat will inform us about which signal (and eventually, which strategy) is prioritized under threat.

In order to do so, we combined a Threat-of-Scream procedure with a modified version of the categorization task initially developed by El Zein et al. (El Zein, Wyart, & Grezes, 2015). The experimental task was a Neutral-Fear emotion categorization task. In each trial, participants were presented with a facial expression of varying intensity (from 0: neutral to 7: high level of emotion strength), paired with direct or averted gaze, and had to categorize the expressed emotion. The concomitant gaze direction was not mentioned to the participants and hence was implicit. To better characterize cognitive mechanisms involved in participant behavior, computational models from signal detection theory were applied on data. Parameters of the models will inform us on how threat transforms the processing of signal either by modulating the perception sensitivity of cue or by biasing our subjective evaluation of them (decision criterion).

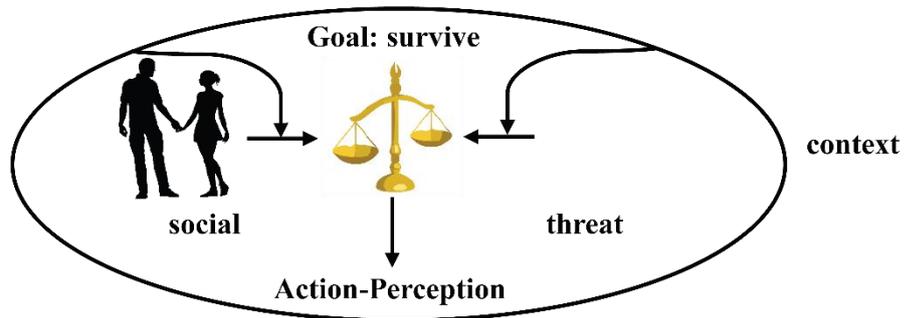
4-Summary of the Chapter

To investigate how social cognition is transformed under threat, experiments presented in this thesis investigated how and why the sense of being threatened impacts action co-representation and perception of fear emotional displays (see **Figure 3-2**). Then, we first validated a within-subject procedure to induce anxiety using the unpredictable delivery of 70-dB aversive distress screams (**Chapter 4**). This procedure has been applied to two well-known paradigms: the social Simon task which allows to assess action co-representation (**Chapter 5**) and a neutral-fear categorization task to investigate the processing of fear emotional display (**Chapter 6**). To understand the nature and dynamics of collective reactions to imminent danger in humans, the instrumentality (i.e. value/social meaning) of experimental factors has been varied. We assumed that the way our cognition will be sensitive to particular factor incentives will inform the function of social cognition under threat. The following experimental section of this thesis will present each of these experiments in detail.

HOW DOES THREAT TRANSFORM SOCIAL COGNITION?

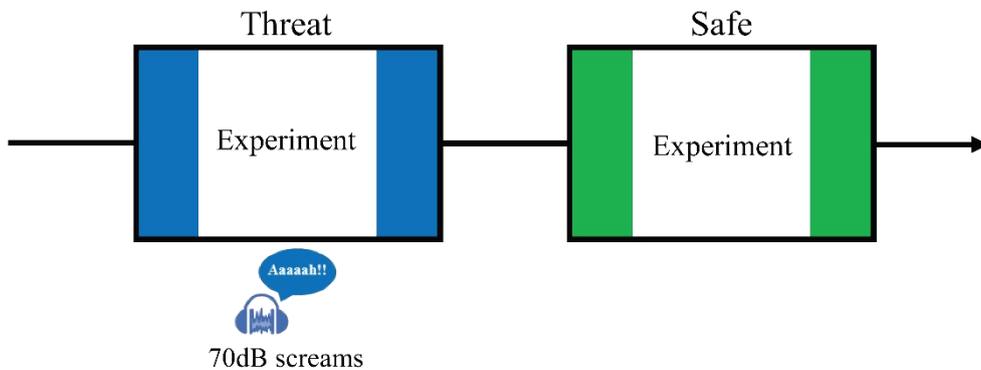
Assumption:

Others can be a safety instrumental signal



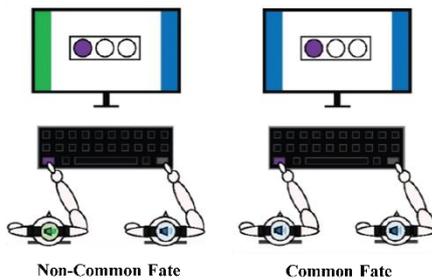
Threat anxiety-inducing manipulation

① Validation of the Threat-of-Scream Paradigm



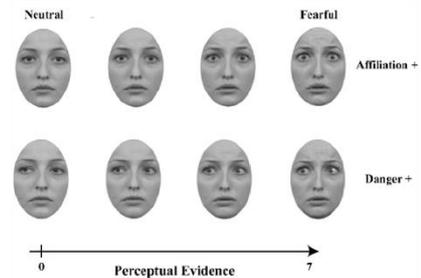
Experiments

② Action Co-representation



Social Simon Task

③ Perception of fearful faces



Neutral-Fear Categorization Task

Instrumentality

Others' resources to help or not

Affiliative vs. danger-related signal

Figure 3-2. Organization of the Ph.D. dissertation - To understand how threat shapes social cognition (i.e. how the value of social cue impacts our action planning and perception), we first validated the threat-of-scream paradigm and we applied it on the two tasks to investigate co-representation of action and perception of fearful face depending on two instrumental modulations: resources to help and affiliative signal.

EXPERIMENTAL STUDIES

INDUCING A 'SENSE OF BEING THREATENED' IN THE LAB VALIDATION OF THE THREAT-OF-SCREAM PARADIGM

In this chapter, we will describe the central method we have used in all studies we conducted: the threat-of-scream paradigm. This paradigm is an acoustic version of the gold-standard threat-of-shock. Threat of unpredictable shocks is an efficient and reliable within-subject procedure to elicit anxiety (i.e. sustained stress) in both humans and animals (Davis et al., 2010; Grillon, 2008). When this project was created, the literature on this procedure raised two questions:

- (i) Is this type of procedure effective through long experimental sessions?
- (ii) Can we use another stimulus more easily applicable in laboratory than the electric shock?

Hence, we chose human distress screams instead of electric shocks. To ensure the safety of participants' audition, the screams were presented at an intensity of 70dB. Since the induction of a sense of being threatened was the main experimental factor in our planned studies, we first validated this paradigm inside two groups of participants (N=26 then N=33) during a one-hour experimental session. To validate this tool, participants' subjective reports as well as their skin conductance level (SCL) were measured. A higher subjective report of anxiety and a higher SCL would demonstrate the induction of a sense of being threatened in threat blocks compared to the time-period in which no screams are delivered. Also, these two increases would be present over the whole experiment. As the following chapter will illustrate, I found a significant difference on SCL and subjective anxiety between threat-of-scream and safe time-periods. These results validate the efficiency of this procedure. Distress screams thus appear to be excellent candidates to investigate responses to ongoing threat in the lab.

The ‘Threat of Scream’ paradigm: A tool for studying sustained physiological and subjective anxiety

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NB2: Supplementary material is available in the Appendix section of the dissertation (p.161)

Abstract

Progress in understanding the emergence of pathological anxiety depends on the availability of paradigms effective in inducing anxiety in a simple, consistent and sustained manner. The Threat-of-Shock paradigm has typically been used to elicit anxiety, but poses ethical issues when testing vulnerable populations. Moreover, it is not clear from past studies whether anxiety can be sustained in experiments of longer durations. Here, we present empirical support for an alternative approach, the ‘Threat-of-Scream’ paradigm, in which shocks are replaced by screams. In two studies, participants were repeatedly exposed to blocks in which they were at risk of hearing aversive screams at any time vs. blocks in which they were safe from screams. Contrary to previous ‘Threat-of-Scream’ studies, we ensured that our screams were neither harmful nor intolerable by presenting them at low intensity. We found higher subjective reports of anxiety, higher skin conductance levels, and a positive correlation between the two measures, in threat compared to safe blocks. These results were reproducible and we found no significant change over time. The unpredictable delivery of low intensity screams could become an essential part of a psychology toolkit, particularly when investigating the impact of anxiety in a diversity of cognitive functions and populations.

Introduction

Given the ubiquity and persistence of anxiety disorders, as well as their massive impact upon quality of life (Leon, Portera, & Weissman, 1995), it is essential that neurobiologists and clinicians be able to determine how anxiety influences human brain physiology and behavioral responses to stress or external threats, along the continuum from normal to pathological conditions. While high anxiety leads to exaggerated estimates of the probability of threat, a certain level of anxiety is crucial for an organism's survival as it ensures optimal sensitivity and decisiveness in the face of possible threat (Bateson, Brilot, & Nettle, 2011; Grillon, 2008; Marks & Nesse, 1994).

The predictability of threat appears to be a major determinant of anxiety-related bodily manifestations, such as modulations of heart rate, startle reflex or skin conductance (Alvarez, Chen, Bodurka, Kaplan, & Grillon, 2011; Davis, Walker, Miles, & Grillon, 2010; Torrisi et al., 2016; Vansteenwegen, Iberico, Vervliet, Marescau, & Hermans, 2008). Indeed, predictable threats lead to phasic and acute fear responses (e.g. startle reflex (Grillon, Baas, Lissek, Smith, & Milstein, 2004)) that are directly associated with the appearance of that threat (e.g. a shock). In contrast, and in agreement with the safety-signal hypothesis (Seligman & Binik, 1977), unpredictable threats induce sustained anxiety-related physiological responses (e.g. startle reflex (Grillon et al., 2004) ; prepulse inhibition, a physiological marker of alertness (Grillon & Davis, 1997)) and enhanced vigilance, reflected in a long-lasting facilitation of the processing of sensory information (Kastner-Dorn et al., 2018).

The Threat of Shock paradigm (hereinafter TOS) has been the gold-standard paradigm to reveal the effects of anxiety on cognitive functions and quantify within-subject individual difference in threat response (for review (Robinson et al., 2013)). TOS consists in alternating blocks in which participants are explicitly told that they could receive an electric shock at any time (unpredictable threat blocks) with blocks in which participants are explicitly told that no such shocks will occur (safe blocks). Such on-off alternations allow experimenters to manipulate the state of anxiety within subjects as each participant can serve as her/his own control. TOS proved to be a reliable method for inducing sustained anxiety, as reflected in participants' higher physiological (startle reflex and elevated tonic skin conductance level) and psychological (higher reports of subjective anxiety) responses during threat versus safe blocks (Bradley et al., 2018; Grillon et al., 2016; Hubbard et al., 2011; Torrisi et al., 2016)

Yet, similarly to all paradigms, TOS has limitations. First, it is not clear whether it can induce sustained anxiety responses for long durations. Experiments that have employed the TOS paradigm have been relatively short (~ 30 minutes). Hour-long experiments using TOS do exist (Engelmann, Meyer, Fehr, & Ruff, 2015) but anxiety manipulation in these studies was mainly assessed using self-ratings of

anxiety states, susceptible to demand effects, and/or local phasic physiological changes, which only represent a few seconds of the participants' physiological state following the electric shock. To our knowledge, few experiments looked at whether induced anxiety could be maintained across several blocks. First, Bublatzky and colleagues (Bublatzky et al., 2013) reported no habituation of tonic skin conductance activity during an experiment lasting only 15 minutes, while Aylward and colleagues (Aylward et al., 2019) reported no habituation on subjective reports of anxiety across a 45-min experiment. Moreover, Bublatzky and colleagues (Bublatzky, Gerdes, & Alpers, 2014) provided promising results, even in the absence of aversive experiences, i.e. when participants believed that they could receive shocks in threat blocks while none were delivered, across repeated sessions within one day. However, in the absence of aversive stimulation, the induced anxiety across repeated test days diminished with different timing across subjective reports and physiological measures. It therefore remains unclear whether TOS, using unpredictable aversive stimulation, is resistant to physiological habituation even though long-duration experiments are necessary when testing several conditions and/or requiring a large number of trials (as in computational modelling).

A second limitation has to do with the appropriateness of TOS for certain study populations. Although well-known for their aversive properties (Schmitz & Grillon, 2012), electric shocks may not be administered to vulnerable and younger populations (notably children). White noise burst has been proposed as an alternative to electric shocks for fear-conditioning protocols that require a large number of trials (e.g. EEG and MEG, see (Sperl, Panitz, Hermann, & Mueller, 2016)). However, the same criticism arises. Aversive noise bursts are often presented at between 95 and 110 dB, an intensity that can potentially be intolerable and which could cause hearing loss following prolonged exposition (European Legislation- directive n° 2003/10/CE). Sounds between 95 and 110 dB not only exceed tolerance (75dB) and danger (85dB) thresholds for audition, they come relatively close to the pain threshold of 120dB.

What methodology can overcome these limitations while generating anxiety in most populations in a sustained and stable way? Threatening stimuli are useful insofar as they are perceived as unpleasant without being painful. In particular, distress screams produced by humans are good candidates as they are evolutionarily and socially meaningful sounds that efficiently signal impending danger to conspecifics (Arnal et al., 2015; Belin & Zatorre, 2015). They are perceived as highly aversive signals and are characterized by distinctive roughness acoustical properties (Anikin, Bååth, & Persson, 2018), which specifically engage subcortical regions known to be critical for swift reactions to danger (Arnal et al., 2015).

Human screams have previously been used during fear conditioning paradigms (e.g. screaming lady paradigm (Lau et al., 2011; Lau et al., 2008)), to investigate, for instance, the mechanisms involved in developmental anxiety (Britton, Lissek, Grillon, Norcross, & Pine, 2011). Stimuli paired with screams induce higher skin conductance (Ahrens et al., 2016) and startle responses (Glenn, Lieberman, & Hajcak, 2012; Haddad, Xu, Raeder, & Lau, 2013) as well as higher subjective anxiety reports (Den, Graham, Newall, & Richardson, 2015) compared to unpaired stimuli. However, as most past studies using screams delivered them with a potentially painful intensity (around or above 90 dB) (Ahrens et al., 2016; Dibbets & Evers, 2017; Geller et al., 2017; Hamm, Vaitl, & Lang, 1989; Lau et al., 2011; Lau et al., 2008), the aversive nature of screams and the potential painful experience may have both contributed to the observed responses. Nevertheless, some studies did succeed in evoking acute fear responses using intensities lower or equal to 80 dB (Den et al., 2015; Glenn, Klein, et al., 2012; Glenn, Lieberman, et al., 2012). Of interest, the fear potential startle was found to be comparable for stimuli conditioned with electric shocks or 80dB screams, even though those conditioned with shocks were reported to be more aversive than those conditioned with screams (Glenn, Lieberman, et al., 2012). If the substitution of shocks by screams is a promising means of generating acute stress, the question remains as to whether human screams can be an efficient tool to induce sustained anxiety in a within-subject paradigm. Of interest, adolescents show elevated startle responses in blocks during which a fearful female face accompanied by a piercing loud scream was presented in an unpredictable manner (as compared to blocks with neutral cues), suggesting that scream stimuli can induce sustained state of anxiety (Schmitz et al., 2011). Moreover, Patel and colleagues (Patel et al., 2016) manipulated anxiety in adolescents performing a working memory task using loud shrieking screams (Threat of Scream paradigm – TOSc). Substituting shocks with screams was successful as participants reported being more anxious and had higher startle responses in threat blocks compared to safe ones. Subjective anxiety of participants was found to be constant while no information was provided about differences in physiological changes over time. Yet, these experiments were short-lasting and the screams were delivered at a high intensity (95-dB).

To further establish the viability of the Threat of Scream paradigm (TOSc) and its promise for research on anxiety, we used human distress screams delivered at low intensity - rather than high intensity screams or electric shocks - to test their efficiency in inducing anxiety during a one-hour experiment. Since distress screams have specific acoustic properties and privileged communicative function, we expected these to be particularly suitable to evoke anxiety in a long-lasting fashion, especially when presented in an unpredictable manner. To determine whether sustained anxiety was induced, we measured subjective reports of anxiety and skin conductance activity; two markers that track

environmental uncertainty (De Berker et al., 2016). We ran the same 1-hour experiment twice, to assess whether the observed effects were replicable. Two conditions had to be met to validate the TOSc paradigm: (i) the unpredictable screams presented at low intensity (<80dB) should modulate anxiety responses, with increased subjective anxiety reports and increased tonic physiological activity (skin conductance) in threat compared to safe blocks, similarly to previous TOS studies; and (ii) sustained state anxiety should be induced for extended periods (here one hour).

Methods

Participants

Twenty-six healthy volunteers (12 females, age 23.6 ± 3.4 years SD) were recruited to participate in Experiment 1 (a sample of the same magnitude as Patel et al. (2016)'s study). Results from the correlation between tonic skin conductance activity and subjective reports of anxiety were used to calculate the sample size needed to replicate this result using G*power. The sample size for replication was estimated at $n = 27$ for an effect size of $d = 0.56$, $\alpha = 0.05$ and $\beta = 0.80$. To anticipate potential exclusions, we aimed at including 35 participants in Experiment 2 (Replication of Experiment 1), and 33 participants could be recruited (18 females, age = 23.89 ± 4.50 years SD).

All participants were right-handed, had normal or corrected-to-normal vision, and had no history of neurological or psychiatric disorders. The experimental protocol was approved by INSERM and the local research ethics committee (Comité de protection des personnes Ile de France III - Project CO7-28, N° Eudract: 207-A01125-48), and it was carried out in accordance with the Declaration of Helsinki. The participants provided informed written consent and were compensated for their participation.

General Procedure

First, participants were recruited thanks to an online advert, which consisted of a short description of the study and included an internet link which directed participants to a Qualtrics survey. Due to the potentially stressful nature of our paradigm and after discussion with the referent medical doctors of our laboratory, we requested that participants fill in, online and anonymously, the French versions of State-Trait Anxiety Inventory Spielberger (Spielberger, 1983) (STAI) and Post-traumatic stress disorder Checklist Scale (Weathers, Litz, Herman, Huska, & Keane, 1993) (PCLS), at least one week before the experiment. Only participants with a score below 40 for the PCLS and below 60 for both STAI state and trait anxiety were able to contact the experimenter, i.e. and were therefore included in the experiment.

Second, and on the day of the experiment, upon arrival at the lab, participants again completed the State-Trait STAI questionnaire on a computer to ensure that their level of anxiety was in the “normal” range (below 60) before the experimental session that aimed at manipulating their anxiety (see **Figures S4-1 & S4-2**).

Third, after providing the instructions regarding the main task, the experimenter installed the skin conductance electrodes. To identify potential physiological non-responders before the main experiment, the experimenter assessed the variation of the physiological signal while participants were asked to imagine a situation during which they fell into really cold water, and this, until stopped by the experimenter. All our participants showed increased physiological response during this mental imagery task; the response then dropped when asked to stop the exercise. Based on this definition of ‘non-responder’, there were no non-responders among our participants.

Fourth, participants started with a 4-minute training session, before performing the main experiment for approximately 1 hour, and were carefully debriefed at the end of the main experiment.

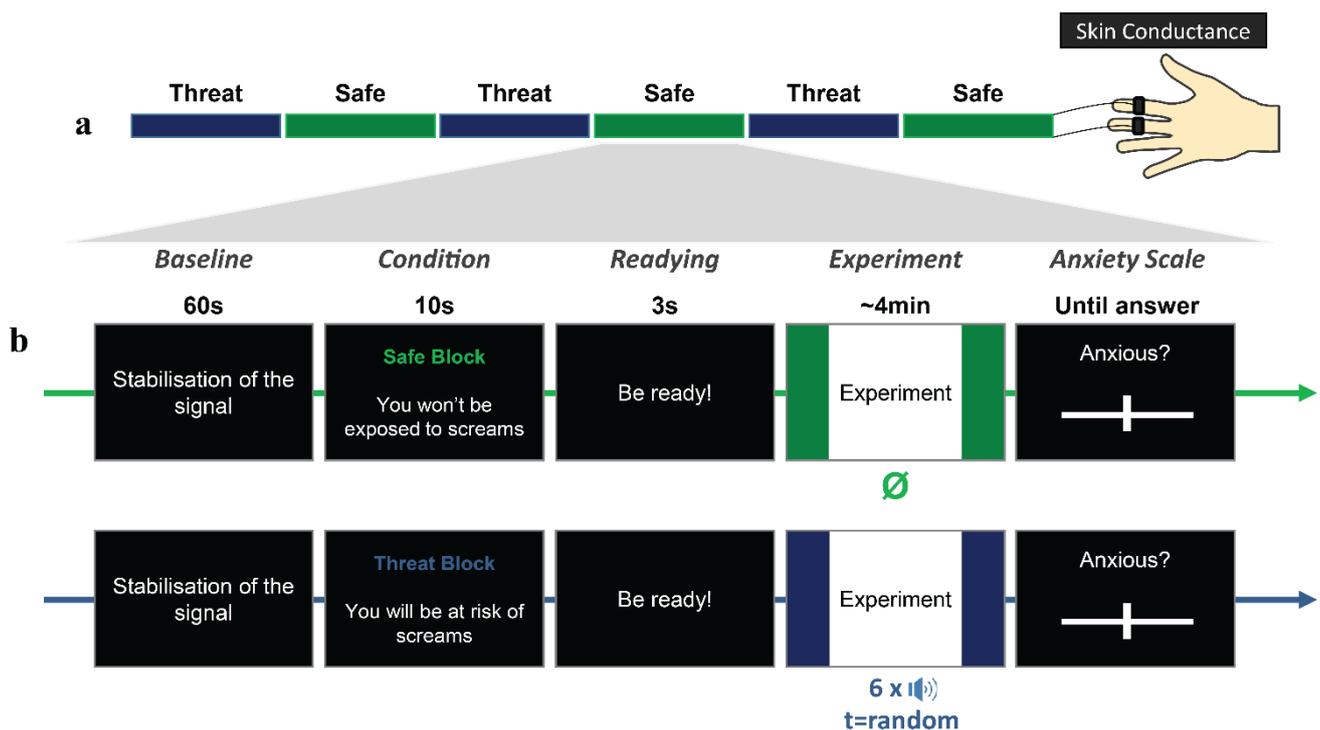


Figure 4-1. The Threat of Scream Design. (a) Temporal organization of the experiment. Participants performed a free action-task, in the two types of alternating blocks (Safe/Threat). (b) Temporal organization of a block. Each block began with one minute of baseline to measure participants’ skin conductance before each block. A written sentence was then presented for 10 sec, providing information about the upcoming nature of the block (Safe or Threat). Each block ended with an anxiety scale. Note that skin conductance activity was measured throughout each block whereas subjective anxiety ratings were only collected at the end of each block.

Screams stimuli

Eight distress screams were used in the present protocol (4 from males and 4 from females). The screams were normalized at -2b using audiosculpt 3.4.5 (<http://forumnet.ircam.fr/shop/fr/forumnet/10-audiosculpt.html>). During both the training session and the main experiment, screams were delivered using Bose headphones (QuietComfort 25) at peak intensity below 70 dB (mean of 68 dB as measured by a sonometer).

The screams were provided by Professor Armony, and had been previously validated (Fecteau et al., 2005) by a group of 60 individuals who rated the stimuli on emotional valence and intensity. However, at the end of the experiment, during the debriefing, we collected ratings for all screams together on an aversive scale (from 0 - not at all aversive to 10 - extremely aversive). Participants rated the screams as moderately aversive (median of 4, **see Figure S4-4, left**). Note however that, compared to past studies, we delivered the screams at a lower intensity (70 dB rather than 85–90 dB as in (Fecteau, Belin, Joannette, & Armony, 2007)). As inducing anxiety relies both on the aversiveness of the delivered stimuli as well as their unpredictability, we also asked participants to rate how much they felt preoccupied by the possibility that a scream would be delivered during threat blocks (this was done during the debriefing). Participants felt relatively preoccupied, i.e. they reported anticipatory anxiety of scream delivery (median of 6 **see Figure S4-4, right**). They often stated that they were wondering when the next scream was to appear.

Experimental design and task

The experiment consisted in an alternation between threat and safe blocks (**see Figure 4-1a**). Participants were informed that during threat blocks, the sides of the screen were blue, meaning that they were at risk of hearing unpredictable distress screams at any time, through their headphones. In contrast, during safe blocks, the sides of the screen were green meaning no screams were to be delivered.

During both threat and safe blocks, participants performed a free action-decision task in a social context, developed by Vilarem et al. (Vilarem, Armony, & Grèzes, 2019). Each trial started with a grey screen of 1000ms, followed by a fixation cross for 500ms. A picture of a scene was then presented which remained on the screen until a response was registered, or until a maximum time of 1400ms in the case of no response (each trial has therefore a duration of 2900ms maximum). The scene depicted a waiting room with four chairs, of which the outer two were empty. The two middle chairs were occupied by two task-irrelevant individuals, one displaying a neutral expression while the other displayed either a neutral, fearful or angry expression. Participants were asked to indicate the seat they

would like to occupy, maintaining fixation on the cross displayed between the faces throughout the trial. In order to make their choice, participants had to left-click on the mouse, move the cursor from the bottom center of the scene and release the click on the chosen seat. The cursor was automatically re-centered at every new trial. Participants were required to make spontaneous choices and were informed that there were no correct or incorrect responses. Importantly here, the number of neutral, fear and anger trials was equal for safe and threat blocks. Data from the task are not presented here, being part of another study (Beaurenaut et al. unpublished). To resume, participants performed a free action-task and were either exposed to screams at any time during threat blocks and to no screams during safe blocks.

The temporal organization of each block was as follow (see **Figure 4-1b**): a black screen with the written instruction “stabilisation of the signal” was first presented for 1 minute during which the physiological baseline of participants was recorded. Second, to inform participants about the nature of the block, the written instruction “Threat Block: at any time, a scream can be presented” or “Safe Block: you will hear nothing during this block” was presented for 10 sec. Third, participants performed the above-described free action-task for about 4 min. Fourth, at the end of each block, participants reported their anxiety level on a continuous scale (from 0: really calm to 100: really anxious), by moving a cursor on the screen using the mouse. The scale was presented on the computer screen and disappeared once the response was given. Finally, to assess physiological variation of participants’ bodily state in threat compared to safe blocks, skin conductance activity was recorded throughout the blocks.

A training session was performed before the main experiment to familiarize participants with the free action-task, the structure of the experiment (the alternation of safe and threat blocks and their associated screen sides’ colors) and the screams. Participants were trained on 2 blocks, one safe and one threat, each of 32 trials. During the threat block, 2 distress screams (one male and one female) were delivered once during two randomly chosen trials from among the 32 (approximately 6% of the trials). Note that the two screams used for the training were different from the 6 screams used during the main experiment.

Participants then performed the main experiment ($M_{\text{duration}} = 65 \text{ min}$, $SD_{\text{duration}} = 5 \text{ min}$), divided into 10 blocks of 96 trials, 5 threat blocks and 5 safe blocks. During each threat block, 6 distress screams were delivered once, randomly during the block (approximately 6% of the trials), either before the grey screen (2 screams), before the fixation cross (2 screams), or at the appearance of the scene (2

screams). The nature (safe or threat) of the first block was counterbalanced across participants: the threat blocks were the blocks 2-4-6-8-10 for even participants and 1-3-5-7-9 for the odd participants.

Skin conductance recordings

Skin conductance activity was recorded using a PowerLab 8/35 amplifier, with a GSR Amp (FE116) unit which uses low, constant-voltage AC excitation (22 mV rms at 75 Hz), and a pair of stainless steel dry bipolar electrodes (3x2,5cm, MLT118F). The electrodes were attached to the participant's left index and ring fingers of the non-dominant hand, using dedicated Velcro. Recordings were performed with LabChart 7 software, at a sampling rate of 1 kHz, with the recording range set to 40 μ S and using initial baseline correction ("subject zeroing") to subtract the participant's absolute level of electrodermal activity from all recordings (devices and software from ADInstruments). Finally, as low-pass filter of 0.05Hz has been proposed as an appropriate filter to eliminate any noise as well as the phasic component of the signal (see (Braithwaite, Watson, Jones, & Rowe, 2013)), we applied this filter to isolate the tonic activity of the skin conductance signal and to minimize the phasic influence of screams during threat blocks on the skin conductance activity. Performing the analyses on raw data signal revealed similar results as those performed on filtered data (see **Figure S4-3**).

Skin conductance level (SCL) processing

The SCL corresponds to the tonic activity of the skin conductance signal. The physiological signal was processed using Labchart 7 and Matlab. For each participant and for each block, we obtained (a) one SCL value corresponding to the averaged signal over the 1-minute baseline at the start of the block (see **Figure 4-1b**), and (b) one SCL value corresponding to the averaged signal over task performance ($M_{\text{Duration of one block}} = 4\text{min}$, $SD = 30\text{s}$). The instruction phase (Condition + Readyng - see **Figure 4-1b**), between 1-minute baseline and the beginning of the free action-task was not included in the averaged signal. Moreover, for threat blocks only, the phasic activity induced by the distress screams (6% of threat block trials) was excluded from the averaged signal. Finally, for each block (whether safe or threat), variation from the baseline was obtained by subtracting the baseline activity from the averaged activity over task performance. We therefore obtained, for each participant, 5 values corresponding to the 5 Safe blocks, and 5 values corresponding to the 5 Threat blocks.

Statistical analyses

All statistical analyses were carried out using JASP Software (JASP Team (2017), JASP (Version 0.8.5.1) [Computer software]). The corresponding tables of results are available in Supplementary materials.

Repeated-measures ANOVAs

For each experiment and for both the physiological variable (SCL) and the subjective reports of anxiety, we ran two-way repeated-measures ANOVAs with Condition (Threat vs. Safe) and Time (Blocks 1 to 5) as within-subject factor. We applied the Greenhouse-Geisser correction to correct for deviations from the assumption of sphericity (the corrected P corrected and the GG- ϵ are reported) and Bonferroni correction for the post-hoc tests (P_{bonf}). Effect sizes (partial eta-squared, η^2_p) are reported together with F and p values. To better examine if SCL and subjective anxiety changed over time, we looked at threat vs. safe difference over time (see **Supplementary Materials**).

Intra-individual correlation

To assess the intra-individual coherence between the physiological state of participants and their subjective experience, we first computed Pearson's r correlation coefficient for each participant between their subjective reports and SCL measures (10 values for each measure and each participant, since the experiment was composed of 10 blocks). We then performed Fisher's r -to- z transformation to normalize Pearson's r correlation coefficients (Howell, 2009) before testing whether the correlation coefficients across participants were different from zero (bidirectional one-sample t -test).

Inter-individual variability

We assessed whether inter-individual variability in trait anxiety could partly explain the variance in our measures of interest (SCL, subjective anxiety, and intra-individual correlation). To do so, we reran the above-described ANOVAs for SCL and subjective anxiety with the scores of the STAI-trait questionnaire as co-variable, and performed a correlation between the intra-individual correlations (used to assess emotion coherence) and the scores of the STAI-trait questionnaire.

Results Study 1

Skin conductance level (SCL)

Participants' tonic skin conductance activity (SCL) was greater during Threat ($M = -0.61$, $SE = 0.39$) relative to Safe ($M = -2.03$, $SE = 0.33$) blocks ($F(1,25) = 17.20$, $p < 0.001$, $\eta^2_p = 0.41$) (see **Figure 4-2a**). We observed a main effect of Time ($F(4,100) = 12.96$, $p_{corr} < 0.001$, $GG-\epsilon = 0.49$, $\eta^2_p = 0.34$), suggesting a decrease of SCL across the experiment. However, there was no significant interaction between Condition and Time ($F(4, 100) = 0.12$, $p_{corr} = 0.92$, $GG-\epsilon = 0.58$, $\eta^2_p = 0.005$), suggesting that the difference in SCL between Safe and Threat did not change with time.

Subjective reports of anxiety

Participants reported higher scores on the anxiety scale at the end of Threat ($M = 37.90$, $SE = 4.27$) compared to Safe ($M = 23.35$, $SE = 3.28$) blocks ($F(1,25) = 15.11$, $p < 0.001$, $\eta^2_p = 0.38$) (see **Figure 4-2b**). While factor Time was not significant ($F(4,100) = 1.84$, $p_{\text{corr}} = 0.16$, $GG-\varepsilon = 0.61$, $\eta^2_p = 0.069$), there was a trend toward *significance* for the interaction term between Condition and Time on subjective reports ($F(4,100) = 2.14$, $p = 0.081$, $\eta^2_p = 0.079$). Based on complementary t-tests (see **Table S4-14**), the interaction appears to be driven by a diminution of the difference in subjective anxiety between Threat and Safe conditions in the fifth and last block (for Blocks 1 to 4, all $p_s < 0.005$ and Cohen's $d > 0.633$; for Block 5, $p = 0.032$ and Cohen's $d = 0.446$).

Intra-individual Correlation

The average of intra-individual correlation estimates between SCL and subjective reports was positive ($\text{Mean}_r = 0.21$, $\text{Mean}_{r\text{-to-}z} = 0.26$), of medium size and statistically different from zero (bidirectional t-test, $t(25) = 2.86$, $p = 0.009$, Cohen's $d = 0.56$, lower 95% CI for Cohen's $d = 0.14$, upper 95% CI for Cohen's $d = 0.97$) (**Figure 4-2c**).

Inter-individual variability

In exploratory analyses, we assessed whether inter-individual variability in anxiety trait, measured by the STAI-trait auto-questionnaire, could explain part of the variance in our measures of interest (SCL, subjective reports of anxiety and intra-individual correlation). No significant interaction or correlation were observed with scores at the STAI-trait questionnaire (all the $p_s > 0.17$, see **Tables S4-17 - S4-19**).

Results Study 2 (Replication)

Skin conductance level (SCL)

Replicating results from Experiment 1 (see **Figure 4-2d**), participants' tonic skin conductance activity (SCL) was higher during Threat ($M = -0.77$, $SE = 0.35$) relative to Safe ($M = -2.00$, $SE = 0.33$) blocks ($F(1,32) = 29.36$, $p < 0.001$, $\eta^2_p = 0.48$). We observed a main effect of Time ($F(4,128) = 12.48$, $p_{\text{corr}} < 0.001$, $GG-\varepsilon = 0.73$, $\eta^2_p = 0.28$), suggesting a decrease of SCL across the experiment. However, there was no significant interaction between Condition and Time ($F(4,128) = 1.35$, $p = 0.25$, $\eta^2_p = 0.041$).

Subjective reports of anxiety

Replicating results from Experiment 1, participants reported higher scores on the anxiety scale at the end of Threat ($M = 39.08$, $SE = 4.55$) compared to Safe ($M = 14.19$, $SE = 2.51$) blocks ($F(1,32) =$

47.84, $p < 0.001$, $\eta^2_p = 0.60$) (see **Figure 4-2e**). There was a trend toward *significance* for the main effect of Time, suggesting that participants' subjective reports decreased in intensity across the experiment ($F(4,128) = 2.47$, $p_{\text{corr}} = 0.083$, $GG-\varepsilon = 0.58$, $\eta^2_p = 0.072$). There was a significant interaction between Condition and Time on subjective reports ($F(4,128) = 4.05$, $p = 0.004$, $\eta^2_p = 0.11$). Post-hoc tests revealed a significant decrease in the difference in subjective anxiety between Threat and Safe conditions between the first and the fourth and fifth blocks (B1vsB4: Mean Difference= 12.36, SE = 3.63, $t(32) = 3.41$, $p_{\text{bonf}} = 0.018$; B1vsB5: Mean Difference= 14.30, SE = 4.20, $t(32) = 3.40$, $p_{\text{bonf}} = 0.018$; all other comparisons $ps > 0.342$, see **Table S4-29**). Note however that the subjective difference between Threat and Safe conditions remained significant in all blocks (all the $p < 0.001$, $0.77 < \text{Cohen's } d < 1.24$) (see **Table S4-31**).

Intra-individual Correlation

Replicating results from Experiment 1, mean of intra-individual correlation between SCL and subjective reports of anxiety was positive ($\text{Mean}_r = 0.33$, $\text{Mean}_{r-t0-z} = 0.40$), of large size and statistically different from zero (Bidirectional T-test- $t(32) = 5.58$, $p < 0.001$, Cohen's $d = 0.97$, lower 95% CI for Cohen's $d = 0.55$ upper 95% CI for Cohen's $d = 1.38$) (see **Figure 4-2f**).

Inter-individual variability

As in Study 1, we assessed whether inter-individual variability in trait anxiety, measured by the STAI trait auto-questionnaire, could explain part of the variance in our measures of interest (SCL, Subjective anxiety and intra-individual correlation). No significant interaction or correlation were observed with the scores in the STAI trait questionnaire (all the $ps > 0.091$, see **Tables S4-34 - S4-36**).

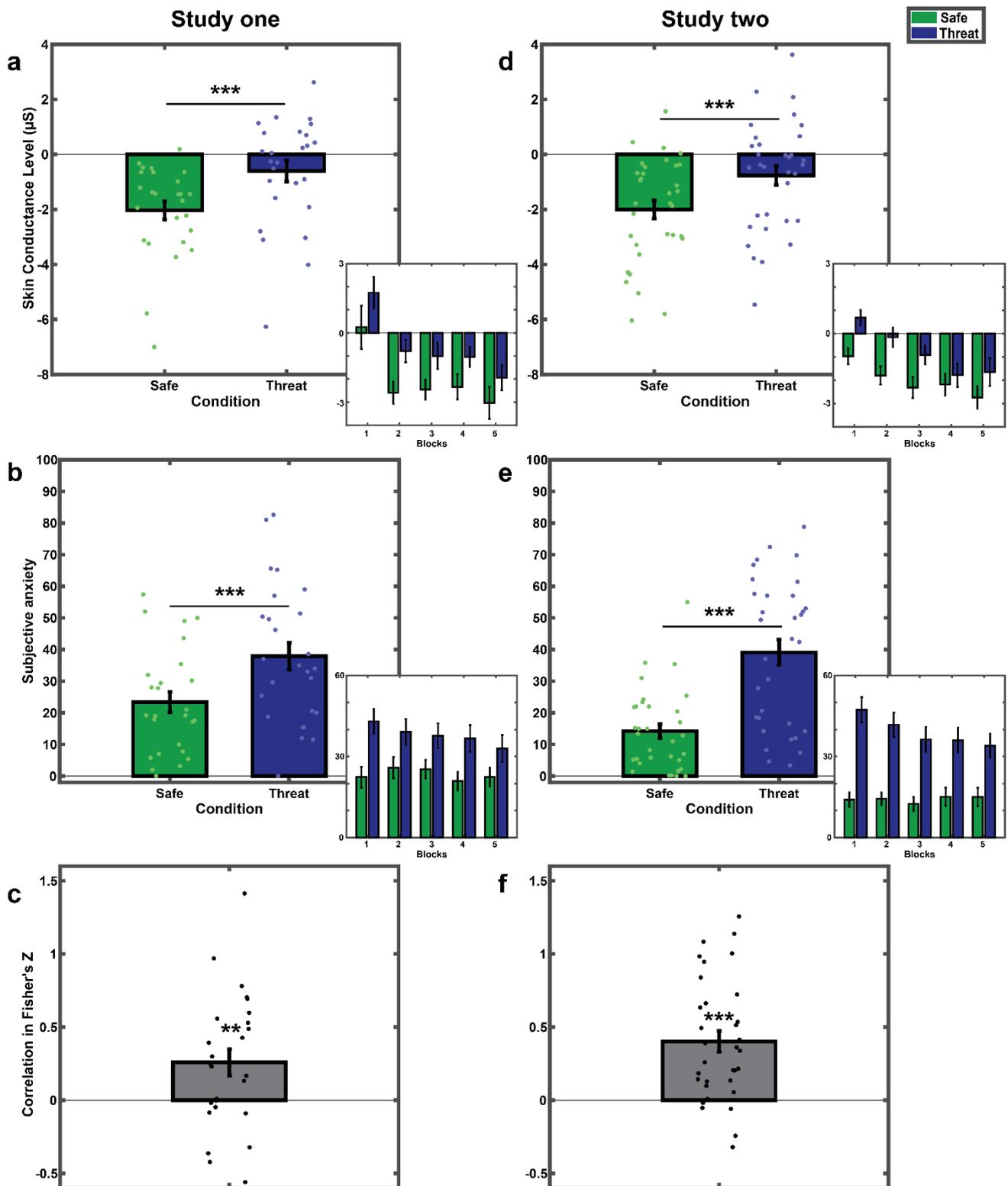


Figure 4-2. Skin Conductance Level (Top), subjective anxiety (Middle) and intra-individual correlation between SCL and subjective anxiety (Bottom) for study one (Left) and its replication study two (Right). Error bars and points represent respectively standard errors and individual data. Miniatures provide descriptive variation of the reported effects relative to each block. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; n.s. = $p > 0.05$.

Discussion

The present experiment aimed at offering additional validation to the Threat-of-Scream paradigm (TOSc (Patel et al., 2016)) by investigating whether sustained anxiety could be induced during a period of 1 hour, using unpredictable distress screams delivered at low sensory intensity (70-dB). We measured two proxies of anxiety, namely subjective reports of anxiety and skin conductance level, and ran the same hour-long experiment twice to assess the replicability of our results. Both experiments revealed higher skin conductance level (SCL) and self-reported anxiety during threat as compared to safe blocks. Moreover, we observed that the difference in SCL between safe and threat blocks remained constant throughout the experiment (or at least, statistically non-distinguishable), and that participants tended to report less anxiety towards the end of the experiment. The physiological state of participants (SCL) and their subjective reports of anxiety were positively correlated and all reported effect sizes were medium to large and replicable. Overall, our findings convincingly demonstrate the robustness of the TOSc paradigm as a tool to assess the relatively long-lasting impact of sustained anxiety with potential applications to a diversity of cognitive functions and populations.

To manipulate anxiety within participants, we used unpredictable human distress screams as aversive cues. Human distress screams are highly salient vocal signals of impending danger. Characterized by distinctive roughness acoustical properties which contribute to their aversiveness (Arnal et al., 2015; Arnal, Kleinschmidt, Spinelli, Giraud, & Mégevand, 2019), they are perceived as communicating fear (Anikin et al., 2018) and convey cues as to caller identity (Engelberg, Schwartz, & Gouzoules, 2019). Past experiments successfully substituted shocks with human screams to generate acute stress during fear conditioning paradigms (e.g. screaming lady paradigm (Lau et al., 2011; Lau et al., 2008)). Comparable physiological responses (fear potential startle) were found for stimuli conditioned with electric shocks and 80dB screams, even if stimuli conditioned with electric shocks were rated as more aversive than those conditioned with screams (Glenn, Lieberman, et al., 2012).

Knowing that unpredictability can induce sustained anxiety provided that the anticipated stimulus is sufficiently aversive (Grillon et al., 2004), we tested whether unpredictable distress screams, delivered at lower sensory intensity (70-dB) than previous experiments (Patel et al., 2017, 2016), could efficiently induce sustained anxiety. Our findings clearly demonstrate that the aversiveness of unpredictable distress screams at low sensory intensity (70-dB) is sufficient to induce sustained anxiety in a within-subject paradigm. Indeed, in addition to a modest but significant increase in self-reported anxiety, participants' skin conductance level increased and a large difference in physiological activity ($\eta^2_p > 0.40$) was found in blocks during which human distress screams were delivered compared to safe blocks in both experiments.

Moreover, we demonstrate that anxiety can be induced for extended periods (here: one hour). We observed in two experiments that changes in tonic physiological activity (skin conductance level) between threat and safe blocks did not seem to be affected by time. Regarding self-reported anxiety, and contrary to Patel et al. (Patel et al., 2017), we observed a decrease in subjective ratings of anxiety over time (significant in Study 2 and trending in Study 1), which could be explained by the duration of our experiment and/or by the intensity of the present screams. Yet, the difference in subjective anxiety between threat and safe conditions remained significant across all blocks. Our results complement previous findings of sustained tonic skin conductance activity during a 15-min study (Bublitzky et al., 2013) and of self-reported anxiety throughout a 30 (Patel et al., 2017) and 45-min experiment (Aylward et al., 2019). Altogether, findings from the current study indicate that unpredictable distress screams, which serve to communicate danger, (i) are efficient in manipulating anxiety within-subject for one hour, and (ii) can be perceived as aversive even at low intensity.

In the present experiment, screams were rare as they occurred in approximately 6% of trials (as in the original version developed by Patel et al. (Patel et al., 2016)). We isolated the tonic skin conductance activity by removing trials over which the exposure to screams could generate phasic activity. Moreover, the difference between threat and safe conditions can be observed by and was stable in the first seconds of the blocks, even when no scream had yet been heard (the first scream was delivered at 37 ± 4 s SD after the beginning of block, see **Figure S4-5**). We therefore believe that our effect is related to the anxiety likely generated by the unpredictable threat context rather than by reactions to the screams themselves.

Subjective reports of anxiety and skin conductance level were found to be positively correlated in both experiments. The association between self-reported experience and observed physiological activity has been referred to as “emotion coherence”. A number of proponents have suggested that coherence across physiological, behavioral (facial expressions), and experiential responses is the definition of an emotion episode (e.g. (Ekman, 1993; Panksepp, 1994; Tomkins, 1962)). This proposition is however debated, as some authors suggest that emotion systems are only loosely coupled (Bonanno & Keltner, 2004; Izard, 1977), or even independent (e.g. (LeDoux & Pine, 2016)). Results from past experiments in healthy subjects are inconclusive as they provided evidence either for a moderate association between physiological responses and self-rated experience (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Dan-Glauser & Gross, 2013; Franklin et al., 2017; Mauss, Levenson, McCarter, Wilhelm, & Gross, 2005; Nandrino et al., 2012) or were consistent with the hypothesis that there is no emotional coherence between subjective and physiological data (Morris, DeGelder, Weiskrantz, & Dolan, 2001; Vuilleumier, Armony, Driver, & Dolan, 2001; Vuilleumier & Pourtois, 2007).

Within the fear conditioning literature, positive correlations between SCR and self-reported experience have been observed (Lovibond, Davis, & O’Flaherty, 2000; Rodriguez, Craske, Mineka, & Hladek, 1999). For instance, Glenn, Lieberman, Hajcak (Glenn, Lieberman, et al., 2012) observed, at a trend level, a convergence between subjective and physiological (fear-potentiated startle) measures of fear, but only for stimuli that were conditioned using electric shocks and not for those conditioned with screams. However, Abend et al. (Abend et al., 2019) revealed a convergence of subjective and psychophysiological measures for CS+ following conditioning, using 95dB female scream. Here, by alternating blocks during which participants were at risk of hearing unpredictable aversive screams with blocks during which no screams were to be delivered (safe blocks), we show that unpredictable distress screams at low sensory intensity (70-dB) are sufficiently aversive to generate emotion coherence, i.e. positive correlation between subjective reports of anxiety and skin conductance level. Such coordinated changes (coherence) across physiological and experiential responses clearly support the efficiency of our manipulation in inducing an emotion (anxiety) episode.

Several limitations to this experiment need to be acknowledged. First, as in the majority of the threat of shock studies (i.e. (Aylward et al., 2017; Balderston, Hsiung, Ernst, & Grillon, 2017)), aversive stimuli were delivered only in threat blocks while participants did not receive any stimulation in safe ones. This difference in stimulation could be involved in the observed SCL differences. Future studies should eliminate this confound. We envision three possibilities here. First, one could avoid stimulation entirely during the task. Indeed, some experiments have either delivered shocks during a shock work-up procedure before the main experiment (Bublitzky et al., 2013; Bublitzky & Schupp, 2012) or never delivered shocks to participants (Costa, Bradley, & Lang, 2015). Subsequent verbal instructions (i.e., “you can be exposed to shocks in this block”) and cues that falsely signal the possibility of a shock were sufficient to elicit autonomic and subjective fear. A second possibility is to deliver the aversive stimuli at the end of the threat block to best isolate their effects (Robinson, Letkiewicz, Overstreet, Ernst, & Grillon, 2011). However, participants appeared to learn that they were in fact safe of shocks in so-called threat blocks when the experiment was of a long duration (Bublitzky et al., 2014). A third possibility is to add monetary stimulation in safe blocks, which causes stimulation and makes these blocks ‘appetitive’ rather than neutral (Bradley et al., 2018; Cohen et al., 2016). Nevertheless, these 3 methods still do not appear to be fully appropriate to specifically investigate long-lasting anxiety.

Second, one may question the specificity of tonic skin conductance activity (SCL) to assess sustained anxiety. SCL is known to be modulated by different factors such as participants’ emotional state, arousal, visual attention and motor activity (Boucsein, 2012; Critchley, 2002). As such, SCL may only represent an indirect marker of anxiety (see (Grillon et al., 2004)), and the present higher SCL during

threat compared to safe blocks may be linked to one or more of these modulators, i.e. higher level of arousal, and/or negative emotional state and/or increase of visual attention. There is however some evidence in the literature that SCL can reflect participant's sustained anxiety. For instance, Doberenz et al. (Doberenz, Roth, Wollburg, Breuninger, & Kim, 2010) revealed elevated SCL in awake panic disorder patients compared to controls, and suggested that it was related to sustained anxiety between panic attacks, i.e. anxious anticipation of future attacks. Recently, and in a more controlled setting, Neueder et al. (Neueder, Andreatta, & Pauli, 2019) show that successful context conditioning is indicated by higher anxiety ratings and skin conductance levels (SCLs) in an anxiety context where an aversive unconditioned stimulus occurred unpredictably vs. a safety context. Finally, De Becker et al. (De Berker et al., 2016) demonstrated that one physiological marker that tracks environmental uncertainty is skin conductance activity. Altogether, these findings indicate that SCL could capture participants' anxiety induced by the unpredictable delivery of screams. Future studies should however confirm our results by measuring the startle reflex, one of the most common readouts in the context of predictable/unpredictable threat (e.g., Grillon et al., 2004; Schmitz et al., 2011).

Third, sustained contextual anxiety, but not phasic fear to a predictable threat, is believed to differentiate anxious from non-anxious individuals (e.g. Grillon, Morgan, Davis, & Southwick, 1998). The present absence of association between our measures of interest, i.e. SCL and subjective report of anxiety, and participants' trait anxiety could be seen as a challenge for the validity of our paradigm. A first potential explanation is that the relatively limited sample size did not provide sufficient power to reliably examine correlations among these measures. However, looking at previous studies that used the threat-of-shock or -scream paradigms to induce state anxiety, the association between participants' trait anxiety and both subjective and physiological measures is unclear. Indeed, most studies in normative samples that we are aware of only report the mean trait anxiety scores of their participants without performing any correlations between trait anxiety and physiological measures (e.g. Grillon et al., 2004, 2020; Grillon & Charney, 2011; Robinson et al., 2011; Sarigiannidis, Grillon, Ernst, Roiser, & Robinson, 2020, with the exception of Patel et al., 2017). Future experiments should therefore further examine the interactions between (shock- and scream-induced) state anxiety and temperamental trait anxiety disposition.

Fourth, there may be an influence of the action-decision task on our anxiety measures. This is indeed a possibility as (a) the present task consists in taking-action decisions in the presence of two task-irrelevant individuals, one of them displaying in 2/3 of the trials a threat-related expression (fear or anger); and (b) Grillon and Charney (Grillon & Charney, 2011) have revealed that the startle reflex was transiently potentiated by fearful faces compared to neutral faces in threat periods, suggesting that

fearful faces can prompt behavioral mobilization in an anxiogenic context. The startle reflex is a reflexive reaction to an unexpected and intense stimulus, which is reliably potentiated by negative emotional states (e.g. Lang, Bradley, & Cuthbert, 1990). According to this definition, phasic skin conductance response following unexpected and negative stimuli may be similarly impacted in threat contexts. Therefore, one could envisage higher phasic skin conductance activity to the screams and to the presence of a threat-related facial expression in threat as compared to safe blocks. However, as we filtered our data in order to reduce the phasic component of the skin conductance activity, we believe that such an effect cannot entirely explain the difference we observed in tonic skin conductance activity (SCL) between threat and safe blocks. Regarding subjective reports of anxiety, we cannot fully exclude the possibility of an influence of the ongoing task (and stimuli), as Grillon and Charney (Grillon & Charney, 2011) observed a significant positive correlation between the startle potentiation score (difference between fear and neutral stimuli) and the increased fear reported by the subjects during threat relative to safe contexts. Future studies are needed to confirm our results, by measuring the startle reflex to startle stimuli in both threat and safe contexts.

Finally, the present study does not demonstrate that the threat-of-scream paradigm leads to longer lasting effects than the threat-of-shock paradigm. However, as electric shocks, which represent a direct physical threat, may be considered more aversive than human screams (electric shocks constitute a threat; screams are signals of impending threat), the associated induced anxiety should be even less susceptible to time. Also, if the aversiveness of the delivered stimuli is one important component in the induction of anxiety, the unpredictability of the aversive stimuli is probably the main component in such paradigms. As both paradigms share these two major components, we are confident that future experiments will provide evidence for long-lasting effects using the threat-of-shock paradigm.

Overall, our study offers support to the TOSc paradigm by showing that: (i) unpredictable distress screams presented at low intensity (<80dB) can induce sustained anxiety as revealed by increased subjective reports of anxiety and increased tonic physiological activity (skin conductance level) during threat compared to safe blocks, similarly to previous threat-of-shock experiments; and that (ii) sustained states of anxiety can be induced for extended periods (here one hour). Distress screams, delivered at lower sensory intensity (70-dB), thus appear to be excellent candidates to overcome the ethical issues associated with exposing vulnerable and young populations to electric shocks and aversive noise, and to experimentally address the emergence of pathological anxiety in a consistent and sustained manner.

Author notes

Author contributions

M.B., J.G. and G.D. designed the study; M.B. and E.T. collected the data; M.B. performed the analysis; M.B., J.G. and G.D. wrote the first draft of the manuscript. All authors reviewed and approved the final manuscript.

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Competing interests

The authors declare no competing financial interests.

Supplementary materials

Data and analysis are available on OSF

link: https://osf.io/f2bvr/?view_only=4a4fda675e8d41f7bf20a9033f013a6f

CHAPTER 5

ACTION CO-REPRESENTATION UNDER THREAT

As social species, many activities in our daily life require interacting with our conspecifics. More particularly, succeeding in coordinating movements represent one of our most incredible, but complex, social abilities. In order to do it efficiently, a set of cognitive mechanisms are involved, such as action co-representation (i.e. the ability to represent others' action plans). Literature on disasters revealed that coordinated actions are still planned in such context: moving obstacle on the exit road or doing legs-up for example. Such joint actions required action co-representation.

How does threat affect our ability to represent others' action plans and our ability to collaborate on physical tasks? This chapter will describe how sustained stress modulates the integration of others' action under threat. Anxiety could either reduce co-representation (CoR) in order to allocate cognitive resources to individual actions, or enhance our ability to integrate others' action plans in order to more easily coordinate with each other. To disentangle these two hypotheses, 40 pairs of participants performed the Social Simon task allowing the measure of CoR abilities, in threat and safe contexts (thanks to the threat-of-scream paradigm validated in **Chapter 4**). As explained in the theoretical part of this dissertation, social action can be planned for different motivation (i.e. considering other's welfare or not). To distinguish the possible sources of interpretation for a modulation of CoR abilities, distress screams were delivered to one or both members of the pair of participants (i.e. sharing or not the same anxiety condition).

As the following chapter will illustrate, our results indicate that: (i) the ability to co-represent others is maintained in a threat environment; (ii) this ability is, however, boosted when one participant is exposed to threat environment while his or her partner is safe. This increase in the ability to co-represent others when one is personally threatened might be due to self-preservative motives: the CoR function could be to recruit social support, particularly in a threatening situation. However, this explanation is debated at the end of this chapter because of several methodological issues

What happen to action co-representation under threat? A Social Simon study

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Highlight

- Action co-representation has never been studied in threat context
- Our results showed that co-representation is maintained under threat contexts
- It is even boosted when participants are under threat near safe partners
- Social buffering took place in presence of co-partners
- Co-representation may promote social strategies essential for one's own survival.

NB1: This article is currently under revision.

NB2: Supplementary material is available in the Appendix section of the dissertation (p.179)

Abstract

Several studies have shown that individuals automatically integrate the actions of other individuals into their own action plans, thus facilitating action coordination. What happens to this mechanism in situations of danger? This capacity could either be reduced, in order to allocate more cognitive resources for individualistic actions, or enhanced to better cooperate under threat. In order to determine the impact of the perception of danger on this capacity, two groups of participants carried out, in pairs, the Simon Social task, which provides a measure of co-representation. The task was performed during so-called ‘threat blocks’ (during which participants could be exposed at any time to an aversive stimulus) and so-called ‘safety blocks’ (during which no aversive stimulation could occur). In a first group of participants, both individuals were exposed at the same time to threat blocks. In a second group, only one of the two participants was exposed to them at a time. Our results indicate that co-representation, an important cognitive mechanism for cooperation, (i) is preserved in situations of danger; and (ii) is reinforced in participants who are confronted alone to threat but in the presence of a safe partner. This last result suggests that one possible function of co-representation could be to recruit social support, both in everyday life and in dangerous contexts.

Introduction

As the COVID-19 sanitary situation has reminded us of, dangers are integral part of our lives. We, humans, are social animals, and we have evolved a series of individual adaptations and collective decision rules to cope with a wide variety of threats, such as disease transmission (Neuberg, Kenrick, & Schaller, 2011; Tybur & Lieberman, 2016), predatory encounters (Caro, 2005) and natural disasters or ecological shocks (Drury & Reicher, 2010; Henrich, 2017). Danger is so much part of our lives that our social inclinations have been suggested to have evolved in response to predatory pressures, with increasing group size being an adaptation to alleviate the costs of vigilance (Lima, 1995; Roberts, 1996), allowing for threat dilution and the preparation of collective responses (Caro, 2005). How are those collective responses to danger even possible in humans? Which are the cognitive mechanisms that allow us to coordinate with others in the face of danger?

Paradoxically, and in spite of the wealth of literature on collective mechanisms in response to danger in other animals, human responses to danger (such as freezing e.g. Hagenaars, Roelofs, Hagenaars, & Stins, 2010 or avoidance of threatening individuals e.g. Vilarem, Armony, & Grèzes, 2019), have largely been studied in complete social isolation. Many of our behavioral strategies are yet social. In other animals, reactions to perceived danger consist of a set of behaviors that cascade. When a threat is detected, social information acquisition processes are put in place, whereby detectors voluntarily or involuntarily inform other individuals of the presence of the danger (Caro, 2005). Once information is passed on to conspecifics, strategies for responding to danger develop. In the animal, these strategies include solo and social flight, concealment, social contact seeking and coordinated attacks on the predator (Caro, 2005).

Beyond the technical difficulties of studying social behavior in the laboratory, another reason why the perception and reaction to danger is rarely considered in its social dimension in humans may be related to the persistent belief that our own responses to danger are fundamentally asocial and/or antisocial (Dezecache, 2015). When threatened, humans run for their lives, and may even trample others to access safety (Le Bon, 1895; Quarantelli, 2001). In fact, those apparently asocial reactions could be inherently social, and flight possibly a strategy to approach familiar conspecifics and places (Mawson, 2005). What's more, humans engage in coordinated actions even when directly exposed to a deadly danger, and in perfect knowledge of the risk. In a study we led on survivors' reactions during Paris terrorist attack (Dezecache et al., 2020), we found leg-up to climb up to exits, votes to decide on the next decisions to be taken and many other coordinated responses to maintain individual and collective safety. These results are consistent with previous studies on the evacuation of the World Trade Center (Fahy & Proulx, 2005) or the London bombing attacks (Drury, Cocking, & Reicher, 2009b) which

report risk taking to help strangers and a sense of unity between survivors, but also with recent behavioral research (e.g. Margittai et al., 2015; Tomova, Saxe, Klöbl, Lanzenberger, & Lamm, 2020; von Dawans, Ditzen, Trueg, Fischbacher, & Heinrichs, 2019; Von Dawans, Fischbacher, Kirschbaum, Fehr, & Heinrichs, 2012) which indicate that anticipated or experienced threats can also promote affiliative and social behaviors, in agreement with the “tend-and-befriend” hypothesis (Taylor, 2006). Altogether, it suggests that our social cognitive capabilities are at work during intensely stressful situations, and that they may even allow us to coordinate and plan actions with others. How is that even possible?

In threat-free situations, successful joint actions (such as moving furniture) are already complex tasks. Agents need to anticipate others’ actions, integrate their own action representations with those of others, to then be able to spatially and temporally coordinate their own action with those of others (Era, Candidi, Gandolfo, Sacheli, & Aglioti, 2018; Knoblich & Sebanz, 2006). Efficient coordination indeed relies on a complex set of cognitive mechanisms (Constable, Pratt, Gozli, & Welsh, 2015; Obhi & Sebanz, 2011; Sebanz & Knoblich, 2009), such as visual and conceptual perspective taking (i.e. abilities to represent others’ visual and reasoning point of view) or action and goals co-representation (i.e. abilities to represent others’ action plans and intention). Co-representation of action (Atmaca, Sebanz, & Knoblich, 2011; Müller, Brass, et al., 2011; Sahai, Desantis, Grynszpan, Pacherie, & Berberian, 2019; Stenzel et al., 2012, 2014; Tsai, Kuo, Hung, & Tzeng, 2008) and of visual information (Fini, Committeri, Müller, Deschrijver, & Brass, 2015; Gobel, Tufft, & Richardson, 2018) is now established for active and intentional biological agent and is associated with affiliative tendencies toward others (Bukowski & Samson, 2016).

What can be expected in threatening situations? Although associated with affiliative tendencies, co-representation may yet be reduced in contexts where it is more costly than useful for the agent, such as in a joint task where the contribution of each co-agent is independent and clearly distributed (Tufft & Richardson, 2019). Co-representation could even be shut down, such as when participants are co-acting in competitive contexts (Iani, Anelli, Nicoletti, Arcuri, & Rubichi, 2011), confronted to hostile conspecifics (Hommel, Colzato, & Van Den Wildenberg, 2009), or under negative moods such as sadness, anger and anxiety (Kuhbandner, Pekrun, & Maier, 2010; Todd, Forstmann, Burgmer, Brooks, & Galinsky, 2015; Todd, Simpson, & Cameron, 2019; Todd & Simpson, 2016). These findings suggest that co-representation mechanisms may be tuned to allow for collaborative activity only when necessary, adjusting the amount of cognitive resources devoted to own vs. others’ actions (Mendl, Fröber, & Dolk, 2018). As co-representing others’ actions can be costly and thus can diminish the

possibility to allocate resources to asocial and self-preservative behaviors, it may be reduced or even interrupted under threatening situations.

On the other hand, as threat situations are inherently social situations (where others are both to be protected and to act with), it may well be that co-representation is maintained or boosted to promote social strategies that survivors described as essential for their own survival. Coherently, co-representation is known to be susceptible to the presence of social indices and favored toward in-group and friendly individuals as well as under cooperative contexts (Aquino et al., 2015; Iani, Anelli, Nicoletti, & Rubichi, 2014; McClung, Jentsch, & Reicher, 2013; Müller, Kühn, et al., 2011). Such increases in co-representation can possibly be explained by the interdependence between co-agents (i.e., others represent an advantage or an obstacle to reach personal goals) (Era, Aglioti, et al., 2018; Iani et al., 2014; Ruys & Aarts, 2010), which modulates the willingness to invest in an interaction (Poortvliet & Darnon, 2010). So far, evidence leads toward contradictory predictions, and as co-representation mechanisms have never been studied in threat contexts, the question remains as to whether and how they are impacted under threat.

Here, we proposed to modify one of the gold-standard paradigms to investigate the cognitive processes underlying joint actions in humans under moderate threat. We used the Social Simon task, commonly used to measure self-other integration (Sebanz, Knoblich, & Prinz, 2003; Sebanz, Knoblich, Prinz, & Wascher, 2006, for review see Dolk et al., 2014, for meta-analysis Karlinsky, Lohse, & Lam, 2017). In the standard Simon task (Hommel, 2011; Simon & Rudell, 1967), a single participant categorize binary non-spatial stimuli (e.g., violet and grey cues) randomly presented to the left or right side of the screen. To do so, participant use two spatially defined keypresses, such as the left and right “Ctrl” keypresses, each of them being associated with one stimulus (e.g. left-violet & right-grey). Even though stimulus location on the screen is completely task-irrelevant, participants are slower to respond when the cue is not spatially aligned with the corresponding keypress (incongruent trials) as compared to when it is aligned (congruent trials). This difference in reaction times, called the Simon Effect (SE), rests upon the fact that, during incongruent trials, spatial and non-spatial information activate two different action plans that compete with each other, thus slowing down participant’s responses to the cue. Hence, when the same participant performs a go/no-go version of the task, i.e. being responsible for only one key-press (e.g. only left-violet), the SE disappears. However, and of interest here, when the same go/no-go version of the task is performed with a conspecific seated next to the participant, such that each of them is responsible for one keypress, the SE re-appears in both members of the dyad. This alter-centric interference, better known as Social SE, may be regarded as an objective measure of self–other integration, typically explained by an automatic co-representation of surrounding

individuals' actions (Sebanz et al., 2003 but see Dolk, Hommel, Prinz, & Liepelt, 2013 for a debate on the underlying mechanisms).

In the present work, dyad of participants performed the Social Simon task under a “threat-of-scream” procedure (Patel et al., 2017, 2016). This procedure consists in alternating time-periods in which participants are at risk of hearing unpredictable aversive distress screams (threat blocks) with time-periods in which no such screams are to be delivered (safe block). Using this procedure, we previously revealed that unpredictable threats (distress screams) generate sustained aversive states in participants, reflected by higher subjective reports of anxiety, higher skin conductance level, and positive correlation between the two measures, in threat compared to safe time periods (Beaurenaut, Tokarski, Dezechache, & Grèzes, 2020). We tested the hypothesis that the alter-centric interference (Social SE) is affected during threat blocks. If such hypothesis is correct, we can better understand how social cognitive capabilities that allow us to coordinate and plan actions with others are engaged during threatening situations. If primary reactions to danger are asocial/anti-social, we should observe a decrease in co-representation, i.e., of the Social SE in threat compared to safe time periods. However, if primary reactions to danger are affiliative, action co-representation could be maintained or enhanced, i.e. we should respectively observe no change or an increase of Social SE in threat compared to safe time periods.

Finally, to best understand the incentives behind potential changes in action co-representation under threat, we created two versions of the Social Simon Task. In the Common fate version, the members of a dyad were simultaneously exposed to distress screams during threat blocks, and were simultaneously safe during safe blocks. In the Non-Common fate version, and for each block, only one member of the dyad at a time was exposed to distress screams, while the other was safe (and the reverse in the next block). If alter-centric interference (Social SE) is influence by the interdependence between co-agents (Era, Aglioti, et al., 2018; Iani et al., 2014; Ruys & Aarts, 2010), this manipulation could indicate whether affiliative tendencies under threat, as measured by Social SE, serve prosocial motives (such as bringing mutual support in the Common fate and/or social support to the individual under threat in Non-Common fate) or self-preservative motives (Dezechache et al., 2017) (recruiting social support from the safety individual in Non-Common fate).

Methods

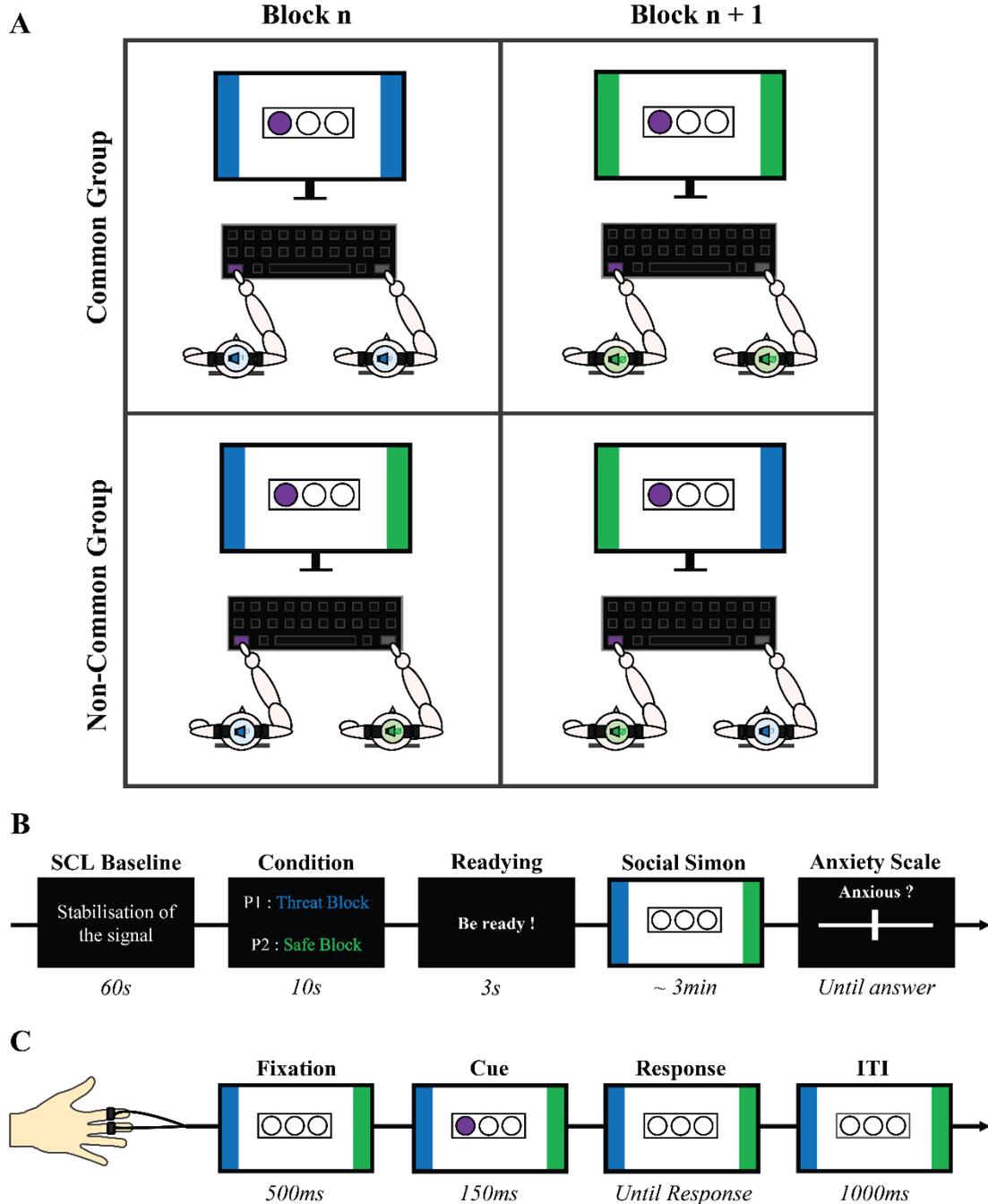


Figure 5-1: Experimental Design. (A) Experimental Settings. Participants in dyads performed the Social Simon task, while either sharing (Common) or not (Non-Common) the experimental context. The blue color bands on the screen indicated to participants that they could be exposed at any time to distress screams (threat blocks) while green color bands indicated that no such screams will be delivered (safe blocks). Participant, whether from the Common or the Non-Common group, performed the Social Simon task alternating threat and safe blocks, and the nature of the first block was counterbalanced across participants. Each participant was responsible for one color cue (e.g. participant 1 – violet, participant 2 - grey) by pressing the associated key-press (e.g. participant 1 – left, participant 2 - right). (B) Temporal organization of one block (here for the Non-Common Group). Each block began with a one-minute baseline to measure participants’ skin conductance before the block. A written sentence was then presented for 10 sec, providing information about the upcoming nature of the block (Safe or Threat) for each participant. At the end of the Social Simon task, participants were requested to rate their anxiety level during the block on a continuous scale. (C) Temporal Organization of a trial (here for the Non-Common Group). Each trial started with a fixation screen for 500ms. A colored cue then appeared for only 150ms followed by the presentation of a screen without the color cue until participant’s response. Skin conductance activity was measured throughout the task and compared to the Baseline.

Participants

Seventy-eight healthy volunteers (38 females, of mean age 23.5 ± 4.3 years SD) were recruited to participate in this study. All participants were right-handed, had normal or corrected-to-normal vision, and had no history of neurological or psychiatric disorders. The experimental protocol was approved by INSERM and the local research ethics committee (Comité de protection des personnes Ile de France III - Project CO7-28, N° Eudract: 207-A01125-48), and it was carried out in accordance with the Declaration of Helsinki. The participants provided informed written consent and were compensated for their participation.

Twenty dyads of same gender (10 dyads of females, of mean age 23.4 ± 4.3 years SD) were randomly assigned to Common group, while nineteen dyads (9 dyads of females, of mean age 23.6 ± 4.5 years SD) were assigned to the Non-Common group. Participants didn't know each other, and were not allowed to talk to each other until the end of the experiment.

General Procedure

First, participants were recruited thanks to an online advert, which consisted of a short description of the study and included an internet link which directed participants to a Qualtrics survey. Due to the potentially stressful nature of our paradigm and after discussion with the referent medical doctors of our laboratory, we requested participants to fill in, online and anonymously, the French versions of State-Trait Anxiety Inventory Spielberger (STAI, Spielberger, 1983) and Post-traumatic stress disorder Checklist Scale (PCLS, Weathers, Litz, Herman, Huska, & Keane, 1993), at least one week before the experiment. Only participants with a score below 40 for the PCLS and below 60 for both STAI state and trait anxiety were able to contact the experimenter, i.e. were included in the experiment.

Second, two days before the experimental session, participants that were included in the experiment filled in online the Liebowitz Social Anxiety Scale (LSAS, Heimberg et al., 1999) and the Trait-STAI questionnaire. On that occasion, an anonymous code was attributed to each participant, and use for both the questionnaires and the behavioral data. Moreover, on the day of the experiment, upon arrival at the lab, the two participants completed on a computer, in two different rooms, the State-STAI questionnaire. This allowed to ensure that their state level of anxiety was in the “normal” range (below 60) before the experimental session that aimed at manipulating their anxiety. LSAS and STAI distribution for each group are provided in Supplementary Material (see **Figure S5-2**) and didn't differ between groups (all $p > 0.28$, see **Tables S5-38 - S5-44**).

Third, after providing the instructions regarding the main task, the experimenter installed the skin conductance electrodes. To identify potential physiological non-responders before the main experiment, the experimenter assessed the variation of the physiological signal while participants were asked to imagine a situation during which they fell into really cold water, and this, until stopped by the experimenter. All our participants showed increased physiological response during this mental imagery task; the response then dropped when asked to stop the exercise. Based on this definition of ‘non-responder’, there were no non-responders among our participants.

Fourth, participants started with a 3-minute training session, before performing the main experiment for approximately 30 minutes, and were carefully debriefed at the end of the main experiment. During the debriefing, participants were notably requested to rate how aversive the screams were for them and how much they felt preoccupied by the possibility that a scream would be delivered during threat blocks (from 0 - not at all to 10 - extremely).

Experimental design and task (Figure 1)

The experiment consisted in a modified version of the gold-standard Social Simon task (Sebanz et al., 2003) (**Figure 5-1A**), performed by dyads of participants during alternating blocks of threat-of-screams or safety. Participants were either assigned to the Common or the Non-Common group. Dyads of participants in the Common group systematically shared the same experimental context: both participants performed the task during blocks before which they were told that they could hear aversive screams at any time (threat blocks) vs. blocks before which they were told that no scream will be heard (safe blocks). Participants were informed that during threat blocks, the color bands located on both sides of the screen will be blue, and that, at any time during the block, unpredictable distress screams could be delivered through their headphones. In contrast, they were informed that during safe blocks, both sides of the screen were to be green, meaning that no screams were to be delivered. The nature of the first block was counterbalanced across dyads of participants.

Contrary to the Common group, dyads of participants in the Non-Common group never shared the same experimental context: participants were informed that when the color band located on their side of the screen was blue, the color band located on the side of the other participant was to be green, meaning that only they were at risk to hear unpredictable distress scream through their headphones (i.e. they were alone in a threat block), whereas the other participant was totally safe. Safe and threat conditions were reversed at the end of each block.

The temporal organization of each block was as follow (**Figure 5-1B**): a black screen with the written instruction “stabilisation of the signal” was first presented for 1 minute during which the physiological

baseline of participants was recorded. Second, to inform participants from the Common group about the nature of the block, the written instruction “Threat Block: at any time, a scream can be presented to both of you at the same time” or “Safe Block: Both of you will hear nothing during this block” was presented for 10 seconds. For the Non-Common Group, the written instruction “Participant X - Threat Block: at any time, a scream can be presented to you and only you” and “Participant Y - Safe Block: You and only will hear nothing during this block” was presented for 10 seconds. Third, participants performed the Social Simon task for about 4 min. Fourth, at the end of each block, participant reported one by one their anxiety level on a continuous scale (from 0: really calm to 100: really anxious), by moving a cursor on the screen using the mouse. The order to report anxiety was randomized and participants were asked to close their eyes and turn their head to allow their co-participant to respond anonymously. The scale was presented on the computer screen and disappeared once the response was given. Finally, to assess physiological variation of participants’ bodily state in threat compared to safe blocks, skin conductance activity was recorded throughout blocks for each participant.

The temporal organization of each trial was as follow (**Figure 5-1C**): at the center of the screen, a rectangle surrounding three horizontally arranged empty circles first appeared for 500ms, after which one of the circles became either violet or grey for 150ms. The colored cue could appear on 3 different locations: on the center circle (10% of the time), on the left one (45% of the time) or on the right one (45% of the time). Each color cue was associated with a button (e.g. violet – “Ctrl Left” or grey – “Enter Right”), and each participant of the dyad was responsible for one key-color cue association. The key-color cue associations were randomized between participants. Participants were requested to respond as soon as they saw the color cue corresponding to their key-press by using their right index finger, regardless of the color cue’s position. After participant responded, an interval of 1000ms was included before the start of the next trial.

A training session was performed before the main experiment to familiarize participants with the Social Simon Task, the structure of the experiment (the alternation of safe and threat blocks and their associated screen side colors) and the screams. Participants were trained on 2 blocks, one safe and one threat, each of 32 trials. During the threat block, 2 distress screams (one male and one female) were delivered once during two randomly chosen trials from among the 32 (approximately 6% of the trials). Note that the two screams used for the training were different from the 6 screams used during the main experiment.

Participants then performed the main experiment, divided into 4 blocks of 90 trials, 2 threat blocks and 2 safe blocks. During each threat block, 6 distress screams were delivered once, randomly during the

block (approximately 6% of the trials), either at the beginning of the trial (2 screams), before the color cue appeared (2 screams), or when it disappeared (2 screams).

Screams stimuli

Eight distress screams were used in the present protocol (4 from males and 4 from females). The screams were normalized at -2b using audiosculpt 3.4.5 (<http://forumnet.ircam.fr/shop/fr/forumnet/10-audiosculpt.html>). During both the training session and the main experiment, screams were delivered using two Bose headphones (QuietComfort 25) at peak intensity below 70 dB (mean of 68 dB as measured by a sonometer). The screams were provided by Professor Armony, and had been previously validated (Fecteau et al., 2005) by a group of 60 individuals who rated the stimuli on emotional valence and intensity. The experimental set up was previously validated in Beaudenaut et al. (Beaudenaut et al., 2020).

Skin conductance recordings

Skin conductance activity was recorded using a PowerLab 8/35 amplifier, with two GSR Amp (FE116) unit which uses low, constant-voltage AC excitation (22 mV rms at 75 Hz), and two pair of stainless steel dry bipolar electrodes (3x2,5cm, MLT118F). The electrodes were attached to the participant's left index and ring fingers of the non-dominant hand, using dedicated Velcro. Recordings were performed with LabChart 7 software, at a sampling rate of 1 kHz, with the recording range set to 40 μ S and using initial baseline correction ("subject zeroing") to subtract the participant's absolute level of electrodermal activity from all recordings (devices and software from ADInstruments). Finally, as low-pass filter of 0.05Hz has been proposed as an appropriate filter to eliminate any noise as well as the phasic component of the signal (see Braithwaite et al., 2013), we applied this filter to isolate the tonic activity of the skin conductance signal and to minimize the phasic influence of screams during threat blocks on the skin conductance activity (see Beaudenaut et al., 2020).

Skin conductance level (SCL) processing

The SCL corresponds to the tonic activity of the skin conductance signal. The physiological signal was processed using Labchart 7 and Matlab. For each participant and for each block, we obtained (a) one SCL value corresponding to the averaged signal over the 1-minute baseline at the start of the block (see **Figure 5-1B**), and (b) one SCL value corresponding to the averaged signal over task performance. The instruction phase (Condition + Readyng - see **Figure 5-1B**), between 1-minute baseline and the beginning of the free action-task was not included in the averaged signal. Moreover, for threat blocks only, the phasic activity induced by the distress screams (6% of threat block trials) was excluded from the averaged signal. Finally, for each block (whether safe or threat), variation from the baseline was

obtained by subtracting the baseline activity from the averaged activity over task performance. We therefore obtained, for each participant, 2 values corresponding to the 2 Safe blocks, and 2 values corresponding to the 2 Threat blocks.

Statistical analyses

All statistical analyses were carried out using JASP Software (JASP Team (2017), JASP (Version 0.8.5.1) [Computer software]). The corresponding tables of results are available in Supplementary materials. The statistical analyses can be divided in two parts.

First, we checked that the threat-of-scream procedure was efficient and had similar impact on both Common and Non-Common groups. To do so, we ran two-way repeated-measures ANOVAs with Condition (Threat vs. Safe) and Time (block 1 to 2) as within-subjects factor and with Group (Common vs. Non-Common) as between-subjects factor on SCL and subjective reports of anxiety as well as t-tests on the debriefing scores of Aversiveness and Preoccupation. Moreover, in an exploratory analysis, we assessed whether the anxiety manipulation could have been impacted when participants were in dyads rather than alone (Classical Simon task performed by 38 participants during alternating threat and safe blocks, **see Supplementary Materials in Appendix Section**). To do so, we ran repeated-measures ANOVAs with Condition (Threat vs. Safe) as within-subjects factor and with Group (Alone vs. Common vs. Non-Common) as between-subjects factor on SCL, subjective reports of anxiety, scores of Aversiveness and Preoccupation.

Second, to determine whether and how sustained anxiety impacted the Social Simon Effect (SE), we analyzed reaction times (RTs). Trials with RTs below 150ms or above 1500ms were considered as incorrect trials and participants with an error rate higher than 10% were excluded for RT analyses (Müller, Brass, et al., 2011). The SE is operationalized as the difference of reaction times between trials where the position of the cue on the screen was spatially incongruent with the location of the button press (e.g. grey cue on the left) and trials where the position of the cue on the screen was spatially congruent with the location of the button press (e.g. grey cue on the right). We ran two-way repeated-measures ANOVA with Condition (Threat vs. Safe) and Congruency (Incongruent vs. Congruent) as within-subjects factor and with Group (Common vs. Non-Common) as between-subjects factor for RTs. Finally, to investigate whether SE during safe and threat blocks rested upon the same mechanisms (Welsh, McDougall, & Weeks, 2009), we computed between-subjects correlations separately for Common and Non-Common groups respectively. Effect sizes (eta-squared, η^2 or Cohen's d) are reported together with F, t, Pearson's r and p values.

Results

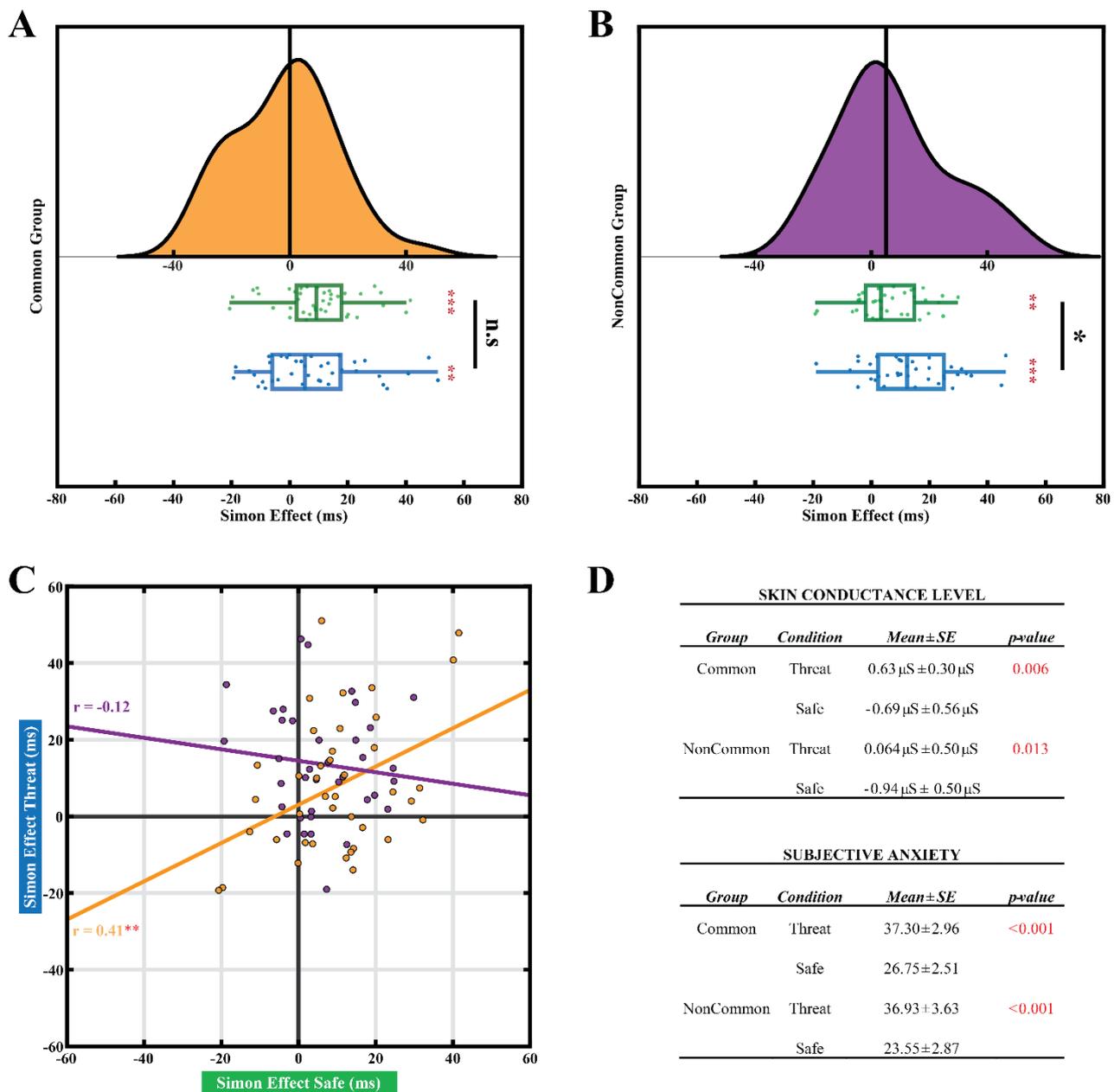


Figure 5-2: Result from the Social Simon task. (A) and (B) Social Simon Effect (SE) for the Common and the Non-Common groups, respectively. Points represent individual data. Distribution in the upper part of each plot represents the difference in Social SE between Threat and Safe blocks and the black line the median of this distribution. The distribution is center to zero for the Common Group while it is shift toward positive values for the Non-Common Group. (C) Between-subjects correlations between the magnitude of the Social SE in safe and threat blocks for the Common Group (Orange) and Non-Common Group (Purple). (D) Skin Conductance level and Subjective reports of anxiety. P-value for t-test contrasting threat against safe blocks within each group are provided. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; n.s. = $p > 0.05$.

Quality check of the threat-of-scream procedure

The electrodes of one participant got unplugged during two blocks, and it was therefore excluded from the SCL analyses (final $n = 77$). Participants' tonic skin conductance activity (SCL) was greater during

Threat relative to Safe blocks ($F(1,75) = 14.62, p < 0.001, \eta^2_p = 0.16$) (**Figure 5-2D**). We observed a main effect of Time ($F(1,75) = 41.060, p < 0.001, \eta^2_p = 0.35$), suggesting a decrease of SCL across the experiment. However, there was no significant interaction between Condition and Time ($F(1, 75) = 0.91, p = 0.34, \eta^2_p = 0.012$), suggesting that the difference in SCL between Safe and Threat blocks did not change with time. No significant interaction with Group was observed, suggesting that SCL activity was similar between Common and Non-Common Groups (all p s < 0.22).

Regarding subjective anxiety, participants reported higher levels of the anxiety at the end of Threat compared to Safe blocks ($F(1,76) = 41.16, p < 0.001, \eta^2_p = 0.35$) (**Figure 5-2D**). There was a *significant* main effect of Time, suggesting that participants' subjective reports decreased in intensity throughout the experiment ($F(1,76) = 7.30, p = 0.009, \eta^2_p = 0.088$). However, there was no significant interaction between Condition and Time on subjective reports ($F(1,76) = 0.002, p = 0.97, \eta^2_p \sim 0$), suggesting that the difference in subjective reports of anxiety between Safe and Threat blocks did not change with time. Moreover, no significant interaction with Group was observed, suggesting subjective reports of anxiety were similar between Common and Non-Common Groups (all p s < 0.25).

In addition, the scores reported at the end of the experimental session regarding the Aversiveness of screams ($t(76) = 0.30, p = 0.77, \text{Cohen's } d = 0.067$) and Preoccupation related to screams delivery ($t(76) = -0.79, p = 0.43, \text{Cohen's } d = -0.18$) didn't differ between Common and Non-Common Groups.

Finally, in an exploratory analysis, we assessed whether our anxiety manipulation could have been impacted when participants were in dyads rather than alone (Classical Simon task performed by 38 participants during alternating threat and safe blocks, see Supplementary Materials). The ANOVAs revealed a significant Group by Condition interaction for the SCL ($F(2,112) = 3.66, p=0.03, \eta^2_p = 0.061$), the Subjective anxiety ($F(2,113) = 6.79, p=0.002, \eta^2_p = 0.11$) and the Preoccupation score ($F(2,113) = 4.70, p=0.011, \eta^2_p = 0.077$) suggesting that overall, the level of sustained anxiety was higher when participants performed the task alone (see **Tables S5-24 – S5-34**) than when performing the task in dyads.

Simon Effect

One participant had an error rate above 10% and was excluded from RTs analyses (final $n = 77$). Neither the main effect of Condition ($F(1,75) = 1.33, p = 0.25, \eta^2 = 0.017$), nor the interactions between Condition and Group ($F(1,75) = 1.64, p = 0.21, \eta^2 = 0.021$), or between Condition and Congruency ($F(1,75) = 2.00, p = 0.16, \eta^2 = 0.026$), or between Congruency and Group ($F(1,75) = 0.14, p = 0.71, \eta^2 = 0.002$) on RTs were found significant. The main effect of Congruency on RTs, which reflected the classical Social SE, was found to be significant ($F(1,75) = 52.32, p < 0.001, \eta^2 = 0.41$). Participant

were slower during incongruent compared to congruent trials. T-tests against zero suggested that the Social SE was present and significant in both Safe and Threat blocks and in both Common and Non-Common groups (all p s < 0.01, see **Tables S5-8 and S5-12**).

Moreover, the triple interaction between Condition, Group and Congruency was found to be significant ($F(1,75) = 4.81$, $p = 0.031$, $\eta^2 = 0.060$). To better understand this interaction, we fitted separated ANOVAs on Common and Non-Common groups respectively. In the Common group, i.e. the two members of the dyad were exposed to the same experimental context, the interaction between Congruency and Condition was not significant ($F(1,39) = 0.36$, $p = 0.55$, $\eta^2 = 0.009$), suggesting that the Social SE was of similar size during Safe and Threat blocks (**Figure 5-2A**). In contrast, in the Non-Common group, i.e. the two members of the dyad were never exposed to the same experimental context, the interaction between Congruency and Condition was significant ($F(1,36) = 5.58$, $p = 0.024$, $\eta^2 = 0.13$), suggesting that the Social SE was increased when participants were exposed to an aversive situation on their own while their partner was safe (**Figure 5-2B**).

Finally, when computing between-subjects' correlations separately for Common and Non-Common groups respectively, a positive and significant correlation was observed between the magnitude of the Social SE during the safety condition and the magnitude of the Social SE during the threat condition, for the Common group ($r = 0.41$, $p = 0.008$). In contrast, no correlation was observed for the Non-Common group ($r = -0.12$, $p = 0.50$) (**Figure 5-2C**).

Discussion

The objective of this study was to determine whether and how one of the crucial mechanisms on which cooperative behaviors rests upon (Era, Candidi, et al., 2018; Knoblich & Sebanz, 2006), i.e. the ability to integrate one's own action representations with those of others, is modified under threat. To this end, dyads of participants jointly performed the Social Simon task (Sebanz et al., 2003; Sebanz, Knoblich, et al., 2006) while being exposed simultaneously (Common group) or not (Non-Common group) to alternating blocks of threat-of-screams or safety (Beaurenaut et al., 2020; Patel et al., 2017). Our results are threefold. First, when two members of a dyad shared the same experimental context, the magnitude of the Social SE, used as a proxy of co-representation, was similar in safe and threat contexts. Second, when only one member of a dyad was under threat while the other was safe, the magnitude of the Social SE was significantly different between safe and threat contexts. Third, the magnitudes of Social SE in safe and threat contexts were positively correlated in dyads sharing the same experimental context. In contrast, when exposed to an aversive situation on their own while their co-performer was safe, most of the participants displayed a Social SE of high magnitude under threat,

irrespective of the magnitude of their Social SE during the safe context, i.e. the magnitudes of Social SE in safe and threat contexts were not correlated. Altogether, these results suggest that self-other integration is maintained under threat and possibly boosted when participants are exposed to an aversive situation on their own while the other participant is safe.

Action co-representation is preserved under threat. When dyads of participants jointly performed the Social Simon task, the observed alter-centric interference, better known as Social SE, is regarded as an objective measure of self–other integration, typically explained by an automatic co-representation of surrounding individuals' actions (Sebanz et al., 2003). Besides replicating previous findings from experiments that used the same task (Karlinsky et al., 2017) in safety context, we further show here that, when exposed to a moderate threat, the co-representation of surrounding others' actions is preserved. Alter-centric interference (Social SE) is known to be modulated by the interpersonal relationship between the members of the dyads. It is notably increased between lovers (Quintard, Jouffre, Croizet, & Bouquet, 2018), friendly and supportive co-actors (Hommel et al., 2009) as well as in-group members (McClung et al., 2013; Müller, Kühn, et al., 2011) but reduced under competitive context (Iani et al., 2011, 2014), following social exclusion (Costantini & Ferri, 2013) or when co-acting with a hostile individual (Hommel et al., 2009). By revealing that under threat, people continue to take into account the actions of others, our findings suggest that the social bonds between the members of the dyads was maintained. They therefore dovetail nicely with converging evidence from field works (Dezecache, 2015; Decache et al., 2020; Drury, Cocking, & Reicher, 2009b; Fahy & Proulx, 2009; Mawson, 2005) and behavioral research (e.g. Margittai et al., 2015; Tomova et al., 2020; von Dawans et al., 2019; von Dawans, Fischbacher, Kirschbaum, Fehr, & Heinrichs, 2012) that show that primary reactions to anticipated or experienced threats are social and affiliative rather than asocial and/or antisocial (Dezecache, 2015). Here, we further suggest that affiliative tendencies under threat could be associated with the maintenance of self-other integration, an ability which could be crucial for survival by facilitating efficient action coordination (Török, Pomiechowska, Csibra, & Sebanz, 2019), cooperation and decisions (Schwenke, Dshemuchadse, Vesper, Bleichner, & Scherbaum, 2017; Wahn, Czeszumski, Labusch, Kingstone, & König, 2020) with others.

Affiliative tendencies under threat were suggested to be motivated by the fact that surrounding others can provide (a) a best estimate of the individual one's own emotional state (emotional comparison motives (Schachter, 1959)), (b) information regarding the nature of the threat (e.g., Kulik, Mahler, & Earnest, 1994), and/or (c) help reduce one's own anxiety level through comfort and mutual support (tend-and-befriends (Taylor, 2006)). While our experiment didn't aim at dissociating these different possibilities, we observed that sustained anxiety, evidenced by increases in skin conductance and in

subjective anxiety ratings in threat compared to safe blocks, was lower in participants who performed the Social Simon task in dyads (for both Common and Non-Common groups) as compared to those who performed the Classical Simon task on their own (see Supplementary Materials). This implies that the mere presence of a conspecific mitigated participants' anxiety responses during threat blocks, a phenomenon labeled social buffering (O'Haire, McKenzie, Beck, & Slaughter, 2015; von Dawans et al., 2012). While reduced in the presence of conspecifics, anxiety responses in the members of dyads were still significantly higher during threat than safe blocks, suggesting that part of the anxiety responses to unpredictable threats is resistant to social buffering (see Kiyokawa, Kawai, & Takeuchi, 2018, for similar results in animals). These results still concur with the idea that under threat, affiliative tendencies could be partly motivated by the fact that the presence of others reduces one's own anxiety level (fear-reduction motives that benefit both members of the dyads). We further show here that affiliative tendencies and related social buffering effects are associated with the maintenance of self-other integration under threat.

Action co-representation under threat is boosted in the presence of a safe individual. To best understand the potential incentives behind changes in action co-representation under threat, the present experimental design quantified the variation of action co-representation according to whether members of the dyads shared (Common) or not (Non-Common) the current situation of danger. Sustained anxiety was successfully induced by threat-of-scream, and importantly didn't differ between shared and non-shared situations. However, while the magnitude of the alter-centric interference (Social SE) was similar in safe and threat contexts when two members of a dyad shared the same experimental context, it was significantly higher in threat as compared to safe contexts when only one member of a dyad was under threat while the other was safe. This result contradicts Schachter (Schachter, 1959) pioneering work where he suggested that under condition of experimentally-induced anxiety, individuals display increased affiliative tendencies towards others perceived to be undergoing the same emotional states (similar others) rather than dissimilar-state others (replicated by Firestone, Kaplan, & Russell, 1973; Zimbardo & Formica, 1963).

What could be the function of a boost in self-other integration, i.e. an extension of social space, in participants that are facing alone a threat, while others are safe? Could it serve cooperative or altruistic motivations toward others? Several findings on peripersonal space bear similarity with those on alter-centric interference observed during the Social Simon task. For instance, the boundaries between self and other peripersonal spaces also blur if the other is a cooperator but not for a competitor (Teneggi, Canzoneri, di Pellegrino, & Serino, 2013). Of interest, Hobeika et al. (Hobeika, Taffou, & Viaud-Delmon, 2019) showed that participants' peripersonal space, which corresponds to their defensive

space (as measured by the detection of threatening looming stimuli), enlarged in the presence of another individual in a cooperative context. They suggested that such extension of the peripersonal space could underlie the altruistic motivation to protect and defend others, notably group members. While this suggestion is appealing, one would somewhat expect the reverse, an extension of the peripersonal space in safe individuals toward others under threat, as in Fossataro et al. (Fossataro, Sambo, Garbarini, & Iannetti, 2016) who revealed increased defensive reactions when observing someone else in danger, as a function of participants' empathic tendency.

Another possible explanation is that self-preservative motives underlie the increased of co-representation toward individuals that are safe, and thus potentially in a best position to help. This suggestion would concur with Rofé's utility affiliative theory (Rofé, 1984), whereby affiliative tendencies depend on the perceived or anticipated benefit and damage of being with another to one's own ability to cope with the anxiety. Hence, the greater the probability that being with another will help coping with the anxiety by either eliminating or reducing the source of threat or by providing a sense of comfort and support (secondary motives), the stronger the tendency to affiliate. In similar vein, Taylor and Lobel (Taylor & Lobel, 1989) proposed that individuals seek out information and affiliation from more fortunate (upward contacts) rather than less fortunate others, and Dezechache et al. (Dezechache et al., 2017) indeed showed that affiliative tendencies decreased toward individuals that are the most exposed to threat. In addition, Doerrfeld et al. (Doerrfeld, Sebanz, & Shiffrar, 2012) revealed that participants paired with a healthy co-actor (i.e., with high resources to help) underestimated the effort which would be necessary to perform a joint task while they overestimated it when paired with an injured partner (i.e. low resources to help). Low et al. (Low, Edwards, & Butterfill, 2020) recently argued that perceiving physical constraints of others' movements shaped the representation of their beliefs, indicating that observer's motor system appraises other's resources to act. Interestingly here, we further observed that while the context (safety or threat) in Common dyads had little impact on the intrapersonal ability to co-represent others (positive correlation between the magnitudes of Social SE), most of the participants in the Non-Common dyads displayed a high level of co-representation under threat, irrespective of its magnitude during the safe context. Altogether, our findings show that facing alone a threat while being surrounded by safe individuals boosts the ability to integrate one's own action representations with those of others, an increase which could promote social strategies essential for one's own survival.

In defense of the social nature of the Social SE. The mechanisms underlying alter-centric interference observed during the Social Simon task and their social nature are debated (see Dolk et al., 2014 for the review). Here, we systematically adopted the action co-representation account (Sebanz et al., 2003),

but the Social SE could also be explained within the referential coding framework (Dolk et al., 2013). This theory suggests the presence of a co-partner provides spatial, perceptual or conceptual reference frames used by the participant to code their actions. Hence, the proponents of action co-representation account argue for the social nature of the task, while those of the referential coding account propose that any sufficiently salient event, irrespective of its social nature, can prompt an alter-centric interference. Past experiments provided several evidence that interpersonal social factors, such as social status (Aquino et al., 2015), group membership (McClung et al., 2013) or perceived interpersonal closeness (Shafaei, Bahrami, & Vaziri-Pashkam, 2019), influenced the magnitude of the alter-centric interference. Proponents of the referential coding framework suggest that the observed social effects are related to the fact that the size of the Social SE is an indicator of the similarity between self- and other-generated alternative events. Such explanation however doesn't hold for the present results of larger Social SE under threat in Non-Common dyads compared to Common dyads. Moreover, this effect was specific to the social context. Indeed, the magnitudes of the classical Simon effect in participants performing the task on their own were of similar size in safe and threat contexts, and correlated as in the Common situation (see **Figure S5-1, Tables S5-19 - S5-23**). Together, we believe our results to clearly favor the social nature of the phenomenon.

Limitations. The present experiments are not without limitations. First, they were conducted in a between-subject design, which was favored in the past to investigate Social SE (Costantini & Ferri, 2013; Kuhbandner et al., 2010), as the social context of an experimental condition can contaminate the subsequent one due to potential long-term effects (Chadwick, Metzler, Tijus, Armony, & Grèzes, 2019; Iani et al., 2014). Still, part of our results could be explained by random variations from the different sampling populations. While we can't control for all possible variables, we checked that Common and Non-Common groups didn't significantly differ in their levels of anxiety traits (LSAS, STAI-T), anxiety state (STAI-E) and induced anxiety (SCL, subjective anxiety, debriefing scores). Second, as we only tested same gender dyads, future studies are needed to generalize our results to mixed gender dyads. Third, we proposed possible explanations for larger SE in Non-Common compared to Common groups, but clearly, further experiments are needed to specifically tackle the possible mechanisms and motives behind this increase, notably the potential role of co-representation in recruiting social support. Finally, while laboratory experiments clearly allow investigating the impact of moderate threat on socio-cognitive mechanism in controlled environments (Kinatader, Ronchi, Nilsson, et al., 2014), one may still question their validity to address behavioral responses in real life situations where individuals are at risk of death.

Conclusion

Overall, the present work strongly supports the idea that, under threat, affiliative tendencies prevail, by showing that action co-representation is maintained and possibly boosted in the presence of safe individuals. We further observed that the mere presence of a conspecific mitigated participants' anxiety responses during threat blocks. We discussed the possibility that affiliative tendencies may be sustained by self-preservative motives, but further experiments are needed before such conclusion can be firmly drawn. Despite its limitations, we think that this study is important in that real-time reactions to threatening situations are seldom observed, and the cognitive mechanisms underlying these reactions are impossible to record. This is necessary to comprehensively understand the nature and dynamics of immediate collective reactions to imminent danger in humans.

Author notes

Author contributions

M.B., J.G. and G.D. designed the study; M.B collected the data; M.B. performed the analysis; M.B., J.G. and G.D. wrote the first draft of the manuscript. All authors reviewed and approved the final manuscript.

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Competing interests

The authors declare no competing financial interests.

Supplementary information

Data and analysis are available on OSF:

https://osf.io/tb9sk/?view_only=0dd2445b91c9422c9735119286645fb7

CHAPTER 6

DISTRESS OR DANGER-RELATED SOCIAL SIGNALS: WHICH ONE IS PRIORITIZED UNDER THREAT?

In dangerous situations, individuals perceive different information in their physical and social environment necessary for making an efficient decision. Traffic signs and emergency exits, for example, are important clues in deciding whether to flee or take shelter from threat. However, facial and bodily expressions from our conspecifics also provide relevant clues about their mental state and these influence our perception (Koizumi et al., 2016), our attentional allocation as well as our action selection (Vilarem et al., 2019). A particularly relevant cue under threat is fear emotional expression.

In this chapter, we tried to understand what types of signals are prioritized under threat. For this purpose, the fear emotional expression is a very interesting tool. Indeed, two distinct social messages can be interpreted depending on the gaze direction displayed, averted or direct: in the former case, the gaze can inform about the presence of a danger in the environment, while in the latter case, the gaze is a signal of vulnerability and affiliation addressed to the observer. The first study carried out on 85 participants brought new evidence confirming these associations between gaze direction and these two possible communicative functions.

Investigating which of these two interpretations is processed preferentially allow us to identify which message is the most relevant in a threatening situation. Thus, 32 participants performed an emotional categorization task during threat and safe blocks. Their behaviors were then fitted using techniques derived from the Signal Detection Theory. Our results showed that anxiety biases our assessment of danger cues (i.e. lower decision criterion), without impacting the processing of affiliation signals. The following chapter details a series of experiments used to investigate fear perception under threat and the possible interpretations explaining the results produced. One particular explanation would be that, under threat, processing danger-related social cues might be modified to prioritize individual's own survival.

Prioritization of danger-related social signals under the experience of threat

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NB: This article is in preparation (draft)

NB2: Supplementary material is available in the Appendix section of the dissertation (p.194)

Abstract

Exposure to threat are almost always social phenomena. Under threat, the combinations of fearful display and gaze orientation emitted by others can provide crucial information about the presence and location of the danger, but also as to whether the signaler is in need or can provide mutual support. While it has been shown that the processing of fearful faces is prioritized under threat, the question remains as to whether the processing of one of the two social meanings conveyed by fearful displays and gaze combinations (signaling danger vs. distress/affiliation) is facilitated when observers are themselves under threat. To address this question, we ran two experiments. The first experiment shows that the appraisal of the two social meanings (signaling danger vs. signaling a need for help / distress) indeed differ between fearful displays associated with either averted or direct gaze respectively. In the second study, participants performed a categorization task (neutral vs. fear) under safe or threat-induced anxiety contexts, while gaze direction and intensity levels of facial expressions were manipulated. Results from classical and model-based analyses indicate that participants' tendency to interpret facial expressions as expressing fear when associated with averted gaze is enhanced when they are in a sustained state of anxiety (under threat) as compared to in a safe state. Altogether, our findings suggest that, under threat, the social signals that convey information about the presence and location of the danger, such as the combinations of fearful facial displays and averted gaze, are prioritized.

Introduction

Despite the common conception that our responses are fundamentally asocial and/or antisocial when faced with a collective threat, converging evidence from field work (Dezecache et al., 2017, 2020; Drury, Cocking, & Reicher, 2009; Fahy & Proulx, 2009; Mawson, 2005; see review by Dezecache, 2015), and behavioral research (Margittai et al., 2015; Tomova et al., 2020; von Dawans et al., 2019, 2012; Von Dawans et al., 2012) revealed that our social cognitive abilities are preserved (rather than shut down). Surprisingly, although exposure to threat are almost always social episodes, little is known about how stressful situations shape the way individuals process social signals emitted by surrounding others, as a function of the social meaning they convey.

When under threat collectively, socio-emotional cues become highly relevant signals. Indeed, threatening contexts not only result in internal body changes that likely are inaccessible to others (i.e. increased sweating or heart rate), but may also be associated with facial and bodily expressions of fear (e.g. Anderson, Monroy, & Keltner, 2018). Interestingly, facial displays of fear convey different social meanings that may be further accentuated by co-emitted gaze orientation. On the one hand, fearful displays signal the presence of a potential threat for both the emitter and the observer which needs to be located and identified (Adams Jr & Kleck, 2005; Cushing et al., 2018; Im et al., 2017; Whalen, 2007). Fearful displays enhance observers' processing of important environmental events in the visual fields, i.e. observers better discriminate expressers' gaze direction and targets in visual periphery (Lee, Susskind, & Anderson, 2013; Phelps et al., 2006), and this even more when they are "pointing to a danger" with the eyes (Bayless, Glover, Taylor, & Itier, 2011; Hadjikhani, Hoge, Snyder, & de Gelder, 2008; Lassalle & Itier, 2013). Fearful facial expressions are more likely to be judged as averting their gaze from the perceiver (Lobmaier, Tiddeman, & Perrett, 2008). Moreover, when associated with averted gaze, fearful displays are more efficiently processed (El Zein, Wyart, & Grèzes, 2015), better and more quickly categorized (Adams & Kleck, 2003, 2005; Hess, Adams, & Kleck, 2007; Sander, Grandjean, Kaiser, Wehrle, & Scherer, 2007), rated as both more intense (Cristinzio, N'diaye, Seeck, Vuilleumier, & Sander, 2010; N'diaye, Sander, & Vuilleumier, 2009; Sander et al., 2007) and more negative (Ewbank, Fox, & Calder, 2010).

On the other hand, fearful displays, by enhancing facial cues of vulnerability and affiliation (Hess et al., 2000; Marsh et al., 2005), communicate distress (Hammer & Marsh, 2015). As such, they can trigger empathetic concern and altruistic motivations in the observer (Batson, Fultz, & Schoenrade, 1987; Nichols, 2001), especially in participants with high prosocial personality profile (Kaltwasser, Moore, Weinreich, & Sommer, 2017), which can result in approach behaviors (Vilarem et al., 2019).

Altogether, these results suggest that under threat, the combinations of fearful displays and gaze orientation emitted by others could provide crucial information about the presence, the nature and location of danger as well as the sources that need or can provide mutual support, but a direct assessment of how these two signals are appraised as a function of gaze orientation is lacking. Moreover, while it has been shown that the processing of fearful faces is prioritized under threat (Bublitzky, Kavcıoğlu, Guerra, Doll, & Junghöfer, 2020; Kavcıoğlu, Bublitzky, Pittig, & Alpers, 2019; Lago et al., 2019; Robinson et al., 2016; Robinson, Letkiewicz, Overstreet, Ernst, & Grillon, 2011), the question remains as to whether the processing of one of the two social meanings conveyed by fearful displays and gaze combinations is facilitated when observers are themselves under threat.

To address these questions, we ran two experiments. The first study investigated whether the explicit appraisal of the two social meanings (signaling danger vs. signaling a need for help / distress) differ between the different combinations of fearful displays and gaze orientation. The second study investigated whether the processing of one of the two social meanings conveyed by fearful displays and gaze combinations is facilitated during a categorization task (neutral vs. fear) under safe or threat-induced anxiety contexts. We performed model-guided analyses of the behavioral data to determine whether threat contexts influence the observers' sensitivity to sensory information and/or their response bias (or criterion).

Study 1

Study 1 consisted in running an online experiment during which participants were requested to explicitly evaluate the extent to which faces, varying in emotion (neutral versus fear) and gaze direction (averted versus direct), conveyed a signal of danger and/or need for help (distress).

Methods

Participants

Eighty-four participants (54 females, 28.9 y.o. \pm 9.5 SD) were recruited online. All participants had normal or corrected-to-normal vision, and had no history of neurological or psychiatric disorders. The experimental protocol was approved by INSERM and the local research ethics committee (Comité de protection des personnes Ile de France III - Project CO7-28, N° Eudract: IRB00003888) and was carried out in accordance with the Declaration of Helsinki. Participants provided online consent.

Stimuli

Stimuli were provided by El Zein et al. (2015) and consisted of facial displays from 36 actors (18 females) adapted from the Radboud Faces Database (Langner et al., 2010) that varied in emotion (neutral or fearful expressions) and gaze direction (direct toward the participant or averted 45° to the

left or right). Faces were modified to remove any visible hair, resized and repositioned so that eyes, nose and mouth appeared within the same circumference. All images were also converted to greyscale and cropped into a 280 x 406 pixels oval centered within a 628 x 429 pixels black rectangle.

Experimental Protocol

Participants were recruited via an online advert. On the first page of the survey (programmed on Qualtrics), participants had to confirm that they matched the inclusion criteria. Then, instructions were given. The experiment was described as a “face evaluation task”. On each trial, a face was to be presented for 300ms. Participants were then requested to assess how much the presented face signaled (i) the presence of a danger and (ii) a need for help, on two separate continuous scales ranging from not at all (0) to extremely (100), the order of which was randomized between participants. To provide their answer, participants had to click on their cursor and move it on the scale before validating their response using the “shift” keypress. They were asked to answer spontaneously and to use the whole scale as much as possible. In addition, as we anticipated potential internet connection problems, participants were allowed to cancel a trial by pressing the “space” keypress if the image did not load correctly on the screen (2% of the trials \pm 8% SD). Each trial ended with participant response. The next trial started after 300m (inter-trial interval). One-hundred and forty four trials were presented, corresponding to thirty-six actors with a fearful or a neutral face associated with an averted or a direct gaze ($36*2*2=144$ trials).

At the end of the experiment, we assessed participants’ ability to discriminate neutral from fearful faces. To do so, images of 18 of the actors were presented to participants, with direct gaze. Nine actors displayed a neutral facial expression while the other nine expressed a fearful one (18 trials in total). The 18 actors were randomly selected as well as their emotional display and both were counterbalanced across subjects. Participants were requested to indicate if the expression of the face was neutral or fearful by pressing respectively the “E” and “P” letter on their keyboard. Each trial ended with participant response, and the next trial started after 300m (inter-trial interval). As before, participants were allowed to cancel a trial by pressing the “space” key.

Statistical analyses

All statistical analyses were carried out using JASP Software (JASP Team (2017), JASP (Version 0.8.5.1)).

Participant exclusion

For each participant, we computed a quality check score (i.e. the percentage of trials where the image loaded correctly) and a categorization score (i.e. percentage of trials where the participant correctly

discriminated fear from neutral expressions). Participants were identified as outliers if the mean of one of the scores deviated from the mean group by 2 SD. Two participants were outliers for the quality score ($\text{Mean}_{\text{Group}} = 98.26\% \pm 8.14\%$, $\text{threshold}_{\text{Outlier}} = 81.98\%$) and 4 for the categorization score ($\text{Mean}_{\text{Group}} = 94.91\% \pm 7.69\%$, $\text{threshold}_{\text{Outlier}} = 79.56\%$). After excluding those participants, the final data sample included 78 participants (50 females, 28.6 y.o. ± 9.2 SD)

Repeated-measures ANOVAs

We ran three-way repeated-measures ANOVAs with Question (Danger vs. Help), Emotion (Neutral vs. Fearful) and Gaze (Averted vs. Direct) as within-subject factors. Effect sizes (partial eta-squared, η^2_p) are reported together with F and p values. If gaze direction impacts on the appraisal of the social signals (danger vs. help) conveyed by fearful faces, a triple interaction should be observed.

Results and conclusion of study 1

While the ANOVA did not reveal any significant main effect of Question ($F(1,77) = 1.57$, $p = 0.21$, $\eta^2_p = 0.020$), a main effect of Emotion was observed ($F(1,77) = 805.89$, $p < 0.001$, $\eta^2_p = 0.91$), such that fearful faces were associated with higher scores for both questions as compared to neutral faces. The ANOVA further revealed a main effect of Gaze ($F(1,77) = 11.66$, $p = 0.001$, $\eta^2_p = 0.13$), an interaction between Question and Emotion ($F(1,77) = 13.75$, $p < 0.001$, $\eta^2_p = 0.15$), Question and Gaze ($F(1,77) = 32.89$, $p < 0.001$, $\eta^2_p = 0.30$), and Emotion and Gaze ($F(1,77) = 39.98$, $p < 0.001$, $\eta^2_p = 0.34$), further characterized by the triple interaction between Question, Emotion and Gaze ($F(1,77) = 7.16$, $p = 0.009$, $\eta^2_p = 0.085$). While Danger scores were significantly higher for Averted as compared to Direct gaze for both Fearful and Neutral faces (see **Figure 6-1**), the Help scores were significantly higher for Direct as compared to Averted Fearful faces, but higher for Averted as compared to Direct Neutral faces (see Supplementary Materials for full results in **Tables S6-1 and S6-2**). Fifty-six of the 78 participants (71%) reported higher Danger scores for Averted compared to Direct Fearful faces, while 60 of the 78 participants (77%) reported higher Help scores to Direct as compared to Averted Fearful faces.

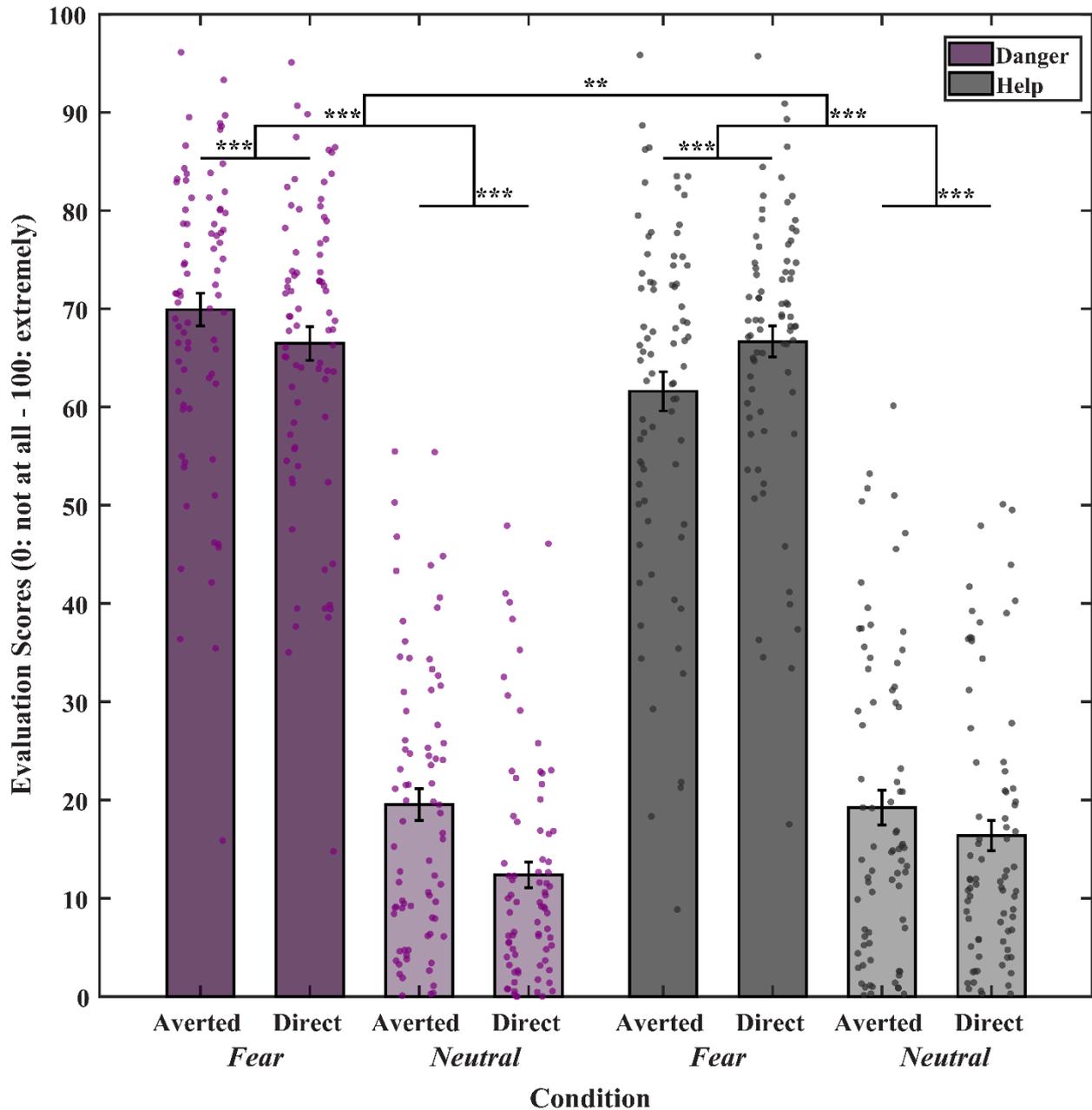


Figure 6-1. Participants' evaluation scores during the face evaluation task. Participants assessed on continuous scales whether fearful (dark color) or neutral (light color) facial expressions associated with averted or direct gaze faces signaled (i) the presence of danger (purple) and (ii) a need for help (grey). Error bars and points represent respectively standard errors and individual data. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; n.s. = $p > 0.05$.

So far, the literature suggested that emotional displays of fear are associated with two potential social meanings: they signal the presence of a potential danger in the environment and/or communicate distress and need-for-help. Here, using explicit ratings of faces, we bring evidence that the two social meanings conveyed by fearful faces are further accentuated by co-emitted gaze orientation, i.e. fearful faces with averted gaze more clearly signal the presence of a danger while fearful faces associated with direct gaze more clearly communicate distress and need for help. These results further confirm that co-

emitted gaze acts as an important contextual information that facilitate the interpretation of fearful facial signals (e.g. El Zein et al. 2015).

Study 2

To determine whether the processing of one of the two social meanings conveyed by fearful displays and gaze combinations is facilitated when observers are themselves under threat, a new group of participants performed a categorization task under safe or threat-induced anxiety contexts while varying gaze direction and intensity levels of fearful expressions.

Materials and methods

Participants

Thirty-two healthy volunteers (17 females, 23 y.o. \pm 4.4 SD) were recruited to participate in Study 2 (a sample of the same magnitude as that recruited in Bublatzky et al. (2020)). All participants were right-handed, had normal or corrected-to-normal vision, and had no history of neurological or psychiatric disorders. The experimental protocol was approved by INSERM and the local research ethics committee (Comité de protection des personnes Ile de France III - Project CO7-28, N° Eudract: 207-A01125-48) and was carried out in accordance with the Declaration of Helsinki. Participants provided informed written consent and were compensated 20€ for their participation.

General Procedure

Participants were recruited via an online advert, which contained a link to a Qualtrics survey. Due to the potentially stressful nature of our paradigm and following discussion with the referent medical doctors of our laboratory, we requested that participants fill in, online and anonymously, the French versions of State-Trait Anxiety Inventory Spielberger (STAI, Spielberger, 1983) and Post-traumatic stress disorder Checklist Scale (PCLS, Weathers et al., 1993), at least one week before the experiment. Only participants with a score below 40 for the PCLS and below 60 for both STAI state and trait anxiety were invited to contact the experimenter and could take part in the experiment.

Also, two days prior participation, participants filled in online the Liebowitz Social Anxiety Scale (LSAS, Heimberg et al., 1999), the Trait-STAI questionnaire, Intolerance of Uncertainty Scale (IUS, Buhr & Dugas, 2002; Freeston, Rhéaume, Letarte, Dugas, & Ladouceur, 1994) and the Social Value Orientation scale (SVO, Murphy & Ackermann, 2014). Moreover, on the day of the experiment, upon arrival at our premises, participants completed the State-STAI questionnaire. This allowed us to ensure that their state level of anxiety was in the “normal” range (below 60) before the experimental session, which aimed at manipulating their anxiety (see **Figures S6-1** for questionnaire scores distributions).

Finally, after being instructed, participants took part in a 2-minute training session, before completing the main experiment for approximately 1 hour. They were debriefed at the end of the main experiment. During the debriefing, participants were notably requested to rate how aversive the screams were and how much they felt preoccupied by the possibility that a scream would be delivered during threat blocks (from 0 - not at all to 10 - extremely).

Scream Stimuli

Eight distress screams were used in the present protocol (4 from males and 4 from females). The screams were normalized at -2b using audiosculpt 3.4.5 (<http://forumnet.ircam.fr/shop/fr/forumnet/10-audiosculpt.html>). During both the training session and the main experiment, screams were delivered using Bose headphones (QuietComfort 25) at peak intensity below 70 dB (mean of 68 dB as measured by a sonometer). The screams were provided by Professor Armony, and had been previously validated (Fecteau et al., 2005) by a group of 60 individuals who rated the stimuli on emotional valence and intensity. The experimental set up was previously validated in Beurenaut et al. (Beurenaut et al., 2020)

Face Stimuli

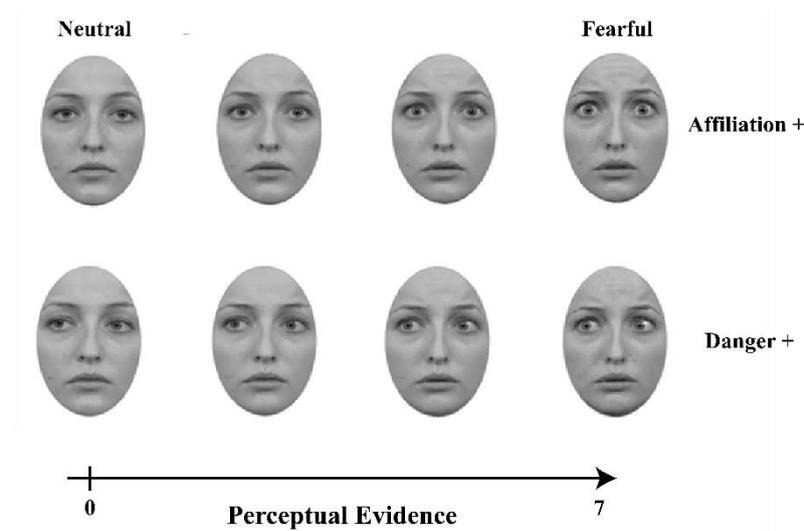


Figure 6-2. Facial signals stimuli - The amount of perceptual evidence (emotional information) on the faces varies from neutral to fear (8 levels of morphs), and each face was associated with direct and averted gaze, which we expected to signal a need for affiliation or danger.

As in study 1, stimuli consisted of 36 actors (18 females) adapted from the Radboud Faces Database (Langner et al., 2010) that varied in emotion (from neutral to fearful expressions) and gaze direction (direct toward the participant or averted 45° to the left or right). Using Adobe Photoshop CS5.1 (Adobe Systems, San Jose CA), faces were modified to remove any visible hair, resized and repositioned so that eyes, nose and mouth appeared within the same circumference. All images were converted to

greyscale and cropped into an oval aperture presented at the center of the screen. To vary the intensity of emotional expressions, faces were morphed from neutral to fearful expressions using software FantaMorph (Abrosoft). Eight levels of morphs were created from neutral (level 0) to fear (level 7) expressions using a simple linear morphing transformation (separately for direct and averted gaze stimuli, **see figure 6-2**). The above described morphed fearful faces were previously used in the El Zein et al. study (El Zein, Wyart, & Grezes, 2015).

Experimental design and task

The experiment consisted in a modified version of the emotion categorization task (El Zein, Wyart, & Grezes, 2015) performed by participants during alternating blocks of threat-of-screams or safety (Threat-of-Scream procedure - Beurenaut et al., 2020) (**see Figure 6-3**). Participants were informed that, during threat blocks, the color bands located on both sides of the screen will be blue, and that, at any time during the block, unpredictable distress screams could be delivered through their headphones. In contrast, they were informed that during safe blocks, both sides of the screen were to be green-colored, indicating that no scream was to be delivered. The order of threat and safe blocks was counterbalanced across participants.

The temporal organization of each block was as follows: First, the written instruction “Threat Block: at any time, a scream can be presented” or “Safe Block: you will hear nothing during this block” was presented for 10 seconds. Second, participants performed the Emotion categorization task for about 4 min. Third, and at the end of each block, participant reported their anxiety level on a continuous scale (from 0: very calm to 100: very anxious), by moving a cursor on the screen using the mouse. The scale was presented on the computer screen and disappeared once the response was given.

The temporal organization of each trial of the Emotion categorization task was as follows: using the Psychophysics-3 Toolbox (Brainard, 1997; Pelli, 1997), stimuli were projected on a black screen. Each trial was initiated with a white oval delimiting the faces that remained throughout the trial. The white oval appeared for approximately 500ms, followed by a white fixation point presented at eye level for approximately 1000ms (to ensure a natural fixation to upcoming faces and avoid eye movements from the center of the oval to eye regions). Then, the morphed face was displayed for 250ms. After face offset, participants were asked to report (2s maximum after face offset) if the face was neutral or fearful. They provided their response by pressing the left “Control” or “Enter” key, localized on an external keyboard, using their left or right index correspondingly (**see Figure 6-3**). A neutral/fear mapping was used (2 possible mapping) and kept constant for each subject, counterbalanced across subjects.

A training session was performed before the main experiment to familiarize participants with the emotion categorization task, the structure of the experiment (the alternation of safe and threat blocks and their associated screen side colors) and the screams. Participants were trained on 2 blocks, one safe and one threat, each consisting of 32 trials. During the threat blocks, 2 distress screams (one male and one female) were delivered once during two randomly chosen trials from among the 32 (approximately 6% of the trials). Note that the two screams used for the training were different from the 6 screams used during the main experiment.

Participants then performed the main experiment, divided into 12 experimental blocks (6 threat blocks, 6 safe blocks), each consisting of 96 trials, balanced in the number of gaze (2), gender (2) and morph levels (8). This resulted in a total of 576 trials (16 trials*36 IDs) presented twice, and 1152 trials for the entire experiment. During each threat block, 6 distress screams were delivered once, randomly during the block (approximately 6% of the trials), either at the beginning of the trial (2 screams), before the face appeared (2 screams), or when it disappeared (2 screams). At the end of each block, the percentage of correct responses was shown to the participants, to keep them motivated.

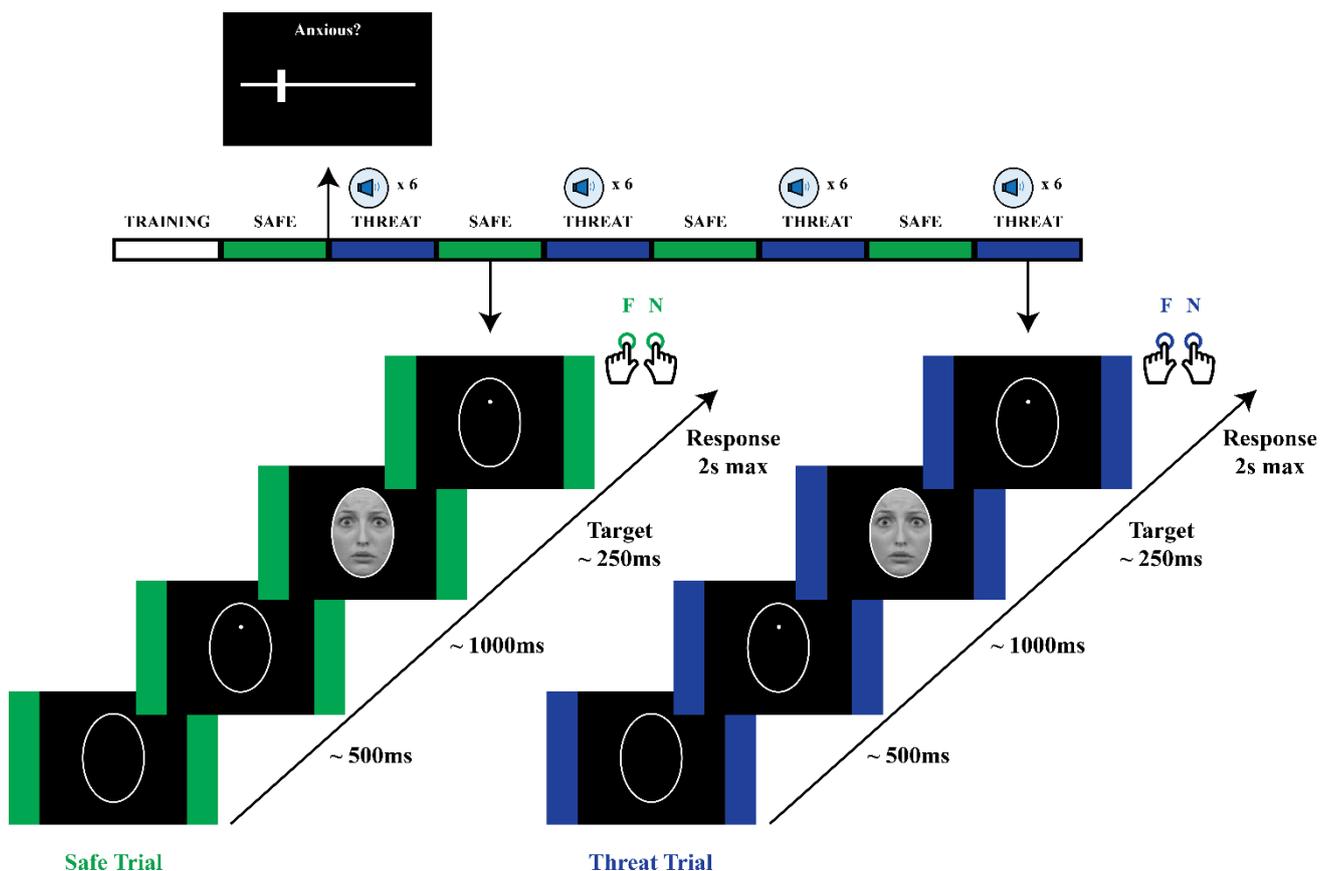


Figure 6-3. Experimental paradigm. Participants performed an experiment under two types of condition indicated by different color band (Green: Safe and Blue: Threat). Participant's task was always to indicate whether the presented faces displayed a neutral or a fearful expression. After each block, the subject indicates its anxiety level on a scale from 0 (relaxed) to 100 (very anxious).

Statistical analyses

All statistical analyses were carried out using JASP Software (JASP Team (2017), JASP (Version 0.8.5.1)).

First, to assess the efficiency of the threat-of-scream procedure, we ran a two-way repeated-measure ANOVA with Condition (Threat vs. Safe) and Time (block 1 to 6) as within-subject factors on subjective reports of anxiety. Descriptive medians of the Aversiveness and Preoccupation debriefing scores were also provided.

Second, to determine whether and how sustained anxiety impacted the emotion categorization task, we analyzed the proportion of fear responses and reaction times (RTs) during Threat and Safe block. We excluded 2 participants from the analyses, as their mean RTs deviated from the mean group by 2 SD ($\text{Mean}_{\text{Group}} = 736 \text{ ms} \pm 151 \text{ ms}$, threshold for Outlier = 434 ms). The final data sample included 30 participants (16 females, 23.6 y.o. ± 4.5 SD). We ran three-way repeated-measures ANOVAs with Condition (Threat vs. Safe), Gaze direction (Direct vs. Averted) and the strength of perceptual evidence (from 0 for neutral to 7 for fear) as within-subject factors on the proportion of fear responses and RTs. Moreover, we assessed whether we could replicate findings from Kavcıoglu et al. (Kavcıoglu et al., 2019), i.e. scores in anxiety trait positively correlated with the number of false alarms (i.e. fear response to neutral faces) in threat context compared to safe context. To do so, we conducted a repeated-measures ANOVA with (Threat vs. Safe) and Gaze direction (Direct vs. Averted) as within-subject factors and STAI-trait scores as a co-variable on the proportion of fear response to neutral faces only (i.e. intensity level = 0).

Third, we performed model-guided analyses of the behavioral data. The SDT (Signal Detection Theory) theoretical framework distinguishes between sensitivity to sensory information, and response bias (or criterion) which reflects the observer's tendency to interpret the signaler as displaying either of the two options (here, fear or neutral decisions). Within this framework, we fitted participant behavior using a model of choice hypothesizing that decisions were formed on the basis of a noisy comparison between the displayed emotion and a criterion. For safe and threat contexts separately, we fitted the data with the simplest model (null model) that could account for each subject's decisions using a noisy, 'signal detection'-like psychometric model to which we included a lapse rate, thereby considering that subjects guessed randomly on a certain proportion of trials:

$$P(\text{fear}) = \phi[\omega * x + b] * (1 - \varepsilon) + 0.5 * \varepsilon$$

where $P(\text{fear})$ corresponds to the probability of judging the face as fear, $\phi(.)$ to the cumulative normal function, ω to the perceptual sensitivity to the displayed emotion, x to a trial-wise array of

evidence values in favor of fear (emotion strength in the stimulus - from 0 for neutral to +7 for an intense display), b to an additive, stimulus-independent bias toward one of the neutral/fear choice, and ϵ to the proportion of random guesses among choices.

We compared the ‘null’ model, which did not allow for influences of gaze direction on the decision process, to three additional models which instantiate two different mechanisms which could account for the observed increase in recognition accuracy for fearful faces combined with averted gaze (**see results study 2**): model 1 (BIAS) where only the bias parameter would be influenced by gaze direction; model 2 (SENSITIVITY), where only the perceptual sensitivity parameter would be influenced by gaze direction; and model 3 (COMPLEX) where both the bias and the sensitivity parameters would vary according to gaze direction. A change in the decision bias implied that the bias toward fear/neutral responses is different for direct and averted gaze and a change on the sensitivity implied that the sensitivity for fear associated with direct gaze is different from the sensitivity for fear associated with averted gaze.

To take into-account inter-individual variability, sensitivity (ω) and bias (b) parameters were estimated for each participant. The four models were fitted independently for Safe and Threat Contexts. We used Bayesian fixed-effect model selection that assume that all participants used the same underlying model to generate their behavior. We calculated the Bayesian information criterion (BIC) for each candidate models to determine which of the four models was more likely to explain the observed data (Burnham & Anderson, 2004; Kass & Raftery, 1995).

As parameters of each model were computed independently for each context, two different scenarios could emerge after model selection: on the one hand, model selection could identify different best models for Safe and Threats contexts, which would indicate that different mechanisms were at play during those two contexts; on the other hand, model selection could identify the same model for Safe and Threats contexts. In the latter case, one could still hypothesize that the underlying mechanism could be modulated differently according to Safe and Threat contexts. To find out, and depending on the best models, we planned to run either a repeated measures ANOVA with gaze direction (direct/averted) and context (safe/threat) as within-subject factors or two-tailed paired t-tests on extracted parameters.

Finally, as the literature describes that fearful faces elicit higher approach-tendencies in population with high prosocial temperament, we checked if Social Orientation Value (used as an index of individual attitudes of cooperation) could explain part of the variance in our measures of interest

(proportion of fear response, RT, model parameters). To do so, we re-ran the above-described ANOVAs with the scores of the SVO questionnaire as co-variable.

For all analyses, effect sizes (partial eta-squared, η^2_p) are reported together with F and p values. We applied the Greenhouse-Geisser correction to correct for deviations from the assumption of sphericity (the corrected P corrected and the GG- ϵ are reported)

Results study 2

Subjective reports of anxiety

Participants reported higher scores on the anxiety scale at the end of Threat ($M = 28.1$, $SE = 3.98$) compared to Safe ($M = 19.8$, $SE = 2.74$) blocks ($F(1,29) = 12.31$, $p = 0.001$, $\eta^2_p = 0.30$). Neither the main effect of Time ($F(5,145) = 1.74$, $p_{\text{corr}} = 0.15$, $GG-\epsilon = 0.74$, $\eta^2_p = 0.057$) nor the interaction between Condition and Time ($F(5,145) = 0.90$, $p_{\text{corr}} = 0.45$, $GG-\epsilon = 0.64$, $\eta^2_p = 0.030$) were found significant on subjective reports. During debriefing, participants rated the screams as moderately aversive (median of 5, see **Figure S6-2**, left) and felt relatively preoccupied by the unpredictability of scream delivery (median of 5 see **Figure S6-2**, right)

Proportion of fear response

The ANOVA revealed a main effect of Intensity ($F(7,203) = 247.31$, $p_{\text{corr}} < 0.001$, $GG-\epsilon = 0.20$, $\eta^2_p = 0.90$), as the proportion of fear responses increased with the strength of emotional evidence for fear displays. The main effect of Gaze was also significant ($F(1,29) = 23.34$, $p < 0.001$, $\eta^2_p = 0.45$), as faces associated with an averted gaze were more often categorized as expressing fear as compared to faces associated with direct gaze. These two main effects were further characterized by an interaction between Gaze and Intensity ($F(7,203) = 7.50$, $p < 0.001$, $\eta^2_p = 0.21$), where the effect of gaze on the proportion of fear responses was smaller for strong emotion evidence. While no effect of Condition was found ($F(1,29) = 0.71$, $p = 0.41$, $\eta^2_p = 0.024$), the Condition by Gaze interaction was significant ($F(1,29) = 5.00$, $p = 0.033$, $\eta^2_p = 0.15$): the difference in proportion of fear responses between averted and direct gaze was higher under Threat than Safe contexts (see **figure 6-4A**). Neither the Condition by Intensity interaction ($F(7,203) = 1.79$, $p_{\text{corr}} = 0.13$, $GG-\epsilon = 0.59$, $\eta^2_p = 0.058$) nor the Condition by Gaze by Intensity interaction ($F(7,203) = 1.15$, $p_{\text{corr}} = 0.34$, $GG-\epsilon = 0.68$, $\eta^2_p = 0.038$) were significant.

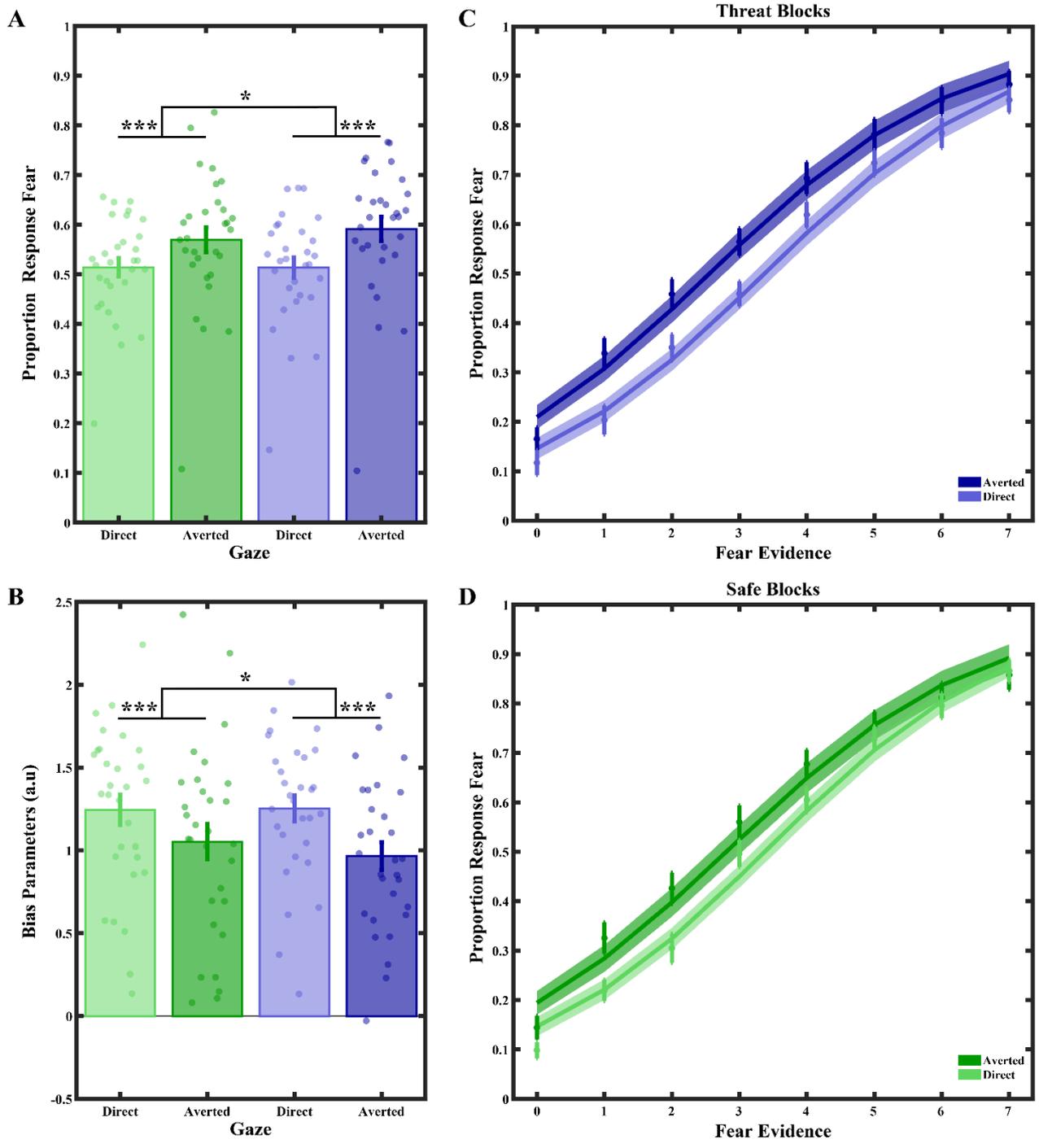


Figure 6-4. A. Proportion of response "Fear" during the categorization task. B. Estimated bias parameters for the winning model for each condition (Green = Safe and Blue = Threat) and for each gaze directions (direct: light, averted: dark). Error bars and points represent respectively standard errors and individual data. C and D. Psychometric functions representing the probability of responding 'fear' as a function of the amount of evidence of fear in the stimulus (0 = neutral to 7 = fear) for both contexts (threat: C, safe: D). The dots and associated error bars correspond to participant data (mean \pm standard error). The curves and the area in transparency respectively indicate the mean predictions and the associated error of the winning BIAS model. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; n.s. = $p > 0.05$.

Reaction Times

The ANOVA revealed a main effect of Intensity ($F(7,203) = 25.25$, $p_{\text{corr}} < 0.001$, $GG-\varepsilon = 0.36$, $\eta^2_p = 0.47$) related to the fact that participants got better as emotion evidence got stronger. The main effect of Gaze was also significant ($F(1,29) = 8.23$, $p = 0.007$, $\eta^2_p = 0.22$), as participants were slower to provide their responses for faces associated with an averted gaze as compared to a direct gaze. These two main effects were further characterized by an interaction between Gaze and Intensity ($F(7,203) = 5.27$, $p_{\text{corr}} < 0.001$, $GG-\varepsilon = 0.52$, $\eta^2_p = 0.15$), the difference in RTs between averted and direct gaze was stronger for weak emotion evidence. While no main effect of Condition was found significant ($F(1,29) = 0.44$, $p = 0.52$, $\eta^2_p = 0.015$), the Condition by Gaze interaction was found significant ($F(1,29) = 4.23$, $p = 0.048$, $\eta^2_p = 0.13$): the difference in RTs between averted and direct gaze was larger under Threat than Safe contexts. Neither the Condition by Intensity interaction ($F(7,203) = 0.54$, $p = 0.80$, $\eta^2_p = 0.018$), nor the triple interaction between Condition, Gaze and Intensity ($F(7,203) = 0.79$, $p = 0.60$, $\eta^2_p = 0.027$) were significant.

Influence of Trait anxiety on false alarm detection

The ANOVA performed on the proportion of fear responses when the faces conveyed no evidence for fear (neutral faces) revealed a main effect of Gaze ($F(1,28) = 10.40$, $p = 0.003$, $\eta^2_p = 0.27$) as the number of false alarms was higher for neutral faces associated with averted as compared to direct gaze. A significant interaction between Condition and Anxiety Trait was found ($F(1,28) = 6.019$, $p = 0.021$, $\eta^2_p = 0.17$). Similarly to what has been observed by Kavcioglu et al. (2019), the difference in false alarms between Threat and Safe contexts was positively correlated ($r = 0.42$; $p = 0.021$) with participants' trait anxiety scores. No further main effects or interactions were found to be significant (all p s > 0.13).

Mechanisms underlying increased recognition of danger-related cues

Bayesian fixed-effect model selection (Bayesian Information Criterion, see **Table 6-1**) showed that an increased decision bias to fearful faces with averted gaze explained the data better than a change in sensitivity, in both Safe and Threat contexts ($BIC_{\text{SafeBias}} = 599.7$, $BIC_{\text{SafeSens}} = 604.52$, $BF_{\text{safe}} = 11.1$; $BIC_{\text{ThreatBias}} = 559.53$, $BIC_{\text{ThreatSens}} = 564.4$, $BF_{\text{Threat}} = 11.4$).

	Null	Bias	Sensitivity	Complex
Safe	601.75	599.71	604.52	602.57
Threat	562.80	559.53	564.40	563.26

Table 6-1. Bayesian information criterion (BIC) for each context and each model candidate

The ANOVA on decision bias parameters (see **figure 6-4B**) revealed that this bias was significantly different between faces associated with averted and direct gaze (main effect of Gaze: $F(1,29) = 20.92$, $p < .001$, $\eta^2p = 0.42$), such that less evidence was required to answer fear for faces associated with averted gaze. While no main effect of Condition was observed ($F(1,29) = 0.28$, $p = 0.60$, $\eta^2p = 0.010$), the interaction between Gaze and Condition was significant ($F(1,29) = 5.88$, $p = 0.022$, $\eta^2p = 0.17$): less evidence was required to answer fear for faces associated with averted vs. direct gaze in Threat vs. Safe contexts. The subjective equality point (SEP) which corresponds to the strength of evidence where a participant provided the same proportion of fear and neutral responses was lower in Threat context ($\text{Mean}_{\text{SEP_Threat}} = 38.68\% \pm 3.4 \text{ SE}$) compared to Safe context ($\text{Mean}_{\text{SEP_Safe}} = 41.84\% \pm 4.2 \text{ SE}$) for faces associated with averted gaze (see **figure 6-4C and 6-4D**).

Influence of prosocial predisposition on the categorization task.

To evaluate if a prosocial temperament could explain part of the variance in our measures of interest (proportion of fear response, RT, model parameters), we re-ran the above-described analyses with the scores of the SVO questionnaire as co-variable. No significant interaction were observed (all the p s > 0.33 , see **Tables S6-16 - S6-18**).

Discussion study 2

We investigated how the experience of threat impacts the perception of fearful facial displays, a relevant social stimulus under threat. As mentioned above, fearful display can simultaneously convey the presence of danger in the environment and a need-for-help or social support signal, with gaze direction playing an important role in the arbitration between the two interpretations. Our results showed that, when participants are themselves under threat, faces associated with averted gaze are more often categorized as expressing fear, as compared to safe blocks. Threat context however does not affect participants' categorization of faces with direct gaze. Model-based analyses of the behavioral data revealed that in both threat and safe contexts, averted gaze direction bias the interpretation of facial expressions (whether neutral or fearful) in favor of the fear responses rather than increasing the perceptual sensitivity to the facial features diagnostic of fear, a shift of the decision criterion that was enhanced under threat. Altogether, our results suggest that under threat, participants are more prone to interpret facial displays as fear when associated with an averted gaze.

General discussion

When collectively exposed to a threat, the social signals emitted by surrounding others become highly relevant signals. Their facial expressions of fear and associated gaze orientation can notably provide crucial information about the presence and location of danger as well as of the social sources that need or can provide mutual support. Here, we assessed whether the processing of one of the two social meanings conveyed by fearful displays and gaze combinations is facilitated when observers are themselves under threat. Our results are twofold. First, participants appraised explicitly fearful faces with averted gaze as more clearly signaling the presence of a danger and fearful faces with direct gaze as more clearly communicating distress and need for help. Second, we reveal that participants interpreted facial expressions as expressing fear when associated with averted gaze, a bias which was found to be enhanced when they were in a sustained state of anxiety (under threat) as compared to in a safe state. Altogether, our findings indicate that threat enhances the processing of social signals conveying information about the presence and location of the danger, i.e. the combinations of fearful facial displays and averted gaze.

In both safe and threat contexts, participants displayed a bias to categorize faces with averted gaze as fearful. One explanation for this facilitated processing of averted-gaze fear combinations rests upon the shared signal hypothesis according to which emotion and eye gaze behavior are associated with behavioral motivational orientations to approach or avoid (Adams Jr & Kleck, 2003, 2005). Within this framework, fear and averted gaze are suggested to be both avoidance oriented, whereas direct gaze is approach oriented. When participants are requested to judge emotional expressions, they are more likely to judge it in a manner that is congruent with the behavioral motivational orientation associated with the perceived gaze direction (and vice versa when requested to judge the gaze direction – e.g. Lobmaier et al., 2008). According to Adams et al. (Adams et al., 2012), fearful displays signal that emitters have perceived a danger in their surrounding environment: when coupled with averted gaze, fearful displays provide clear information about the location of the threat, whereas when coupled with direct gaze, the conveyed signal is ambiguous as the emitter could be signaling a danger or a need for help (Im et al., 2017). This could explain why averted-gaze fear combinations are rated as more intense (Cristinzio et al., 2010; N'diaye et al., 2009; Sander et al., 2007) and negative (Ewbank et al., 2010), and perceived to signal greater danger than fear with direct gaze (present Study 1).

To our knowledge, the present study is the first to investigate how fearful faces are processed under threat contexts depending of gaze orientation. Here, participants' bias to categorize faces with averted gaze as fearful was enhanced in threat as compared to safe context, without impacting on the categorization of faces with direct gaze. Previous studies that explored how fearful faces are processed

under threat exclusively used faces displaying direct gaze. They show that sustained anxiety, induced using the threat-of-shock paradigm, prompts faster identification (Robinson, Charney, Overstreet, & Grillon, 2012), enhanced the processing of (Robinson et al., 2011), the attentional capture by (Lago et al., 2019; Robinson et al., 2016; Robinson et al., 2011) and the defensive mobilization to fearful faces (indexed by fear-startle reflex, Grillon & Charney, 2011). Bublatzky and colleagues (Bublatzky, Kavcıoğlu, Guerra, Doll, & Junghöfer, 2020; Kavcıoğlu et al., 2019) recently revealed that participants were biased to categorize faces as fearful in threat contexts (but not for other emotions, such as happy or angry faces). Similar findings were observed in children using the Trier Social stress test (Chen et al., 2014). Here however, by contrasting fearful faces with both averted and direct gaze, we provide evidence that participants' bias only applied to averted faces. This finding suggest that threat biases the processing of social cues towards those that are perceived to signal greater danger and/or provide information about the location of the danger.

By inducing sustained anxiety in participants, both the threat-of-shock (above-mentioned) and threat-of-screams paradigms appear to be efficient tools to reproduce threat-related biases observed in trait anxious individuals. Indeed, there are considerable evidence that individuals with high levels of anxiety show biased processing of threatening information (Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & Van Ijzendoorn, 2007; Hu, Gendron, Liu, Zhao, & Li, 2017; March, Gaertner, & Olson, 2017; White, Skokin, Carlos, & Weaver, 2016). Moreover, high trait-anxious individuals may be particularly sensitive to threat contexts, as they more frequently erroneously categorized neutral faces as fearful in threat compared to safe blocks (Kavcıoğlu et al., 2019, present experiment).

Differential threat processing observed in anxiety were suggested to be potentially driven by multiple cognitive biases: a bias in prior expectation for the likelihood of threat occurrence, a bias (weaker criterion) in stimulus evaluation and a bias in selective attention (e.g. Mogg, Garner, & Bradley, 2007; White et al., 2016). Among the past studies that investigated the impact of anxiety on gaze-emotion processing, it has been observed that high trait-anxious participants are more likely judged the gaze direction of fearful faces as looking away (Hu et al., 2017) and show an enhanced orienting to the eye gaze of faces with fearful expressions relative to other expressions (neutral, happy, anger, see Fox, Mathews, Calder, & Yiend, 2007). The findings, in association with the known difficulty of high trait-anxious individuals in disengaging attention from fearful faces (Leleu, Douilliez, & Rusinek, 2014), could provide a potential explanation for the present slower reaction times to categorize faces with averted as compared to direct gaze under threat-induced anxiety contexts.

While our model-based analysis clearly show that threat contexts lead to a weaker criterion in stimulus evaluation for faces with averted gaze, we believe that our specific findings for averted gaze cannot be explain by an expectation bias that the fear response was more likely to be correct. The present weaker criterion in stimulus evaluation for faces with averted gaze is consistent with results from our first study, i.e. participants' explicitly appraisal of faces (fearful and neutral) with averted gaze as more clearly signaling the presence of a danger, yet, future studies are needed to assess whether these two measures are correlated within the same group of participants. Interestingly, rapid presentation of the faces (<300ms) is associated with facilitated processing of averted-gaze fear combinations within the magnocellular pathway while longer presentation (>800ms) is associated with facilitated processing of direct-gaze fear combinations within the slower parvocellular pathway (Adams et al., 2019; Adams et al., 2012; Cushing et al., 2018). Moreover, the same team (Im et al., 2017) recently revealed that anxiety trait enhances fast magnocellular processing of averted-gaze fear combinations while disrupting parvocellular processing of direct-gaze fear combinations. These results suggest that both the chosen time of presentation (250 ms) and the anxiety manipulation could lead to the prioritized processing of fearful faces with averted gaze that convey a clear signal of danger. Distress signals may only be processed once the nature and the location of the danger has been identified.

Conclusion

Although exposure to threat are almost always social episodes, little is known about how social and stressful situations shape the way individuals process social signals emitted by surrounding others, as a function of the social meaning they convey. Our research not only shows that fearful facial display's message (danger vs. support offer or recruitment) depends on gaze orientation, but also that the perception of averted facial display as fearful is increased when the perceiver is herself experiencing a threat. Future studies should more carefully assess the affective state of the participants when examining emotional facial perception.

AUTHOR NOTES

Author contributions

M.B., G.O., E.M., J.G. and G.D. designed the study; G.O. and M.B. collected the data; M.B. performed the analysis with the assistance of G.O. and E.M.; M.B., G.D. and J.G. wrote the first draft of the manuscript. All authors reviewed and approved the final manuscript.

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Competing interests

The authors declare no competing financial interests.

GENERAL DISCUSSION

CHAPTER 7

SOCIAL COGNITION UNDER ANXIETY-INDUCING CONTEXTS

1-Summary of the findings

The neuroscience literature seldom includes the presence of others in models of defensive reactions to danger. By contrast, the social sciences (but also the ethological community) emphasizes the importance of others (their presence and potential recruitment) for individual survival. The fact that organisms are social in contexts of exposure to danger means we should renew our account of how we process threat information, when we are ourselves under threat.

Then, what happens to social cognition when we face a danger? Our approach was to investigate whether some of the mechanisms involved in emotional perception and joint action are modulated under threat. In order to perform collective action with others, we need to take them into account: we need to perceive the signals they conveyed and to adapt our action to them.

To place people in threat situations, we validated a tool able to generate anxiety episodes (a major component of threat) using unpredictable delivery of aversive distress screams, in order to investigate how it modulates action co-representation and perception of danger-related and distress-related signals conveyed by our congeners. Specifically, this dissertation detailed 3 studies designed to investigate how social cognition is transformed under threat:

- (1) the validation of the threat-of-scream paradigm by using skin conductance activity and subjective reports as proxy of the induced anxiety state (**Chapter 4**),
- (2) how the social Simon effect, a proxy of how much participants represented the action of their co-partners, is modulated under a threat-of-scream procedure (**Chapter 5**),
- (3) how fearful faces, relevant social signals observable during a dangerous situation, are processed under a threat-of-scream procedure (**Chapter 6**).

Furthermore, we tried to understand why human social abilities are maintained (or not) under threat. To do so, we changed the social message of different contextual cues while assessing action and perception under threat. We assumed that the function of social cognition under threat could be inferred by how the action-perception loop is influenced by the presence of others and the modulation of the social signals they conveyed. We will detail for each study how these factors were experimentally operationalized.

1.1-Validation of the Threat-of-Scream

To investigate the modulation of socio-cognitive functions under threat in a lab-controlled environment, through an ethical and easy way, we validated a new version the threat-of-screams paradigm (Patel et al., 2017, 2016). It is an experimental tool modulating anxiety in a within-subject design by delivering (threat blocks) or not (safe blocks) unpredictable low-intensity aversive screams. Importantly, we checked that the anxiety manipulation was efficient during one hour without habituation. Thus, we assessed the skin conductance level (SCL), used as a proxy of physiological anxiety, on 26 participants and their subjective reports of anxiety during threat and safe blocks. We observed that both SCL and subjective reports increased when participants were exposed to 70dB aversive distress screams compared to when they were in safe blocks. The physiological increase was constant through time while participants reported to be less stressed at the end of the experiment compared to the beginning. These results were replicated in a second group of 33 participants. Interestingly, emotion coherence was found in both groups, as an intra-individual correlation between our two anxiety measures was revealed. However, the anxiety trait of participants did not interact with any results previously revealed in this study. Altogether, this suggests that the threat-of-screams paradigm is an efficient tool to manipulate participant feelings of being threatened which appears by a robust physiological and subjective emotion episode.

1.2-Action co-representation under threat

Successful social interactions require integrating information from others while being able to distinguish them from our own representation (Milward & Sebanz, 2016). Using the Social Simon Task (Sebanz et al., 2003) under a threat-of-scream procedure, we explored whether self-other integration was shut down, maintained or boosted under threat. To best explain the incentives behind potential changes in action co-representation under threat, participants performed the task either with a second threatened participant (N=40) or either with a safe participant (N=38). First, results showed that Social Simon Effect were not significantly different when both participants were together under threat or under safe blocks. Second, the Social Simon Effect was higher when only one participant was threatened in co-presence with a safe partner. Finally, to examine the involvement of sharing the experimental room with a second participant during threat-anxiety inducing context, a third group of participants performed the classical version of the Simon task (one participant responsible for the two-colored cues) with alternating threat and safe blocks. Interestingly, we observed a phenomenon akin to social buffering, as subjective reports of anxiety and skin conductance level were together lower when the task was performed with a second participant than alone. Altogether, these results suggest that participants benefited from the presence of others as it reduced their anxiety. Also, co-

representation is maintained when participant felt threatened, confirming that social cognition is still engaged under a threat-of-scream procedure. Interestingly, we observed that co-representation is increased under threat when one participant is near of a safe one. This effect may be explained by representing the safe participant as an available resource of help. Under this interpretation, the function of co-representation could be to recruit social support (notably when we feel threatened).

1.3-Perception of fear emotional displays under threat

When human-beings face a threatening situation, they are surrounded by different kinds of source of information (Haghani et al., 2016). The detection of threat and relevant safety cues in our environment is crucial for individual's survival as these clues allow us to choose the most appropriate defensive responses (Davidson et al., 2004; Öhman, 2009; Öhman & Mineka, 2001). One major social signal conveyed under threat are fearful emotional displays. Fearful emotional displays convey two signals depending of gaze orientation: averted gaze informs on the position of a potential danger while direct gaze is associated with signal of distress, and potentially seeking support from others (these two spontaneous interpretations were confirmed by an online experiment we conducted, which is detailed in **Chapter 6**). Using a Fear-Neutral categorization task combined with a threat-of-scream procedure, our results suggest that being threatened favors the detection of danger-related signals, without changing our perception of distress ones. Model-based analyses of the behavioral data revealed that in both threat and safe contexts, averted gaze direction biases the interpretation of facial expressions (whether neutral or fearful) in favor of the fear responses, a shift of the decision criterion that was enhanced under threat. We proposed that, under threat, participants are more prone to interpret facial displays as fear when associated with an averted gaze, a bias which may be useful to maximize safety.

1.4-Conclusion of the findings

During this Ph.D. project, we first succeeded to validate a psychological toolkit to investigate how the sense-of-being threatened, associated with an anxiety episode (physiological and subjective manifestation), impact socio-cognitive mechanisms. We therefore used this tool to investigate how being under threat impact two crucial functions for human interactions: representing others' actions and processing of non-verbal signals conveyed by human faces. First, our results showed that social cognition is still at work under threat. Thus, it is relevant to integrate social cognition when modelling human defensive reactions. In both studies, participants were particularly sensitive to danger-related cues and the presence of safety partners. We proposed that participants' prioritization of these contextual cues can be explained by the fact that they possibly bring auto-protection advantages (i.e. maximizing survival). Obviously, our experiments are not without limitations which challenge this

proposition. In addition, social cues associated with distress signals conveyed by others seemed to be processed similarly in threat and in safe contexts. Altogether, this dissertation supports the idea that social cognition is rather transformed than shut down under threat. We speculate that one possible function of social strategies under threat may be to serve self-preservative motives, as described in the haunted house study led by Dezechache et al. (Dezechache et al., 2017), even if more direct evidence is needed to clearly identify the role of social cognition under threat.

2-The threat-of-scream paradigm: a relevant tool to induce anxiety

In the context of this thesis, we wanted to focus on individuals' behavior in threatening situations, i.e. measuring the modulation of socio-cognitive functions during time-periods in which participants were exposed to danger compared to time-periods in which they felt safe. Research on the anticipation of electric shock showed that under threat, the body (through physiological manifestation (Bradley et al., 2018)) and our cognitive system (i.e. attention, detection (Balderston et al., 2017)) prepare themselves to react quickly (i.e. behavioral mobilization for urgent situation to avoid specifically aversive stimuli (Grillon & Charney, 2011; Mkrtchian, Roiser, & Robinson, 2017; Sarigiannidis et al., 2020)). The threat-of-shock paradigm (Robinson et al., 2013) seemed to be the most relevant starting point. As explained in Chapter 4, we worked with low acoustical intensity (instead of electric shocks or loud sound (Patel et al., 2017, 2016; Robinson et al., 2013) to ensure that it did not present any risk to the participants. Indeed, it is difficult to evaluate the acoustic sensitivity of each participant and to identify if they have already been exposed to loud sound during the last 24 hours. Our threat-of-scream validation offers two original controls. First, about screams intensity: screams would be more suitable for long experimental designs than electric shocks but they induce anxiety at lower intensities. Moreover, the screams we presented were between 10 and 35 dB below the sound level usually used in the literature, which could lead to significant differences in results. Second, we propose to check whether the induced anxiety is long lasting (i.e. one hour).

2.1-Validation of the Threat-of-Scream paradigm: from 60 to 200 participants

In Chapter 4, we described the validation of this methodological tool through two groups of approximately 30 participants: it is able of inducing an emotional episode which takes the form of a prolonged activation of the autonomic nervous system (without statistical reduction over time) and an increase in subjective anxiety (which seems to decrease slightly over time). The anxiety scores obtained after the publication of the Threat-of-Scream validation may help us to confirm the validity of this tool as well as its limitations. Throughout three studies, 207 participants performed a cognitive task mixed with a Threat-of-Scream procedure. These participants can be divided into two groups.

Firstly, 127 out of 207 performed it by being alone in the room, either doing an action-decision task in the presence of emotional expression (fear/anger), a Simon task, or doing a categorization task of fear emotion. Out of these 127 participants, skin conductance level (SCL) has been measured on 97 of them, while subjective reports of anxiety, preoccupation and aversiveness scores were collected from all participants. Descriptively, 81% of them reported being more anxious in threat blocks than in the safety ones and 82% of them showed more electrodermal activity in threat relative to safe blocks. There was a small but significant positive inter-individual correlation between the two variables ($r=0.33$, $p < 0.01$). No effect of time on skin conductance activity was observed in the different studies. Nevertheless, an habituation trend on subjective reports was observed in a first one-hour study, significant in a second one-hour study but not significant in a third one-hour and on a thirty-minute study. Finally participants described screams as moderately aversive (median of 4 out of a scale of up to 10) but reported being particularly preoccupied by the possibility that a scream would be delivered during threat blocks (median of 6).

Then, 78 participants carried out a Social Simon task in which they had to share the experimental box with a second participant. The electrodermal activity was recorded on 77 of them and once again the subjective reports of anxiety, preoccupation and aversiveness scores related to scream delivery were collected from all the participants. As described in Chapter 5, a phenomenon akin to social buffering was observed. When two subjects were in the same room, only 69% of them showed more electrodermal activity in threat relative to safe blocks, even if 76% of them reported being more stressed in threat compared to safe blocks. Consistently, even if paired participants rated the aversiveness of screams similarly to single participants (median of 4), the latter reported being less concerned about the possibility that a scream would be delivered (median of 4).

Taken together, these results suggest that this paradigm is effective for inducing anxiety in participants, which is characterized by: (i) an over-activation of the autonomic nervous system (SCL) that appears to be stable over time and (ii) a subjective experience reported as moderately negative but potentially prone to habituation. Furthermore, the observed social buffering effect induced by the presence of a social partner can be identified as piece of evidence (perhaps more indirect) of the induction of a state of anxiety that has been attenuated.

Also, even though anxiety induction by electric shocks has been used to investigate many cognitive functions, the use of sound has only been tested on two cognitive functions: verbal working memory (Patel et al., 2017, 2016) and cognitive control in response to emotional stimuli (Cohen et al., 2016). Moreover, several studies suggest that sympathetic activation induced by acoustic stimuli is weaker

than the activation induced by shocks (Ferry & Nelson, 2020.; Glenn, Lieberman, & Hajcak, 2012). One of the main reasons is that, while electric shocks represent a real threat to physical integrity, sound is a more indirect threat because it signals the presence of danger rather than being a danger itself, probably by possessing features that are been selected to maximize aversiveness (via sound roughness) to our auditory system (Arnal et al., 2015).

Moreover, the sounds we presented were of lower intensity than those used in previous studies. We wondered whether the level of anxiety induced by distress screams would be sufficient to induce behavioral changes (i.e. modulate cognitive functions). Randomly presented at 70dB, the distress screams proved to be effective in modulating co-representation: in fact, it depended on whether the participant shared the same emotional state as his or her partner or not. Moreover, we were able to replicate several results obtained by the team of Bubkatzky et al. (Kavcioglu et al., 2019; Schellhaas et al.) that used electric shocks: an increased bias in identifying faces of fear, an increase in false alarms in individuals with anxious temperaments when they are in threat blocks as well as an absence of threat effect in face storage (**see Appendix**). All these results indicate that the induced level of anxiety was high enough to modify participants' behaviors, as much as when an electric shock was used. We thus recommend inducing anxiety with low-intensity screams instead of electric shocks (which may be particularly useful for developmental studies).

2.2-Limitations of the Threat-of-Scream paradigm

As discussed in the Chapter 4, one of the empirical limitations of this method is that it may not be influenced by participants' predisposition to anxiety. Under threat-of-shock paradigm, very few studies reported having included self-reporting scores in their analyses. Under the Threat-of-Scream paradigm, the study led by Patel et al. (Patel et al., 2017) showed a variation of the startle reflex when splitting participants into high versus low anxiety group using responses at the STAI-Trait auto-questionnaire. In the studies reported in this dissertation, participants systematically completed a series of questionnaires assessing their predisposition to anxiety: STAI-T (all studies), Liebowitz Social Anxiety Scale (LSAS, studies 2 and 3) and Intolerance of Uncertainty Scale (IUS, study 3). Nevertheless, as already mentioned in the Chapter 4 discussion, our studies separately included cohorts that were probably too small to identify inter-individual differences.

However, we obtained STAI-T Scores for 207 participants, 176 of them having analyzable electrodermal response. We checked whether, when grouping all our participants together, inter-individual variability in trait anxiety could explain the sensitivity to our anxiety manipulation. To do so, we performed linear regressions including anxiety trait, duration of experiment and presence of a

co-partner, and we modeled separately the skin conductance level and subjective reports of anxiety (see Table 7-1). We observed that anxiety trait does not explain the variance of our two variables of interest (SCL and subjective reports), while co-presence explains both variables. The time factor seems to be important for modelling subjective responses, but not physiological ones. Overall, these linear models seem to confirm the absence of an anxiety trait effect, the presence of social buffering when the experiment is shared, and a subjective (but not physiological) habituation of participants to the procedure.

To conclude, this absence of anxiety trait effect does not seem to be explained by the size of our cohorts. This lack of effect can be explained by: first, the non-inclusion of individuals with a score at the STAI-T above 60 eliminates the most anxious participants and therefore perhaps the most sensitive to our manipulation; second, the generation of an anxiety episode may be sensitive only to certain components of anxiety temperament. New studies using the Threat-of-Scream paradigm should keep including LSAS and IUS questionnaires to investigate whether other sub-components of anxiety trait promote our anxiety induction.

	STAI-Trait		Time		Co-presence	
	β	p	β	p	β	p
Skin Conductance (N = 176)	0.021	0.25	-0.19	0.18	-0.98	0.018
Subjective Anxiety (N = 207)	0.019	0.90	-3.11	0.003	-14.13	> 0.001

Table 7-1: Coefficients and p-values for the linear regressions on Skin Conductance Level and Subjective reports of Anxiety including anxiety temperament (STAI-Trait), the duration of the experiment (Time) and the social context (Co-presence of others or not) as regressors.

2.3-Future directions for the Threat-of-Scream paradigm

Future directions can be proposed to pursue the validation of the threat-of-scream procedure. First, if some aspects indicate that anxiety induction using distress screams seems to be comparable to electric shock induction, more direct evidence must be provided. In the same way that shocks and screams have been compared for the NPU paradigm (Ferry & Nelson, 2020), investigating these two anxiety methods in a within-subject design could be a relevant way to compare them. Furthermore, the literature on experimental anxiety usually records the startle reflex (instead of the SCL) since it is a more accurate marker for measuring anxiety. Replication with this biomarker can be expected. Also, Aylward and Robinson (Aylward & Robinson, 2017) recently proposed the Sustained Attention to Response Task (SART) as an interesting methodological tool to provide a non-subjective measure to evaluate the generated anxiety. They showed that the random presentation of electric shocks can

reliably modify participants' responses by improving their detection rate of distracting stimuli and by slowing down reactions to target stimuli as previously described in the literature. But more importantly, this effect is consistent through the test and retest of participants several times over the following months. Insofar as Aylward and Robinson's code is accessible online, we consider verifying whether such consistent results can be obtained with our distress screams.

3-Social cognition and defensive reactions under threat

During this dissertation, we try to propose a motivational framework to predict social actions that take place in situations of danger (such as those observed during Bataclan Paris attacks). Based on these observed behaviors, two presuppositions can be made: (i) the mechanisms essential to social interactions, such as the perception of socio-emotional signals and the coordination of action, are still at work under threat and (ii) that the function of these mechanisms may first favor the detection of individuals who can provide social or physical support and then facilitate the implementation of collective action with them. A corollary of such assumptions is that social actions only take place if it is the best strategy to adopt in a given context. In this chapter, we will first discuss (cautiously) how the results obtained support these presuppositions and how they might be aligned with the currently proposed taxonomy of defensive responses under threat.

3.1-Social Cognition is not shut down under threat

The results obtained in our studies are in favor of a maintained capacity to handle social stimuli in threatening situation. Firstly, when participants performed a task in pairs compared to when they are alone, the anxiety markers we measured decreased (subjective anxiety reports, preoccupation score due to the possibility that a scream will appear and skin conductance level). This suggests that sharing a threat context influences (i) our subjective experience of stress and (ii) our body's readiness to respond to danger. Based on Central Fear Generator model (Fanselow & Pennington, 2018), physiological and subjective stress are coupled with the behavioral response elicited by an emotion episode. Of interest, the review of the literature carried out in Chapter 2 highlighted a strong relationship between (i) anxiety level and perception, (ii) anxiety level and value attribution to contextual clues and (iii) anxiety level and decision making/action choices. Consequently, it is very likely that the presence of others will impact the type or the intensity of our defensive reaction⁴.

⁴ It is important to note that this model is currently under debate: it has been proposed by LeDoux & Pine (LeDoux & Pine, 2016) that the subjective and conscious response of fear and anxiety are underpinned by circuits different from those involved in physiological readiness and behavioral response. In any case, our argumentation makes also sense using this second model as physiological modulation has been observed.

Moreover, the results we have obtained show first of all that the action plans of others are still taken into consideration in a threatening situation. Indeed, if we assume that the Social Simon Effect is a marker of co-representation, this mechanism does not seem to be interrupted when we feel threatened. To our knowledge, this is the first study investigating the cognitive processes involved in joint actions in a sustained anxiety context. Our results suggest that individuals may predispose the cognitive resources necessary to initiate collective actions when a danger occurs. In line with the field studies, our results support the credibility of the disaster survivors' testimonies describing cooperative actions (leg-up or moving furniture), since the mechanisms necessary for these actions would be preserved. Second, similar to several studies reviewed in Chapter 2, the processing of social signals from others is also active in threatening situations. As a result, it is very likely that the cues communicated by our social partners will be taken into account to influence our action choices in situations of danger. To conclude on this first part, these results suggest the presence of others to play an important role in the way of behaving in threatening situations. Indeed, the presence of others can influence our anxiety level, be an important source of information and be at the origin of behavioral outcomes that cannot be achieved alone (i.e. leg-up).

3.2-Co-representation: an opportunity to recruit social support?

The study carried out by Dezechache and al. (Dezechache et al., 2020) pointed out that social action (i.e. performed with a social partner) could be planned for a wide variety of reasons: individual motives to ensure one's own survival, cooperatively for mutual benefit or in a totally altruistic way. Moreover, the implementation of these strategies appear to depend on the cost of these actions (i.e. being injured) or on the possibility of planning another strategy associated with a higher probability of survival. On the basis of these findings, we investigated reactions, particularly collective ones, within a motivational research framework, i.e. how mechanisms are modulated according to the cues' value (i.e. their instrumentalities) present in the environment.

As a first step, we investigated how our ability to integrate others' action plans into our own action plans is influenced by the presence of a social partner being threatened at the same time as us or not. Our results showed that co-representation (measured by the magnitude of the Social Simon effect) is particularly increased in a situation of threat when we are in the presence of a safe social partner. The co-representation mechanism seems to be sensitive to contextual variations in a situation of threat, as it has been observed in everyday situation (Iani et al., 2014; Ruys & Aarts, 2010). It is therefore appropriate to explore which ones influence this mechanism. We interpreted the increase of co-representation as the result of the presence of a social partner with resources to provide assistance.

This is in line with the view that our cognition aligns with that of individuals who can help us in a threatening situation. Interestingly, co-representation is not increased when individuals are safe but in the presence of a threatened co-partner. This result gives particular weight to the interpretation that co-representation function may be to recruit social support since individuals with potential resources to help do not integrate others' representations to a greater extent. Under threat, our cognition may be oriented toward other for self-preservation motives.

However, the interpretation that safe co-partners represents an available resource of social support remains speculative as different criticisms can be made. The first is that the Social Simon Task consists of two independent sub-tasks for each participant. The performance of one player does not influence the performance of the other and does not influence the probability of receiving a scream. Furthermore, participants were forbidden to communicate with each other. As a result, our experimental setting did not allow any form of assistance between participants. Based on that, it is very unlikely that participants believed they can receive assistance during the experimental session. Nevertheless, many effects in social cognition are based on beliefs that can be very easily induced. For example, presenting an image of a gaze is sufficient to induce a belief of being observed and to impact many cognitive functions (Conty, Gimmig, Belletier, George, & Huguet, 2010; Haley & Fessler, 2005; Hazem, Beurenaud, George, & Conty, 2018; Hazem, George, Baltazar, & Conty, 2017). This belief of receiving help from a safety partner is for us the most possible interpretation of our data. However, while fear and gaze combinations were assessed online in order to associate them with a particular social message (danger or affiliation), we had no explicit verbal clues from participants about how supportive their safe partner is perceived. Future research should help to confirm this interpretation.

3.3-Is minimal safety required to perform collective action under threat?

The field literature repeatedly emphasized that the riskier the situation, the less social the strategy is reported. The maintenance of social norms declines when survival rates are low (Frey et al., 2010) and the number of supportive behaviors decrease if the risk of being injured or the probability to reach safety by escaping are high (Dezecache et al., 2020; Vieira, Schellhaas, Enström, & Olsson, 2020). Consistently, laboratory experiments showed evidence that participants' choices are highly driven by risk-aversion mechanisms (Mkrtchian et al., 2017; Robinson, Bond, & Roiser, 2015; Robinson, Overstreet, et al., 2013). The main conclusion that can be drawn is that collective action is not a 'by default option' as it is preferred only when a minimal sense of safety is met.

The results of our categorization task may be in favor of this hypothesis. We observed that, under threat, anxiety did not modulate the perception of direct fearful face (predominantly associated with a

need for help/affiliation social message). On the contrary, participants' behavior revealed that, under threat, the decision criterion to detect fear is lowered when faces are associated with an averted gaze (predominantly assessed as a danger-related signal). In this experimental context, the source of danger is never provided to participants. One potential explanation of those results is that, to behave in an adaptive way and to reach safety, it is important to identify where the source of threat is. Fearful face with an averted gaze can be particularly relevant as it provides information on threat localization (Hadjikhani et al., 2008). Our results may suggest that when they threatened, participants prioritize social cues that provide information about the source of threat; i.e. impact our appraisal of socio-emotional cues to meet a minimal sense of safety (i.e. secure our own survival in a first step). However, this remains speculative and further investigations are needed to confirm the role of the prioritization of danger-related cues.

3.4-Statistical limitations of our interpretations

Caution should be exercised with some of the interpretations proposed above as statistical limitations can be identified in this work. The literature detailed in the theoretical part of this dissertation seems to strongly suggest that social cognition would be at a minimum maintained, even boosted to potentially set up collective actions. The literature led us to two main hypotheses:

- 1) the mechanisms investigated could be intact (Hypothesis 0, our natural socio-cognitive capacities would remain the same),
- 2) the mechanisms investigated could be increased (Alternative Hypothesis H1, others would be particularly salient in threatening situations).

According to our operational hypotheses, they assumed that the non-rejection of H0 would be informative (i.e. to discuss and conclude on non-significant p-value). It is important to keep in mind that a non-significant test does not allow us to formally conclude that there is no difference, even if this hypothesis is one of the possible ones. Our two interpretations "co-representation is maintained" (i.e. no difference of co-representation when threat is shared by both participants) and "affiliation signals are similarly processed" (i.e. no impact of threat on direct fearful face detection) under threat can't be totally conclusive. We are aware of this limitation. Bayesian statistics are programmed in order to better interpret our results.

3.5-Sociality in the taxonomy of defensive reactions

Studies described in this manuscript have only been able to investigate two mechanisms and their modulation under threat, and only in presence of a single contextual factor (shared threat or gaze direction). While these results feed our understanding of sociality in situations of danger, the level of

evidence remains too low to provide a theoretical framework that would allow us to clearly predict reactions of individuals in threatening situations. Nevertheless, a few lines of thought can be opened up.

A particularly interesting starting point for thinking about the influence of others on defensive reactions would be Oliveira and Faustino's opinion paper "Social information use in threat perception" published in 2017 (Oliveira & Faustino, 2017). Based on collective defensive reactions observed in animal kingdom, the authors proposed a unifying conceptual framework describing the influence of three different social mechanisms on threat responses (see **Table 7-2**). Thanks to the perception of social information conveyed by others, a defensive reaction can be either initiated or enhanced through respectively social contagion (i.e. the perceived signals conveyed by others alarm individual of a missed threat detection) or social facilitation (i.e. the perceived signals from others confirmed individual's detection of threat). Also, this defensive reaction can be decreased through social buffering (i.e. social signals which help to cope with stress). Ultimately, the presence of others (compared to the same situation but alone) could, depending on the shared social signal, shift our position on the axis defining 'threat intensity' parameter in the models of individual reactions presented in Chapter 1.

Presence of social partners?



Direct Threat Information	Social Information (indirect threat)	Threat Response	Social Phenomena
+	0	++	Individual Threat Response
+	-	+	Social Buffering
-	+	+	Social Contagion
+	+	+++	Social Facilitation

Table 7-2. Influence of the type of social information on threat response. Direct threat information corresponds to the threat information perceived by the individual. Social information represents the threat signal conveyed by social partners. Individual threat response is the combination of both information. Depending of the social cue conveyed by others, it can be initiated, amplified or attenuated the initial threat defensive response. Adapted from Oliveira and Faustino (2017).

To what extent, our results might contribute to the model we presented at the beginning of the manuscript? First of all, it is important to consider where we are in the spatio-temporal axis of this model when the participants carry out a threat-of-scream procedure. This axis is subdivided into four phases (see **Figure 7-1**): safe, pre-encounter threat, post-encounter threat and circa-strike threat. During the threat blocks, the participants know that they can receive an aversive stimulus at any time: they are in anticipation of an approaching threat. Consequently, participants would be in the post-encounter phase (i.e. the threat is present but not attacking). It is possible that, during screams delivery, participants enter and then leave the circa-strike phase. It would be very interesting to investigate later

whether the transitions between these two states (post-encounter/circa-strike) were involved or even necessary in the emergence of the effects found in our studies or not. Regarding safe blocks, it could either put participants in a safe state (i.e. as close as possible to everyday social cognition), or either in an intermediate state (i.e. pre-encounter where threat is not present but the probability of encountering it in the near future is high). This second proposition is plausible insofar as the safe blocks precede a future threat block.

Our results showed that the Threat-of-Scream paradigm effectively induced an anxiety episode. The literature defends this state induces a hypervigilance phenomenon which should favor risk-assessment behaviors (Blanchard, Blanchard, Tom, & Rodgers, 1990). Detecting salient signals in the environment would then be possible. According to our data and the observations/testimonies of disaster survivors, our social partners would play an important role in threatening situations. We propose that the detection of conspecifics under threat would generate three possible reactions. The first would be a decrease in our stress response through social buffering. This phenomenon would consequently reduce our perception of threat intensity. This reduction in intensity would, in turn, influence human potential behavioral outcomes. Second, the social signals conveyed by others can provide information on the ongoing threat: for example, fearful faces we studied in Chapter 6 provide information on both threat intensity (through the emotional intensity displayed) and its position (communicated by gaze direction). This information would allow individuals to disambiguate the context in order to maximize its survival. Following this, a strategy can be put in place: either individual or collective.

The safety hints present in the environment could help to disentangle between these two main types of strategies. If the assumption we made based on Dezechache et al's studies (2017, 2020) are correct, the presence, for example, of an easily accessible emergency exit should favor individual strategies (i.e. to flee). Conversely, the availability of social partners who can be helpful in restoring our homeostasis (i.e. either by reducing our anxiety or by helping us to escape the threatening situation) should favor collective strategies. This would manifest through the organization of collective actions, which requires co-representation of our social partners (as long as a minimal sense of safety is met). These actions could ensure group escape (i.e. leg-up) or the implementation of collective attacks (as observed in ethology studies (Caro, 2005)).

This proposal offers meaningful links between the different key parameters from the models of individual reaction to threat (i.e. ambiguity, threat intensity, temporal distance to threat) and those resulting from the investigation of sociality in threat situations that we have defended (social buffering, social cues, instrumental cues, collective action/co-representation). Although it undoubtedly remains

speculative, it encourages interdisciplinarity by imagining bridges between the findings of neurosciences, cognitive psychology, ethology and the social sciences.

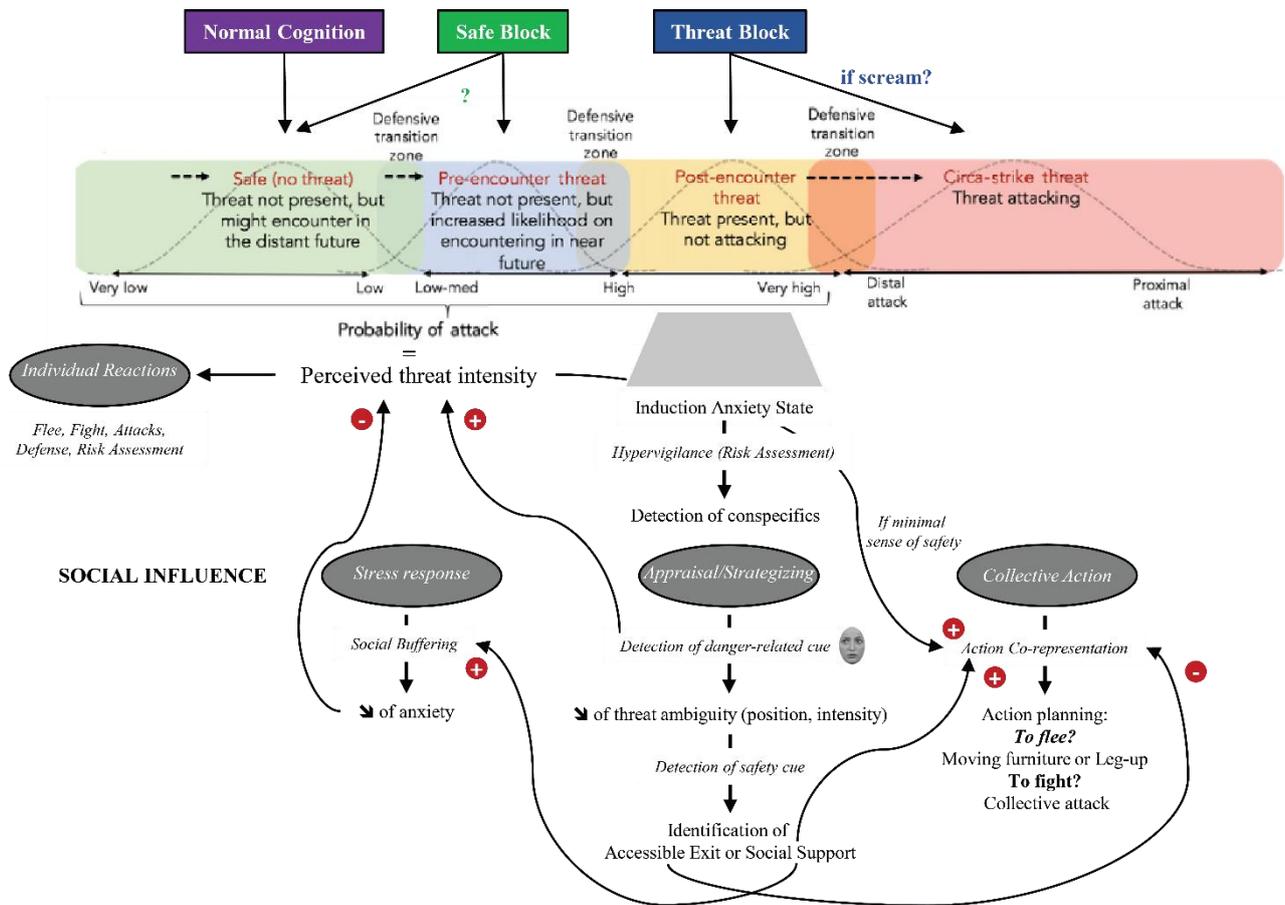


Figure 7-1. Sketch of a unifying model between the previously defined taxonomy of human defensive reaction, the assumptions raised by field studies and the results we obtained. Threat-of-scream allowed to investigate individuals' reaction during post-encounter phase. We proposed that the detection of social partners under anxiety can influence individuals' stress response, our decision making, and the organization of collective actions. Presence of others can modulate ambiguity and intensity factors and consequently impact future action planned under threat which can be collective or individual depending of external environmental factors (possibility to escape, resources of social partners, sense of safety). Adapted from Mobbs et al. (2020).

4-Perspectives and future directions

In order to keep understanding how social cognition is modified in threatening situations, several directions can be undertaken. Here, we propose five future directions to complement the studies we have conducted. Firstly, we will propose solutions to confirm our interpretation about the modulation of the Social Simon effect under threat. Secondly, it is possible to pursue the investigation of the self-other balance in threatening situations by studying other phenomena of co-representation. Then, in order to predict all social behaviors in threat contexts, it is essential to vary the experimental parameters that allow us to mimic these situations in the laboratory. Next, we will question the role of inter-individual variability in the emergence of these social strategies. Finally, we will remind that the understanding of social cognition under threat is only possible in an interdisciplinary context.

4.1-Collective action and social support

As explained above, the assumption that the increase of co-representation in the Non-common group is explained by the fact safe co-partners represents an available resource of social support is questionable. To overcome this limitation, two different alternatives can be developed. The first would be to reinforce the belief that the second participant can provide assistance or not. Of interest, Doerrfeld et al. (Doerrfeld et al., 2012) revealed that the perception of clues that the co-partner with whom the participants had to perform a motor task was injured, impacted future action planning. Similarly, a recent study (Low et al., 2020) showed that the representation of participants' beliefs can be influenced by the perception of others' physical constraints (preventing them from performing some movements). These two studies seem to indicate that simple visual cues are powerful to modify participant's beliefs about the state of their social partners, since the observer's motor system tracks other people's resources to act. Consequently, our study on Social Simon Effect in a threatening situation could be replicated by performing the task in the presence of a confederate who would be injured/constrained vs. healthy/unconstrained.

The other alternative is to work with joint action tasks in which the actions of each participant are mutually dependent to achieve a common goal. In the study led by Torok et al. (Török et al., 2019), participants can choose between two pathways that allow them to reach a target (see **Figure 7-2**). They can choose to perform a movement that is either low-cost for them but more costly for the partner or vice versa. This design makes it possible to assess more explicitly whether in threatening situations, participants choose more often strategies that minimize their own costs (self-preservation tendency) or those of their partner (pro-social tendency). With the same aim, Le bars et al. (Le Bars, Devaux, Nevidal, Chambon, & Pacherie, 2020) designed a joint action task to test how action coordination takes place when the cost-benefit ratio of actions differs for each player. In this task, the participants have to coordinate their actions in order to move a cursor in a given time from the center of the screen to one of the four possible targets located in each corner of the screen. Each target is associated with a payoff matrix for each player (fair, unfair or null according to the trials). One of the two partners can only move the cursor vertically, while the other can only move it horizontally. Depending on how the trials are organized, if each player decides to maximize his or her own winnings, the target may tend towards the same option or towards a null option (as shown at the **bottom right in Figure 7-2**). This task would be particularly elegant for investigating in a threat context, the real-time human motor coordination according to the consequences of one's actions for oneself and others.

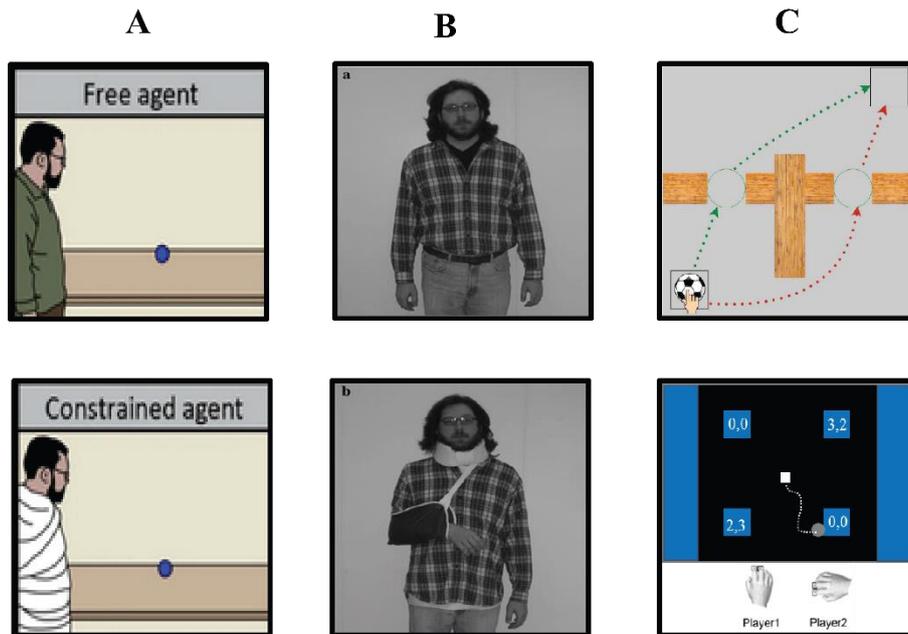


Figure 7-2. Future direction to investigate the influence of resources availability on joint action task under threat. Task can be performed using constrained (A) or injured confederate (B) or can be designed to study joint action between dependent actions (C). Adapted from: (A) Low et al. (2020), (B) Doerrfeld et al. (2012) and (C) Torok et al. (2018) & Le bars et al. (2020).

4.2-Alter-centric cognition and self-other balance

In order to better understand the organization of social behaviors in situations of danger, an efficient strategy would be to pursue the investigation of alter-centric cognition when we feel threatened. In the present project, only one form of co-representations was investigated: motor representations. However, in order to be coordinated spatially and temporally with actions of others, other representations are also necessary (Constable et al., 2015; Obhi & Sebanz, 2011; Sebanz & Knoblich, 2009): the representation of other people's goals and intentions, the representation of visual information of the things that others perceive at a given moment or the representation of the way they are reasoning. The amount of evidence on the relevance and the automaticity of these processes in our social interactions as well as the level of complexity of these representations have increased considerably over the last few years (Capozzi, Cavallo, Furlanetto, & Becchio, 2014; Obhi & Sebanz, 2011; Surtees, Apperly, & Samson, 2016). For example, individual represent features (Elekes, Varga, & Király, 2016) and position of objects (Cavallo, Ansuini, Capozzi, Tversky, & Becchio, 2017; Costantini, Committeri, & Sinigaglia, 2011; Freundlieb, Kovács, & Sebanz, 2016) or semantic of words (Freundlieb, Kovács, & Sebanz, 2018) perceived by their partners as well as the parameters of their actions, such as deviation (Curioni, Vesper, Knoblich, & Sebanz, 2019; Schmitz et al., 2017), velocity (Vesper, Schmitz, & Knoblich, 2016; Vesper, van der Wel, Knoblich, & Sebanz, 2011) or order of movements (Schmitz, Vesper, Sebanz, & Knoblich, 2018).

What happens to all these capabilities under threat? The Threat-of-Scream paradigm is a tool that can be applied to the large range of tasks already designed and available in the literature to study self-other integration. This tool therefore opens up a field of immense possibilities in terms of collaboration and future research directions. As an example, in spring 2021, a collaboration with the Dr. Romand-Monnier will begin to investigate how visual perspective-taking (Samson et al., 2010) is modified in threatening situations; with the same idea that an increased altercentric bias would be associated with a cognition oriented towards others. Also, another self-other component which has been relatively ignored in this manuscript and which it would be essential to investigate is the peripersonal space. Peripersonal space (PPS), is defined as the space where physical interactions between the body and the external world occur (Serino, 2019; Vieira, Pierzchajlo, et al., 2020). It has been shown that the PPS representations were modified by the social context and the presence of the tool in the environment (Holmes, Calvert, & Spence, 2004; Pellencin, Paladino, Herbelin, & Serino, 2018). PPS extended up to include the space around cooperative co-partners but not competitive ones (Hobeika et al., 2019; Teneggi et al., 2013). In addition, it has been observed that individuals' PPS is modulated when they perceive a threat inside the PPS of a social partner, resulting from the embodiment of others' perception of threat (Fossataro et al., 2016). Of interest, PPS has been defined as "the space in which the world can become threatening and dangerous, requiring protective behaviors" (de Vignemont, 2018; de Vignemont & Iannetti, 2015). Consequently, we believe that PPS boundaries can be modulated to protect others or to recruit social support (if others is perceived as a relevant safety cue). The investigation of this mechanism would then be particularly aligned with the issues highlighted by this dissertation.

4.3-Socio-cognitive mechanisms and threat parameters

As pointed out above, using "Threat-of-Scream" paradigm, only a small part of the spectrum of defensive behavior is studied. In this paradigm, participants shift from one state to another (and vice versa): a state of safety or a state of anxiety caused by the anticipation of a potential threat⁵. Many factors remain to be studied in order to understand how social cognition is transformed in all possible situations of danger we may encounter. As a reminder, Blanchard et al. (Blanchard & Blanchard, 2008) have identified five parameters modulating our defensive actions in situations of danger: distance to the danger, intensity of the threat, ambiguity about the source of the danger, the possibility to escape or to hide. Dezechache et al. (Dezechache et al., 2020) having observed that supportive behavior decreased if individuals are under fire and with the possibility to escape, it would be relevant to

⁵ As explained above, it is possible that during scream delivery, participants may go from a state of anxiety to a state of fear. The role of this transition in the observed phenomena will have to be monitored in future studies.

evaluate how threat intensity and the presence of an emergency exits influence the perception of affiliation signals. One possibility would be to have a group of participants perform a dot-probe task between two categories of stimuli (see **Figure 7-3**), socio-affiliative signals vs. signals indicating an emergency exit, while varying the intensity of the threat (absent, weak or strong) by modulating the intensity of screams (still below the danger to audition threshold). If the observations in the Dezechache et al. study are correct, then the attentional bias for exit signals (relative to social signals) should increase with threat intensity.

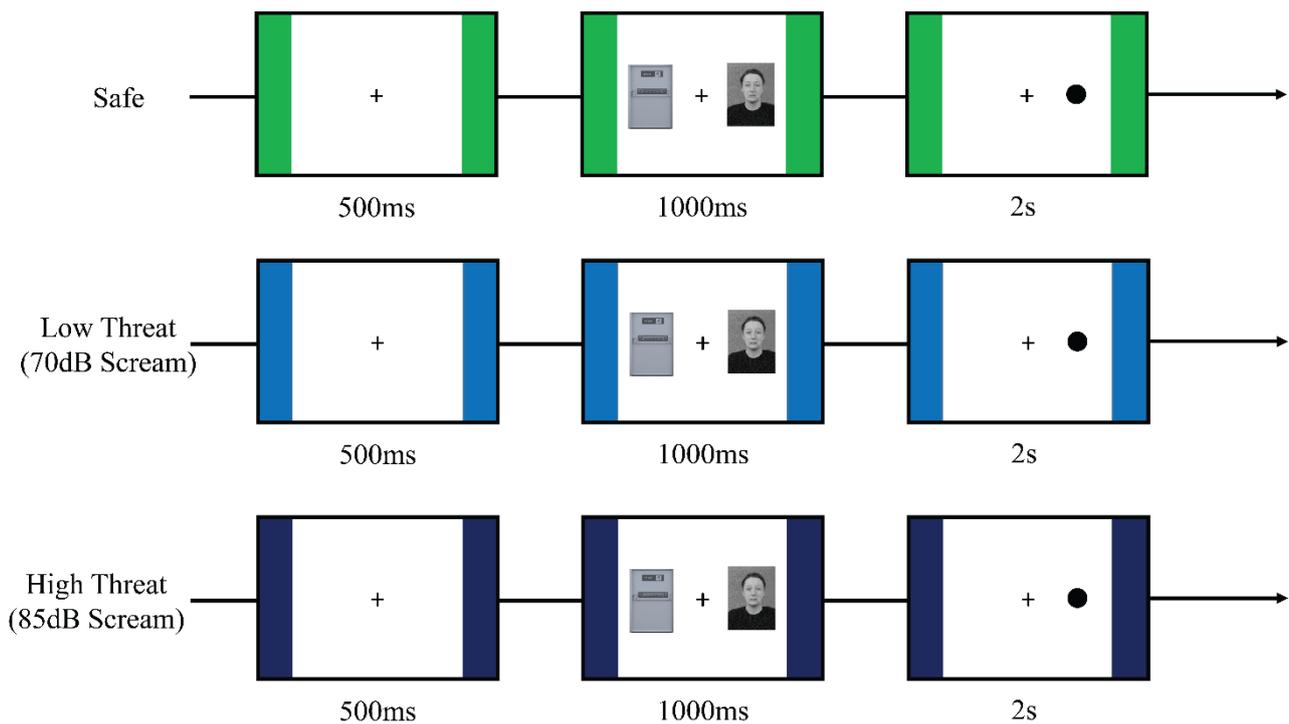


Figure 7-3. Experimental design of a dot-probe task to investigate attentional bias between cue signaling possibility to escape and affiliation signal, depending on threat intensity.

Furthermore, we suggested that affiliation signals might be more relevant in a second stage, in order to elicit cooperation strategies once the source of the threat is clearly perceived and identified. Unfortunately, the temporal component was not taken into account in our studies, which makes interpretations such as "safety first" very speculative. Also, if fear stimulus associated with an averted gaze is associated with the social function of specifying the location of danger (i.e. ambiguity factor) to others, no feedback on the true position of the source was given to the participants. Thus, we propose two follow-up studies to our categorization task. The first one would consist in varying the duration of the faces presentation by proposing two temporalities: 250ms vs. 800ms. Recent fMRI results obtained by Cushing et al. (Cushing et al., 2018) seem to support a two-stage processing: an early processing of threat information and a late processing of affiliation signals conveyed by fearful faces. Consistent with these results, we hypothesize that fast presentation of our stimuli in threat situations would

prioritize danger signals (i.e. averted gaze) while affiliation signals would be prioritized in a longer presentation (i.e. direct gaze). The use of models from the Signal Detection Theory will again be informative here: they will allow us to replicate the increased bias (i.e. to averted gaze) we previously obtained for a 250ms presentation, but also to identify which mechanism is involved in the prioritization of affiliate signals (if such result is observed for 800ms presentation). The second follow-up study would be to investigate the perception of the combination of gaze and expression of fear when the position of the threat is already indicated to participants. In this context, the averted fear gaze becomes non-informative. This study will investigate what happens to the direct gaze in such context (i.e. when ambiguity about threat is overcome).

4.4-Does inter-individual variability matter when investigating social cognition under threat?

One of the points that require to be deeper investigated in this project is inter-individual variability. Several traits related to anxiety were measured in our different studies: general anxiety, social anxiety or anxiety to uncertainty. These scores were acquired to control the anxiety trait level of the recruited participants. They were not used as a co-variable to explain the effects we obtained. One of the main reasons is that, given the number of questionnaires used, the probability of obtaining a false positive was high. Moreover, our experimental designs included three to four experimental factors at the same time. The addition of a co-variable would most likely have made the understanding of the investigated phenomena more complex (for the same reason, gender has not been integrated as a co-variable). Moreover, the size of our samples would have been too small to be able to conclude on such analyses. A replication on a larger sample size might allow us to investigate the influence of trait anxiety variability on the ability to co-represent and detect social signals in threat situations. The only score we used as a covariate is the Social Value Orientation score (Murphy & Ackermann, 2014), which has been associated several times with affiliate tendencies in the literature (Kaltwasser et al., 2017; Moussaïd & Trauernicht, 2016). It therefore allowed us to establish a strong *a priori* prediction we wanted to test (i.e. prosocial individuals should be more sensitive to direct fearful faces). Nevertheless, no effect was observed, even if we again believe that replication with a larger group of participants is necessary. For the same reasons, we believe that questionnaires measuring empathy capacities should be added for our future studies as they explain the variability of prosocial behavior in threatening situations (Tomova et al., 2017; Vieira, Schellhaas, et al., 2020) but also the plasticity of co-representation mechanisms in our daily social interactions. They would have been highly relevant for the identification of the functions of the mechanisms we measured (in particular to distinguish whether the effects we observed can be explained as truly reflecting self-preservative motives or rather by empathic concern towards others).

4.5-A longitudinal interdisciplinarity research axis

One of the biggest challenges associated with this research question is to collect empirical data which are both ecologically valid and experimentally meaningful (i.e. to be easily interpretable). In this manuscript, we have shown that field-based studies in ethology and social psychology can inform neuroscience models of defense circuits under threat. Nevertheless, these data are mainly based on video observations (Gu, Liu, Shiwakoti, & Yang, 2016) or subjective reports (Dezecache, 2015; Drury, 2018) which suffer from several biases that make their interpretation complicated. In order to identify which factors influence the behaviors observed in real life and why they occur, the contribution of experimental psychology seems necessary insofar as it provides a much more controlled and therefore more informative working environment. In return, it has been obviously argued that there are ethical and practical issues in recreating real-life dangerous situations in the laboratory (Vieira, Schellhaas, et al., 2020). Consequently, the validity of such data can be criticized and qualified to be too reductionist. However, it is important first to point out that, independently of this debate, our data at least provide new evidence on human social cognition in situations of moderate and prolonged anxiety as well as insights about the cognitive differences observed in people suffering from anxiety disorders (Robinson et al., 2013). Secondly, it is likely that the sociocognitive processes targeted at laboratory under low-risk context are the same as the ones implicated in more extreme forms of danger (but probably in an intensified way).

So how to deal with this trade-off between experimental control and validity? In order to do so, it is necessary to keep dialoguing between these different fields. Building theoretical bridges, as we tried to do in this dissertation, will allow researchers to make progress in this area. Threat situation is highly complex. As a results, individual emotional responses can be highly variable. Nevertheless, we have many approaches to overcome this issue (i) which are highly complementary, (ii) which provide specific data at different scales, and (iii) which allow us to travel along this continuum between ecological validity and controllable environment (see **Table 7-3**).

	Hypothetical study	« Classical » Lab experiment	VR experiment	Drills	Case studies / Field Study
<i>Setting</i>	Laboratory	Laboratory	Laboratory	Real-world	Real-world
<i>Experimental control?</i>	Yes	Yes but less than VR	Yes	Limited	no
<i>Type of data</i>	Subjective (statement)	Subjective, behavior, (neuro)physio	Subjective, behavior, (neuro)physio	Subjective, behavior	Subjective, behavior
<i>Use of stressors</i>	No (only hypothetical)	limited	limited	limited	yes
<i>Ecological validity?</i>	Very Low	Low	Medium	High if unannounced limited if announced	High
<i>Adjusting experimental settings?</i>	Yes	Yes	Yes	Limited	No
<i>Exact replication?</i>	Yes	Yes	Yes	Limited	No
<i>Time and Cost for data collection</i>	Very low	Low	Low	Medium	High

Table 7-3: Comparison of research methods to investigate threat. Adapted from Kinateder, Ronchi, Nilsson, et al. (2014).

The results of the studies we have conducted and described in this manuscript will not by themselves answer the big question of "what happens to social cognition in threatening situations?". However, they do provide data that can and should be continuously highlighted with other studies conducted in laboratory, as well as with behaviors observed in real life to provide qualitative and quantitative predictive models. Some mathematical models try to simulate the behavior of crowds observed in disaster or attack situations by combining parameters representing both physical environmental constraints and socio-cognitive phenomena (Cheng & Zheng, 2018; Verdière et al., 2015). As an example (von Sivers et al., 2016), it has been shown that social identity and helping behaviors undertaken under threat were efficient model parameters to efficiently simulate the evacuation timing during the London bombing attacks. It is in this spirit of continuity that future projects in this field should be pursued.

5-Conclusion

The work conducted here was inspired by collective behaviors that have been observed during disasters or attacks to question how our socio-cognitive functions are modified in such contexts. We have identified two target functions which are the co-representation and perception of social signals that we have studied in the laboratory under conditions of sustained anxiety. We then discussed how the modulation of these mechanisms could underlie these so-called behaviors. During the course of this

dissertation, we presented how we went back and forth between real life and laboratory once a time. Obviously, considering the complexity and variability of threat situations, this work needs to be done repeatedly to provide a clear picture of the social behaviors under threat. Nevertheless, this dissertation has made it possible to legitimize the place of others and collective actions in models predicting reactions to dangers. It provided a review of the literature on sociality in situations of danger by attempting to harmonize results from various fields with extremely varied approaches. It defends in particular a motivational approach (i.e. cost-benefit ratio) to understand the diversity of behaviors emerging in threat situations, both at individual and collective level. Empirically, it first provides a tool to pursue the study of social cognition in threat situations: the threat-of-scream paradigm. Then, through two studies, it brought new evidence to defend the importance of social cognition under threat. These results were compared with models describing the taxonomy of defense reactions in order to propose a unified framework between results from research in neuroscience, social sciences and cognitive psychology. To validate such framework, it is still necessary to identify the list of environmental factors (and combinations of factors) that influence our behavior and how. Ultimately, this dissertation is an invitation to interdisciplinarity because, as stated in the first words of this manuscript, "there are a need for interdisciplinarity in this regard".

APPENDIX

SUPPLEMENTARY INFORMATION 1

SUPPLEMENTARY MATERIAL AND APPENDIX TO CHAPTER 4

Supplementary Material

Description

The present work aimed at assessing the efficiency of a new version of TOSc paradigm during which we delivered unpredictable human distress screams at low intensity (70dB instead of 95dB used in the past). In the main manuscript, we discussed findings related to tonic skin conductance activity (which represent the physiological activity of participant through the entire block) and subjective scores of anxiety reported by participants at the end of each block. This supplementary document provides detailed about the Methods (the characteristics of the sampling distribution, debriefing that concluded the experimental session, signal quality check) as well as the tabs of results for all the analyses reported in the main text (Statistics, Repeated Measures ANOVA, Post Hoc Comparisons and One Sample T-Test Against Zero).

Methods – Supplementary information

Participants

We provide the mean and SD, as well as the distribution of scores to STAI state and trait questionnaires, for each experiment.

Table S4-1. Characteristics of the sample of Study one

Size	Gender	Age	STAI-State	STAI-Trait
26	12 F/14 M	23.6 ± 3.4 y.o SD	28.9 ± 6.1 SD	37.4 ± 7.2 SD

Table S4-2. Characteristics of the sample of Study two

Size	Gender	Age	STAI-State	STAI-Trait
33	18 F/15 M	23.9± 4.5 y.o SD	26.6 ± 5.9 SD	38.7± 9.6 SD

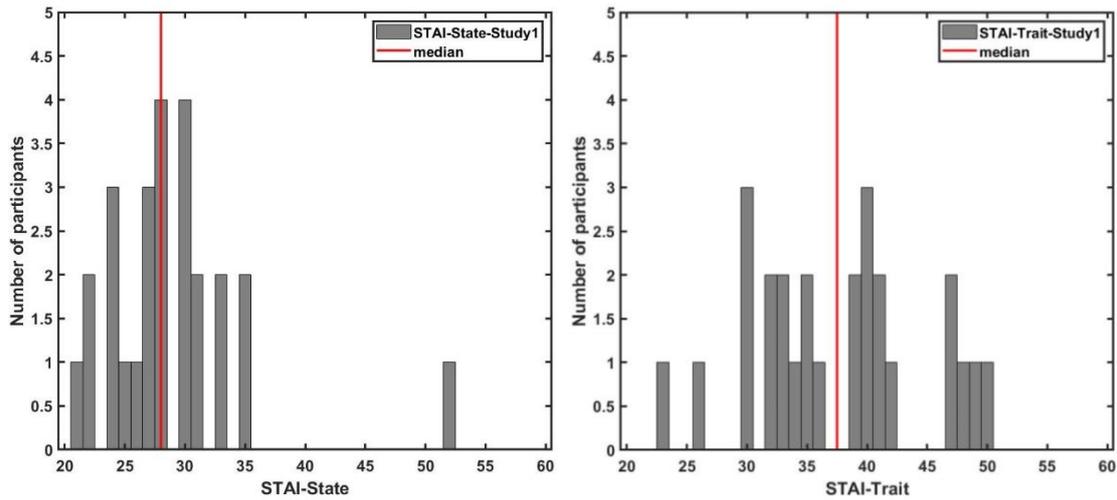


Figure S4-1. Distribution of STAI-State (Left) and STAI-Trait (Right) questionnaires of Study one

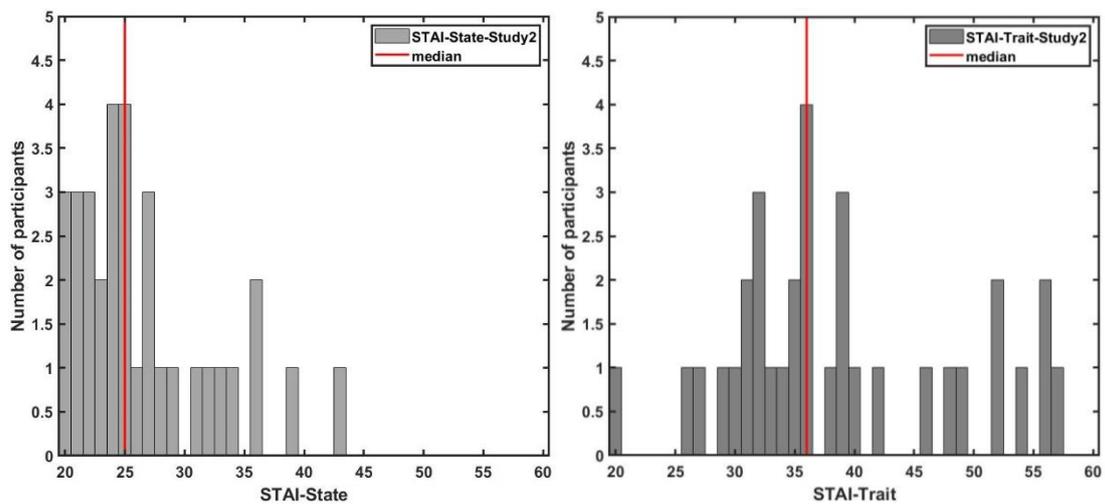


Figure S4-2. Distribution of STAI-State (Left) and STAI-Trait (Right) questionnaires of Study two

Filter quality check

We show skin conductance response to scream ($\max(\text{RED } 1\text{ to } 6\text{ s following a scream}) - \text{Mean}(\text{RED } 1\text{ s before a scream})$) for the raw data as well as for the filtered data. Low-pass filter of 0.05Hz appears efficient to reduce the phasic influence of screams (see **Figure S4-3 Left**). Moreover, and importantly, this filter didn't affect SCL values. As it can be seen, the values of SCL before and after filter are similar (see **Figure S4-3 Right**).

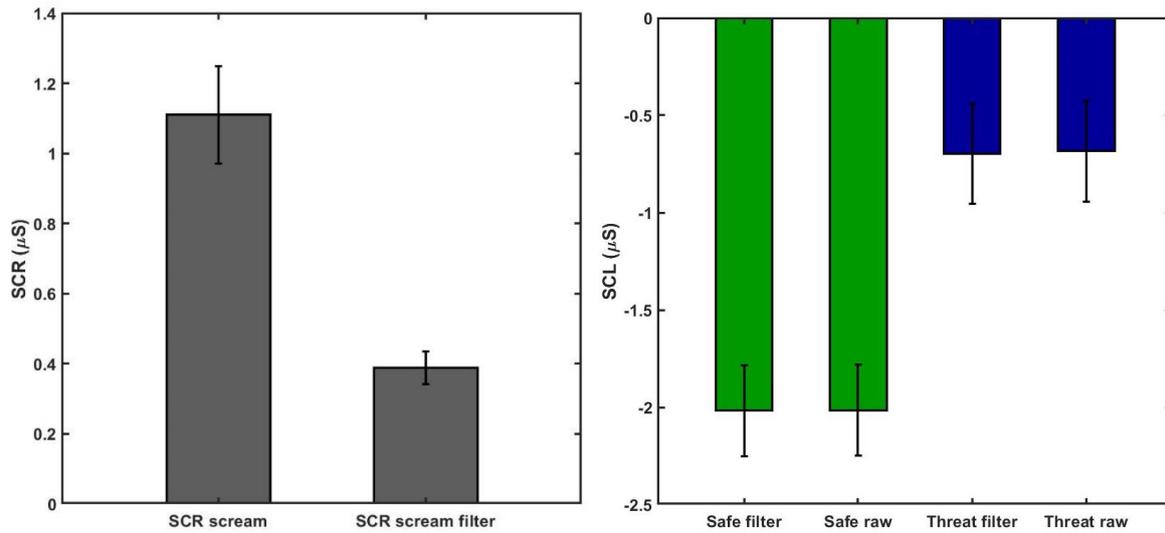


Figure S4-3. SCR to scream (Left) and SCL before and after filter correction (Right).

Debriefing with participants

We collected ratings for all screams together on an aversive scale (from 0 - not at all aversive to 10 - extremely aversive). Participants rated the screams as moderately aversive (median of 4, see **Figure S4-4**, left). Inducing anxiety relies both on the aversiveness of the delivered stimuli as well as on their unpredictability. We therefore also asked participants to rate how much they felt preoccupied by the possibility that a scream would be delivered during threat blocks (this was done during the debriefing). Participants felt relatively preoccupied, i.e. they reported anticipatory anxiety of scream delivery (median of 6 see **Figure S4-4**, right).

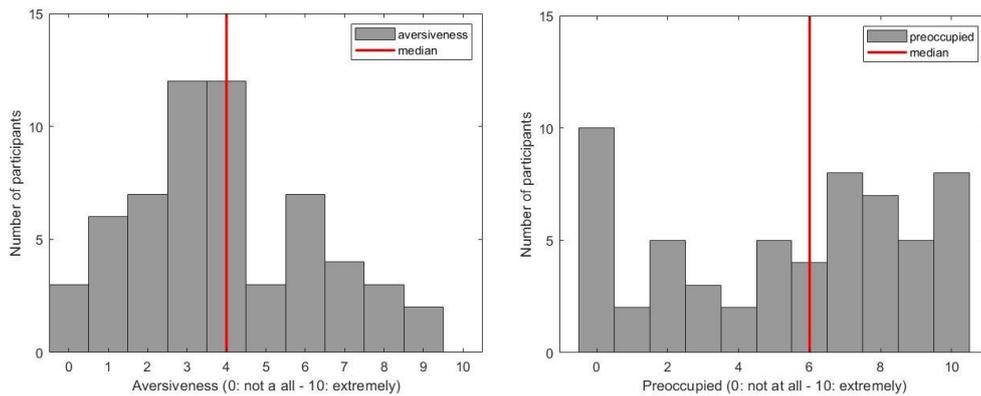


Figure S4-4. Distribution of participant’s aversiveness (Left) and preoccupation ratings (Right).

Experiment 1 – Supplementary results

Skin Conductance Level

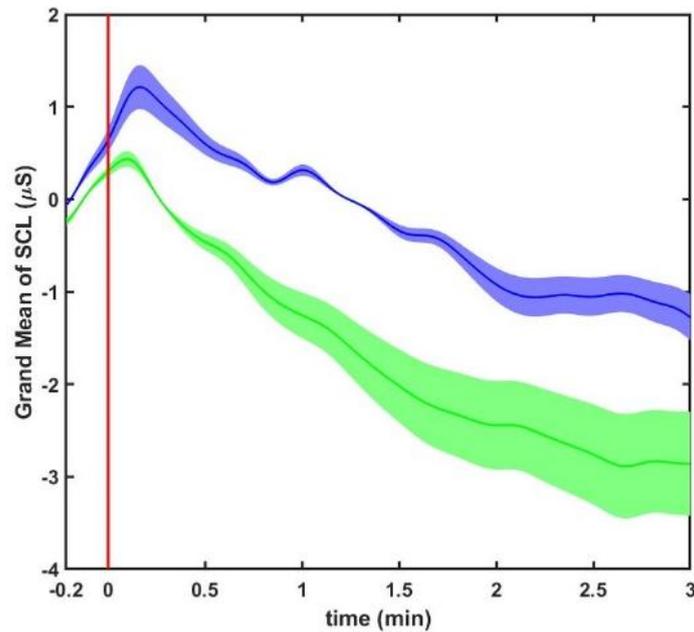


Figure S4-5. Grand mean of skin conductance activity across the duration of one block, for threat (blue curve) and safe (green curve) conditions separately. Shaded error bars indicate SEM. At t = -0.2 min, the type of block (“Threat or Safe”) was announced. At t = 0 (red line), the decision-task began.

Table S4-3. Within Subjects Effects of Repeated Measures ANOVA (Condition & Time) on SCL

	Sphericity Correction	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	None	132.517	1.000	132.517	17.204	< .001	0.41
	Greenhouse-Geisser	132.517	1.000	132.517	17.204	< .001	0.41
Residual	None	192.565	25.000	7.703			
	Greenhouse-Geisser	192.565	25.000	7.703			
Time	None	372.006 ^a	4.000 ^a	93.002 ^a	12.958 ^a	< .001 ^a	0.34
	Greenhouse-Geisser	372.006 ^a	1.972 ^a	188.634 ^a	12.958 ^a	< .001 ^a	0.34
Residual	None	717.709	100.000	7.177			
	Greenhouse-Geisser	717.709	49.303	14.557			
Condition * Time	None	3.528 ^a	4.000 ^a	0.882 ^a	0.115 ^a	0.977 ^a	0.01
	Greenhouse-Geisser	3.528 ^a	2.324 ^a	1.518 ^a	0.115 ^a	0.917 ^a	0.01
Residual	None	769.397	100.000	7.694			
	Greenhouse-Geisser	769.397	58.088	13.245			

Note. Type III Sum of Squares

^a Mauchly's test of sphericity indicates that the assumption of sphericity is violated ($p < .05$).

Table S4-4. Test of Sphericity for Repeated Measures ANOVA (Condition & Time) on SCL

	Mauchly's W	Approx. X ²	df	p	Greenhouse-Geisser ε	Huynh-Feldt ε	Lower Bound ε
Condition	1.000 ^a	NaN ^a	NaN ^a	NaN ^a	1.000 ^a	1.000 ^a	1.000 ^a
Time	0.130	47.783	9	< .001	0.493	0.535	0.250
Condition * Time	0.164	42.337	9	< .001	0.581	0.644	0.250

^a Singular error SSP matrix: The repeated measure has only two levels, or more levels than observations. When the repeated measure has two levels, the assumption of sphericity is always met.

Table S4-5. Descriptive Statistics (ANOVA) - SCL

Condition	Time	Mean	SD	N
Threat	B1	1.740	3.533	26
	B2	-0.791	2.448	26
	B3	-1.003	2.876	26
	B4	-1.035	2.224	26
	B5	-1.943	2.783	26
Safe	B1	0.245	4.755	26
	B2	-2.590	2.475	26
	B3	-2.457	2.184	26
	B4	-2.334	2.771	26
	B5	-3.036	3.512	26

Table S4-6. Post Hoc Comparisons - ANOVA (Time) on SCL_Threat - SCL_Safe

		Mean Difference	SE	t	Cohen's d	p _{bonf}
Threat_B1-Safe_B1	Threat_B2-Safe_B2	-0.304	1.361	-0.223	-0.044	1.000
	Threat_B3-Safe_B3	0.041	1.457	0.028	0.005	1.000
	Threat_B4-Safe_B4	0.196	1.428	0.137	0.027	1.000
	Threat_B5-Safe_B5	0.401	1.418	0.283	0.056	1.000
Threat_B2-Safe_B2	Threat_B3-Safe_B3	0.345	0.713	0.484	0.095	1.000
	Threat_B4-Safe_B4	0.500	0.466	1.073	0.210	1.000
	Threat_B5-Safe_B5	0.706	0.735	0.960	0.188	1.000
Threat_B3-Safe_B3	Threat_B4-Safe_B4	0.155	0.911	0.170	0.033	1.000
	Threat_B5-Safe_B5	0.361	1.019	0.354	0.069	1.000
Threat_B4-Safe_B4	Threat_B5-Safe_B5	0.205	0.823	0.250	0.049	1.000

Note. Cohen's d does not correct for multiple comparisons.

Note. Bonferroni adjusted confidence intervals.

Table S4-7. Descriptive Statistics (ANOVA) on SCL_Threat - SCL_Safe

TimeXcondition	Mean	SD	N
Threat_B1-Safe_B1	1.495	6.479	26
Threat_B2-Safe_B2	1.799	2.383	26
Threat_B3-Safe_B3	1.454	3.355	26
Threat_B4-Safe_B4	1.299	2.967	26
Threat_B5-Safe_B5	1.093	3.041	26

Table S4-8. One Sample T-Test Against 0 for SCL_Threat - SCL_Safe

	t	df	p	Cohen's d	95% CI for Cohen's d	
					Lower	Upper
Threat_B1-Safe_B1	1.176	25	0.251	0.231	-0.161	0.618
Threat_B2-Safe_B2	3.849	25	< .001	0.755	0.312	1.186
Threat_B3-Safe_B3	2.210	25	0.036	0.433	0.027	0.832
Threat_B4-Safe_B4	2.232	25	0.035	0.438	0.031	0.837
Threat_B5-Safe_B5	1.833	25	0.079	0.360	-0.041	0.753

Note. Student's t-test.

Note. For the Student t-test, effect size is given by Cohen's *d*.

Subjective Anxiety

Table S4-9. Within Subjects Effects of Repeated Measures ANOVA (Condition & Time) on Subjective Anxiety

	Sphericity Correction	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	None	13753.388	1.000	13753.388	15.107	< .001	0.377
	Greenhouse-Geisser	13753.388	1.000	13753.388	15.107	< .001	0.377
Residual	None	22760.312	25.000	910.412			
	Greenhouse-Geisser	22760.312	25.000	910.412			
Time	None	1046.946 ^a	4.000 ^a	261.737 ^a	1.841 ^a	0.127 ^a	0.069
	Greenhouse-Geisser	1046.946 ^a	2.434 ^a	430.053 ^a	1.841 ^a	0.159 ^a	0.069
Residual	None	14217.654	100.000	142.177			
	Greenhouse-Geisser	14217.654	60.862	233.607			
Condition * Time	None	792.977	4.000	198.244	2.143	0.081	0.079
	Greenhouse-Geisser	792.977	2.883	275.051	2.143	0.105	0.079
Residual	None	9252.823	100.000	92.528			
	Greenhouse-Geisser	9252.823	72.075	128.377			

Note. Type III Sum of Squares

Table S4-10. Test of Sphericity for Repeated Measures ANOVA (Condition & Time) on Subjective Anxiety

	Mauchly's W	Approx. X²	df	p	Greenhouse- Geisser ϵ	Huynh- Feldt ϵ	Lower Bound ϵ
Condition	1.000 ^a	NaN ^a	NaN ^a	NaN ^a	1.000 ^a	1.000 ^a	1.000 ^a
Time	0.240	33.412	9	< .001	0.609	0.679	0.250
Condition * Time	0.510	15.778	9	0.072	0.721	0.825	0.250

^a Singular error SSP matrix: The repeated measure has only two levels, or more levels than observations. When the repeated measure has two levels, the assumption of sphericity is always met.

Table S11. Descriptive Statistics (ANOVA) on Subjective Anxiety

Condition	Time	Mean	SD	N
Threat	B1	43.000	23.091	26
	B2	39.115	24.438	26
	B3	37.692	23.306	26
	B4	36.731	25.373	26
	B5	32.962	25.677	26
Safe	B1	22.346	19.781	26
	B2	25.808	20.151	26
	B3	25.269	17.676	26
	B4	20.923	17.202	26
	B5	22.423	17.936	26

Table S4-12. Post Hoc Comparisons - ANOVA (Time) on Subjective Anxiety_Threat - Subjective Anxiety_Safe

	Mean Difference	SE	t	Cohen's d	p_{bonf}
Threat_B1-Safe_B1	Threat_B2-Safe_B2	7.346	4.926	1.491	0.292
	Threat_B3-Safe_B3	8.231	4.567	1.802	0.353
	Threat_B4-Safe_B4	4.846	4.807	1.008	0.198
	Threat_B5-Safe_B5	10.115	4.152	2.436	0.478
Threat_B2-Safe_B2	Threat_B3-Safe_B3	0.885	3.126	0.283	0.056
	Threat_B4-Safe_B4	-2.500	3.487	-0.717	-0.141
	Threat_B5-Safe_B5	2.769	2.873	0.964	0.189
Threat_B3-Safe_B3	Threat_B4-Safe_B4	-3.385	3.149	-1.075	-0.211
	Threat_B5-Safe_B5	1.885	2.890	0.652	0.128
Threat_B4-Safe_B4	Threat_B5-Safe_B5	5.269	2.902	1.816	0.356

Note. Cohen's d does not correct for multiple comparisons.

Note. Bonferroni adjusted confidence intervals.

Table S4-13. Descriptive Statistics (ANOVA) on Subjective Anxiety_Threat - Subjective Anxiety_Safe

TimeXcondition	Mean	SD	N
Threat_B1-Safe_B1	20.654	26.068	26
Threat_B2-Safe_B2	13.308	21.012	26
Threat_B3-Safe_B3	12.423	19.265	26
Threat_B4-Safe_B4	15.808	22.578	26
Threat_B5-Safe_B5	10.538	23.646	26

Table S4-14. One Sample T-Test Against 0 for Subjective Anxiety_Threat - Subjective Anxiety_Safe

	t	df	p	Cohen's d	95% CI for Cohen's d	
					Lower	Upper
Threat_B1-Safe_B1	4.040	25	< .001	0.792	0.344	1.228
Threat_B2-Safe_B2	3.229	25	0.003	0.633	0.206	1.050
Threat_B3-Safe_B3	3.288	25	0.003	0.645	0.216	1.063
Threat_B4-Safe_B4	3.570	25	0.001	0.700	0.264	1.125
Threat_B5-Safe_B5	2.273	25	0.032	0.446	0.038	0.845

Note. Student's t-test.

Note. For the Student t-test, effect size is given by Cohen's *d*.

Intra-individual correlation

Table S4-15. One Sample T-Test Against 0 for Intra-individual Correlation

	t	df	p	Cohen's d	95% CI for Cohen's d	
					Lower	Upper
r_to_z_-Fisher Normalization	2.856	25	0.009	0.560	0.141	0.969

Note. Student's t-test.

Note. For the Student t-test, effect size is given by Cohen's *d*.

Table S4-16. Descriptive Statistics (t-test) on Intra-individual Correlation

	N	Mean	SD	SE
r_to_z_-Fisher Normalization	26.000	0.256	0.457	0.090

STAI-Trait and Skin conductance level (SCL)

Table S4-17. Within Subjects Effects of Repeated Measures ANOVA (Condition & Time) on SCL with Z-score STAI-Trait

	Sphericity Correction	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	None	1.252	1.000	1.252	0.165	0.688	0.007
	Greenhouse-Geisser	1.252	1.000	1.252	0.165	0.688	0.007
Condition * ZST	None	10.919	1.000	10.919	1.443	0.241	0.057
	Greenhouse-Geisser	10.919	1.000	10.919	1.443	0.241	0.057
Residual	None	181.646	24.000	7.569			
	Greenhouse-Geisser	181.646	24.000	7.569			
Time	None	5.486 ^a	4.000 ^a	1.372 ^a	0.184 ^a	0.946 ^a	0.008
	Greenhouse-Geisser	5.486 ^a	1.970 ^a	2.784 ^a	0.184 ^a	0.829 ^a	0.008
Time * ZST	None	3.582 ^a	4.000 ^a	0.896 ^a	0.120 ^a	0.975 ^a	0.005
	Greenhouse-Geisser	3.582 ^a	1.970 ^a	1.818 ^a	0.120 ^a	0.884 ^a	0.005
Residual	None	714.126	96.000	7.439			
	Greenhouse-Geisser	714.126	47.292	15.100			
Condition * Time	None	52.130 ^a	4.000 ^a	13.032 ^a	1.745 ^a	0.146 ^a	0.068
	Greenhouse-Geisser	52.130 ^a	2.210 ^a	23.591 ^a	1.745 ^a	0.181 ^a	0.068
Condition * Time * ZST	None	52.444 ^a	4.000 ^a	13.111 ^a	1.756 ^a	0.144 ^a	0.068
	Greenhouse-Geisser	52.444 ^a	2.210 ^a	23.734 ^a	1.756 ^a	0.180 ^a	0.068
Residual	None	716.952	96.000	7.468			
	Greenhouse-Geisser	716.952	53.032	13.519			

STAI-Trait and Subjective anxiety

Table S4-18. Within Subjects Effects of Repeated Measures ANOVA (Condition & Time) on Subjective Anxiety with Z-score STAI-Trait

	Sphericity Correction	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	None	13758.162	1.000	13758.162	14.534	< .001	0.377
	Greenhouse-Geisser	13758.162	1.000	13758.162	14.534	< .001	0.377
Condition * ZST	None	40.833	1.000	40.833	0.043	0.837	0.002
	Greenhouse-Geisser	40.833	1.000	40.833	0.043	0.837	0.002
Residual	None	22719.478	24.000	946.645			
	Greenhouse-Geisser	22719.478	24.000	946.645			
Time	None	1167.583 ^a	4.000 ^a	291.896 ^a	2.027 ^a	0.097 ^a	0.078
	Greenhouse-Geisser	1167.583 ^a	2.390 ^a	488.479 ^a	2.027 ^a	0.133 ^a	0.078
Time * ZST	None	392.404 ^a	4.000 ^a	98.101 ^a	0.681 ^a	0.607 ^a	0.028
	Greenhouse-Geisser	392.404 ^a	2.390 ^a	164.169 ^a	0.681 ^a	0.535 ^a	0.028
Residual	None	13825.249	96.000	144.013			
	Greenhouse-Geisser	13825.249	57.366	241.002			
Condition * Time	None	734.440	4.000	183.610	1.954	0.108	0.075
	Greenhouse-Geisser	734.440	2.810	261.343	1.954	0.133	0.075
Condition * Time * ZST	None	233.913	4.000	58.478	0.622	0.648	0.025
	Greenhouse-Geisser	233.913	2.810	83.236	0.622	0.593	0.025
Residual	None	9018.910	96.000	93.947			
	Greenhouse-Geisser	9018.910	67.446	133.720			

STAI-Trait and Intra-individual correlation

Table S4-19. Pearson Correlation between intra-individual correlation and Z-score STAI-Trait

		r_to_z_-Fisher Normalization
ZST	Pearson's r	-0.103
	p-value	0.617

Experiment 2 – Supplementary results

Skin Conductance Level

Table S4-20. Within Subjects Effects of Repeated Measures ANOVA (Condition & Time) on SCL

	Sphericity Correction	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	None	125.907	1.000	125.907	29.359	< .001	0.478
	Greenhouse-Geisser	125.907	1.000	125.907	29.359	< .001	0.478
Residual	None	137.234	32.000	4.289			
	Greenhouse-Geisser	137.234	32.000	4.289			
Time	None	183.408 ^a	4.000 ^a	45.852 ^a	12.484 ^a	< .001 ^a	0.281
	Greenhouse-Geisser	183.408 ^a	2.916 ^a	62.891 ^a	12.484 ^a	< .001 ^a	0.281
Residual	None	470.124	128.000	3.673			
	Greenhouse-Geisser	470.124	93.322	5.038			
Condition * Time	None	17.859	4.000	4.465	1.353	0.254	0.041
	Greenhouse-Geisser	17.859	3.338	5.351	1.353	0.259	0.041
Residual	None	422.344	128.000	3.300			
	Greenhouse-Geisser	422.344	106.804	3.954			

Note. Type III Sum of Squares

^a Mauchly's test of sphericity indicates that the assumption of sphericity is violated ($p < .05$).

Table S4-21. Test of Sphericity for Repeated Measures ANOVA (Condition & Time) on SCL

	Mauchly's W	Approx. X²	df	p	Greenhouse-Geisser ϵ	Huynh-Feldt ϵ	Lower Bound ϵ
Condition	1.000 ^a	NaN ^a	NaN ^a	NaN ^a	1.000 ^a	1.000 ^a	1.000 ^a
Time	0.514	20.264	9	0.017	0.729	0.810	0.250
Condition * Time	0.641	13.541	9	0.140	0.834	0.943	0.250

^a Singular error SSP matrix: The repeated measure has only two levels, or more levels than observations. When the repeated measure has two levels, the assumption of sphericity is always met.

Table S4-22. Descriptive Statistics (ANOVA) on SCL

Condition	Time	Mean	SD	N
Threat	B1	0.683	1.885	33
	B2	-0.162	2.366	33
	B3	-0.922	2.363	33
	B4	-1.787	2.944	33
	B5	-1.652	3.433	33
Safe	B1	-0.974	1.956	33
	B2	-1.797	2.256	33
	B3	-2.316	2.592	33
	B4	-2.187	2.754	33
	B5	-2.743	2.763	33

Table S4-23. Post Hoc Comparisons - ANOVA (Time) on SCL_Threat - SCL_Safe

		Mean Difference	SE	t	Cohen's d	p _{bonf}
Threat_B1-Safe_B1	Threat_B2-Safe_B2	0.022	0.485	0.045	0.008	1.000
	Threat_B3-Safe_B3	0.263	0.694	0.379	0.066	1.000
	Threat_B4-Safe_B4	1.258	0.661	1.902	0.331	0.662
	Threat_B5-Safe_B5	0.566	0.716	0.790	0.138	1.000
Threat_B2-Safe_B2	Threat_B3-Safe_B3	0.241	0.602	0.401	0.070	1.000
	Threat_B4-Safe_B4	1.236	0.655	1.886	0.328	0.683
	Threat_B5-Safe_B5	0.544	0.586	0.929	0.162	1.000
Threat_B3-Safe_B3	Threat_B4-Safe_B4	0.994	0.584	1.702	0.296	0.985
	Threat_B5-Safe_B5	0.303	0.561	0.540	0.094	1.000
Threat_B4-Safe_B4	Threat_B5-Safe_B5	-0.691	0.736	-0.940	-0.164	1.000

Note. Cohen's d does not correct for multiple comparisons.

Note. Bonferroni adjusted confidence intervals.

Table S4-24. Descriptive Statistics (ANOVA) on SCL_Threat - SCL_Safe

TimeXcondition	Mean	SD	N
Threat_B1-Safe_B1	1.657	2.526	33
Threat_B2-Safe_B2	1.635	2.587	33
Threat_B3-Safe_B3	1.394	2.472	33
Threat_B4-Safe_B4	0.400	2.582	33
Threat_B5-Safe_B5	1.091	3.021	33

Table S4-25. One Sample T-Test Against 0 for SCL_Threat - SCL_Safe

	t	df	p	Cohen's d	95% CI for Cohen's d	
					Lower	Upper
Threat_B1-Safe_B1	3.769	32	< .001	0.656	0.275	1.029
Threat_B2-Safe_B2	3.632	32	< .001	0.632	0.254	1.003
Threat_B3-Safe_B3	3.239	32	0.003	0.564	0.192	0.928
Threat_B4-Safe_B4	0.889	32	0.381	0.155	-0.190	0.497
Threat_B5-Safe_B5	2.075	32	0.046	0.361	0.006	0.711

Note. Student's t-test.

Note. For the Student t-test, effect size is given by Cohen's *d*.

Subjective Anxiety

Table S4-26. Within Subjects Effects of Repeated Measures ANOVA (Condition & Time) on Subjective Anxiety

	Sphericity Correction	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	None	51113.482	1.000	51113.482	47.844	< .001	0.599
	Greenhouse-Geisser	51113.482	1.000	51113.482	47.844	< .001	0.599
Residual	None	34187.018	32.000	1068.344			
	Greenhouse-Geisser	34187.018	32.000	1068.344			
Time	None	1900.558 ^a	4.000 ^a	475.139 ^a	2.472 ^a	0.048 ^a	0.072
	Greenhouse-Geisser	1900.558 ^a	2.324 ^a	817.702 ^a	2.472 ^a	0.083 ^a	0.072
Residual	None	24603.042	128.000	192.211			
	Greenhouse-Geisser	24603.042	74.377	330.790			
Condition * Time	None	2116.655	4.000	529.164	4.046	0.004	0.112
	Greenhouse-Geisser	2116.655	3.311	639.242	4.046	0.007	0.112
Residual	None	16739.345	128.000	130.776			
	Greenhouse-Geisser	16739.345	105.958	157.981			

Note. Type III Sum of Squares

^a Mauchly's test of sphericity indicates that the assumption of sphericity is violated ($p < .05$).

Table S4-27. Test of Sphericity for Repeated Measures ANOVA (Condition & Time) on Subjective Anxiety

	Mauchly's W	Approx. X ²	df	p	Greenhouse-Geisser ϵ	Huynh-Feldt ϵ	Lower Bound ϵ
Condition	1.000 ^a	NaN ^a	NaN ^a	NaN ^a	1.000 ^a	1.000 ^a	1.000 ^a
Time	0.291	37.593	9	< .001	0.581	0.629	0.250
Condition * Time	0.641	13.547	9	0.140	0.828	0.935	0.250

^a Singular error SSP matrix: The repeated measure has only two levels, or more levels than observations. When the repeated measure has two levels, the assumption of sphericity is always met.

Table S4-28. Descriptive Statistics (ANOVA) – Subjective Anxiety

Condition	Time	Mean	SD	N
Threat	B1	47.303	26.789	33
	B2	41.727	25.790	33
	B3	36.303	26.052	33
	B4	36.030	26.687	33
	B5	34.030	25.576	33
Safe	B1	14.000	15.383	33
	B2	14.364	13.212	33
	B3	12.455	14.992	33
	B4	15.091	19.106	33
	B5	15.030	19.404	33

Table S4-29. Post Hoc Comparisons - ANOVA (Time) on Subjective Anxiety_Threat – Subjective Anxiety_Safe

		Mean Difference	SE	t	Cohen's d	P _{bonf}
Threat_B1-Safe_B1	Threat_B2-Safe_B2	5.939	3.923	1.514	0.264	1.000
	Threat_B3-Safe_B3	9.455	4.581	2.064	0.359	0.472
	Threat_B4-Safe_B4	12.364	3.631	3.405	0.593	0.018
	Threat_B5-Safe_B5	14.303	4.204	3.402	0.592	0.018
Threat_B2-Safe_B2	Threat_B3-Safe_B3	3.515	3.508	1.002	0.174	1.000
	Threat_B4-Safe_B4	6.424	2.904	2.212	0.385	0.342
	Threat_B5-Safe_B5	8.364	4.203	1.990	0.346	0.552
Threat_B3-Safe_B3	Threat_B4-Safe_B4	2.909	3.995	0.728	0.127	1.000
	Threat_B5-Safe_B5	4.848	4.980	0.974	0.169	1.000
Threat_B4-Safe_B4	Threat_B5-Safe_B5	1.939	3.481	0.557	0.097	1.000

Table S4-30. Descriptive Statistics (ANOVA) Subjective Anxiety_Threat – Subjective Anxiety_Safe

TimeXcondition	Mean	SD	N
Threat_B1-Safe_B1	33.303	26.984	33
Threat_B2-Safe_B2	27.364	26.535	33
Threat_B3-Safe_B3	23.848	22.857	33
Threat_B4-Safe_B4	20.939	25.172	33
Threat_B5-Safe_B5	19.000	24.384	33

Table S4-31. One Sample T-Test Against 0 for Subjective Anxiety_Threat – Subjective Anxiety_Safe

	t	df	p	Cohen's d	95% CI for Cohen's d	
					Lower	Upper
Threat_B1-Safe_B1	7.090	32	< .001	1.234	0.774	1.684
Threat_B2-Safe_B2	5.924	32	< .001	1.031	0.602	1.450
Threat_B3-Safe_B3	5.994	32	< .001	1.043	0.612	1.464
Threat_B4-Safe_B4	4.779	32	< .001	0.832	0.430	1.224
Threat_B5-Safe_B5	4.476	32	< .001	0.779	0.384	1.165

Note. Student's t-test.

Note. For the Student t-test, effect size is given by Cohen's *d*.

Intra-individual correlation

Table S4-32. One Sample T-Test Against 0 for Intra-individual Correlation

	t	df	p	Cohen's d	95% CI for Cohen's d	
					Lower	Upper
r_to_z_-Fisher Normalization	5.579	32	< .001	0.971	0.551	1.381

Note. Student's t-test.

Note. For the Student t-test, effect size is given by Cohen's *d*.

Table S4-33. Descriptive Statistics (t-test) on Intra-individual Correlation

	N	Mean	SD	SE
r_to_z_-Fisher Normalization	33.000	0.402	0.414	0.072

STAI-Trait and Skin conductance level (SCL)

Table S4-34. Within Subjects Effects of Repeated Measures ANOVA (Condition & Time) on SCL with Z-score STAI-Trait

	Sphericity Correction	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	None	125.915	1.000	125.915	28.447	< .001	0.479
	Greenhouse-Geisser	125.915	1.000	125.915	28.447	< .001	0.479
Condition * ZST	None	0.019	1.000	0.019	0.004	0.948	0.000
	Greenhouse-Geisser	0.019	1.000	0.019	0.004	0.948	0.000
Residual	None	137.214	31.000	4.426			
	Greenhouse-Geisser	137.214	31.000	4.426			
Time	None	183.481 ^a	4.000 ^a	45.870 ^a	12.270 ^a	< .001 ^a	0.284
	Greenhouse-Geisser	183.481 ^a	2.878 ^a	63.762 ^a	12.270 ^a	< .001 ^a	0.284
Time * ZST	None	6.567 ^a	4.000 ^a	1.642 ^a	0.439 ^a	0.780 ^a	0.014
	Greenhouse-Geisser	6.567 ^a	2.878 ^a	2.282 ^a	0.439 ^a	0.717 ^a	0.014
Residual	None	463.557	124.000	3.738			
	Greenhouse-Geisser	463.557	89.205	5.197			
Condition * Time	None	17.892	4.000	4.473	1.345	0.257	0.042
	Greenhouse-Geisser	17.892	3.340	5.357	1.345	0.262	0.042
Condition * Time * ZST	None	9.804	4.000	2.451	0.737	0.569	0.023
	Greenhouse-Geisser	9.804	3.340	2.935	0.737	0.546	0.023
Residual	None	412.540	124.000	3.327			
	Greenhouse-Geisser	412.540	103.545	3.984			

Note. Type III Sum of Squares

^a Mauchly's test of sphericity indicates that the assumption of sphericity is violated ($p < .05$).

STAI-Trait and Subjective anxiety

Table S4-35. Within Subjects Effects of Repeated Measures ANOVA (Condition & Time) on Subjective Anxiety with Z-score STAI-Trait

	Sphericity Correction	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	None	51185.115	1.000	51185.115	50.981	< .001	0.622
	Greenhouse-Geisser	51185.115	1.000	51185.115	50.981	< .001	0.622
Condition * ZST	None	3063.006	1.000	3063.006	3.051	0.091	0.090
	Greenhouse-Geisser	3063.006	1.000	3063.006	3.051	0.091	0.090
Residual	None	31124.012	31.000	1004.000			
	Greenhouse-Geisser	31124.012	31.000	1004.000			
Time	None	1900.320 ^a	4.000 ^a	475.080 ^a	2.403 ^a	0.053 ^a	0.072
	Greenhouse-Geisser	1900.320 ^a	2.319 ^a	819.478 ^a	2.403 ^a	0.090 ^a	0.072
Time * ZST	None	92.347 ^a	4.000 ^a	23.087 ^a	0.117 ^a	0.976 ^a	0.004
	Greenhouse-Geisser	92.347 ^a	2.319 ^a	39.823 ^a	0.117 ^a	0.915 ^a	0.004
Residual	None	24510.695	124.000	197.667			
	Greenhouse-Geisser	24510.695	71.887	340.961			
Condition * Time	None	2116.067	4.000	529.017	4.024	0.004	0.115
	Greenhouse-Geisser	2116.067	3.227	655.741	4.024	0.008	0.115
Condition * Time * ZST	None	437.334	4.000	109.333	0.832	0.508	0.026
	Greenhouse-Geisser	437.334	3.227	135.524	0.832	0.487	0.026
Residual	None	16302.012	124.000	131.468			
	Greenhouse-Geisser	16302.012	100.037	162.961			

Note. Type III Sum of Squares

^a Mauchly's test of sphericity indicates that the assumption of sphericity is violated ($p < .05$).

STAI-Trait and Intra-individual correlation

Table S4-36. Pearson Correlation between intra-individual correlation and Z-score STAI-Trait

		r_to_z -Fisher Normalization
ZST	Pearson's r	-0.020
	p-value	0.913

Appendix to Chapter 4

Cardiac activity was recorded on participants from study one for exploratory purposes in order to understand if our results were replicable on a second physiological variable. The cardiac acquisition and processing were based on the study of Messerotti Benvenuti and colleagues (Messerotti Benvenuti, Buodo, Mennella, & Palomba, 2015). The electrocardiogram (ECG) was recorded using Ag/AgCl surface electrodes. They were placed on the participant's chest in a lead II configuration. A band-pass filtered (0.3–100 Hz) was applied on one signal and were digitized at a sample rate of 1000 Hz. For

three participants, one electrode was unplugged, and the cardiac signal was not recorded during the experimental session (final N=23). Heart rate was computed as the inter-beat interval of the ECG using a modified 'ECG processing' Matlab script (initially developed by Sergey Chernenko). Heart rate was first computed inside the entire duration of each block and was analyzed with repeated measures ANOVAs with Condition (Threat vs. Safe) and Time (Blocks 1 to 5) as within-subject factors. Then, we computed the heart rate after each scream. To do so, heart rates were determined for eight time windows of one second after each scream and compared to eight time windows before each scream. Heart rates were relative to a one second baseline period before the first time window. Repeated measures ANOVAs with Scream (Before vs. After) and Windows (1 to 8s) as within-subject factor were performed on heart rate variation.

Within a block, ANOVA revealed a main effect of Condition ($F(1,22) = 4.87$, $p = 0.038$, $\eta^2_p = 0.18$): heart rates were slower during threat relative to safe blocks. We observed an effect of Time, heart rates being decreased as the experiment progressed ($F(4,88) = 14.78$, $p_{\text{corr}} < 0.001$, $GG-\epsilon = 0.70$, $\eta^2_p = 0.40$). We did not observe a significant interaction between Time and Condition ($F(4,88) = 0.43$, $p = 0.79$, $\eta^2_p = 0.019$). The main effect of Scream did not reach significance but heart rates tended to be slower after than before a scream ($F(1,22) = 3.33$, $p = 0.081$, $\eta^2_p = 0.13$). We observed no main effect of Windows ($F(4,88) = 0.54$, $p_{\text{corr}} = 0.64$, $GG-\epsilon = 0.39$, $\eta^2_p = 0.024$). The interaction between Windows and Scream was not significant either ($F(7,154) = 1.15$, $p = 0.33$, $\eta^2_p = 0.050$).

Our cardiac results suggest that under unpredictable threat, heart rate decreases. For Lojowska and colleagues (Lojowska et al., 2015), heart rate deceleration is associated with an increase of attention as well as an enhancement of visual navigation. Our results seem to be consistent with, on one hand, theoretical models on defensive behavior which suggests the possibility to be attacked induces freezing strategies to facilitate the appraisal of the environment and on the other hand, threat-of-shock studies, which defend that uncertain risky contexts induce hypervigilance. However, while we can exclude the activity induced by screams from the global skin conductance activity, it is difficult to do it with the cardiac signal without creating an artefact. As we did not present additional stimuli in the safe condition, we can exclude our effect to be only explained by the presentation of seldom stimuli in threat blocks, independently of the stimuli valence, as we notably observed a propensity of the cardiac signal to decelerate just after a scream. When discussing with researchers having used to record cardiac activity, we realized we needed to be careful with our interpretation without a "stimulation-control" inside our safe blocks. In addition, because of technical problems, the final sample size is too small while the cardiac activity is really variable. For these reasons, we decided to provide these results in the Appendix and to describe them in a speculative way.

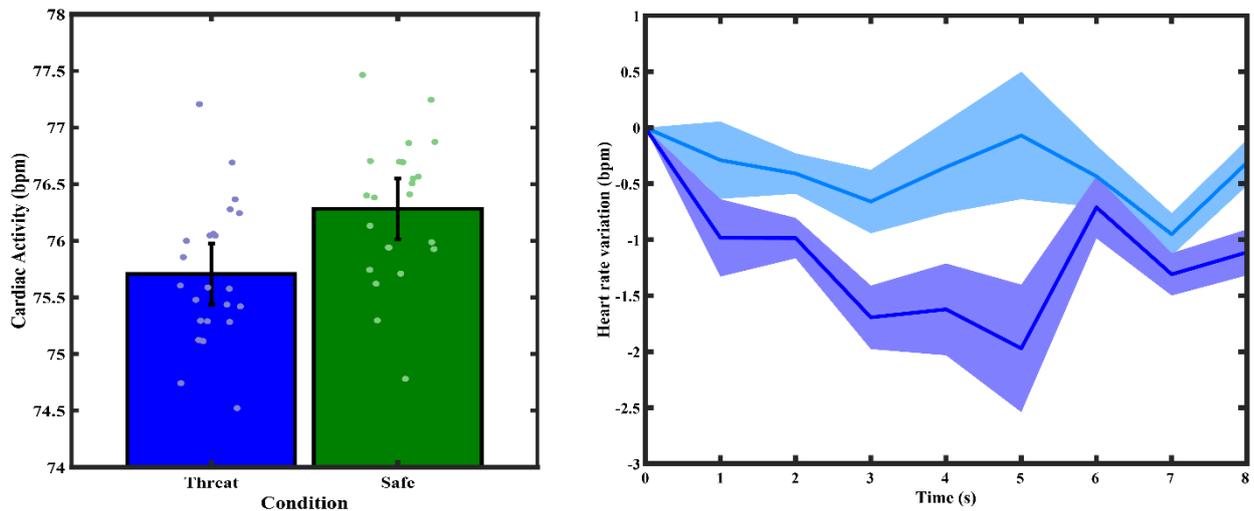


Figure A4-1. Left: heart rate mean during threat (blue) and safe (green) conditions. Right: heart rate variation over time before (Light blue) and after (Dark blue) the delivery of aversive scream. Shaded error bars indicate SEM.

Table A4-1. Within Subjects Effects of Repeated Measures ANOVA (Condition & Time) on Heart rate

	Sphericity Correction	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	None	18.845	1.000	18.845	4.866	0.038	0.181
	Greenhouse-Geisser	18.845	1.000	18.845	4.866	0.038	0.181
Residual	None	85.193	22.000	3.872			
	Greenhouse-Geisser	85.193	22.000	3.872			
Time	None	371.982 ^a	4.000 ^a	92.996 ^a	14.781 ^a	< .001 ^a	0.402
	Greenhouse-Geisser	371.982 ^a	2.806 ^a	132.560 ^a	14.781 ^a	< .001 ^a	0.402
Residual	None	553.643	88.000	6.291			
	Greenhouse-Geisser	553.643	61.735	8.968			
Condition * Time	None	5.305	4.000	1.326	0.431	0.786	0.019
	Greenhouse-Geisser	5.305	3.502	1.515	0.431	0.761	0.019
Residual	None	270.865	88.000	3.078			
	Greenhouse-Geisser	270.865	77.051	3.515			

Note. Type III Sum of Squares

^a Mauchly's test of sphericity indicates that the assumption of sphericity is violated ($p < .05$).

Table A4-2. Test of Sphericity for Repeated Measures ANOVA (Condition & Time) on Heart rate

	Mauchly's W	Approx. X ²	df	p	Greenhouse-Geisser ϵ	Huynh-Feldt ϵ	Lower Bound ϵ
Condition	1.000 ^a	NaN ^a	NaN ^a	NaN ^a	1.000 ^a	1.000 ^a	1.000 ^a
Time	0.410	18.190	9	0.034	0.702	0.815	0.250
Condition * Time	0.747	5.960	9	0.745	0.876	1.000	0.250

^a Singular error SSP matrix: The repeated measure has only two levels, or more levels than observations. When the repeated measure has two levels, the assumption of sphericity is always met.

Table A4-3. Within Subjects Effects of Repeated Measures ANOVA (Scream & Windows) on Heart rate variation

	Sphericity Correction	Sum of Squares	df	Mean Square	F	p	η^2_p
Scream	None	68.636	1.000	68.636	3.334	0.081	0.132
	Greenhouse-Geisser	68.636	1.000	68.636	3.334	0.081	0.132
Residual	None	452.962	22.000	20.589			
	Greenhouse-Geisser	452.962	22.000	20.589			
Windows	None	18.156 ^a	7.000 ^a	2.594 ^a	0.539 ^a	0.804 ^a	0.024
	Greenhouse-Geisser	18.156 ^a	2.737 ^a	6.633 ^a	0.539 ^a	0.641 ^a	0.024
Residual	None	741.189	154.000	4.813			
	Greenhouse-Geisser	741.189	60.216	12.309			
Scream * Windows	None	22.850 ^a	7.000 ^a	3.264 ^a	1.154 ^a	0.333 ^a	0.050
	Greenhouse-Geisser	22.850 ^a	2.444 ^a	9.351 ^a	1.154 ^a	0.330 ^a	0.050
Residual	None	435.804	154.000	2.830			
	Greenhouse-Geisser	435.804	53.762	8.106			

Note. Type III Sum of Squares

^a Mauchly's test of sphericity indicates that the assumption of sphericity is violated ($p < .05$).

Table A4. Test of Sphericity for Repeated Measures ANOVA (Scream & Windows) on Heart rate variation

	Mauchly's W	Approx. X²	df	p	Greenhouse-Geisser ϵ	Huynh-Feldt ϵ	Lower Bound ϵ
Scream	1.000 ^a	NaN ^a	NaN ^a	NaN ^a	1.000 ^a	1.000 ^a	1.000 ^a
Windows	0.001	129.150	27	< .001	0.391	0.452	0.143
Scream * Windows	7.977e -4	138.770	27	< .001	0.349	0.396	0.143

^a Singular error SSP matrix: The repeated measure has only two levels, or more levels than observations. When the repeated measure has two levels, the assumption of sphericity is always met.

Supplementary Material

Description

The present work investigates how the social Simon Effect (used as a proxy for co-representation of action) is modified under a shared (or not) threat context (Common vs. Non Common Group). To do so, we merge the Social Simon task designed by Sebanz et al. (2003) with a threat-of-scream procedure. We used SCL and subjective reports of anxiety to assess the efficiency of the threat-of-scream procedure and analyzed RT to compute the Social Simon Effect. This supplementary document provides details about the Methods as well as the full tables for all the analyses reported in the main text. We also report on a supplementary study corresponding to a classical version of Simon task (one participant responsible for the two color cues) with alternating threat and safe blocks. This supplementary study allowed us to check the differences between a solo and joint design about anxiety and cognitive interference. We observed two interesting results. First, threat didn't impact the classical Simon effect suggesting that the effect of threat on the Social Simon is specific to a joint design. Then, we observed that anxiety induction is stronger when participant is alone, suggesting that the presence of conspecifics mitigates anxiety of participants. All the methods, results and tabs related to this supplementary study are available in this document.

Summary

- Supplementary Results-Social Simon:** tabs for Social Simon (Common and NonCommon Group)
- Supplementary Study-Classical Simon:** Methods and results for the Classical Simon (Alone Group) including “**Exploratory result-Social Buffering**” part in which we compared the anxiety induction between the 3 groups.
- Demographic Information:** Auto-questionnaire, Gender, Age for the 3 Groups

Supplementary Results – Social Simon

Skin Conductance Level

Table S5-1. Within-Subjects Effects of Repeated Measures ANOVA (Condition, Time & Group) on SCL

	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	102.163	1	102.163	14.619	< .001	0.163
Condition * Group	1.678	1	1.678	0.240	0.626	0.003
Residual	524.121	75	6.988			
Time	239.170	1	239.170	41.060	< .001	0.354
Time * Group	0.418	1	0.418	0.072	0.790	0.001
Residual	436.867	75	5.825			
Condition * Time	3.591	1	3.591	0.910	0.343	0.012
Condition * Time * Group	5.902	1	5.902	1.496	0.225	0.020
Residual	295.890	75	3.945			

Note. Type III Sum of Squares

Table S5-2. Descriptive Statistics (ANOVA) - SCL

Condition	Time	Group	Mean	SD	N
Threat	B1	C	1.650	2.337	40
		NC	0.879	3.186	37
	B2	C	-0.681	2.900	40
		NC	-0.750	2.779	37
Safe	B1	C	-0.144	3.506	40
		NC	-0.065	2.995	37
	B2	C	-1.488	4.472	40
		NC	-1.816	3.803	37

Subjective Anxiety

Table S5-3. Within-Subjects Effects of Repeated Measures ANOVA (Condition, Time & Group) on Subjective Anxiety

	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	11160.707	1	11160.707	41.158	< .001	0.351
Condition * Group	156.245	1	156.245	0.576	0.450	0.008
Residual	20608.617	76	271.166			
Time	1132.215	1	1132.215	7.299	0.009	0.088
Time * Group	203.010	1	203.010	1.309	0.256	0.017
Residual	11789.545	76	155.126			
Condition * Time	0.088	1	0.088	0.002	0.969	0.000
Condition * Time * Group	0.267	1	0.267	0.005	0.945	0.000
Residual	4315.903	76	56.788			

Table S5-4. Descriptive Statistics (ANOVA) on Subjective Anxiety

Condition	Time	Group	Mean	SD	N
Threat	B1	C	40.000	20.698	40
		NC	38.079	23.665	38
	B2	C	34.600	19.263	40
		NC	35.789	22.849	38
Safe	B1	C	29.475	17.907	40
		NC	24.605	19.808	38
	B2	C	24.025	16.958	40
		NC	22.500	19.335	38

*Reaction Time***Table S5-5.** Within-Subjects Effects of Repeated Measures ANOVA (Condition, Congruency & Group) on RT

	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	417.198	1	417.198	1.329	0.253	0.017
Condition * Group	512.685	1	512.685	1.634	0.205	0.021
Residual	23537.257	75	313.830			
Congruency	6837.164	1	6837.164	52.320	< .001	0.411
Congruency * Group	18.871	1	18.871	0.144	0.705	0.002
Residual	9800.900	75	130.679			
Condition * Congruency	172.089	1	172.089	1.996	0.162	0.026
Condition * Congruency * Group	414.332	1	414.332	4.806	0.031	0.060
Residual	6465.660	75	86.209			

Table S5-6. Descriptive Statistics (ANOVA) on RT

Condition	Congruence	Group	Mean	SD	N
Threat	Cong	C	385.056	42.772	40
		NC	388.027	45.367	37
	Inc	C	393.165	44.418	40
		NC	401.770	49.535	37
Safe	Cong	C	384.483	43.878	40
		NC	386.932	41.948	37
	Inc	C	394.243	50.194	40
		NC	393.041	43.158	37

Simon Effect – Group Common

Table S5-7. Within-Subjects Effects of Repeated Measures ANOVA (Condition & Congruency) on RT

	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	2.557	1	2.557	0.007	0.935	0.000
Residual	14850.074	39	380.771			
Congruency	3193.233	1	3193.233	17.748	< .001	0.313
Residual	7016.759	39	179.917			
Condition * Congruency	27.248	1	27.248	0.356	0.554	0.009
Residual	2985.350	39	76.547			

Table S5-8. One Sample T-Test Against 0 for SE

	t	df	p	Cohen's d	95% CI for Cohen's d	
					Lower	Upper
Safe	4.304	39	< .001	0.681	0.332	1.021
Threat	2.926	39	0.006	0.463	0.134	0.786

Note. Student's t-test.

Note. For the Student t-test, effect size is given by Cohen's *d*.

Table S5-9. Descriptive Statistics (t-test) on SE

	N	Mean	SD	SE
Threat_SE	40	8.109	17.528	2.771
Safe_SE	40	9.760	14.342	2.268

Table S5-10. Pearson Correlations between the SE in Threat and Safe Condition

		Threat_SE
Safe_SE	Pearson's r	0.411
	p-value	0.008

Simon Effect – Group NonCommon

Table S5-11. Within-Subjects Effects of Repeated Measures ANOVA (Condition & Congruency) on RT

	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	892.646	1	892.646	3.699	0.062	0.093
Residual	8687.183	36	241.311			
Congruency	3645.193	1	3645.193	47.134	< .001	0.567
Residual	2784.141	36	77.337			
Condition * Congruency	539.227	1	539.227	5.578	0.024	0.134
Residual	3480.310	36	96.675			

Note. Type III Sum of Squares

Table S5-12. One Sample T-Test Against 0 for SE

	t	df	p	Cohen's d	95% CI for Cohen's d	
					Lower	Upper
Safe	3.340	37	0.002	0.542	0.198	0.880
Threat	5.833	37	< .001	0.946	0.558	1.325

Note. Student's t-test.

Note. For the Student t-test, effect size is given by Cohen's *d*.

Table S5-13. Descriptive Statistics (t-test) on SE

	N	Mean	SD	SE
Threat_SE	37	13.743	14.745	2.424
Safe_SE	37	6.108	11.429	1.879

Table S5-14. Pearson Correlations between the SE in Threat and Safe Condition

		Threat_SE
Safe_SE	Pearson's r	-0.115
	p-value	0.499

Supplementary Study- Classical Simon

To better understand our effect in a joint design, we decided to investigate the classical Simon effect (where one participant takes charge of all responses) under threat. First, it will help us understand whether threat impacts co-representation or merely cognitive performance, independently of the social nature of the Social Simon task. If results showed that threat doesn't impact the Simon effect while it modifies alter-centric interference during the Social Simon task, this difference should necessarily be conditioned by the social context. Then, it will allow us to control if our anxiety manipulation is sensitive to the presence of an affiliative conspecifics in the experimental room.

Materials and Methods

Thirty-eight healthy volunteers (19 females, 22.9 age \pm 2.8 years SD) were recruited similarly than for the social Simon task. Here, participants performed the classical version of the Simon task through safe and threat blocks (Hommel, 2011; Simon & Rudell, 1967). In this case, the participant was alone and responsible for the 2 key-color cue associations. Participants responded using their 2 thumbs to facilitate the recording of SCL. The temporal organization of a trial, the number of trials and the temporal organization of blocks as well as the number of blocks were the same than for the Social Simon version. Regarding skin conductance recording, as participant needed to use their non-dominant hand to answer, electrodes were exceptionally attached to the middle phalanges of the middle and ring fingers. Otherwise, the same set up was applied on SCL recording. To control that participant answers

with the left hand did not generate motor artefact on skin conductance recording, we computed the absolute value of variation of skin conductance activity 1.5s after pressing the left (i.e. hand with electrodes) or right (i.e. hand without electrodes) key. We observed no difference between right and left hand keypress ($t(37) = 1.60, p = 0.12, \text{Mean Difference} = 0.003\mu\text{S}, \text{SE} = 0.002\mu\text{S}$) which confirmed that answering with the hand where the electrodes were attached didn't contaminate the electrophysiological signal. Subjective Anxiety, SCL and RT were analyzed identically to the Social Simon data.

Results

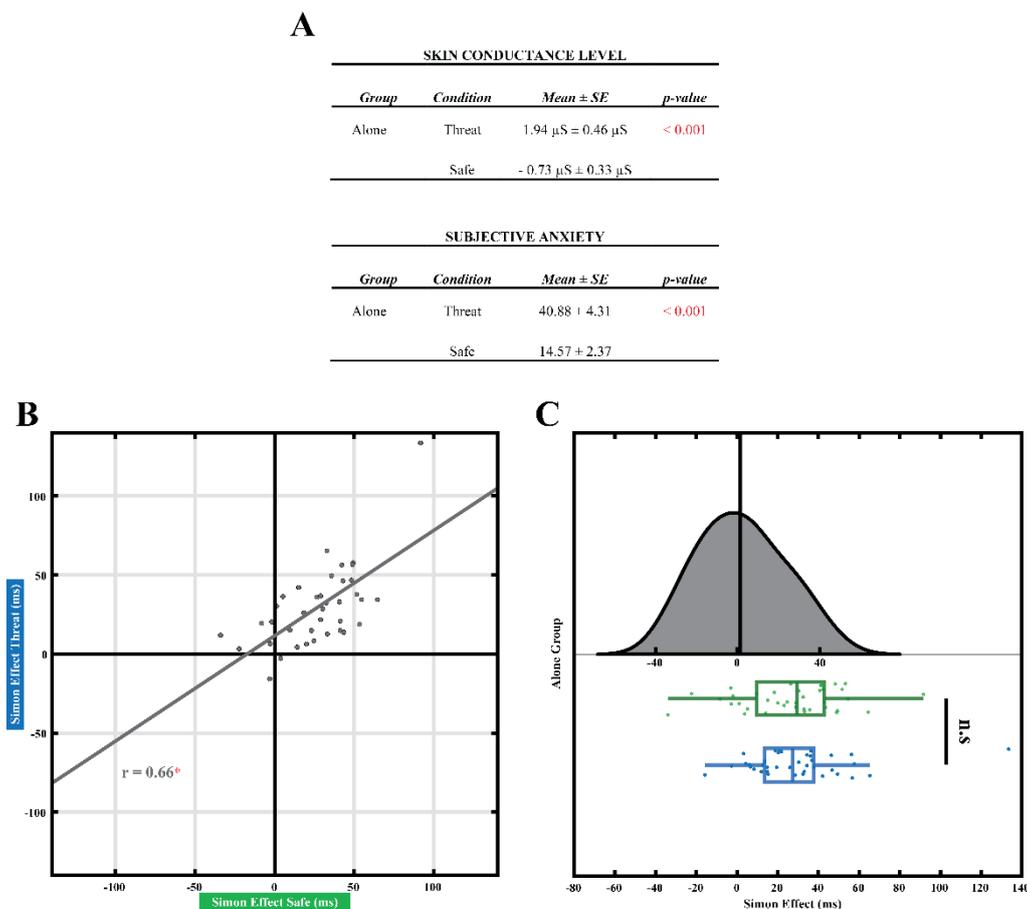


Figure S5-1: (A) Skin Conductance level and Subjective reports of anxiety. P-value for t-test contrasting threat against safe blocks are provided. (B) Between-subjects correlations between the magnitude of the Social SE in safe and threat blocks for the Alone Group. (C) Simon Effect for the Alone group. Points represent individual data. Distribution in the upper part of the plot represents the difference of Simon Effect in Threat and Safe block and the black line the median of this distribution. The distribution is center to 1ms. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; n.s. = $p > 0.05$.

Skin Conductance Level

Participants' tonic skin conductance activity (SCL) was greater during Threat relative to Safe blocks (**Figure S5-1A**). We observed a main effect of Time suggesting a decrease of SCL across the

experiment. However, there was no significant interaction between Condition and Time, suggesting that the difference in SCL between Safe and Threat did not change with time

Table S5-15. Within-Subjects Effects of Repeated Measures ANOVA (Condition & Time) on SCL

	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	272.223	1	272.223	25.752	< .001	0.410
Residual	391.132	37	10.571			
Time	185.502	1	185.502	35.759	< .001	0.491
Residual	191.938	37	5.188			
Condition * Time	3.769	1	3.769	0.470	0.497	0.013
Residual	296.678	37	8.018			

Note. Type III Sum of Squares

Table S5-16. Descriptive Statistics (ANOVA) - SCL

Condition	Time	Mean	SD	N
Threat	B1	3.204	3.937	38
	B2	0.680	2.723	38
Safe	B1	0.213	2.373	38
	B2	-1.682	3.005	38

Subjective Anxiety

Participants reported higher scores on the anxiety scale at the end of Threat compared to Safe blocks (**Figure S5-1A**). There is no significant main effect of Time. However, there is a significant interaction between Condition and Time on subjective reports explained by respectively a small decreased and a small increase of subjective anxiety during the second threat (-3.92) and safe block (+1.45).

Table S5-17. Within-Subjects Effects of Repeated Measures ANOVA (Condition & Time) on Subjective Anxiety

	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	26315.789	1	26315.789	39.378	< .001	0.516
Residual	24726.711	37	668.289			
Time	58.132	1	58.132	0.431	0.515	0.012
Residual	4987.368	37	134.794			
Condition * Time	273.789	1	273.789	4.066	0.051	0.099
Residual	2491.711	37	67.344			

Note. Type III Sum of Squares

Table S5-18. Descriptive Statistics (ANOVA) on Subjective Anxiety

Condition	Time	Mean	SD	N
Threat	B1	42.842	28.703	38
	B2	38.921	26.346	38
Safe	B1	13.842	16.433	38
	B2	15.289	15.856	38

Reaction Time

ANOVA revealed a significant trend to a main effect of Condition on RT suggesting that reaction time was faster in threat block compared to safe. ANOVA revealed a main effect of Congruency on RT, typical of the Simon effect. Participant answered slowly during incongruent trials compared to congruent ones. But interaction between Congruency and Condition was found not significant. T-test against zero suggested that the Simon Effect was induced in both conditions (**Figure S5-1C**).

Table S5-19. Within-Subjects Effects of Repeated Measures ANOVA (Condition & Congruency) on RT

	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	1153.057	1	1153.057	3.092	0.087	0.077
Residual	13798.403	37	372.930			
Congruency	30141.971	1	30141.971	57.681	< .001	0.609
Residual	19334.874	37	522.564			
Condition * Congruency	52.434	1	52.434	0.482	0.492	0.013
Residual	4023.810	37	108.752			

Note. Type III Sum of Squares

Table S5-20. Descriptive Statistics (ANOVA) on RT

Condition	Congruency	Mean	SD	N
Threat	Cong	449.427	60.239	38
	Inc	478.766	67.680	38
Safe	Cong	456.110	56.983	38
	Inc	483.100	63.249	38

Table S5-21. One Sample T-Test Against 0 for SE_Threat - SE_Safe

	t	df	p	Cohen's d	95% CI for Cohen's d	
					Lower	Upper
Safe	6.655	37	< .001	1.080	0.674	1.476
Threat	7.162	37	< .001	1.162	0.744	1.570

Note. Student's t-test.

Note. For the Student t-test, effect size is given by Cohen's *d*.

Table S5-22. Descriptive Statistics (t-test) on SE

	N	Mean	SD	SE
Threat_SE	38	29.339	25.252	4.096
Safe_SE	38	26.989	24.999	4.055

Between-Subject Correlation

To investigate if shared phenomena took place under safe and threat conditions, we computed a between-subject correlation. Results revealed a positive correlation ($r = 0.66$) between the magnitude of the Simon Effect in the safe and the threat condition (**Figure S5-1B**).

Table S5-23. Pearson Correlations between the SE in Threat and Safe Condition

		Threat_SE
Safe_SE	Pearson's r	0.656
	p-value	< .001

Exploratory result – Social Buffering

To control if our anxiety manipulation is impacted by a joint task design, we performed an Anova on Skin Conductance Level and subjective anxiety with Condition (Threat versus Safe) as within-subject factor and Group (Alone vs. Common vs. NonCommon) as between-subject factor. The Anova revealed that the difference between Threat and Safe were higher in Alone Group compared to the two others groups for both SCL and subjective anxiety. Moreover, at the end of the experiment, we also asked participants to rate how aversive the screams were for them and how much they felt preoccupied by the possibility that a scream would be delivered during threat blocks (from 0 - not at to 10 - extremely). We performed an Anova on both scores with group as factors. If aversiveness score were similar for our 3 groups, Anova revealed that the preoccupation score was higher for the alone Group. Altogether, these result suggest that a phenomenon of social buffering (i.e. the presence of an affiliative conspecific mitigates stress responses in a subject) took place in a joint design compared to the alone group. Interestingly, preoccupation scored correlated positively the increase of both SCL and subjective anxiety confirming that unpredictability of screams matter in the anxiety manipulation but seems to be regulated by the presence of conspecifics (see **Tables S5-24 - S5-34**).

Debriefing Participants

Table S5-24. ANOVA (Group) on Preoccupation scores

Cases	Sum of Squares	df	Mean Square	F	p	η^2
Group	84.652	2.000	42.326	4.704	0.011	0.077
Residual	1016.857	113.000	8.999			

Note. Type III Sum of Squares

Table S5-25. Post Hoc Comparisons on Preoccupation scores

		Mean Difference	SE	t	p _{holm}
A	C	2.014	0.680	2.964	0.011
	NC	1.500	0.688	2.180	0.063
C	NC	-0.514	0.680	-0.757	0.451

Table S5-26. Descriptive Statistics (ANOVA) on Preoccupation scores

Group	Mean	SD	N
A	6.039	3.247	38
C	4.025	2.812	40
NC	4.539	2.933	38

Table S5-27. ANOVA (Group) on Aversiveness scores

Cases	Sum of Squares	df	Mean Square	F	p	η^2
Group	16.236	2.000	8.118	1.432	0.243	0.025
Residual	640.454	113.000	5.668			

Note. Type III Sum of Squares

Table S5-28. Descriptive Statistics (ANOVA) on Aversiveness scores

Group	Mean	SD	N
A	5.079	2.223	38
C	4.375	2.317	40
NC	4.211	2.591	38

Skin Conductance Level

Table S5-29. Within-Subjects Effects of Repeated Measures ANOVA (Condition & Group) on SCL

	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	159.823	1	159.823	39.156	< .001	0.259
Condition * Group	29.842	2	14.921	3.656	0.029	0.061
Residual	457.147	112	4.082			

Note. Type III Sum of Squares

Table S5-30. Post Hoc Comparisons - ANOVA (Group) on SCL Difference between Safe and Threat

		Mean Difference	SE	t	p _{holm}
A	C	1.354	0.647	2.092	0.077
	NC	1.671	0.660	2.533	0.038
C	NC	0.318	0.652	0.487	0.627

Table S5-31. Pearson Correlations between the Preoccupation Score and SCL

		Pearson		Spearman	
		r	p	rho	p
Threat-safe	- Preoccupation	0.294 **	0.001	0.264 **	0.004

* p < .05, ** p < .01, *** p < .001

Subjective Anxiety

Table S5-32. Within-Subjects Effects of Repeated Measures ANOVA (Condition & Group) on Subjective Anxiety

	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	16261.411	1	16261.411	81.064	< .001	0.418
Condition * Group	2722.288	2	1361.144	6.785	0.002	0.107
Residual	22667.664	113	200.599			

Note. Type III Sum of Squares

Table S5-33. Descriptive Statistics (ANOVA) on Subjective Anxiety Difference between Safe and Threat

		Mean Difference	SE	t	p _{holm}
A	C	15.766	4.537	3.475	0.002
	NC	12.934	4.595	2.815	0.012
C	NC	-2.832	4.537	-0.624	0.534

Table S5-34. Pearson Correlations between the Preoccupation Score and Subjective Anxiety

		Pearson		Spearman	
		r	p	rho	p
Threat-safe	- Preoccupation	0.497 ***	< .001	0.446 ***	< .001

* p < .05, ** p < .01, *** p < .001

Demographic Information

First, we provide here the characteristics of each Group (age, gender, auto-questionnaire scores for STAI and LSAS) and the distributions of scores for each auto-questionnaire. Then, we checked if participants were similar in general and social anxiety trait as well as anxiety state scores (assessed by the auto-questionnaires). Anova revealed that NonCommon Group was associated with a score of general anxiety trait slightly higher than the Alone Group (MeanDifference = 4.92, SE = 2.04, p = 0.052). Otherwise, no other difference was found significant between our three groups.

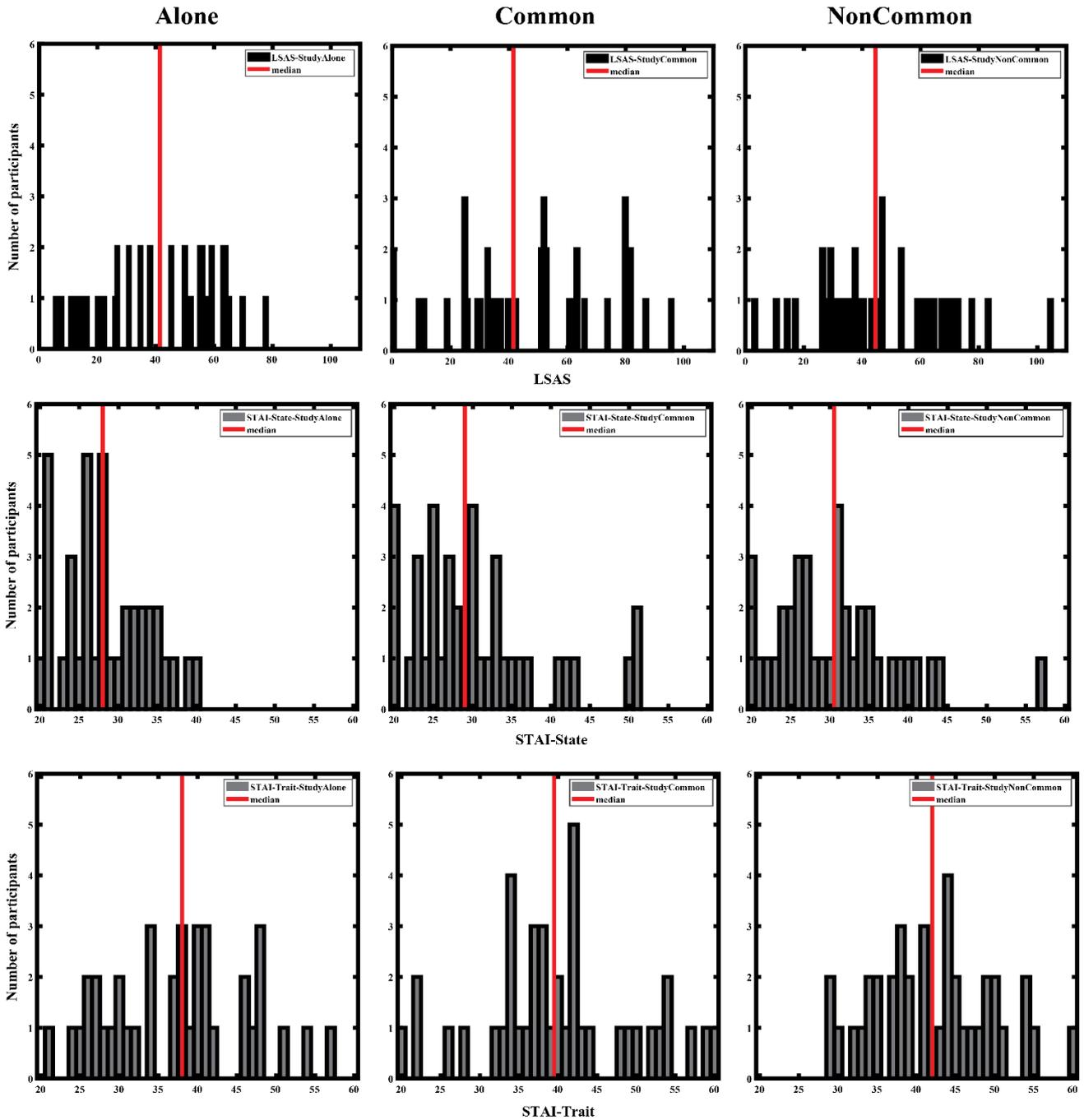


Figure S5-2. Distribution of STAI-State, STAI-Trait and LSAS for each group

Table S5-35. Characteristics of the sample of Alone Group

Size	Gender	Age	STAI-State	STAI-Trait	LSAS
38	19 F/19 M	22.9 ± 2.8 y.o SD	28.5 ± 5.4 SD	37.2 ± 8.9 SD	40.5 ± 20.1 SD

Table S5-36. Characteristics of the sample of Common Group

Size	Gender	Age	STAI-State	STAI-Trait	LSAS
40	20 F/ 20 M	23.4 ± 4.3 y.o SD	30.5 ± 8.3 SD	40.2 ± 9.8 SD	47.1 ± 25.7 SD

Table S5-37. Characteristics of the sample of NonCommon Group

Size	Gender	Age	STAI-State	STAI-Trait	LSAS
38	18 F/20 M	23.6 ± 4.5 y.o SD	30.7 ± 7.8 SD	42.2 ± 7.7 SD	46.3 ± 22.1 SD

*Group comparison (auto-questionnaire)***Table S5-38.** ANOVA (Group) on STAI-E

Cases	Sum of Squares	df	Mean Square	F	p	η^2_p
Group	111.543	2.000	55.771	1.045	0.355	0.018
Residual	6029.216	113.000	53.356			

Note. Type III Sum of Squares

Table S5-39. Descriptive Statistics (ANOVA) on STAI-E

Group	Mean	SD	N
C	30.450	8.268	40
NC	30.711	7.843	38
A	28.500	5.421	38

Table S5-40. ANOVA (Group) on STAI-T

Cases	Sum of Squares	df	Mean Square	F	p	η^2_p
Group	466.739	2.000	233.370	2.952	0.056	0.050
Residual	8934.321	113.000	79.065			

Note. Type III Sum of Squares

Table S5-41. Post Hoc Comparisons on STAI-T

		Mean Difference	SE	t	p _{holm}
C	NC	-1.958	2.014	-0.972	0.333
	A	2.963	2.014	1.471	0.288
NC	A	4.921	2.040	2.412	0.052

Table S5-42. Descriptive Statistics (ANOVA) on STAI-T

Group	Mean	SD	N
C	40.200	9.832	40
NC	42.158	7.723	38
A	37.237	8.940	38

Table S5-43. ANOVA (Group) on LSAS

Cases	Sum of Squares	df	Mean Square	F	p	η^2
Group	1001.765	2.000	500.882	0.961	0.386	0.017
Residual	58890.442	113.000	521.154			

Note. Type III Sum of Squares

Table S5-44. Descriptive Statistics (ANOVA) on LSAS

Group	Mean	SD	N
A	40.474	20.209	38
C	47.100	25.706	40
NC	46.263	22.061	38

Appendix to Chapter 5

This article is currently *under revision*. Integrating the remarks of reviewers was not possible before the submission of this dissertation. I believed that it is important for the readers to be aware of the main criticisms noticed by the reviewers to judge the quality of this study now that it has been peer-reviewed. Both reviewers appreciated the research question and the approach we have chosen to answer it. At the same time, they raised a series of critical yet constructive comments. I will summarize here the main remarks of the review.

First, reviewers reminded us that it is complicated to conclude on a null effect: reviewers suggested that this study doesn't provide evidence that "co-representation is preserved under threat". Then, they discussed the possibility that our sample size is probably too small for a between-subject comparison and that our p-value is close to statistical significance. They questioned the possibility that our effect is a false positive. In addition, they believed that our correlation in the common group is likely to be driven by four outliers (two on the lower and two on the upper side). For them, Bayesian statistics are recommended to understand the level of evidence brought by our study.

Then, the reviewers wondered if our results can really be interpreted in terms of altruism and self-preservative motives in a task in which there is no potential for self-preservative or helping behaviors. Indeed, participants are independently responsible for one color cue and threat is independent of participants' behaviors. Moreover, the difference of reaction time could be explained by low-level interpretations.

We want to thank the reviewers and the editor for their comments and we will try to discuss part of them inside the discussion part of this dissertation.

Supplementary Material

Description

The present work aimed at assessing (i) the influence of gaze direction (direct / averted) on the communication functions of fearful faces (distress signal / danger signal); (ii) the impact of threat on distress versus danger signal prioritization. First, we confirmed that gaze orientation modulates the signal conveyed by fearful faces: direct gaze is more associated with a need-for-help signal while averted gaze is more associated with danger-related information. Then, we showed that threat induce a bias in the detection of danger-related information, without impacting the perception of affiliation signals.

This supplementary document provides details about the Methods (the characteristics of the sampling distribution and debriefing that concluded the experimental session of study 2) as well as the tabs of results for all the analyses reported in the main manuscript.

Supplementary Results – Study One

Table S6-1. Within-Subjects Effects of Repeated Measures ANOVA (Question, Gaze & Emotion) on Score

	Sum of Squares	df	Mean Square	F	p	η^2_p
Question	189.362	1	189.362	1.570	0.214	0.020
Residual	9286.375	77	120.602			
Emotion	378989.893	1	378989.893	805.891	< .001	0.913
Residual	36211.113	77	470.274			
Gaze	681.400	1	681.400	11.659	0.001	0.132
Residual	4500.157	77	58.444			
Question * Emotion	1368.360	1	1368.360	13.753	< .001	0.152
Residual	7660.938	77	99.493			
Question * Gaze	1602.722	1	1602.722	32.894	< .001	0.299
Residual	3751.740	77	48.724			
Emotion * Gaze	1315.093	1	1315.093	39.979	< .001	0.342
Residual	2532.908	77	32.895			
Question * Emotion * Gaze	171.828	1	171.828	7.155	0.009	0.085
Residual	1849.147	77	24.015			

Note. Type III Sum of Squares

Table S6-2. Descriptive Statistics (ANOVA) - Score

Question	Emotion	Gaze	Mean	SD	N
Danger	F	A	69.918	14.849	78
		D	66.477	15.226	78
	N	A	19.521	14.334	78
		D	12.372	11.545	78
Help	F	A	61.600	17.641	78
		D	66.668	13.984	78
	N	A	19.225	15.597	78
		D	16.388	13.517	78

Supplementary Results – Study Two

Subjective Anxiety

Table S6-3. Within-Subjects Effects of Repeated Measures ANOVA (Condition & Time) on Subjective Anxiety

	Sphericity Correction	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	None	6291.736	1.000	6291.736	12.310	0.001	0.298
	Greenhouse-Geisser	6291.736	1.000	6291.736	12.310	0.001	0.298
Residual	None	14822.681	29.000	511.127			
	Greenhouse-Geisser	14822.681	29.000	511.127			
Time	None	978.314 ^a	5.000 ^a	195.663 ^a	1.742 ^a	0.129 ^a	0.057
	Greenhouse-Geisser	978.314 ^a	3.715 ^a	263.347 ^a	1.742 ^a	0.151 ^a	0.057
Residual	None	16290.769	145.000	112.350			
	Greenhouse-Geisser	16290.769	107.733	151.215			
Condition * Time	None	574.781 ^a	5.000 ^a	114.956 ^a	0.895 ^a	0.486 ^a	0.030
	Greenhouse-Geisser	574.781 ^a	3.200 ^a	179.632 ^a	0.895 ^a	0.452 ^a	0.030
Residual	None	18618.303	145.000	128.402			
	Greenhouse-Geisser	18618.303	92.793	200.642			

Note. Type III Sum of Squares

^a Mauchly's test of sphericity indicates that the assumption of sphericity is violated ($p < .05$).

Table S6-4. Test of Sphericity for Repeated Measures ANOVA (Condition & Time) on Subjective Anxiety

	Mauchly's W	Approx. X²	df	p	Greenhouse-Geisser ϵ	Huynh-Feldt ϵ	Lower Bound ϵ
Condition	1.000 ^a	NaN ^a	NaN ^a	NaN ^a	1.000 ^a	1.000 ^a	1.000 ^a
Time	0.327	30.302	14	0.007	0.743	0.866	0.200
Condition * Time	0.199	43.735	14	< .001	0.640	0.729	0.200

^a Singular error SSP matrix: The repeated measure has only two levels, or more levels than observations. When the repeated measure has two levels, the assumption of sphericity is always met.

Table S6-5. Descriptive Statistics (ANOVA) - Subjective Anxiety

Condition	Time	Mean	SD	N
S	1	19.167	18.436	30
	2	20.167	17.354	30
	3	23.567	23.453	30
	4	19.333	18.291	30
	5	18.667	16.336	30
	6	17.700	16.949	30
T	1	29.233	22.411	30
	2	32.267	22.954	30
	3	27.500	23.236	30
	4	27.767	24.228	30
	5	27.267	25.712	30
	6	24.733	22.545	30

Probability of fear response

Table S6-6. Within-Subjects Effects of Repeated Measures ANOVA (Condition, Gaze & Intensity) on P(*fear*)

	Sphericity Correction	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	None	0.021	1.000	0.021	0.710	0.406	0.024
	Greenhouse-Geisser	0.021	1.000	0.021	0.710	0.406	0.024
Residual	None	0.851	29.000	0.029			
	Greenhouse-Geisser	0.851	29.000	0.029			
Gaze	None	1.043	1.000	1.043	23.342	< .001	0.446
	Greenhouse-Geisser	1.043	1.000	1.043	23.342	< .001	0.446
Residual	None	1.295	29.000	0.045			
	Greenhouse-Geisser	1.295	29.000	0.045			
Intensity	None	54.068 ^a	7.000 ^a	7.724 ^a	247.314 ^a	< .001 ^a	0.895
	Greenhouse-Geisser	54.068 ^a	1.365 ^a	39.612 ^a	247.314 ^a	< .001 ^a	0.895
Residual	None	6.340	203.000	0.031			
	Greenhouse-Geisser	6.340	39.583	0.160			
Condition * Gaze	None	0.031	1.000	0.031	4.998	0.033	0.147
	Greenhouse-Geisser	0.031	1.000	0.031	4.998	0.033	0.147
Residual	None	0.181	29.000	0.006			
	Greenhouse-Geisser	0.181	29.000	0.006			
Condition * Intensity	None	0.063 ^a	7.000 ^a	0.009 ^a	1.789 ^a	0.091 ^a	0.058
	Greenhouse-Geisser	0.063 ^a	4.157 ^a	0.015 ^a	1.789 ^a	0.133 ^a	0.058
Residual	None	1.022	203.000	0.005			
	Greenhouse-Geisser	1.022	120.547	0.008			
Gaze * Intensity	None	0.265	7.000	0.038	7.500	< .001	0.205
	Greenhouse-Geisser	0.265	4.855	0.055	7.500	< .001	0.205
Residual	None	1.024	203.000	0.005			
	Greenhouse-Geisser	1.024	140.782	0.007			
Condition * Gaze * Intensity	None	0.033 ^a	7.000 ^a	0.005 ^a	1.149 ^a	0.334 ^a	0.038
	Greenhouse-Geisser	0.033 ^a	4.775 ^a	0.007 ^a	1.149 ^a	0.337 ^a	0.038
Residual	None	0.826	203.000	0.004			
	Greenhouse-Geisser	0.826	138.465	0.006			

Note. Type III Sum of Squares

^a Mauchly's test of sphericity indicates that the assumption of sphericity is violated ($p < .05$).

Table S6-7. Test of Sphericity for Repeated Measures ANOVA (Condition, Gaze & Intensity) on P(*fear*)

	Mauchly's W	Approx. X ²	df	p	Greenhouse- Geisser ε	Huynh- Feldt ε	Lower Bound ε
Condition	1.000 ^a	NaN ^a	NaN ^a	NaN ^a	1.000 ^a	1.000 ^a	1.000 ^a
Gaze	1.000 ^a	NaN ^a	NaN ^a	NaN ^a	1.000 ^a	1.000 ^a	1.000 ^a
Intensity	6.493e-6	315.969	27	< .001	0.195	0.201	0.143
Condition * Gaze	1.000 ^a	NaN ^a	NaN ^a	NaN ^a	1.000 ^a	1.000 ^a	1.000 ^a
Condition * Intensity	0.053	77.805	27	< .001	0.594	0.706	0.143
Gaze * Intensity	0.250	36.671	27	0.105	0.694	0.850	0.143
Condition * Gaze * Intensity	0.176	46.026	27	0.013	0.682	0.833	0.143

^a Singular error SSP matrix: The repeated measure has only two levels, or more levels than observations. When the repeated measure has two levels, the assumption of sphericity is always met.

Table S6-8. Descriptive Statistics (ANOVA) - P(*fear*)

Condition	Gaze	Intensity	Mean	SD	N
S	D	0	9.815	8.623	30
		1	21.574	11.913	30
		2	30.463	15.823	30
		3	48.889	15.724	30
		4	58.796	15.545	30
		5	70.741	15.961	30
		6	77.685	16.594	30
	A	0	14.722	13.235	30
		1	32.685	17.319	30
		2	42.130	17.109	30
		3	54.630	18.774	30
		4	65.648	17.786	30
		5	73.148	17.859	30
		6	78.704	20.247	30
T	D	0	12.685	13.950	30
		1	20.463	15.379	30
		2	34.815	14.102	30
		3	44.907	13.571	30
		4	59.907	14.270	30
		5	69.630	14.824	30
		6	75.463	17.630	30
	A	0	17.593	13.198	30
		1	33.611	16.334	30
		2	44.815	16.028	30
		3	54.537	16.205	30
		4	67.222	17.498	30
		5	76.204	18.493	30
		6	82.130	17.968	30
	7	85.556	17.874	30	

Reaction Time

Table S6-9. Within-Subjects Effects of Repeated Measures ANOVA (Condition, Gaze & Intensity) on RT

	Sphericity Correction	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	None	0.007	1.000	0.007	0.435	0.515	0.015
	Greenhouse-Geisser	0.007	1.000	0.007	0.435	0.515	0.015
Residual	None	0.435	29.000	0.015			
	Greenhouse-Geisser	0.435	29.000	0.015			
Gaze	None	0.018	1.000	0.018	8.279	0.007	0.222
	Greenhouse-Geisser	0.018	1.000	0.018	8.279	0.007	0.222
Residual	None	0.064	29.000	0.002			
	Greenhouse-Geisser	0.064	29.000	0.002			
Intensity	None	0.683 ^a	7.000 ^a	0.098 ^a	25.251 ^a	< .001 ^a	0.465
	Greenhouse-Geisser	0.683 ^a	2.492 ^a	0.274 ^a	25.251 ^a	< .001 ^a	0.465
Residual	None	0.784	203.000	0.004			
	Greenhouse-Geisser	0.784	72.278	0.011			
Condition * Gaze	None	0.006	1.000	0.006	4.259	0.048	0.128
	Greenhouse-Geisser	0.006	1.000	0.006	4.259	0.048	0.128
Residual	None	0.038	29.000	0.001			
	Greenhouse-Geisser	0.038	29.000	0.001			
Condition * Intensity	None	0.004	7.000	6.069e -4	0.540	0.803	0.018
	Greenhouse-Geisser	0.004	5.675	7.487e -4	0.540	0.767	0.018
Residual	None	0.228	203.000	0.001			
	Greenhouse-Geisser	0.228	164.571	0.001			
Gaze * Intensity	None	0.060 ^a	7.000 ^a	0.009 ^a	5.265 ^a	< .001 ^a	0.154
	Greenhouse-Geisser	0.060 ^a	3.623 ^a	0.016 ^a	5.265 ^a	< .001 ^a	0.154
Residual	None	0.328	203.000	0.002			
	Greenhouse-Geisser	0.328	105.065	0.003			
Condition * Gaze * Intensity	None	0.007	7.000	0.001	0.791	0.596	0.027
	Greenhouse-Geisser	0.007	5.254	0.001	0.791	0.563	0.027
Residual	None	0.272	203.000	0.001			
	Greenhouse-Geisser	0.272	152.364	0.002			

Note. Type III Sum of Squares

^a Mauchly's test of sphericity indicates that the assumption of sphericity is violated ($p < .05$).

Table S6-10. Test of Sphericity for Repeated Measures ANOVA (Condition, Gaze & Intensity) on RT

	Mauchly's W	Approx. X ²	df	p	Greenhouse- Geisser ε	Huynh- Feldt ε	Lower Bound ε
Condition	1.000 ^a	NaN ^a	NaN ^a	NaN ^a	1.000 ^a	1.000 ^a	1.000 ^a
Gaze	1.000 ^a	NaN ^a	NaN ^a	NaN ^a	1.000 ^a	1.000 ^a	1.000 ^a
Intensity	0.007	130.815	27	< .001	0.356	0.392	0.143
Condition * Gaze	1.000 ^a	NaN ^a	NaN ^a	NaN ^a	1.000 ^a	1.000 ^a	1.000 ^a
Condition * Intensity	0.376	25.840	27	0.533	0.811	1.000	0.143
Gaze * Intensity	0.092	63.037	27	< .001	0.518	0.601	0.143
Condition * Gaze * Intensity	0.314	30.666	27	0.291	0.751	0.936	0.143

^a Singular error SSP matrix: The repeated measure has only two levels, or more levels than observations. When the repeated measure has two levels, the assumption of sphericity is always met.

Table S6-11. Descriptive Statistics (ANOVA) - RT

Condition	Gaze	Intensity	Mean	SD	N
S	D	0	742.046	112.525	30
		1	767.961	123.637	30
		2	774.997	124.517	30
		3	790.650	140.797	30
		4	772.148	135.060	30
		5	757.551	135.374	30
		6	731.933	132.037	30
	A	0	777.457	134.126	30
		1	790.522	129.385	30
		2	788.325	134.195	30
		3	792.941	150.773	30
		4	762.010	124.740	30
		5	747.031	128.439	30
		6	723.059	126.325	30
T	D	0	751.546	105.302	30
		1	763.174	112.489	30
		2	784.548	121.495	30
		3	793.149	116.952	30
		4	763.515	128.056	30
		5	747.161	120.259	30
		6	736.745	123.596	30
	A	0	713.863	120.813	30
		1	788.688	143.846	30
		2	803.008	139.171	30
		3	797.683	128.805	30
		4	789.079	121.029	30
		5	784.144	146.312	30
		6	754.435	121.630	30
7	735.837	131.483	30		
7	709.460	118.364	30		

False Alarms

Table S6-12. Within-Subjects Effects of Repeated Measures ANOVA (Condition & Gaze) on False Alarms with Z-score STAI-Trait

	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	142.040	1	142.040	2.443	0.129	0.080
Condition * STAI-T	349.935	1	349.935	6.019	0.021	0.177
Residual	1628.010	28	58.143			
Gaze	682.163	1	682.163	10.401	0.003	0.271
Gaze * STAI-T	10.309	1	10.309	0.157	0.695	0.006
Residual	1836.463	28	65.588			
Condition * Gaze	1.608	1	1.608	0.055	0.816	0.002
Condition * Gaze * STAI-T	0.164	1	0.164	0.006	0.941	0.000
Residual	814.201	28	29.079			

Note. Type III Sum of Squares

Table S6-13. Pearson Correlations between STAI-T and Threat-Safe False Alarms

		Threat-Safe
STAI-T	Pearson's r	0.421
	p-value	0.021

Bias Parameter

Table S6-14. Within-Subjects Effects of Repeated Measures ANOVA (Condition & Gaze) on Bias

	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	0.047	1	0.047	0.282	0.599	0.010
Residual	4.784	29	0.165			
Gaze	1.734	1	1.734	20.922	< .001	0.419
Residual	2.403	29	0.083			
Condition * Gaze	0.070	1	0.070	5.879	0.022	0.169
Residual	0.346	29	0.012			

Note. Type III Sum of Squares

Table S6-15. Descriptive Statistics (ANOVA) - Bias

Condition	Gaze	Mean	SD	N
Threat	Direct	-1.254	0.429	30
	Averted	-0.965	0.460	30
Safe	Direct	-1.245	0.498	30
	Averted	-1.053	0.581	30

Social Orientation Value

Table S6-16. Within-Subjects Effects of Repeated Measures ANOVA (Condition, Gaze & Intensity) on P(*fear*) with Z-score SVO

	Sphericity Correction	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	None	188.150	1.000	188.150	0.657	0.425	0.023
	Greenhouse-Geisser	188.150	1.000	188.150	0.657	0.425	0.023
Condition * SVO	None	279.346	1.000	279.346	0.975	0.332	0.034
	Greenhouse-Geisser	279.346	1.000	279.346	0.975	0.332	0.034
Residual	None	8021.845	28.000	286.494			
	Greenhouse-Geisser	8021.845	28.000	286.494			
Gaze	None	10427.278	1.000	10427.278	22.858	< .001	0.449
	Greenhouse-Geisser	10427.278	1.000	10427.278	22.858	< .001	0.449
Gaze * SVO	None	181.806	1.000	181.806	0.399	0.533	0.014
	Greenhouse-Geisser	181.806	1.000	181.806	0.399	0.533	0.014
Residual	None	12773.192	28.000	456.185			
	Greenhouse-Geisser	12773.192	28.000	456.185			
Intensity	None	585353.054 ^a	7.000 ^a	83621.865 ^a	363.279 ^a	< .001 ^a	0.928
	Greenhouse-Geisser	585353.054 ^a	1.518 ^a	385504.939 ^a	363.279 ^a	< .001 ^a	0.928
Intensity * SVO	None	125.782 ^a	7.000 ^a	17.969 ^a	0.078 ^a	0.999 ^a	0.003
	Greenhouse-Geisser	125.782 ^a	1.518 ^a	82.838 ^a	0.078 ^a	0.877 ^a	0.003
Residual	None	45116.494	196.000	230.186			
	Greenhouse-Geisser	45116.494	42.515	1061.181			
Condition * Gaze	None	305.628	1.000	305.628	4.725	0.038	0.144
	Greenhouse-Geisser	305.628	1.000	305.628	4.725	0.038	0.144
Condition * Gaze * SVO	None	18.376	1.000	18.376	0.284	0.598	0.010
	Greenhouse-Geisser	18.376	1.000	18.376	0.284	0.598	0.010
Residual	None	1811.172	28.000	64.685			
	Greenhouse-Geisser	1811.172	28.000	64.685			
Condition * Intensity	None	603.065 ^a	7.000 ^a	86.152 ^a	1.701 ^a	0.111 ^a	0.057
	Greenhouse-Geisser	603.065 ^a	4.117 ^a	146.487 ^a	1.701 ^a	0.153 ^a	0.057
Condition * Intensity * SVO	None	143.163 ^a	7.000 ^a	20.452 ^a	0.404 ^a	0.899 ^a	0.014
	Greenhouse-Geisser	143.163 ^a	4.117 ^a	34.775 ^a	0.404 ^a	0.811 ^a	0.014
Residual	None	9925.309	196.000	50.639			

		Greenhouse-Geisser	9925.309	115.272	86.103			
Gaze * Intensity		None	2512.335	7.000	358.905	6.961	< .001	0.199
		Greenhouse-Geisser	2512.335	4.863	516.591	6.961	< .001	0.199
Gaze * Intensity * SVO		None	174.048	7.000	24.864	0.482	0.847	0.017
		Greenhouse-Geisser	174.048	4.863	35.788	0.482	0.784	0.017
Residual		None	10106.101	196.000	51.562			
		Greenhouse-Geisser	10106.101	136.172	74.216			
Condition * Gaze * Intensity		None	338.469 ^a	7.000 ^a	48.353 ^a	1.161 ^a	0.327 ^a	0.040
		Greenhouse-Geisser	338.469 ^a	4.974 ^a	68.048 ^a	1.161 ^a	0.332 ^a	0.040
Condition * Gaze * Intensity * SVO		None	252.828 ^a	7.000 ^a	36.118 ^a	0.867 ^a	0.533 ^a	0.030
		Greenhouse-Geisser	252.828 ^a	4.974 ^a	50.830 ^a	0.867 ^a	0.504 ^a	0.030
Residual		None	8162.802	196.000	41.647			
		Greenhouse-Geisser	8162.802	139.271	58.611			

Note. Type III Sum of Squares

^a Mauchly's test of sphericity indicates that the assumption of sphericity is violated ($p < .05$).

Table S6-17. Within-Subjects Effects of Repeated Measures ANOVA (Condition, Gaze & Intensity) on RT with Z-score SVO

	Sphericity Correction	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	None	6521.464	1.000	6521.464	0.42 ₃	0.521	0.015
	Greenhouse-Geisser	6521.464	1.000	6521.464	0.42 ₃	0.521	0.015
Condition * SVO	None	3147.325	1.000	3147.325	0.20 ₄	0.655	0.007
	Greenhouse-Geisser	3147.325	1.000	3147.325	0.20 ₄	0.655	0.007
Residual	None	431691.763	28.000	15417.563			
	Greenhouse-Geisser	431691.763	28.000	15417.563			
Gaze	None	18291.461	1.000	18291.461	8.06 ₇	0.008	0.224
	Greenhouse-Geisser	18291.461	1.000	18291.461	8.06 ₇	0.008	0.224
Gaze * SVO	None	578.109	1.000	578.109	0.25 ₅	0.618	0.009
	Greenhouse-Geisser	578.109	1.000	578.109	0.25 ₅	0.618	0.009

Residual	None	63490.010	28.000	2267.500			
	Greenhouse-Geisser	63490.010	28.000	2267.500			
Intensity	None	682779.036 ^a	7.000 ^a	97539.862 ^a	24.7 ₆₉ ^a	< .001 ^a	0.469
	Greenhouse-Geisser	682779.036 ^a	2.476 ^a	275782.228 ^a	24.7 ₆₉ ^a	< .001 ^a	0.469
Intensity * SVO	None	12288.057 ^a	7.000 ^a	1755.437 ^a	0.44 ₆ ^a	0.872 ^a	0.016
	Greenhouse-Geisser	12288.057 ^a	2.476 ^a	4963.286 ^a	0.44 ₆ ^a	0.684 ^a	0.016
Residual	None	771852.791	196.000	3938.024			
	Greenhouse-Geisser	771852.791	69.322	11134.290			
Condition * Gaze	None	5643.709	1.000	5643.709	4.11 ₂	0.052	0.128
	Greenhouse-Geisser	5643.709	1.000	5643.709	4.11 ₂	0.052	0.128
Condition * Gaze * SVO	None	1.832	1.000	1.832	0.00 ₁	0.971	0.000
	Greenhouse-Geisser	1.832	1.000	1.832	0.00 ₁	0.971	0.000
Residual	None	38427.319	28.000	1372.404			
	Greenhouse-Geisser	38427.319	28.000	1372.404			
Condition * Intensity	None	4248.494	7.000	606.928	0.53 ₂	0.810	0.019
	Greenhouse-Geisser	4248.494	5.689	746.760	0.53 ₂	0.774	0.019
Condition * Intensity * SVO	None	4450.009	7.000	635.716	0.55 ₇	0.790	0.020
	Greenhouse-Geisser	4450.009	5.689	782.181	0.55 ₇	0.755	0.020
Residual	None	223599.648	196.000	1140.815			
	Greenhouse-Geisser	223599.648	159.299	1403.652			
Gaze * Intensity	None	59561.322 ^a	7.000 ^a	8508.760 ^a	5.15 ₉ ^a	< .001 ^a	0.156
	Greenhouse-Geisser	59561.322 ^a	3.606 ^a	16518.924 ^a	5.15 ₉ ^a	0.001 ^a	0.156
Gaze * Intensity * SVO	None	4796.627 ^a	7.000 ^a	685.232 ^a	0.41 ₅ ^a	0.892 ^a	0.015
	Greenhouse-Geisser	4796.627 ^a	3.606 ^a	1330.312 ^a	0.41 ₅ ^a	0.778 ^a	0.015
Residual	None	323284.989	196.000	1649.413			
	Greenhouse-Geisser	323284.989	100.958	3202.174			
Condition * Gaze * Intensity	None	7426.789	7.000	1060.970	0.78 ₃	0.602	0.027
	Greenhouse-Geisser	7426.789	5.211	1425.285	0.78 ₃	0.568	0.027

Condition * Gaze * Intensity * SVO	None	6677.195	7.000	953.885	0.70 4	0.669	0.025
	Greenhouse-Geisser	6677.195	5.211	1281.430	0.70 4	0.627	0.025
Residual	None	265632.500	196.000	1355.268			
	Greenhouse-Geisser	265632.500	145.901	1820.639			

Note. Type III Sum of Squares

^a Mauchly's test of sphericity indicates that the assumption of sphericity is violated ($p < .05$).

Table S6-18. Within-Subjects Effects of Repeated Measures ANOVA (Condition & Gaze) on Bias with Z-score SVO

	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition	0.047	1	0.047	0.273	0.606	0.010
Condition * SVO	0.004	1	0.004	0.023	0.879	0.001
Residual	4.780	28	0.171			
Gaze	1.734	1	1.734	20.746	< .001	0.426
Gaze * SVO	0.063	1	0.063	0.756	0.392	0.026
Residual	2.340	28	0.084			
Condition * Gaze	0.070	1	0.070	5.756	0.023	0.171
Condition * Gaze * SVO	0.005	1	0.005	0.393	0.536	0.014
Residual	0.341	28	0.012			

Note. Type III Sum of Squares

Auto-questionnaire Scores

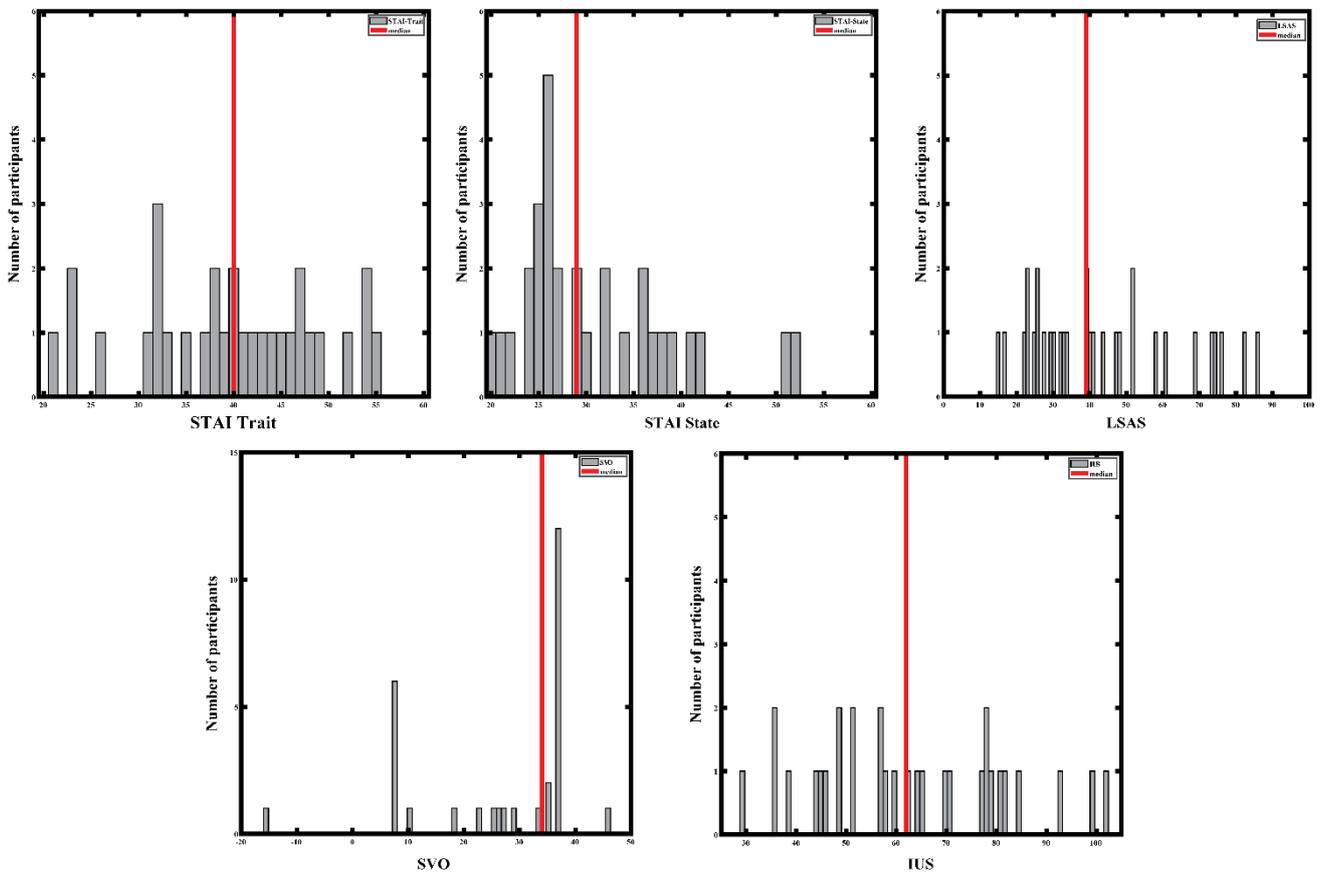


Figure S6-1. Distribution of STAI-Trait (Upper-Left), STAI-State (Upper-Center), LSAS (Upper-Right), SVO (Bottom-Left) and IUS (Bottom-Right) scores

Debriefing Scores

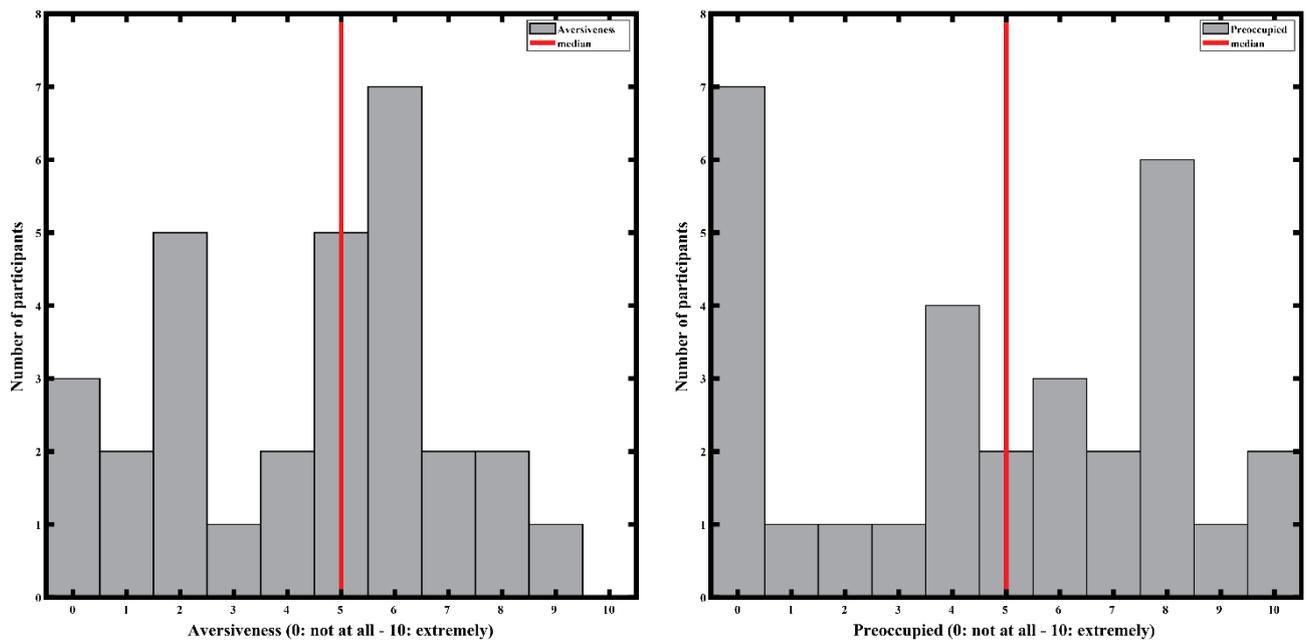


Figure S6-2. Distribution of participant's aversiveness (Left) and preoccupation ratings (Right).

Appendix to Chapter 6

In addition to the appraisal online experiment and the Fear-Neutral Categorization task, we built a third experiment not reported in this article. We wanted to check (in a totally exploratory way) how face encoding is impacted under threat. We assumed that if threat promotes cognitive mechanisms such as perceiving (orienting attention) the ones able to restore their homeostasis, participants will better encode faces under threat. To our knowledge, only three studies investigated this research question (Bolton & Robinson, 2017; Garibbo, Aylward, & Robinson, 2019; Schellhaas et al., 2020). Two of them (Bolton & Robinson, 2017; Garibbo, Aylward, & Robinson, 2019) observed a decrease of participant's performance in an old-new recognition task of faces presented under threat while one (Schellhaas et al., 2020) reported no effect of threat on retrieval abilities.

To test that, we also used an old-new task (see **Figure A6-1**). During the previously described categorization task, half of the identities (randomly assigned for each participant) were presented under threat, the other half under safe blocks: 18 identities were encoded under threat, while 18 identities were encoded during safe blocks. Following the categorization task, the same 32 participants performed an old-new task. They were instructed to report 1) if they already saw the face during the previous experiment and 2) the context of the presentation (threat or safe blocks). The experiment was composed of 68 trials with 36 old faces coming from the Radboud Face Data (Langner et al., 2010) and 32 news faces coming from Chicago Face Database (Ma, Correll, & Wittenbrink, 2015). The new faces were similarly modified as the faces we used in the categorization task. Each trial was initiated with a white oval delimiting the faces that remained throughout the trial. The white oval appeared for approximately 500ms, followed by a white fixation point presented at eye level for approximately 1000ms. Then, the face was displayed for 1.3s. After face offset, participants were asked to answer (up to 5 seconds) the question "Did you see this face in the previous experiment?". If the participant answered yes, they needed to precise if they saw this face under threat or safe block (again up to 5s to answer).

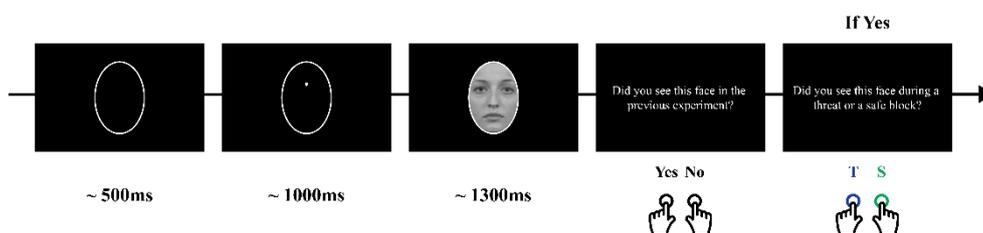


Figure A6-1: Experimental paradigm of the Old-New Recognition task.

The two outliers previously identified for the categorization task were excluded from the old-new analyses. In addition, the dataset of one participant was not saved (Matlab technical issue). The final

data sample included 29 participants ($M_{\text{age}} = 23.3$, $SD_{\text{age}} = 4.4$, 15 women). We computed the accuracy score for both questions and T-tests with Condition (face encoded in Threat vs. Safe blocks) as a within-subject factor were performed on these accuracy scores. Results showed that participants were not better to recognize faces which were displayed under threat compared to safe blocks ($t(28) = 1.47$, $p = 0.15$, Cohen's $d = 0.27$). Moreover, participants' abilities to report the type of blocks in which they saw the face were not influenced by the condition ($t(28) = -1.07$, $p = 0.29$, Cohen's $d = -.20$).

Altogether, these results suggest that anxiety did not favor face encoding. Our results are consistent with similar studies which investigated social memory under threat. However, the MEG investigation led by Schellhaas and al. (Schellhaas et al., 2020) of the neural signatures of encoding and retrieval processes showed sustained activation of several clusters involved in early attention directed toward motivationally relevant information. These MEG clusters suggest faces to be relevant under threat even if participants are not able to remember their identities. In our case, it is important to mention that one of our main experimental factors is gaze direction. Under threat, participants tended to exaggerate the threat information conveyed by fearful face, by reporting seeing fear more often when the face was associated with an averted gaze. We believe that this result is consistent with an amplified bias under threat for averted gazes. This kind of bias suggests that others are more a source of information than support in threat situations. Thus, it is not surprising, based on our hypothesis, that the encoding is not improved. In addition, several studies have shown a cueing effect of the gaze, especially when it is associated with fear emotional display (Bayliss, Schuch, & Tipper, 2010; Kuhn & Tipples, 2011; Mathews, Fox, Yiend, & Calder, 2003; Putman, Hermans, & Van Honk, 2006; Tipples, 2006). It is therefore very likely that participants did not focus on the face but on the environment around it. A replication using eye-tracking could confirm this hypothesis.

Table A6-1. Paired t-test on accuracy scores

	t	df	p	Cohen's d
Q1-Threat - Q1-Safe	1.469	28	0.153	0.273
Q2-Threat - Q2-Safe	-1.069	28	0.294	-0.198

Note. Student's t-test.

Table A6-2. Descriptive Statistics (t-test) - accuracy

	N	Mean	SD	SE
Q1-Threat	29	0.657	0.177	0.033
Q1-Safe	29	0.613	0.184	0.034
Q2-Threat	29	0.450	0.131	0.024
Q2-Safe	29	0.488	0.132	0.025

ARTICLES AND SCIENTIFIC COMMUNICATIONS

Articles

During my master's and doctoral training, I had the opportunity to participate in several other experiments that resulted in published (or future) articles:

Self in the other: social contact enhances bodily self-awareness irrespective of sensory modality.

Hazem N., Beurenaut M., George N., Conty L. (2018) - Scientific Reports

Abstract

Human self-awareness is arguably the most important and revealing question of modern sciences. Converging theoretical perspectives link self-awareness and social abilities in human beings. In particular, mutual engagement during social interactions—or *social contact*—would boost self-awareness. Yet, empirical evidence for this effect is scarce. We recently showed that the perception of eye contact induces enhanced bodily self-awareness. Here, we aimed at extending these findings by testing the influence of social contact in auditory and tactile modalities, in order to demonstrate that social contact enhances bodily self-awareness irrespective of sensory modality. In a first experiment, participants were exposed to hearing their own first name (as compared to another unfamiliar name and noise). In a second experiment, human touch (as compared to brush touch and no-touch) was used as the social contact cue. In both experiments, participants demonstrated more accurate rating of their bodily reactions in response to emotional pictures following the social contact condition—a proxy of bodily self-awareness. Further analyses indicated that the effect of social contact was comparable across tactile, auditory and visual modalities. These results provide the first direct empirical evidence in support of the essential social nature of human self-awareness.

Does social contact influence bodily self-awareness independently of the contact modality?

Hazem N., Beurenaut M., George N., Conty L. (2016) - International Journal of Psychophysiology (conference paper)

I've also been involved in several on-going project inside the team led by Julie Grèzes and Rocco Menzella on the contribution of goal-directed processes during decision-making in socio-emotional contexts (implying motor kinematics, reinforcement learning or neuroimaging). Data are still under analysis.

Posters

- > A Method to Induce Sustained Anxiety Using Aversive Sounds: Validation of the ‘Threat of Screams’ Paradigm - Beurenaut, Dezechache & Grèzes, ICPS, Palais des congrès de Paris, 2019
- > The impact of anticipatory distress scream on skin conductance and subjective anxiety: validation of the Threat of Scream paradigm - Beurenaut, Dezechache & Grèzes, Colloquium of young researcher in Cognitive Science, Paris, 2019
- > Can we Induce Sustained Anxiety Using Aversive Distress voices? Validation of the ‘Threat of Screams’ Paradigm - Beurenaut, Dezechache & Grèzes, iCog5: Interdisciplinary Approaches to Higher Cognitive Function, University of Reading, 2019
- > How stress modulate the impact of emotional cues on action-related decision? Beurenaut, Vilarem, Mennella, Dezechache & Grèzes, Departement of Cognitive Studies Day, Paris, 2018
- > Stress modulates the impact of emotional cues on action-related decision, Beurenaut, Vilarem, Mennella, Dezechache & Grèzes, ESCAN, Leiden (Netherlands), 2018
- > Social Cognition faces danger, Doctoral School day (Cerveau, Cognition et Comportement ED3C) - Beurenaut, Dezechache & Grèzes, Paris, 2018
- > Social Contact and Self-Awareness: Impact of Tactile And Vocal Contact on Interoceptive Awareness - Beurenaut, Hazem, George & Conty, Trace Workshop, Nanterre (France), 2017

Oral Communication

- > Social cognition under threat anxiety inducing contexts - Beurenaut, Dezechache, Grèzes - RTP "Evolutionary Human Sciences", HumanEvoWeek, online, 2020
- > Impact of a situation of sustained anxiety on the ability to represent others' action - Beurenaut, Dezechache, Grèzes – Psy Seminar Lille Neuroscience et Cognition, online, 2020
- > How joint action and perception of social cues are impacted during stressful context? - Beurenaut, Dezechache, Grèzes – Eye Think Team Meeting, UCL, London, 2019
- > La cognition sociale à l’épreuve du danger: comment expliquer nos réactions face à la menace? - Beurenaut, Dezechache, Grèzes, Cogtalk by Cognivence, Paris (France), 2019
- > What happens to my action co-representation when I am in a dangerous situation? - Beurenaut, Dezechache, Grèzes, Colloquium of young researcher in Cognitive Science, Paris (France), 2019
- > Action Co-representation Under Threat - Beurenaut, Dezechache, Grèzes, Joint Action Meeting VIII, Genoa (Italy), 2019
- > Sociality in danger situations - Investigation of implicit markers of prosociality - Beurenaut, Dezechache, Grèzes, Affective Neuroscience Workshop (organized by Lou Safra and Morgan Beurenaut), Paris, 2018

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RÉSUMÉ

Nos réactions en réponse à une menace ont très été souvent considérées comme individualistes et antisociales. Cependant, plus de cinquante ans de recherche en sociologie et en psychologie sociale indiquent que les humains favorisent des stratégies sociales lorsqu'ils sont en danger. En effet, des cas de coopération et d'entraide sont souvent rapportés dans la littérature sur les catastrophes naturelles ou sur les attentats. Pour mettre en œuvre de telles stratégies, il est nécessaire que des mécanismes cognitifs permettant de traiter les signaux sociaux véhiculés par les autres afin d'agir avec eux soient : mise en place, maintenus et voire optimisés en situations d'anxiété intense. Comprendre comment le danger reconfigure la perception de notre environnement social, comment nous représentons les autres et leurs actions, ainsi que les motivations sous-jacentes à de telles stratégies, représente un défi théorique important. Pour aborder cette question, nous avons mené 3 études. Dans la première, nous avons validé une méthode intra-sujet pour induire de l'anxiété de manière soutenue et stable : le paradigme du 'Threat-of-Scream' qui consiste à alterner des blocs dans lesquels les participants sont à risque d'entendre des cris de détresse aversifs à tout moment (blocs de menace) avec des blocs dans lesquels ils ne sont pas du tout exposés à des stimuli aversifs (blocs de sécurité). Dans une deuxième étude, nous avons utilisé cette procédure pour étudier comment la co-représentation d'action (c'est-à-dire la capacité à intégrer automatiquement les actions d'autrui dans nos propres plans d'action pour faciliter la coordination de nos actions) est affectée sous la menace. Les résultats semblent montrer que la co-représentation (évaluée en mesurant l'amplitude de l'effet Simon Social) est maintenue en contextes de menace et semble être particulièrement accrue lorsque les participants sont exposés à un danger à proximité de partenaires en sécurité. Nos résultats suggèrent que la fonction potentielle de la co-représentation d'action pourrait être de promouvoir des stratégies sociales essentielles pour sa propre survie. Enfin, la troisième étude s'est intéressée à la manière dont les visages exprimant de la peur sont perçus sous la menace. En effet, selon la direction du regard qui leur est associée, ils peuvent être évalués soit comme signalant la présence d'une menace potentielle dans le milieu environnant (regard dévié), soit comme un signal de détresse et de besoin d'aide potentiel (regard direct). À l'aide d'une tâche de catégorisation, nous avons cherché à savoir si les signaux liés au danger ou les signaux de détresse étaient favorisés lorsque les participants étaient à risque d'entendre des cris aversifs. Nous avons observé que l'évaluation des signaux liés au danger véhiculés par les expressions faciales de peur est priorisée en contextes de menace, et cela sans moduler l'évaluation des signaux de détresse. Dans l'ensemble, nos résultats suggèrent que si les stratégies sociales sont maintenues sous la menace, elles pourraient être soutenues par des motivations d'autoprotection.

MOTS CLÉS

Cognition sociale ; Anxiété ; Prosocialité ; Menace ; Co-représentation ; Expression émotionnelle

ABSTRACT

Individual reactions to threat are very often thought as individualistic and antisocial. However, more than fifty years of work in sociology and social psychology indicate that humans favor social strategies when confronted with threat. Indeed, cases of cooperation and mutual aid are often reported in the literature on disasters. To implement such strategies, psychological mechanisms that allow us to process social signals conveyed by others in order to act with them must be in place and these mechanisms must be maintained and even optimized in situations of intense anxiety. Understanding how danger reconfigures how we perceive our social environment and how we represent others and their actions, as well as the incentives of such strategies, is an important theoretical challenge. To tackle this issue, we led 3 studies. In the first one, we validated a within-subject method to induce anxiety in a sustained manner: the threat-of-scream paradigm which consists in alternating blocks in which participants are at risk of hearing aversive distress screams at any time (threat blocks) with blocks in which they are not exposed to aversive stimuli at all (safe blocks). In a second study, we used this procedure to investigate how co-representation of action (i.e. the ability to automatically integrate the actions of other individuals into our own action plans to facilitate action coordination) is impacted under threat. Results showed that co-representation (assessed by measuring the magnitude of the classical Social Simon Effect) is maintained under threat contexts and seems to be particularly boosted when participants are exposed to danger near safe partners. Our results suggest that the potential function of co-representing others' actions could be to promote social strategies essential for one's own survival. Finally, the third study addressed how facial displays of fear are perceived under threat. Indeed, depending on their associated gaze direction, they can either be appraised as signaling the presence of a potential threat in the surrounding environment (averted gaze), or as a signal of distress and potential need of help (direct gaze). Using a categorization task, we investigated if danger-related or distress-related signals were prioritized under the threat-of-scream procedure. We observed that the appraisal of danger-related signals transmitted by facial displays of fear is increased under threat contexts, with no impact on the appraisal of distress signals. Altogether, our results suggest that while social strategies are maintained under threat, they might be sustained by self-preservation motives.

KEYWORDS

Social Cognition ; Anxiety ; Prosociality ; Threat ; Co-representation ; Emotional display