



The interplay of action selection and attention allocation in response to social threat

Emma Vilarem

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The interplay of action selection and attention allocation in response to social threat

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Table of contents

Remerciements	3
Abstract	4
Résumé	5
INTRODUCTION	6
I. Emotion: expressions and functions?.....	7
I.1. Intra-personal function: protect oneself	8
I.2. Inter-personal function: communicate to others.....	12
I.3. Relationship to action: anchor communication	16
II. Action: a facet of emotion?	19
II.1. Methodological challenges.....	20
II.2. Summary of the findings	26
III. Attention: shaped by action?	27
III.1 Threat attentional biases.....	28
III.2. Action-related attentional biases	32
IV. Our scientific question.....	38
EXPERIMENTAL SECTION	43
PART 1: Action and covert attentional responses to threat – Behavioural and pupillometry studies (Experiments 1 to 3)	44
PART 2: Action and overt attentional responses to threat – A saccade study (Experiment 4)	85
PART 3: Action and covert attentional responses to threat – An EEG study (Experiment 5)	104
DISCUSSION	117
CONCLUSION	130
APPENDIX A: Post-tests in Experiments 1 to 5	131
APPENDIX B: Papers and scientific communications	134
REFERENCES	137

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Abstract

Everyday action decision-making entails to take into account affordances provided by the environment, along with social information susceptible to guide our decisions. But within social contexts conveying potentially threatening information and multiple targets for action, as when entering a subway car, how do we decide very quickly where to sit while gauging the presence of a potential danger? Existing motor theories posit that action selection between competing options is biased by sensory information and determines attention allocation toward the endpoint of the selected action, while theories of emotion suggest attentional biases toward threat cues. The work conducted during my PhD (5 main studies in healthy human subjects) aimed at addressing this apparent contradiction by investigating action and attentional processes in a realistic social context providing action opportunities.

In the first study, spontaneous action choices and kinematics revealed that threat-related angry and fearful displays impact people's free choice differently, i.e. favoured the selection of actions that avoided angry and approached fearful individuals. The second study further showed that attention was allocated to the space of the scene corresponding to the endpoint of the actions prioritized by those angry and fearful displays. Crucially, the third study evidenced that this effect disappeared when action opportunities were removed from the experimental context. Saccadic behaviour recorded in the fourth study allowed to access the development of attention allocation over time, and crucially revealed that attention was first quickly oriented toward threat before being directed toward the endpoint of the chosen action. Finally, the last EEG experiment suggested that avoiding angry displays and approaching fearful ones were the safer actions in the face of threat, although the corresponding analysis are still ongoing and must then be cautiously discussed. Altogether, these findings shed light on the mechanisms underlying the influence of threat displays on action and attention processes when embedded in a realistic social context.

Résumé

Les décisions d'action que nous prenons au quotidien nécessitent de considérer les affordances fournies par notre environnement, ainsi que les informations sociales susceptibles de guider nos décisions. Mais dans un contexte véhiculant à la fois des informations sociales potentiellement menaçantes et de multiples opportunités d'action, comme lorsque l'on entre dans une rame de métro en cherchant un siège, comment choisissons nous rapidement le siège où s'asseoir tout en évaluant la présence d'un danger potentiel ? Dans un tel contexte, les théories motrices proposent que la sélection d'une action parmi différentes possibilités est biaisée par les informations sensorielles en provenance de l'environnement, et peut guider notre attention vers la finalité de l'action choisie ; cependant, les théories des émotions suggèrent que notre attention est capturée par les informations menaçantes. Le travail réalisé au cours de cette thèse (5 études chez le sujet sain) a visé à questionner cette apparente contradiction en étudiant les processus liés à l'action et à l'attention dans un contexte social réaliste doté d'opportunités d'action.

Dans notre première étude, les choix spontanés d'action et les informations cinématiques ont révélé que les expressions de colère et de peur ont un impact différent sur la sélection d'action, et favorisent les actions permettant d'éviter les individus en colère et d'approcher les individus effrayés. La seconde étude a montré que l'attention peut être allouée vers la finalité des actions privilégiées par les expressions de colère et de peur. La troisième étude a démontré, de façon cruciale, que cet effet attentionnel disparaît lorsque les opportunités d'action sont retirées du contexte expérimental. De plus, l'activité saccadique enregistrée lors de la quatrième étude a permis d'explorer le développement de l'allocation attentionnelle au cours du temps, et a établi que l'attention était rapidement dirigée vers les visages émotionnels, puis réorientée vers la finalité de l'action choisie. Notre dernière étude en électroencéphalographie a suggéré qu'éviter la colère et approcher la peur sont les actions les plus sûres face à la menace, bien que ces analyses soient toujours en cours et requièrent donc d'être discutées avec précaution. Pour conclure, l'ensemble de nos données mettent en lumière les mécanismes sous-tendant l'influence des signaux de menace sur les processus liés à l'action et l'attention au sein d'un contexte social réaliste.

INTRODUCTION

Every day, the decisions we make entail the consideration of action opportunities provided to us by our environment. Imagine you are entering a subway car and must quickly decide where to sit; one essential piece of information to collect is the location of the potential seats. However, when selecting the endpoint of your course of action, other information concerning your immediate environment might come into play and prioritize one or more of these potential seats. As social animals, a relevant signal that often biases our attention and our decisions is other individuals in our immediate environment. For example, what if, in our subway scenario, some of these individuals seem particularly hostile? How do physical and social signals compete for the allocation of our attention and the selection of the best target for action?

The work conducted in my PhD aimed at addressing the relationship between emotions, action and attention in realistic environments. In our view, one of the most adequate contexts in which to study these interwoven processes is the context of threat. Indeed, critical to an organism's survival is its ability to detect and deploy an appropriate response to imminent danger. My project thus aims at studying the interplay between attention and action processes in the face of threat.

Besides adopting a context which urge participants to act, we also integrated a key feature of our daily environment to our experimental designs, namely the presence of action opportunities. Indeed, throughout evolutionary history, organisms have faced the challenges of constant interaction with a complex and ever-changing environment that continuously offers opportunities and demands for action. Implementing the latter within experimental paradigms could strengthen their ecological validity and help shed light on the motor and attentional systems functioning within complex forms of interaction. Hence, the paradigms used throughout my PhD work manipulate action opportunities by

using a social context that affords (or does not afford) different actions, within which we investigate participants' action and attentional responses.

Further, in order to better understand these complex behaviours, we took advantage of the richness of the experimental approach to collect various measures. Through 5 main studies using healthy human subjects, I have thus recorded data concerning movement kinematics, pupil dilation, saccadic behaviour and electroencephalographic activity so as to obtain the most comprehensive possible picture of the interplay between action and attentional processes occurring in the face of threat.

The introduction will be organized as follows: first, I will review the threat-related emotion literature, focusing on facial displays and their associated communicative functions; second I will describe the findings of studies addressing the relationship between threat and action, along with the methodological challenges they pose; third I will question the relevance of studying attention allocation with regards to action selection; fourth I will finally discuss the importance of bridging the gap between emotion and motor domains to investigate action decision-making in the face of threat within realistic social contexts providing action opportunities.

I. Emotion: expressions and functions?

Finding a consensual definition to describe what emotions are is a longstanding quest. If we turn back to the Latin etymology of the word, emotions are referred to as a force that "*moves out, removes, agitates*". The work conducted in my PhD takes this definition literally and investigates the action side of the multifaceted process that are emotions. And what better context in which to explore this facet than one that challenge your survival, urging you to detect an impending danger and to act upon it as fast as possible? Hence, in this chapter, I will focus on threat-related emotions, namely anger and fear, and their associated facial expressions. Using an evolutionary framework, I will describe their different functions and their relationship to action.

I.1. Intra-personal function: protect oneself

“[Arguments for an evolutionary basis of emotions] are strengthened by the adaptive utility of the behaviour systems linked to the emotions: protecting oneself from intruders, predators, and rivals; warding these off and threatening them; obtaining food and drink; detecting and contacting mates; seeking shelter; protecting the young; submitting to the more powerful”.

As put forward by Frijda (2008), emotions appear to have evolved to serve two main functions: to protect the emitter and communicate relevant information to the observer, respectively described in the literature as intra- and inter-personal functions.

The intra-personal function characterizes the process by which emotions prepare the emitter to initiate situation-appropriate actions in order to successfully face environmental challenges (Levenson, 1999). These actions can include automatic defensive responses (e.g. freezing when facing a predator) as well as goal-directed actions (e.g. carefully watching prey to attack it most successfully). However, there is an ongoing debate regarding the causality that relates emotions to behaviours in the emitter, with some authors arguing that behaviour gives rise to emotion (“I am sad because I cry” – (James, 1890; Lange, 1885), appraisal theories positing that behaviour (e.g. facial expressions) is a component of emotions (Scherer, 1984), whereas evolutionary theories propose that emotion give rise to behaviour (“I am sad therefore I cry” – (Anderson & Adolphs, 2014; Panksepp, 2004). Although, this summary simplifies the richness of contemporary emotion theories (Coppin & Sander, 2010), and the complexity of current debate regarding what emotions are (Adolphs, 2017 versus Barrett, 2017), I will embrace here the evolutionary framework to describe the relationship between emotions and action in the emitter.

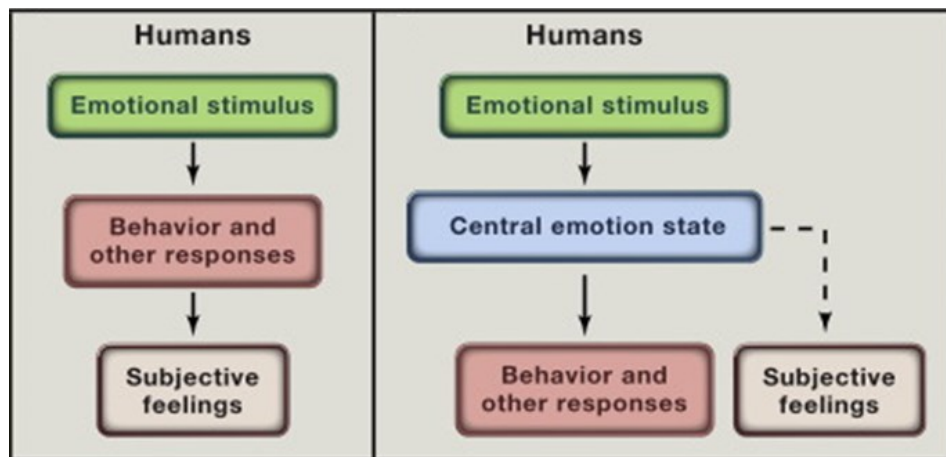


Figure 1. From Anderson & Adolphs (2014). The left panel describes the psychological appraisal theories' view according to which behaviour are evoked by emotional stimuli without triggering a causative emotional state. The right panel describes the authors' view according to which emotional states evoked by emotional stimuli mediate the responses to emotional stimuli.

In a recent review, Anderson & Adolphs (2014) formulated a framework to study emotions across species, and to specify the direction of the relationship that binds them to their associated behaviours (Figure 1). According to their view, the exposure to an emotion-eliciting stimulus produces “*internal, central emotional states*”. These emotional states would then mediate the development of externally observable behaviours, as well as of associated cognitive, somatic and physiological responses. In parallel to those responses, subjective feelings would be produced in humans and would allow for the verbal report of emotional states. The authors further proposed that these emotional states would play an important role in the expression of emotions in animals as well, irrespective of whether or not they have a subjective perception of those states. Hence, according to this framework, behaviours associated with emotions (facial expressions, action tendencies ...) would be a product of emotional states, both in humans and animals.

It has been proposed that the building of the relationship that links emotions to their associated behaviours results from functional adaptations to phylogenetically recurrent situations (Cosmides & Tooby, 1995; Tooby & Cosmides, 1990, 2008). According to this perspective, emotion states are modes of operation that have been designed to solve adaptive problems and which, to this end, govern the construction of organized behavioural sequences. Functional adaptation would allow specific courses of action to be favored when facing situations that have been repeated over evolutionary time (e.g. foraging, escaping predators...), with regards to the individual's emotional state. Thus, according to this view, stimuli provoke emotional states that organize action appropriate to situations, but also shift attention, prioritize goals, affect physiology, among other changes (Cosmides & Tooby, 1995). Along the same theoretical line, Plutchik (2001) further specified that the complex chain of events composing emotions includes feelings, psychological changes, impulses to action and specific goal directed behaviors.

Thus, emotions, by prompting adapted behaviours, would increase the probability of survival by helping individuals overcome environmental challenges. In particular, facial expressions of emotions that are thought to have evolved to modify preparedness for perception and action (Darwin, 1872). This functional role is, notably, proposed to be achieved through sensory regulation, with facial configurations either enhancing or decreasing sensory intake, therefore altering the exposure to the emotion-eliciting situation in an adaptive way (Susskind et al., 2008).

In order to test this assumption, Susskind et al. (2008) investigated the putative role of fear to increase sensory vigilance (Phelps, Ling, & Carrasco, 2006; Taylor & Whalen, 2014) by asking participants to judge the size of their visual field as they displayed fearful expressions. Participants reported a larger visual field under fearful displays relative to neutral; a finding further corroborated by an increase in eye aperture measured in the same participants. Moreover, participants detected peripheral targets at farther eccentricities relative to neutral, and executed faster eye movements during target

localization (Figure 2a, 2b). Similar results were found when exploring the olfactory channel, with increased dilation of the nasal passage and higher respiratory volume (Figure 2, 2d). Fearful facial displays would thus enhance sensory acquisition in the visual and olfactory channels in order to improve danger detection (Susskind et al., 2008).

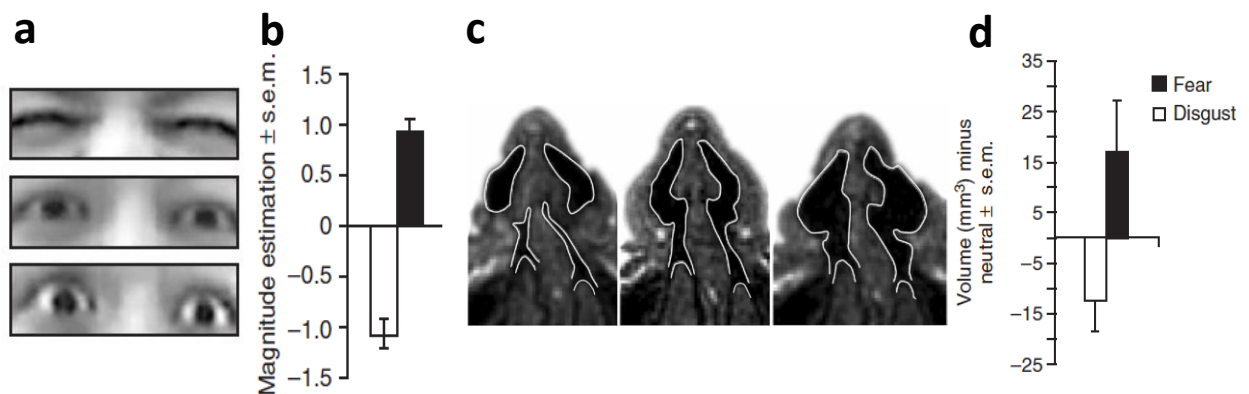


Figure 2. Adapted from Susskind et al. (2008). a) Average eye opening from participants posing disgust, neutral and fear expressions (from top to bottom row). b) Change in estimated visual-field size for fear and disgust expressions relative to neutral expressions. c) Passageways to the inferior turbinate of the respiratory mucosa while posing disgust, neutral and fear expression (from left to right panel). d) Change in overall air cavity volume for fear and disgust expressions relative to neutral.

These findings were supported by the study of other emotional expressions (e.g. disgust facial expressions and its associated reduction of sensory intake - Chapman, Kim, Susskind, & Anderson, 2009; Susskind et al., 2008) that corroborated the sensory regulation intra-personal function of facial expressions of emotion, while raising the question of other aspects that might have shaped their evolution. Indeed, in some cases, the occurrence of these emotional displays seems unrelated to their original physiological function (e.g. disgust in response to morally reprehensible acts – Chapman, Kim, Susskind, & Anderson, 2009; Shariff & Tracy, 2011) and suggest they serve another function.

1.2 Inter-personal function: communicate to others

Besides surviving hostile environments, humans, among other species, also evolved to navigate social relationships. Hence, facial expressions of emotion are also thought to have evolved to communicate information to the observer thereby serving an inter-personal function (Dezecache, Mercier, & Scott-Phillips, 2013). Evolutionary accounts posit that emotional displays convey critical information about the emitter's affective state and associated behavioural intentions (Fridlund, 1994; Keltner & Haidt, 1999). Studies investigating how facial expressions of emotion are perceived by observers, provided data supporting the hypothesis that the interpersonal function of emotions has shaped the configuration of facial expressions. Findings on the perception of angry and fearful expressions are particularly interesting because, beyond their shared threat-relatedness, these displays convey different social signals to the observers and allow the investigation of how facial expressions contribute to social perception.

1.2.a. The case of Anger

Angry facial expressions are a well-established signal of intention to challenge another individual aggressively and are thus perceived as a direct threat by the observer (Sander, Grandjean, Kaiser, Wehrle, & Scherer, 2007). Indeed, highly similar expressions are displayed by nonhuman primates prior to and during aggressive contests over food, mates, and other evolutionarily important resources (de Waal, 1986). Evolutionary theories propose that the function of these expressions would be to communicate that the emitter is about to aggress the observers (Fridlund, 1994). The possible mechanism underlying this threat effect could be that angry facial expressions have evolved to enhance the perceived physical strength of the emitter.

In a recent paper, Sell and colleagues (2014) suggested that in the case of conflict, natural selection favored displaying a configuration of muscle activations that amplified the assessment of the emitter's

fighting ability. In humans, those configurations would enhance cues of physical strength, leading the authors to propose that angry facial expressions would be an adaptation for amplifying these cues. To test their hypothesis, they manipulated the major facial modifications characterizing angry displays in avatar faces and asked raters to evaluate the perceived strength of these faces. Their results indicated that facial features corresponding to angry displays increased the perceived physical strength of the emitter, even when manipulated independently from each other. This relationship between anger and physical strength is further reflected by the findings that men who are physically stronger get angry more easily and tend to consider aggression the best way to settle conflicts (Sell, Tooby, & Cosmides, 2009).

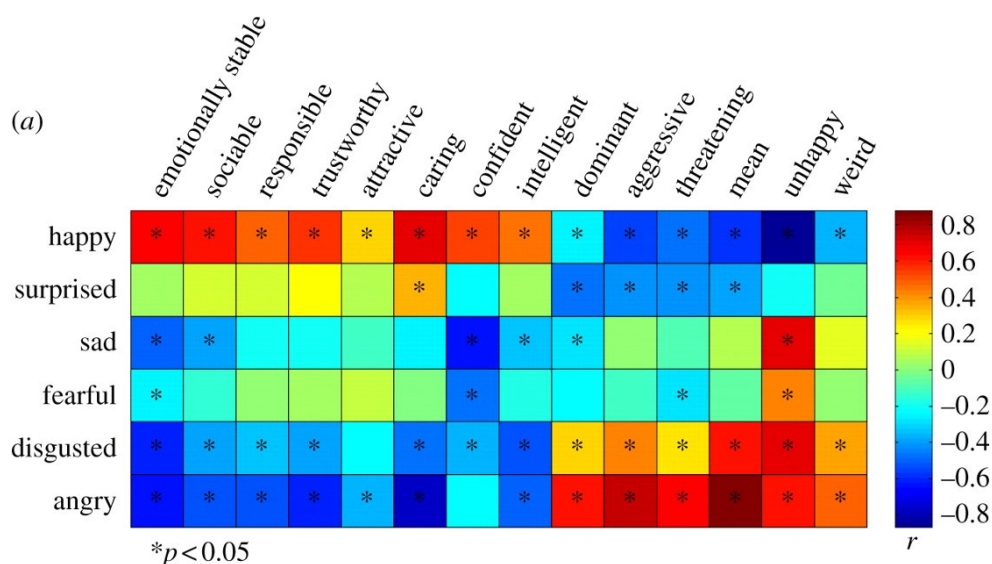


Figure 3. From Said et al. (2011). Correlations between trait and emotion judgments of emotionally neutral faces. The colour of the square corresponds to the magnitude of the correlation coefficient, and the asterisk to significant correlations between trait and emotion judgments.

Finally, when correlating trait judgments with emotion judgments performed on a set of neutral faces, one study has revealed that faces rated as angry were negatively correlated to “positive traits” such as “trustworthy” and “caring”, and positively correlated to “negative traits” such as “threatening” and

“aggressive” (Figure 3), further indicating that anger is perceived as signaling a direct threat (Said, Moore, Norman, Haxby, & Todorov, 2010).

Together, these studies suggest that angry displays communicate a threatening signal that might emerge from an increased perceived probability of being aggressed and defeated.

I.2.b. The case of Fear

The case of fear and its associated social function is interesting because it is more ambivalent than anger. As anger, fear is a threat-related signal that warns the observer of danger in the environment (Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003; Springer, Rosas, McGetrick, & Bowers, 2007). However, contrary to anger, the emitter of the fearful display seems to convey the threatening signal without being perceived as a threat himself. As shown in the study previously cited by Said et al. (2011), the judgment of fear is negatively correlated to the “threatening” trait, and the valence associated with fearful judgments is close to 0 on a scale from -1 (negative) to 1 (positive). To better understand this paradox it is helpful to turn to the comparative literature for insight as it allows for the investigation of the social function of facial expressions by examining their similarities across evolutionary related species, and the context in which they occur.

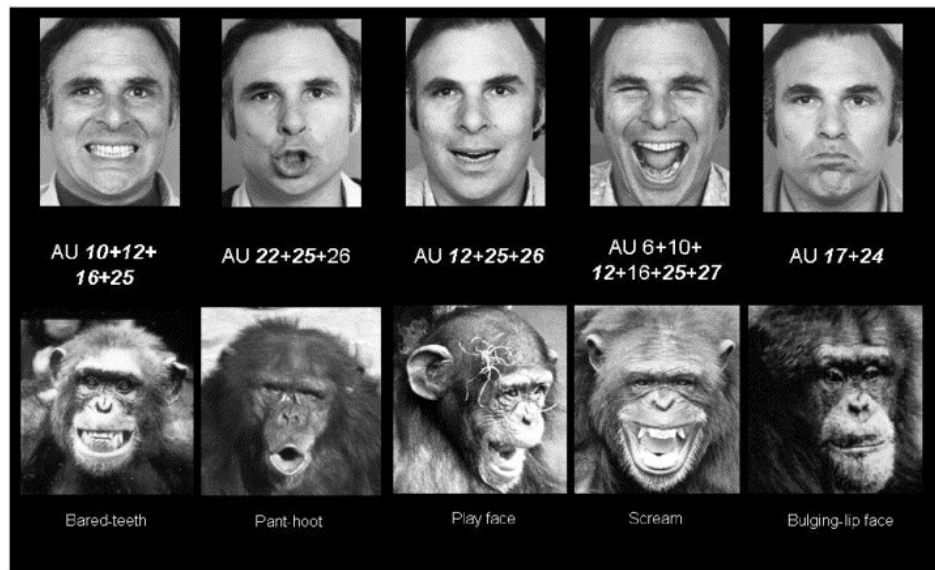


Figure 4. From Parr & Waller (2006). Prototypical chimpanzee facial expressions and homologous facial movements in a human. The identical Action Units (AU) shared by the two expression examples are highlighted in bold italics. The configuration AU10 + 12 + 16 + 25 (the same movements as in the prototypical chimpanzee bared-teeth face) on the top left corner is most often described as showing fear (Wallbott and Ricci-Bitti, 1993).

Ethology provides particularly relevant information in the case of fear, because the facial display that is proposed to be analogous to the human fearful facial display, namely the “bared-teeth” display (also referred to as “fear grin” or “grimace”), is one of the most extensively studied facial expression in animals (Figure 4) (Parr & Waller, 2006).

The literature reveals that fearful expressions are displayed to serve different social functions depending on the species social-ecological context. In wolves for instance, the fear grin display is mostly associated with submissive behaviours observed, for example, when animals are greeting a dominant conspecific or human being. They will approach that conspecific in a low position with flattened ears and extruded tongue as if with a licking intention (Fox, 1970). These facial and postural displays make the wolf appear smaller in size and mimic the behaviours of juveniles, thereby communicating submission and inhibiting aggression (Hammer & Marsh, 2015). But the bared-teeth display can also be observed in affiliative contexts and signal to conspecifics that the emitter has non-aggressive and affiliative intentions. Indeed, a study by Waller & Dunbar (2005) on chimpanzees

revealed that the bared-teeth facial expression significantly increased affiliative behaviours (e.g. holding out hands) between emitter and observer in the 10 minutes following a display. These results suggest that the bared-teeth display functions either to communicate submission, or to increase affiliation and reduce distance between individuals (Hammer & Marsh, 2015).

Data in humans further confirm these observations by indicating that fearful faces are rated by observers as appearing babyish (Marsh, Ambady, & Kleck, 2005), submissive and highly affiliative (Hess, Blairy, & Kleck, 2000). Along with the observations on animals, these results suggest that the social function of fear might be to promote appeased interactions and prosocial behaviours.

These findings suggest that facial expressions of emotion indeed convey relevant and important signals to others, thereby explaining how they became a fundamental building block of social interactions. The following paragraph questions the behavioural responses that these signals produce in the observer.

I.3. Relationship to action: anchor communication

As previously mentioned, emotions are proposed to bear a communicative function. But the stability of this communicative function throughout the course of evolution further implies that it has led to beneficial and adaptive behaviours. Indeed, communication occurs *“when an action (a signal) produced by an individual organism causes a change (a reaction) in another organism, where both the signal and the reaction have been designed for these purposes”* (Scott-Phillips, 2008), and persists only if the signal produces a reaction that benefits both the emitter and the observer. Otherwise, the signal would stop being emitted, or attended to (Dezecache et al., 2013). According to this framework, emotional signals have co-evolved with the observers’ behavioural responses (Dezecache, Jacob, & Grèzes, 2015), so that the latter are adapted to the former, hence ensuring shared benefits. This

assumption would imply that facial expression of emotions in the emitter are closely related to action processes in the observer.

Evidence of such a relationship has been provided by neuroimaging findings indicating motor-related activity triggered by the mere processing of emotional stimuli. Although several studies have shown that threat can trigger activity in *subcortical* areas involved in the elaboration of defensive responses (periaqueductal gray, hypothalamus - e.g. Pichon, de Gelder, & Grèzes, 2011), other studies have revealed co-activations of the amygdala, which plays a pivotal role in emotion-related functions, and *cortical* motor areas in response to the perception of threat-related emotional faces or bodies. Interestingly, such co-activations have been observed in a myriad of tasks, ranging from explicit/implicit emotion categorization (Conty, Dezechache, Hugueville, & Grèzes, 2012; Grèzes, Adenis, Pouga, & Armony, 2013; Pichon, de Gelder, & Grèzes, 2009) to passive viewing (De Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Grosbras & Paus, 2005), independently of attentional control (Pichon, de Gelder, & Grèzes, 2011) or consciousness (Van den Stock et al., 2011). This reveals that the engagement of motor-related regions can be independent of task demands, reflecting a deeply rooted mechanism.

Moreover, a functional and anatomical connection between cortical motor areas and the amygdala has been uncovered (Ahs et al., 2009; Grezes, Valabregue, Gholipour, & Chevallier, 2014; Grèzes, Wicker, Berthoz, & De Gelder, 2009; Qin, Young, Supekar, Uddin, & Menon, 2012; Roy et al., 2009; Voon et al., 2010), suggesting that these regions work in tandem to allow the brain to prepare adaptive responses to threatening signals (Figure 5). The functional role of motor-related areas has been further demonstrated by Transcranial Magnetic Stimulation (TMS) studies in which the disruption of the motor cortex has led to an impairment of facial recognition of threat-related emotions (anger and fear), but not of positive ones (happiness) (Balconi & Bortolotti, 2012, 2013).

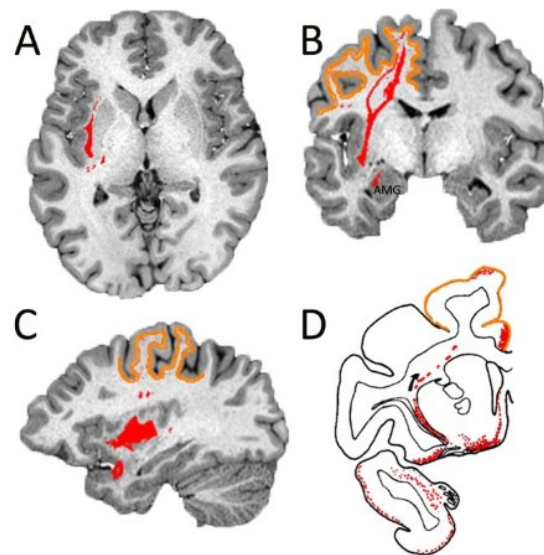


Figure 5. From Grèzes et al. (2014). A,B,C) Reconstructed structural tracts (red) from the amygdala to several motor-related areas (orange) as found with probabilistic fiber tracking dMRI. D) Neuronal tracing showing the paths from the basal nucleus of the amygdala of a monkey to lateral premotor cortex and motor cingulate cortex [modified from Avendano et al. 1983].

Finally, a recent paper has revealed that the brain parametrically encodes the strength of threat signals in the motor cortex (El Zein, Wyart, & Grèzes, 2015). In this EEG study, participants were asked to categorize morphed facial expressions of fear and anger of varying emotional intensity and gaze direction. Regressions of the motor-related mu frequency band with emotional intensity indicated that only threat-signaling emotions were encoded in response preparation signals overlying the motor cortex at 200ms following face presentation. This early representation of threat-related signals in the motor cortex support the contribution of the motor pathway during the processing of negative social signals. Taken together, these findings uphold a strong connection between emotion and motor circuits, enabling the brain to react swiftly and efficiently to threat signals (Ohman & Mineka, 2001).

Conclusion of Chapter 1.

Facial expression of emotions have evolved to serve an intra-personal function preparing the emitter to face environmental challenges, and an inter-personal function allowing the emitter to

communicate information to observers. Indeed, the configuration of facial displays can communicate different signals, as shown by the literature on threat-related emotions indicating that anger signals imminent threat, while fear, despite its threat-relatedness, signals submission and appeasement. Moreover, evolutionary theories suggest that these emotional displays have co-evolved with the behavioural response of the observers. Neuroimaging study corroborated this relationship between emotion and action by showing robust activation of motor-related areas during emotion processing. The question that I will discuss in the next chapter is whether the behavioural response of the observer reflects the social function of the perceived emotional display. And particularly, do action tendencies favoured by angry and fearful facial expressions differ accordingly to their associated social functions.

II. Action: a facet of emotion?

In the emotion domain, the relationship between emotional displays and action tendencies have been investigated through two main perspectives. One line of research argues that the mere perception of an emotional stimulus will trigger the corresponding motivational system and elicit an automatic behavioural response as a function of its valence (negative-avoidance and positive-approach – Bargh, 1997). Alternatively, the discrete action programme perspective, proposes that emotions can be associated with discrete action-programmes that have evolved to cope with specific survival challenges (Levenson, 2011; Panksepp, 2004). Although studies investigating the relationship between emotions and action have mainly focused on the *emitter's* reactions to emotional stimuli, predictions regarding the *observer's* behavioural responses can be drawn within an evolutionary framework. Indeed, evolutionary theoretical accounts suggest that emotional signals have co-evolved with the observers' behavioural responses; the implication being that the observer's response should reflect the social function of the perceived expression (Dezecache et al., 2015).

In the following paragraphs, I will give an overview of behavioural paradigms that have been employed to investigate this question. I will detail the methodological challenges these studies have encountered

in order to highlight the importance of using appropriate response modality and experimental designs to study motor processes. I will mostly present studies including (at least) threat-related facial expressions but I will occasionally broaden this review to studies using non-facial threat stimuli in order to give a comprehensive view of how the question of the emotion-action relationship has been tackled to date.

II.1. Methodological challenges

First, investigating motor processes in response to threat is methodologically challenging due to the numerous steps composing the elaboration of motor responses: identification of the goal and its associated intention, planning of the action toward this goal, and finally the programming and execution of the action. Consequently, uncovering the relationship between threat-related emotions and action requires the use of suitable paradigms and appropriate measures.

Button-press tasks. Some studies have tried to characterize the influence of threatening stimuli on motor responses by using button-press tasks. In these tasks, participants are presented with a stimulus, whose threat-related aspect is generally irrelevant to the ongoing task, and are asked to respond by pressing a button. For instance, using stimuli representing either a person directing a firearm toward or away from the observer, Fernandes and colleagues (2013) investigated the speed with which participants were able to report whether two bars appearing peripherally to the stimuli were identical (Figure 6). Their results revealed that participants were quicker to respond when the stimuli displayed in the center of the screen depicted a firearm directed toward themselves as compared to stimuli depicting a firearm directed away from themselves. The authors interpreted this decrease as reflecting an increased motor preparation in the face of threat.

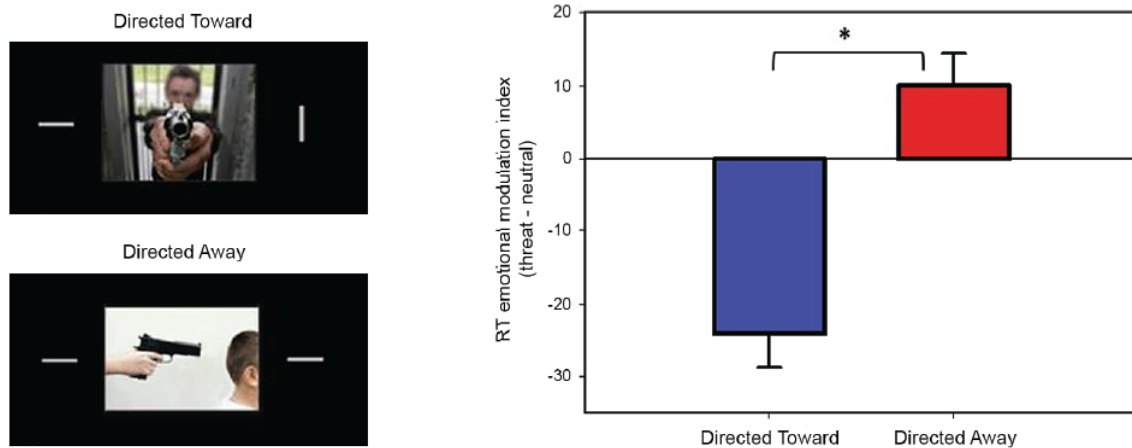


Figure 6. Adapted from Fernandes et al. (2013). The left panel shows example stimuli of the “Directed Toward” and “Directed Away” conditions. The right panel shows the modulation of reaction times by emotional content, with decreased reaction times in response to Directed Toward stimuli, compared to Directed Away.

However, running reaction times studies is not ideal when trying to address specific steps of the motor process. Indeed, registering one single discrete measure cannot disentangle the latency to act from the action duration itself and leads to the compression of all the different steps of the motor process into a unique measure. This ambiguity is further reflected by the fact that opposite reaction times effects can both be interpreted with respect to the threatening property of the stimulus. For example, in another button-press study, Sagliano, Cappuccio, Trojano, & Conson (2014) interpreted an increase in reaction times while categorizing approaching threatening stimuli as reflecting a freezing response. Thus, employing measures and response modalities that allow to decompose different steps of the motor process, such as movements, would help disentangle these different steps. For instance, the latency to act could be used as a proxy for freezing responses whereas the speed of movement execution could offer insights regarding motor preparation processes.

Joystick and manikin tasks. The joystick and manikin tasks allow participants to realize movements, or to move a character on the screen. They generally exploit stimulus-response affective compatibility effects, which rely on the rationale that perceiving positive information immediately facilitates

approach behaviour, whereas perceiving negative information immediately facilitates avoidance behaviour (Chen & Bargh, 1999). Although joystick tasks require participants to execute a movement using a joystick in response to a stimulus, manikin tasks do not require participants to realize a movement per se, but instead to move a figure on the screen via repeated button presses.

In joystick tasks requiring flexion-extension movements, the compatibility effect is based on the theory that approach is characterized by pulling movements (i.e. muscle flexion) whereas avoidance corresponds to pushing movements (i.e. muscle extension). As such, pulling positive stimuli and pushing negative stimuli would be automatic responses associated with shorter reaction times (“specific muscle activations account” in (Eder & Rothermund, 2008). For instance, a seminal study by (Solarz (1960) demonstrated that participants are faster to pull cards with positive words towards them and to push cards with negative words away from them. Yet, in manikin tasks, the compatibility effect is based on the direction of the figures movement caused by the button presses, either toward or away from a stimulus, rather than on the movement itself.

However, the “affective compatibility” effects that are generally revealed in these tasks are highly dependent upon how movements and responses are labelled, and upon what instructions are given (see Laham, Kashima, Dix, & Wheeler, 2015; Phaf, Mohr, Rotteveel, & Wicherts, 2014 for meta-analyses). Indeed, studies investigating action tendencies in response to anger and fear have yielded discrepant results and revealed both approach and avoidance tendencies in response to each emotion, depending on the context (Bossuyt, Moors, & De Houwer, 2014; Enter, Spinhoven, & Roelofs, 2014; Jennifer L. Hammer & Marsh, 2015; Marsh, Ambady, & Kleck, 2005; Wilkowski & Meier, 2010). For instance, Marsh, and colleagues (2005) have demonstrated that fearful expressions facilitated approach, pulling movements whereas angry expressions facilitated avoidance, pushing movements. But Wilkowski & Meier (2010) later found that participants were faster to initiate approach movements toward angry facial expressions and tended to be faster to initiate avoidance movements away from

fearful facial expressions, this time regardless of whether arm extensions or arm flexions were involved.

These results were further questioned by evidence revealing that different factors, such as the evaluative context, can moderate the strength of this effect (“evaluative coding account” from Eder & Rothermund, 2008). Bossuyt, Moors, & De Houwer (2014) have notably shown that the superordinate goals associated with approach and avoidance could determine the compatibility effects. Indeed, their results indicated that anger was associated with avoidance and fear with approach if avoidance allowed one to dominate/aggress and approach allowed one to be submissive. Conversely, anger was associated with approach and fear with avoidance if approach allowed one to dominate/aggress and avoidance allowed one to be submissive. Thus, manipulating the instrumentality of each action tendency and construing them either as aggressive or non-aggressive influenced results.

Altogether, these discrepant findings suggest that the effects revealed by such stimulus-response compatibility paradigms are dependent upon the way tasks are designed or communicated. Moreover, despite their use of movement as response modality, these studies generally did not exploit movement parameters and restricted their analyses to reaction times.

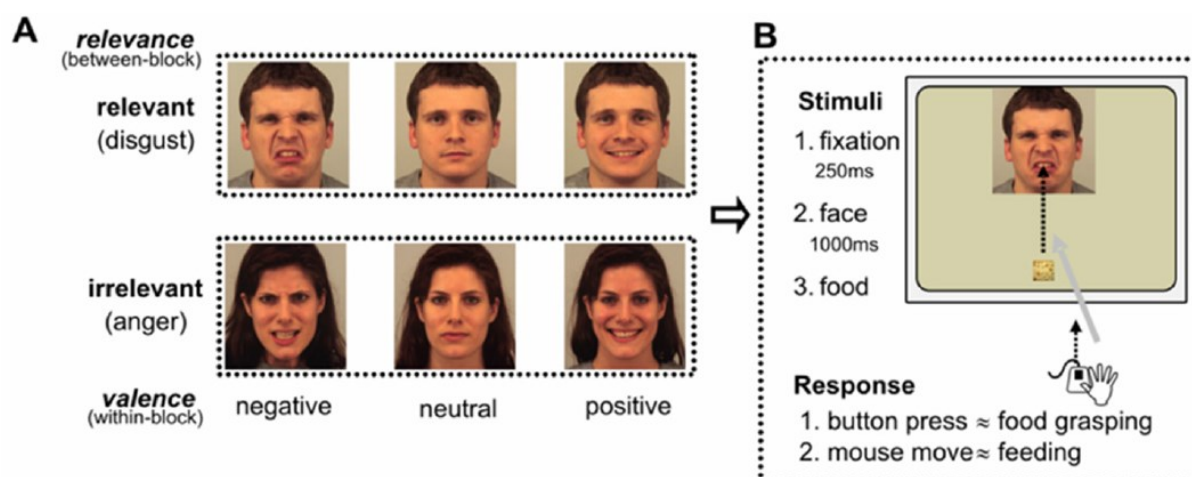


Figure 7. From Ferri et al. (2010). A) Examples of the stimuli. B) Feeding procedure.

Pointing and reaching tasks. Ferri and colleagues (2011) were the first, to our knowledge, to use a paradigm involving emotional faces that allowed to record kinematic parameters such as movement latency, duration and velocity. In their task, participants had to “feed” an actor by using their mouse to grasp a food item and direct it to the actor’s mouth (Figure 7). The actors displayed either a neutral, disgust, happy or angry expression, such that the relevance of the emotional displays was manipulated with regards to the purpose of the action. Their results did not reveal any significant differences between anger and the other emotional displays on any of the kinematic parameters, most probably due to the irrelevance of this emotional display in such feeding context.

In another study by De Valk et al. (2015), participants were presented with a screen where neutral and emotional (fearful and angry) faces and bodies were presented, to which they had to point to as quickly as possible. The results revealed shorter reaction times for angry faces and bodies as compared to neutral ones, which was interpreted as reflecting an increased readiness to act. However, no significant differences were found between angry and fearful displays, or between fearful and neutral displays. Moreover, no kinematic parameters were recorded, although they would have allowed investigating possible differences between angry and fearful, and fearful and neutral motor responses despite similar reaction times.

Finally, one team has recently used a pointing task to investigate the relationship between action and emotional displays, and used emotional displays as distractors rather than as targets (Ambron & Foroni, 2015; Ambron, Rumiati, & Foroni, 2016). This approach is interesting because in everyday life, we do not only interact with people head on but our courses of action is also susceptible to their influence. In these tasks, participants were instructed to move a stylus from a starting point to a target point while a distractor face was presented on the left or right side of the target. The spatial attraction toward the faces, reflected by a deviation in the trajectories toward the distractor, was recorded as a marker of motor distractibility. However, these studies were inconclusive in showing specific effects

of threat-related emotion (anger) on kinematic parameters (no significant difference between angry and happy displays, or angry and neutral displays). Moreover, their choice of a dot target for action might have limited the scope of the results by lacking some ecological validity. Indeed, we propose that using targets whose properties afford actions might be of relevance when studying goal-directed actions.

Standing tasks. While the tasks previously presented focused mainly on goal-directed actions, standing tasks have been shown to be relevant to investigate defensive freezing responses. In order to study body immobility, researchers have used stabilometric force platforms on which participants had to stand as they were presented threat-related stimuli. In a study by Roelofs, Hagenars, & Stins (2010), participants were asked to passively attend to emotional stimuli while their body sway was recorded. Interestingly, their results revealed that viewing angry faces reduced the natural body sway when compared with neutral or happy faces (Figure 8). This effect, triggered by a social threat display, was interpreted as a freeze-like behaviour, reflecting how the body can enter a state of immobility when facing danger.

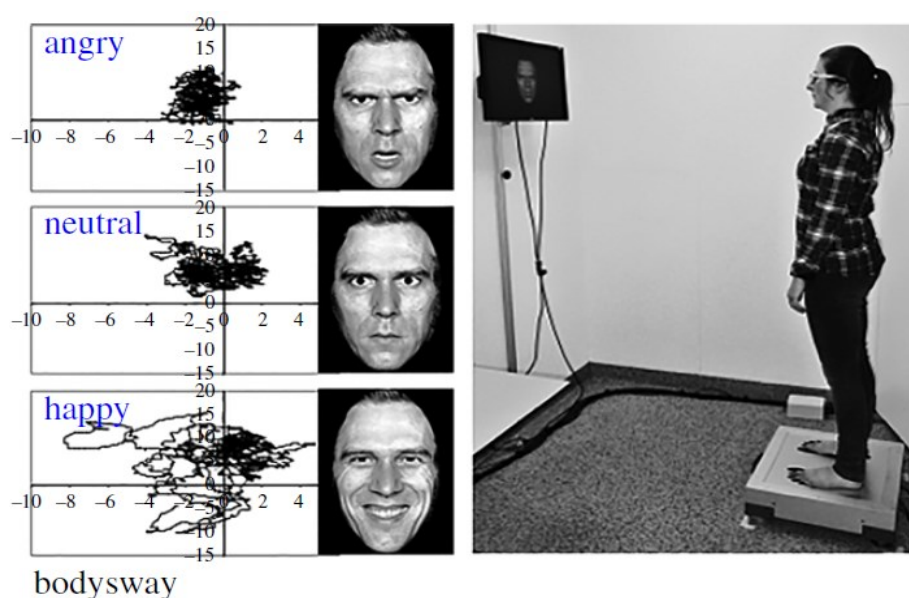


Figure 8. From Roelofs, 2017. Stabilometric force platform registering body sway. (a) Example of time series of body sway displacements (in millimeters in the anterior–posterior as well as lateral dimensions) in response to angry, neutral and happy faces.

A follow-up study replicated these findings using a task wherein subjects had to step back or step forward in response to angry and happy faces (Stins et al., 2011). The results indicated that pre-movement postural immobility was increased and lasted longer when participants had to step toward an angry face, compared to a smiling one, demonstrating increased freezing when they have to go against their natural bias of avoiding negative and approaching positive information.

These findings have been further extended in a recent study (Gladwin, Hashemi, van Ast, & Roelofs, 2016) that showed that the possibility of actively preparing for action in the face of threat could also influence freezing responses. In this study, participants were presented with images of a threatening individual inclined to shoot at them. Participants were either armed (i.e. able to avoid being shot by shooting the individual) or unarmed (i.e. helpless). The body sway data revealed an increased freezing response in the condition where participants were able to shoot at the threatening individual compared to the condition where they were unarmed and helpless. These data suggest that freezing could be a state of “attentive immobility” that might actively prepare further defensive responses. Additionally, the absence of significant effects on reaction times in this task highlights the relevance of taking into account the richness of motor behaviours (e.g. here, postural sway) by tracking their different facets.

II.2. Summary of the findings

Although promising methods have been employed (e.g. body sway measures, mouse-tracking tasks), motor responses to angry and fearful displays appear to be a challenging object of study. Indeed, stimulus-response compatibility paradigms have shown that, depending on the context, these emotional displays can trigger both approach and avoidance tendencies in the observer. Consequently, they seem to contradict the theory that negatively-valenced information systematically prompts avoidance in the observer, suggesting that the social meaning of these expressions matters.

While evidence corroborates that angry expressions signal a direct threat (increased action readiness and freezing responses), the action tendency they trigger in the observer remains to be clarified. In the case of fear, few studies have investigated their associated motor responses and experimentation is therefore needed to understand what behavioural response these displays are able to prompt.

Conclusion of Chapter 2.

The review of the literature investigating the relationship between threat-related emotion and action, and the heterogeneity of their results, highlights the difficulty in tackling this question. Nevertheless, some measures seem well suited to investigate motor responses to threat displays (e.g. consistent results in body sway measurements). Hence, this review calls for the use of paradigms involving neither flexion-extension movements, nor away/toward response labels, that are susceptible to bias the observed effects. The use of ecological experimental designs, notably contexts and targets for action that naturally afford action tendencies in the observer, would possibly allow to better study spontaneous strategies. Moreover, the use of adapted measures such as kinematics, allowing for the study of freezing as well as attraction to an alternative choice, could help investigate the different steps involved in motor processes. The following chapter questions the relevance of looking at action by tackling another mechanism, more precisely through the perspective of attention.

III. Attention: shaped by action?

Being able to detect the location of potential danger in the environment is crucial for survival and must be a quick, efficient and deeply rooted mechanism (LeDoux, 1996). In the emotion domain, the allocation of attention in response to threat-related stimuli has been widely investigated, and a great number of studies have indeed demonstrated that these stimuli have a privileged status and bias attention allocation (see review by Cisler & Koster, 2010). However, these studies have rarely investigated subsequent behavioural responses associated with this early orienting of attention

toward threat, although even if reacting appropriately to threat is as crucial for survival as being able to accurately detect it. Yet, in the motor domain, attention allocation has been shown to be closely related to motor planning (Fagioli, Ferlazzo, & Hommel, 2007; Kirsch, 2015; Wykowska, Schubö, & Hommel, 2009). Then, in the following paragraphs, I will review findings of the two lines of research and present recent evidence suggesting that attentional responses to threat could be investigated with regards to action responses.

III.1 Threat attentional biases

Allocation of attention to threat has been explored using a variety of stimuli and paradigms, ranging from visual search paradigms including photographs of spider or threat-related expressions, to spatial cueing tasks using fear-conditioned shapes. The vast majority of these studies have demonstrated that threat-related information captures, or prioritizes, attention as compared to non-threatening stimuli.

Visual search tasks. In one of the first visual search paradigm operationalizing this question, Öhman, Flykt, & Esteves (2001) asked participants to detect a deviant stimulus among a complex set of pictures while manipulating the threat-relatedness of the deviant to be spotted. The hypothesis they wanted to test was whether threat-related information would automatically capture attention, owing to evolutionary contingencies, and thus be detected faster than non-threatening information. They observed that threat-related deviants were indeed found more quickly than non-threatening ones, and that the speed of detection of the former was not affected by the size of the set, contrary to that of the latter, thereby highlighting how threat-related information was prioritized. Interestingly, this phenomenon has been observed with phylogenetically (spiders, snakes: Ohman et al. 2001; Soares et al. 2009) as well as with ontogenetically (guns: Fox, Griggs, & Mouchlianitis, 2007) threat-relevant stimuli.

Numerous studies have similarly replicated this threat pop out effect using angry faces (Calvo, Avero, & Lundqvist, 2006; Eastwood, Smilek, & Merikle, 2001; E. Fox et al., 2000; Pinkham, Griffin, Baron, Sasson, & Gur, 2010; Tipples, Young, Quinlan, Broks, & Ellis, 2002). The so-called “anger superiority effect” has been mainly observed using schematic stimuli but a study by Pinkham and colleagues (2010) further extended this effect to real angry faces, controlled for their emotional expressiveness, embedded in a crowd of heterogeneous faces (Figure 9). Their results revealed that angry facial expressions were detected faster and more accurately than happy faces, in crowds of both neutral and emotional distractors. Thus, using a more ecologically valid design, this study confirmed the prioritized processing that angry faces trigger.



Figure 9. From Pinkham et al. (2010). Example stimulus matrix from the visual search task showing an angry face among neutral faces.

Spatial cueing tasks. Other studies using spatial cueing tasks (MacLeod, Mathews, & Tata, 1986) aimed at testing whether threat-related stimuli can bias attention. In this paradigm, a threat-related and a neutral stimulus are presented on the screen, followed by a target appearing either at the same location as the threatening stimulus or behind the neutral one. Targets appearing behind threat-

related stimuli were shown to be detected faster, hence reflecting a biased allocation of attention toward the threat-related stimulus at the onset of the target (Lipp & Derakshan, 2005; Mogg & Bradley, 1999).

Interestingly, the effect was replicated using fear-conditioned stimuli whose threat-relatedness was not based on their physical properties but on their association to threat during the experiment (Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2005; Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2004; Notebaert, Crombez, Van Damme, De Houwer, & Theeuwes, 2011; Preciado, Munneke, & Theeuwes, 2017; Van Damme, Crombez, Hermans, Koster, & Eccleston, 2006). In a recent study, coloured circles were associated with electric shocks before the experiment only, and then served as spatial cues, along with other neutral circles. The results indicated a faster detection and an increased perceptual sensitivity for the targets presented at the same location as the fear-conditioned circles, thereby suggesting that threatening stimuli modulate the efficacy of sensory processing (Preciado et al., 2017).

It is important to note however that some spatial cueing tasks, such as the dot probe task, show discrepant results regarding the automaticity of attentional capture by emotional stimuli (for a review, see Puls & Rothermund, 2017).

Filtering tasks. Another way to test attentional biases to threat-related information is to design paradigms in which participants are required to filter out distracting information in order to perform the task. Thus, in these paradigms, different stimuli compete for attentional resources and the ability to accurately filter distracting information could reflect the salience of the distractors.

Vuilleumier and colleagues (2001) designed a paradigm where participants, who were presented with four images on the screen, two houses and two neutral or fearful faces, had to report whether or not the houses or the faces were identical. In one condition, participants had to attend to the faces while

in the other, they had to ignore the faces in order to concentrate on the houses (Figure 10). The results revealed that reaction times decreased when participants had to match the houses stimuli in the presence of fearful faces, compared with neutral faces. These findings indicated that fearful faces automatically exploited attentional resources, thereby interfering with the ongoing task. Other findings from tasks where competing stimuli are superimposed (Dickie & Armony, 2008) or flanker paradigms (Fenske & Eastwood, 2003) have corroborated this result.

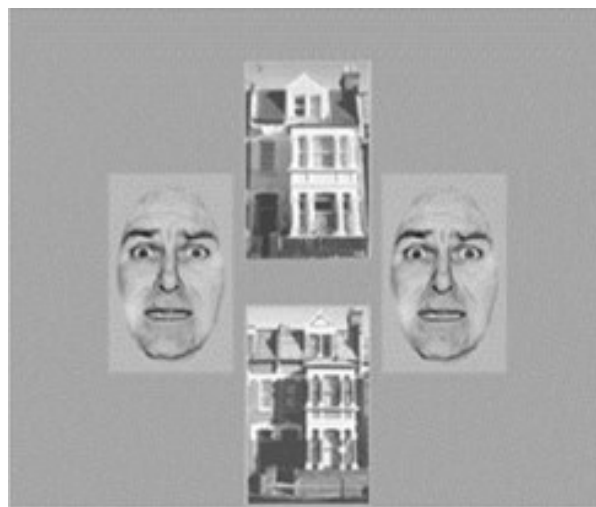


Figure 10. From Vuilleumier et al. (2001). Example stimulus of the filtering task.

Altogether, these results highlight the priority with which threat-related stimuli are consistently processed and the advantage this confers to individuals to accurately detect threat. But, in the face of threat, it is also crucial to select an appropriate action in order to eventually reach a place of safety, and paradigms are thus needed to understand whether attentional biases to threat influence subsequent motor responses. Although using non-threatening stimuli, the motor domain has addressed the question of the interplay between attention and action by jointly studying attention and motor planning (Rizzolatti, Riggio, Sheliga, 1994).

III.2. Action-related attentional biases

III.2.a. Eye movements

The “premotor theory of attention” (Rizzolatti, Riggio, Dascola, & Umiltá, 1987) proposes that attention can be drawn to a point in space only when the oculomotor programme for moving toward this point is ready to be executed, and that the same mechanisms governs overt (eye movements) and covert (shift of attention) orienting. Hence, according to this theory, attention is deployed to a given point in accordance to the parameters of the motor program and action selection should affect attention allocation.

Numerous studies have explored the relationship between eye movements and attention orienting. For instance, Craighero and colleagues (2004) have investigated the functionality of this relationship by exploiting the Posner effect, namely the increased ability to detect an incoming target when its location has been previously cued (Posner, 1980). Their paradigm aimed at testing whether this enhancement remained in circumstances where a target was presented at a location to which no saccades could be executed, thereby dissociating oculomotion from attention orienting. In order to constrain eye movements, participants wore a patch covering one of their eyes and the task was run on a screen which was rotated, both manipulations making it difficult to saccade toward the temporal hemifield (Figure 11). The results revealed no perceptual benefit in processing a validly cued target when it appeared at a location where no eye movements could be executed (i.e. in the temporal hemifield), although a benefit was found when the target appeared in the nasal hemifield where movements could be executed or within both hemifields when the screen was placed in a frontal position.

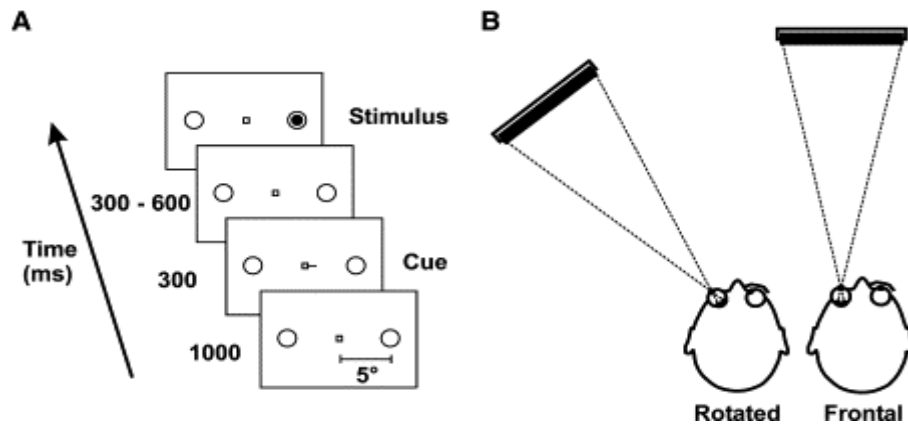


Figure 11. From Craighero et al. (2004). (A) Illustration of the events occurring during a valid trial. (B) Schematic illustration of frontal and rotated conditions here performed by the left eye, with a patch covering the right eye.

Although these results corroborate the relation between eye movements and covert shifts of attention supported by the premotor theory of attention developed by Rizzolatti and colleagues (1987), recent evidence revised this theory by showing that under some circumstances, oculomotion and covert attention dissociate from each other (Belopolsky & Theeuwes, 2009, 2012). Using different paradigms, Belopolsky and Theeuwes (2012) demonstrated that shifting attention is indeed associated with saccade programming, as revealed by faster saccade reaction times when participants had to make an eye movement toward a target whose location matched the cue location. However, while this facilitating effect confirmed the assumption made by the premotor theory of attention, the authors showed that maintenance of attention could be a particular case.

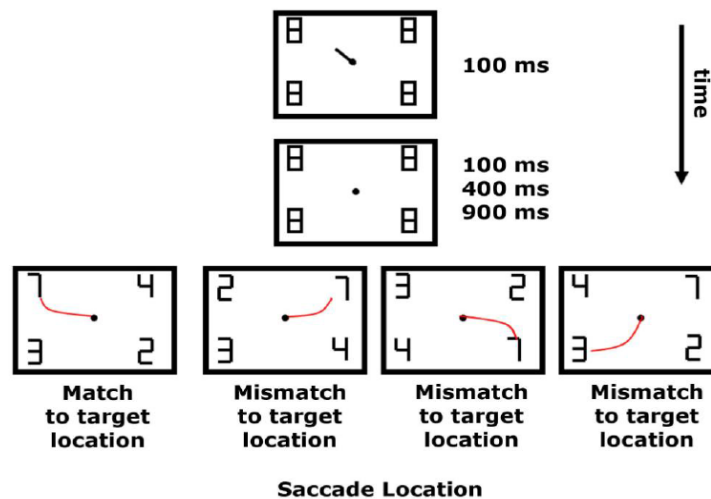


Figure 12. From Belopolsky & Theeuwes (2012). Experimental design of the experiment where participants had to shift their attention toward a cued location and maintain it until the target determining the endpoint of the saccade appeared. Here, targets 1,2,3,4 refers respectively to top left, top right, bottom right, bottom left (correct saccades are illustrated by the thin red line).

Evidence came from a task where participants were cued to covertly attend (without moving their eyes) to a location where a target would appear, and to later make an eye movement to the location defined by the target identity. Importantly, there was a low probability that the target matched the location of the saccade endpoint (only in 25% of the trials). To elicit a maintenance of attention at the target location, the time between the onset of the cue and the onset of the target was manipulated and participants had to maintain their attention at the cued location from 200ms to 1000ms. The results revealed longer saccade reaction times when the saccade endpoint matched the target location (for instance, cue toward the top left corner, and target 1 – see Figure 12), thereby suggesting that saccadic programmes had been suppressed when attention had to be maintained at a location to which there was a low probability of making an eye movement. Thus, although these findings confirmed that the covert orienting is associated with saccade programming, they revealed that they can dissociate in circumstances where attention has to be maintained at a location without the intention of making an eye movement, probably for economical reasons.

III.2.b. Manual actions

Besides studies investigating the relationship between attention orienting and eye movements, others have explored the relationship between the observation, or preparation, of manual actions and attention allocation (Fagioli et al., 2007; Kirsch, 2015; Wykowska et al., 2009).

In a study by Fagioli et al. (2007), participants had to prepare a pointing or grasping action before performing a visual detection task after which the action was to be executed. Importantly, the visual detection task consisted in detecting a deviant in size or in location among a set of stimuli, these features being chosen for their relevance with regards to the two types of actions (e.g. the size of an object is relevant to define the aperture size of a grasping action). The results of their experiment indicated that participants were quicker at detecting a deviant in size from a set of stimuli when they were preparing a grasping movement, and faster to detect a deviant in location when they were preparing a reaching movement. Interestingly, the perceptual features that were favored in the attention task corresponded to the properties of the movement being prepared. The authors concluded that action planning can orient attention towards the features of the stimulus that are relevant to the action that has previously been selected.

Another set of experiments by Kirsch (2015) have shown that action planning can even bias the perceived position of movement-unrelated objects. In these experiments, participants were asked to prepare a mouse movement toward an endpoint that was precisely indicated to them via a numerical cue (7 possible locations from far right to far left – Figure 13), and had to estimate the distance of a target from the middle of the screen while they were preparing the action. The results of these studies revealed that participants were biased to judge the location of a target accordingly to the endpoint of their action, with the magnitude of the biases reflecting the eccentricity of the endpoints (e.g. maximum rightward bias in distance estimation when the endpoint of the action was on the far right). These findings were further corroborated by evidence showing that low-level visual function is

modulated during preparation for a voluntary movement (Rolfs, Lawrence, & Carrasco, 2013), and that fluctuations of visual contrast sensitivity are time-locked to the movement onset (Benedetto, Spinelli, & Morrone, 2016; Tomassini, Ambrogioni, Medendorp, & Maris, 2017).

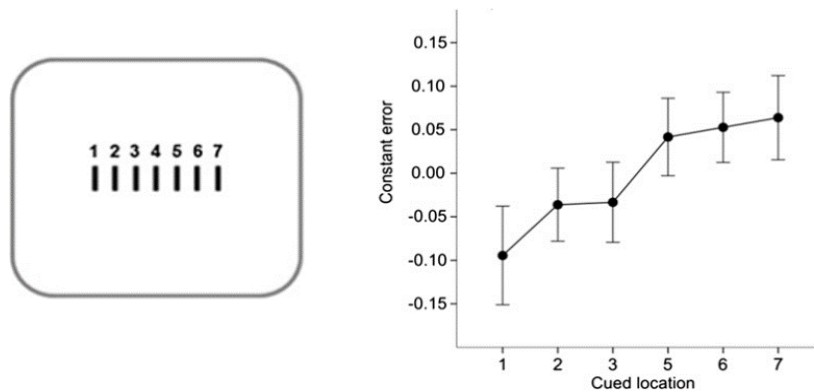


Figure 13. Adapted from Kirsch (2015). On the left panel are presented the numerical cues corresponding to the different location of movements' endpoints, from 1 for a movement ending to the far left, to 7 for a movement ending to the far right. On the right panel is presented the error in judgment of the target position given the cued location of movements' endpoints. Positive values represent a rightward bias, and negative values represent a leftward bias.

These studies suggest that motor planning, when it serves oculomotion or manual responses, can guide attention toward the endpoint of the chosen action. Although these effects were demonstrated using tasks including non-threatening stimuli, they raise the question of the existence of a similar mechanism when planning an action in response to threat-related displays: are threat-related attentional biases the mere reflection of action tendencies in the observer? This assumption seems counterintuitive given the body of research demonstrating attentional bias *toward* threat. However, in these tasks, participants are not presented with action opportunities allowing them to react adaptively to threat.

Interestingly, a recent experiment by Vogt, Koster, & De Houwer (2016) provided compelling evidence that when actions allowing participants to avoid a threatening noise are available, attention could no longer be tuned toward threat. Using an attentional cueing paradigm combined with a secondary Go-No-Go task (see Figure 14), they compared attentional prioritization of coloured cues signaling an

imminent threat (the subsequent occurrence of an aversive noise) and cues allowing participants to instrumentally reach safety. These instrumental safety cues consisted of specific colour patches that could reduce the probability of threat, provided participants responded correctly to these cues (Go response) in the secondary task. Their results revealed that when the safety signal, allowing to decrease the probability of threat, was distinct from the threat signal itself (different colour patches), attention prioritized instrumental safety signals over threat signals, with shorter reaction times to probes when they replaced safety signals compared to threat signals. But when the colour patch that could diminish the probability of threat was the threat signal itself, attention prioritized threat signals.

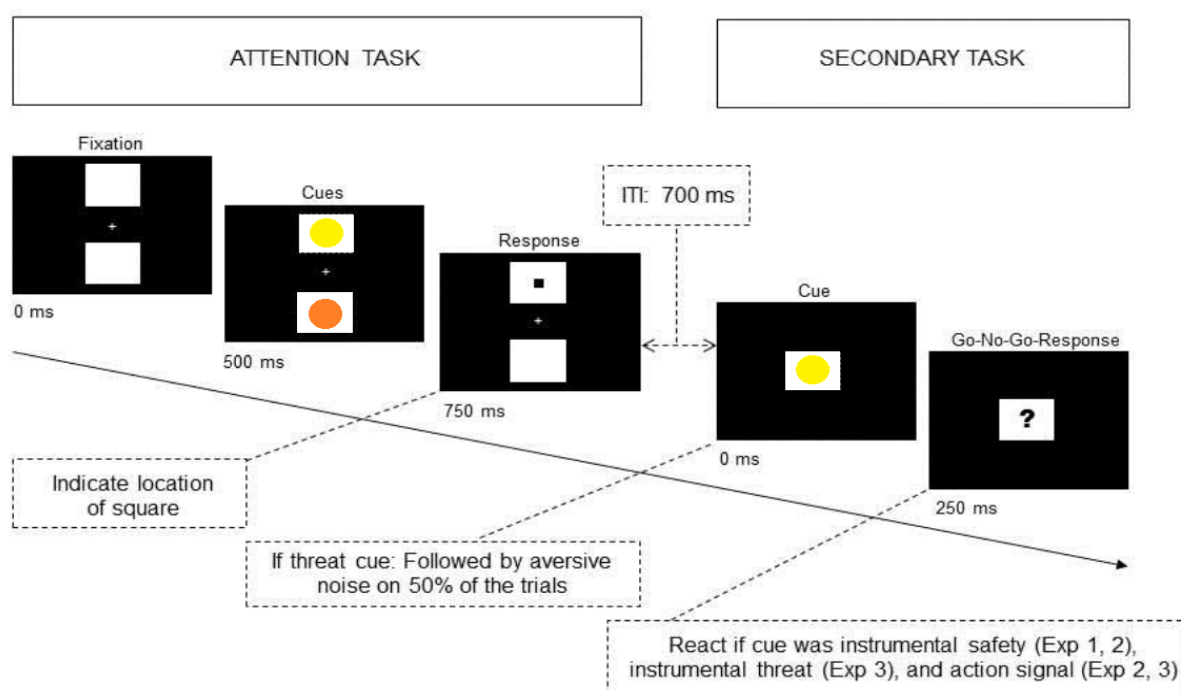


Figure 14. From Vogt et al. (2016). Schematic overview of a trial of the combined dot probe and secondary tasks. In the attention task, participants had to report the location of the square appearing after the patches offset. In the secondary task, they had to press the spacebar if the stimulus presented was the safety signal or the threat signal, depending on the paradigm.

These findings suggest that attention can be allocated to the signals that are most instrumental in reaching safety in a threatening context, and underline the importance of studying responses to threat in environments including action opportunities.

Conclusion of Chapter 3.

Attention biases toward threat have been widely investigated in the literature, but rarely in tandem with their associated motor responses. Yet, studies have shown that motor planning can influence attention allocation, and recent findings suggest that attention can be withdrawn from threat signals when available actions allow participants to reach safety. Future experiments are thus needed to understand the interplay between attention and action responses to social threat within ecological environments providing action opportunities.

IV. Our scientific question

The previous chapters provide conceptual and methodological guidelines with regards to the study of motor processes in response to emotional displays.

First, studying “natural” action tendencies in response to threat-related expressions would benefit from ecologically valid free choice tasks where participants respond spontaneously to emotional displays, while being constrained as little as possible by the tasks demands and by the need to fulfil experimenters’ expectations.

Second, in order to understand action decision-making processes, it seems crucial to use a continuous measure of processing that can provide information about choice dynamics, such as movement kinematics parameters (Lepora & Pezzulo, 2015). One way to record these movement kinematics is to use mouse-tracking methods that can capture an individual’s attraction to competing

response options during a choice task, by reflecting the real-time spatial deviation of a participant's hand to the competing option when en route to the ultimate response (Freeman & Ambady, 2010).

In the emotion domain, this method has been mostly used in social categorization tasks and hand trajectories have been shown to capture individual's response biases (Cloutier, Freeman, & Ambady, 2014; Hehman, Stoler, & Freeman, 2015). In the motor domain, this method has shed light on how action decision making unfolds over time, notably by showing that an overt action can begin early in the decision process and be continuously revised, with action dynamics reflecting the choice uncertainty (Lepora & Pezzulo, 2015). Hence, such data are of great relevance when investigating action decision-making in response to emotional display because they allow us to understand how, under what circumstances and to what extent two actions tendencies can compete for selection in the face of threat, thereby shedding light on mechanisms that remain to be understood.

Third, besides using appropriate methods and measures, we believe that using ecological paradigms is important to study the interplay between action and emotion processes. As put by Pezzulo & Cisek (2016), human cognition has to be studied using *"experiments that reflect conditions that are as ecologically valid as possible, as opposed to conditions designed to face subjects with problems that do not capture the fundamental challenges to which the brain has adapted"*. In the emotion domain, the paradigms that are most commonly used require participants to respond to bodiless faces displaying a stereotypical emotional expression and presented on a plain background. Although these paradigms manipulate stimuli in such way to allow the study of specific cognitive mechanisms, and therein are needed, they do not reflect both the richness of our (social) environment, and the realism of our everyday actions.

One way to design more ecological paradigms is to integrate key features of our natural environment into experimental designs such as, when studying motor processes, action opportunities (affordances). Affordances were originally described by Gibson (1979) as the set of motor possibilities that an object

in the environment offers an individual. According to his view “the observer may or may not perceive or attend to the affordance, according to his needs, but the affordance, being invariant, is always there to be perceived” (Gibson, 1979). Indeed, despite their pervasive nature, the way affordances are processed can depend upon the context, the goals and intentions of the observer, which, together, will prioritize one action over a set of different possible actions that the object affords (Maranesi, Bonini, & Fogassi, 2014).

For instance, in the context of a subway car, the prevailing affordance of a seat would be a sitting action. Though, when entering the subway car for a few stops only, the affordances offered by the empty seats might not be attended to. However, after a long workday, the sitting actions afforded by the subway seats might be more susceptible to be perceived. Yet again, at rush hour, the selection of the seat might be influenced not only by the observer’s state, but also by the presence of other individuals. Indeed, everyday action decision-making entails taking into account the action opportunities provided by the environment, along with social information susceptible to guide our decisions. Hence, if the subway car is busy, the observer will choose a seat while taking into account the surrounding individuals.

This example can generalize to many situations where our courses of action might be shaped by our social environment, thereby reinforcing the relevance of incorporating action opportunities to experimental designs when investigating the relationship between emotion and action.

Fourth, given the data suggesting a relationship between action selection and attention allocation, it seems of great relevance to also address the question of the relationship between emotion and action through the perspective of attention. Indeed, if social information biases action selection, and if action selection biases attention allocation, a paradigm testing attention allocation in the presence of threat-related information and using an environment providing action opportunities might give insightful results. Moreover, using direct behavioural measures of attention allocation such

as saccades can help obtain a comprehensive view of the relationship between attention, action and threat, notably regarding its development in time.

Following these directions, we have designed an action-related decisions task where i) participants make spontaneous free choices between two available actions in response to threat-displays, ii) we continuously track movements' parameters, iii) ecological opportunities for action are provided by the environment. This task will allow us to test whether threat-related facial expressions can shape action selection, as reflected by the proportion of choice and movement kinematics. Moreover, in order to investigate the relationship between attention allocation and action selection, we have i) run the same paradigm while recording saccadic behaviour, ii) designed a task where participants have to detect a cue using the same experimental context. Finally, the action-related decisions task has been run while recording electroencephalographic activity so as to better understand the time course of these different processes occurring in the face of threat.

Accordingly to the evolutionary framework, we formulate the hypotheses that threat displays will influence action selection by favoring specific actions reflecting the social function of the perceived expression. Moreover, regarding attention responses to threat, we propose that incorporating action opportunities to the experimental context might reconcile the present opposite findings from the emotion and motor domains by showing that the presence of affordances can shape attention allocation under social threat (Figure 15).

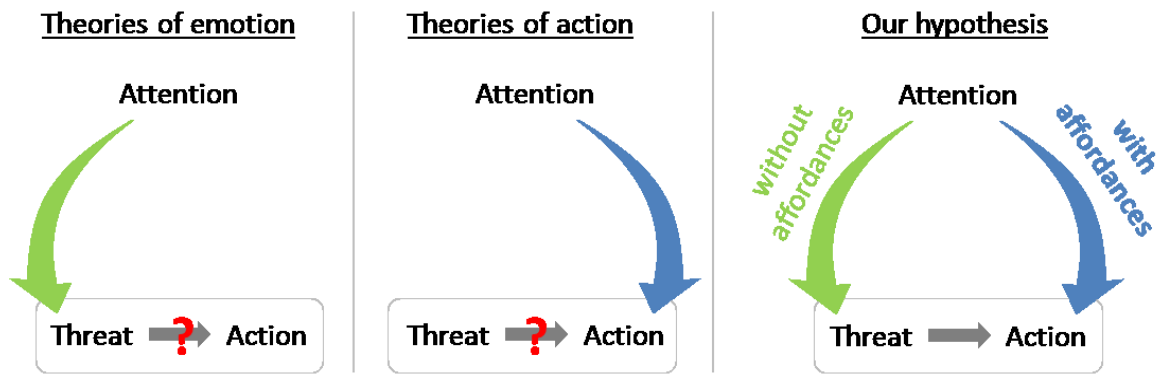


Figure 15. The left panel describes the current view in the emotion domain which assumes that attention is drawn to threat-related information, irrespective of the associated behavioural responses to threat. The middle panel describes the current view in the motor domain which assumes that attention allocation can be guided by action selection, without making clear predictions about the relationship between threat and action. The right panel describes our proposition that the presence of action opportunities in the environment can shape attention allocation, accordingly to the action that will be selected in the face of threat.

EXPERIMENTAL SECTION

PART I: Action and covert attentional responses to threat – Behavioural and pupillometry studies (Experiments 1 to 3)

This part will present a submitted paper combining 3 behavioural studies, and a complementary pupillometry analysis.

Action opportunities modulate attention allocation under social threat.

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Abstract

When entering a subway car affording multiple targets for action, how do we decide, very quickly, where to sit while gauging the presence of a potential danger? Although existing motor theories posit that action selection between competing options is biased by sensory information and determines attention allocation toward the endpoint of the selected action, theories of emotion suggest attentional biases toward threat cues. To address this apparent contradiction, we explored spontaneous action choices and attention allocation in a realistic context offering competing potential actions, in the presence of threat-related angry and fearful displays. Participants chose the actions that avoid angry and approach fearful individuals, respectively, and allocated their attention to the endpoint of the prioritized actions. Our findings establish that in a realistic context offering competing affordances, threat-related distractors shape both action selection and attention allocation accordingly to their social function.

In our natural environment, we are continuously confronted with opportunities for action. Consider, for example, the everyday scenario of entering a subway car and having to decide, very quickly, where to sit. In such situations affording several potential targets for action, it is suggested that our brain prepares multiple competing actions in parallel while collecting sensory information to select the most appropriate one regarding that situation (Cisek, 2007). These maps of action opportunities (affordances) need also to include social information, such as potential interactions with surrounding individuals (Bach, Bayliss, & Tipper, 2011; Ferri, Campione, Dalla Volta, Gianelli, & Gentilucci, 2011; Sartori, Begliomini, Panozzo, Garolla, & Castiello, 2014; Sebanz, Knoblich, & Prinz, 2003). The question arises as to what type of information guides the selection of our imminent actions in social contexts.

One key piece of information that can influence action decision-making is the emotion expressed by others (Dezecache et al., 2015; Grezes, 2011). Indeed, evolutionary accounts posit that emotional displays serve a communicative function by conveying critical information about the sender's affective state and associated behavioural intentions (Fridlund, 1994; Keltner & Haidt, 1999). Moreover, emotional displays are thought to have co-evolved with the observers' behavioural responses so that the latter reflect the social function of the perceived expression (Dezecache et al., 2013). Within such a framework, the emotional displays others produce should influence the selection of our upcoming actions in social contexts, according to their social function.

Returning to our everyday scenario of entering a subway car where different potential actions are competing, we would more likely choose to sit next to a person with a neutral facial expression than to one displaying a threatening, and especially angry, expression. Yet, within the evolutionary framework, the prediction would be different for fearful displays because anger and fear, while sharing the same valence, convey different social meaning. Indeed, while facial expressions of anger evolved to enhance cues of strength and communicate a probability to be aggressed and defeated to the observer (Sell et al., 2014), fearful facial expressions evolved to enhance cues of vulnerability and

promote prosocial behaviours (Hammer & Marsh, 2015). Here, we investigate whether different facial expressions (i.e., anger and fear) influence people's free choice in the presence of competing targets for action, accordingly to their social function. In particular, when in the subway car, would we sit away from angry individuals but next to fearful individual ones?

Further, we explore the potential coupling between action and attentional responses to threat displays in the presence of competing targets for action. Indeed, investigating action processes entails to also consider how potential targets for action are represented within the attentional system, visuo-spatial information being critical for specifying actions' parameters (Cisek & Kalaska, 2010). The motor domain literature has investigated this interplay between attention and action, and has demonstrated that planning an action can automatically guide attention (whether covert or overt) toward the endpoint of the chosen action, so as to extract action-relevant information (Fagioli et al., 2007; Kirsch, 2015; Wykowska et al., 2009). Along with the premotor theory of attention, which argues that attention allocation to a specific location corresponds to preparing a movement toward that location (Sheliga et al. 1994), such findings predict that, when entering in a subway car, our attention should be allocated toward the seat we intend to sit on.

Yet, if among the passengers, one appears as potentially threatening, would our attention be diverted from our destination? Findings from the emotion literature suggest that attention would be oriented toward threat, past research having mainly established that threatening stimuli quickly and efficiently attract attention (Koster, Crombez, Verschuere, Van Damme, & Wiersema, 2006; Notebaert, Crombez, Van Damme, De Houwer, & Theeuwes, 2011; Ohman & Mineka, 2001; Vuilleumier & Huang, 2009 - but see Puls & Rothermund, 2017). However, these studies, by investigating *early* attentional responses in experimental contexts devoid of opportunities for action, have failed to address how such attentional biases predict behavioural responses (Cisler & Koster, 2010). Moreover, one could hypothesize that the presence of a potentially dangerous individual would prompt the preparation of

an escape plan, leading attention to be deployed away from the individual, rather than toward him. As such, the literature from the motor and the emotion domains predicts that, in the presence of several targets for action, the source of potential threat and the best target for action in that situation will compete for attentional priority. Using a spatial attention paradigm, we investigated how the presence of competing targets for action impact people's attention allocation under threat.

We created an original setting that allowed us to record participants' spontaneous choices between competing actions in a realistic context, in the presence of emotional displays (Exp. 1). Our stimuli represented a room with four seats. The two middle seats were occupied by two individuals, while the two outer seats remained empty, leaving the opportunity for two potential actions. At the same time, the facial expressions of the seated individuals were manipulated so that one always displayed a neutral expression while the other displayed either a neutral, fearful or angry expression of varying intensity. As participants were asked to freely choose where they would like to sit, any influence of instructions, arbitrary movements or response labels was prevented on observed effects (Laham et al., 2015). To indicate their choice, participants were requested to perform a mouse movement whose kinematic parameters were continuously collected, allowing to disentangle different stages of the action process. Furthermore, to investigate whether the presence of competing targets for action also impact people's attention allocation under threat, we conducted two additional experiments, using a spatial attention design. While the first spatial attention experiment (Exp. 2) used the exact same stimuli as described above, the second one (Exp. 3), by masking the action-related context, addressed the modulatory effect of action possibilities on attention allocation. We predicted that anger and fear displays, signalling aggression (Sell, Cosmides, & Tooby, 2014) and affiliation (Hammer & Marsh, 2015) respectively, would favour the selection of actions that avoid angry and approach fearful individuals, and trigger attention to the endpoint of these threat-prioritized actions. Crucially, if action-related

processes modulate attention allocation, we hypothesize that this modulatory effect should disappear when action opportunities are removed from the experimental context (Exp. 3).

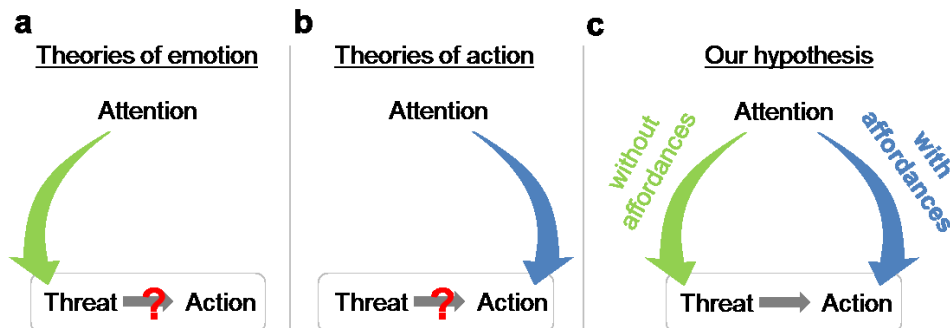


Figure 1. Experimental hypothesis and predictions. a) Theories of emotion have demonstrated attentional biases toward threats. However, they have failed to investigate whether these biases reflect upcoming behavioural responses, and to establish a clear relationship between threat displays and upcoming behavioural responses. b) Alternatively, theories of action suggest that attention allocation is guided by action selection. c) We propose to clarify these links by investigating i) whether attention can be allocated to the endpoint of an action that is prioritized by a specific threat, ii) whether the presence of action opportunities is a requisite to the guiding of attention by threat-prioritized actions, and finally iii) whether these prioritized actions reflect the social meanings of threat displays.

Methods

1. Participants

Three groups of participants were tested: 20 (9 males, mean age: 23.0 ± 3.6 years) participated in an action-related decision study, 25 (13 males, mean age: 22.4 ± 2.3 years) took part in the spatial attention study, and, finally, 27 (11 males, mean age: 23.0 ± 3.1 years) took part in a spatial attention control 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 licensed by the local research ethics committee (Comité de protection des personnes Ile de France III - Project CO7-28, N° Eudract: 207-A01125-48) and carried out in accordance with the Declaration of Helsinki. The participants provided informed written consent and were paid for their participation.

2. Stimuli

The stimuli reproduced a realistic social environment and consisted of photographs depicting a waiting room with four seats, where the two middle seats were occupied by two individuals (a pair of females or males) and the two outer seats were empty (**See Figure 2a**). Pairs' identities were matched by controlling for gender as well as invariant trustworthiness and threat facial traits. Faces varied in emotion (neutral, angry or fearful expressions) and in intensity (4 levels of morphs for anger and fear, created from the neutral to the emotional expression using a simple linear morphing transformation), and were equalized in perceived emotional intensities (for details: El Zein, Wyart, & Grèzes, 2015). In order to study the influence of Anger and Fear independently from each other and exclude emotion contrast effects (Paulus & Wentura, 2016), one actor of the pair always displayed a neutral expression while the other displayed either a neutral, angry or fearful expression. The identities, as well as the side of the actor expressing emotions, were fully counterbalanced. Please refer to the supplementary material for further details.

This resulted in 480 trials: 10 pairs x (2 emotional expressions x 4 levels of morphs + 1 neutral expression x 4 repetitions) x 2 emotional actor's identity x 2 emotional actor's side.

3. Experimental procedure and data analyses

General experimental procedure. Participants were seated 60 cm from eye to screen so that the eccentricity to the central fixation cross was of 4.5 degrees for the centre of the faces, and of 8 degrees

for the centre of the seats. In each study, participants underwent training until their accuracy in the task reached 60% and then completed the experiment. They were informed of their percentage of correct responses at the end of each block and were asked to maximize it.

The experiments were run using Matlab Psychtoolbox R2012b.

General statistical analyses. In all our experiments, we rejected invalid trials including nonresponses, incorrect responses (see below) and reaction times (RTs) inferior to 250ms. Statistical analyses were performed using Matlab R2012b and PASW Statistics 18. All data are expressed as mean (m) and Confidence Intervals (CI). For kinematics analyses, General Linear Models were used. For comparisons between conditions, repeated-measures ANOVAs were performed, and a Greenhouse-Geisser correction was applied when the assumption of sphericity was not met. When necessary, post hoc analyses with paired Student's t-tests were used. Independent Student's t-tests were performed to compare groups' performance. Partial eta squared (η^2_p) is reported as the effect size of the F statistics and Cohen's d (d) as the effect size of the t statistics. A value of $\eta^2_p = 0.1/d=0.2$ represents a small effect size, $\eta^2_p = 0.06/d=0.5$ a medium one and over $\eta^2_p = 0.14/d=0.8$ a large effect size.

3.1. Action-related decisions study

Experimental procedure. The experiment was designed as follows: participants were first exposed to a grey screen for 1000ms, then a fixation cross was superimposed upon the grey screen for 500ms, followed by the appearance of the scene. Participants were asked to choose which seat they would like to occupy in the scene as they maintained fixation on the cross displayed between the faces throughout the trial. They were given a maximum response time of 1400ms to indicate their choice by clicking on the mouse, moving the cursor from the bottom centre of the scene to the chosen seat, and releasing the click. An example of a trial is depicted in Figure 1A. Participants were requested to make

spontaneous free choices and were instructed that there were no correct choices in this task. Nevertheless, they were instructed that their movements needed to be correctly performed for their responses to be registered. A correct movement was defined by the release of the click on one of the seats within 1400ms after scene onset, and was signalled to the participants by the appearance of their portrait (taken prior to the experiment) superimposed on the scene at the release location, for 300ms (the maximum scene duration for correct movements was thus 1400ms + 300ms). If the click release was not made on the seat, or did not occur within 1400ms, the trial was considered incorrect. The end of the trial was triggered either by the mouse release or 1400ms after scene onset in the absence of a response.

Data analyses. We excluded data from two participants due to outlier performance on movement accuracy (lower than the mean accuracy minus two standard deviations). Because high anxiety is known to impact attention allocation to threat (for a review, see Grupe 2013), we limited our sample to subclinical population and excluded one participant presenting a clinical anxiety score based on the State-Trait Anxiety Inventory (STAI) administered before the study. We therefore analysed the data of 17 participants for this study. Participants' responses were first analysed by calculating the proportion of trials in which they decided to sit next to the neutral or emotional individual. Moreover, we conducted a raw time analysis on peak velocity measures which consisted in generating 60 time bins along the original (non-normalized) movement time, between 0ms and 1200ms, and computing the peak velocity of each trajectory.

3.2. Spatial Attention Study

Experimental procedure. The experiment was designed as follows: participants were first exposed to a grey screen for 1000ms, the scene appeared for 200ms and then, a cue (an upright or an inverted "T") was superimposed upon the scene for 400ms at a fixed location, on either outer seat. The scene

was then replaced by a grey screen for 800ms. Participants had a maximum of 1200ms (400ms cue presentation + 800ms grey screen) from the onset of the cue to report whether the T was upright or inverted by pressing the corresponding key, regardless of the side where the “T” appeared. The trial ended after the keypress or at the end of the 800ms grey screen in the absence of a response. Importantly, participants had to answer while focusing on a fixation cross displayed between the faces throughout the trial. They were requested to use their peripheral vision to discriminate the “T” and were instructed not to look at the surrounding scene. The mapping between the responses (upright or inverted) and the keys was counterbalanced between participants.

Data analyses. Data of one participant were excluded due to a misunderstanding of instructions. We therefore analysed the data of 24 participants for this study.

3.3. Spatial Attention Control Study

Experimental procedure. This experiment was designed to directly evaluate whether the presence of action possibilities determines emotion-specific attention allocation. The task and design were identical to the Spatial Attention study, except that a mask was superimposed on the scene to hide all the information susceptible to be associated with opportunities of action, leaving only the faces visible (See Figure 3c).

Data analyses. Data of two reaction times outlier (lower than the mean accuracy minus two standard deviations) were excluded. We therefore analysed the data of 25 participants for this study.

4. Data availability

The data that support the findings of this study are available from the corresponding author upon request.

Results

Impact of task-irrelevant emotional displays on action choices. Participants were presented at each trial with a scene representing a room with four seats where the two middle seats were occupied by two individuals. While one of those two individuals displayed a neutral expression, the other displayed either a neutral, angry or fearful expression, of varying intensity (4 levels of emotion strength for each emotion). Participants were asked to freely choose where they would like to sit by moving their mouse cursor toward one of the two available outer seats, as accurately and quickly as possible, and were informed that there was no correct response (**See Figure 2a**). Crucially, the subjects were first trained on neutral stimuli and conducted the experimental task only once they were able to realize the movements while fixating the central cross throughout the trial. The presence of emotional expressions was never mentioned to the participants.

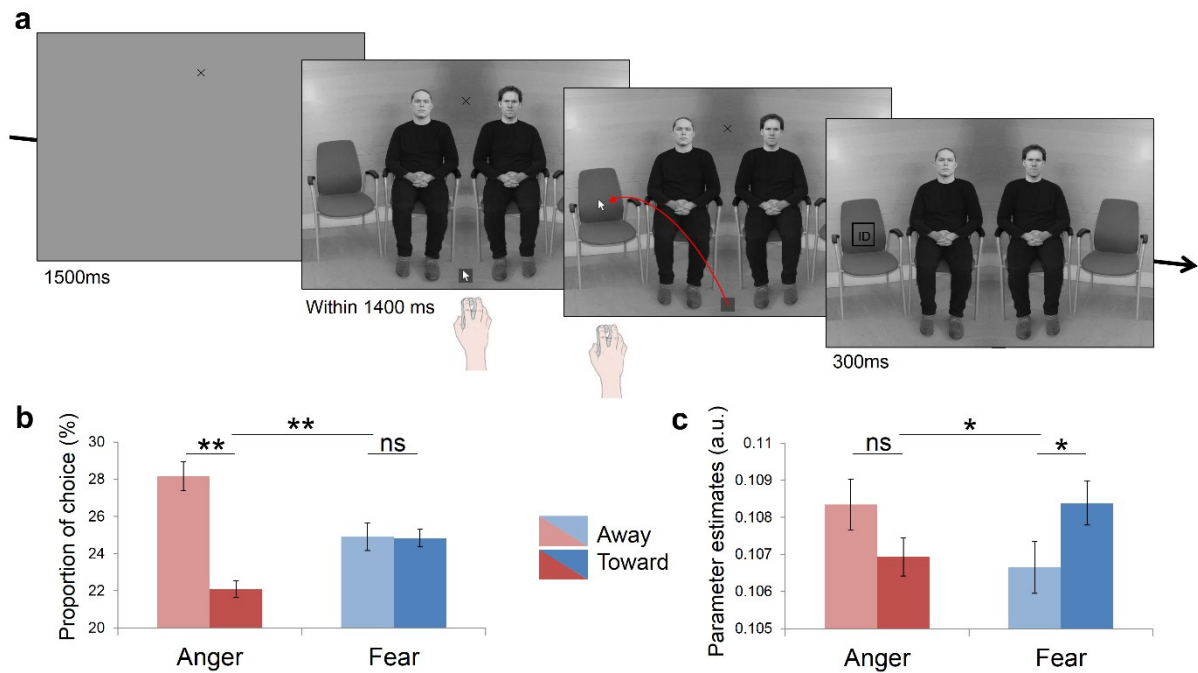


Figure 2. Action-related decisions study. a) Time course of a trial where participants have to indicate where they would like to sit by moving their cursor from the bottom centre to the chosen seat. The face of the participant appeared for 300ms after the offset of the movement. Please note that the pair of identities displayed on the stimuli was not used in this experiment and was selected for illustration purpose only, according to Radboud Faces Database permission. b) Emotion-by-Side interaction on the proportion of choice. c) Emotion-by-Side interaction on the parameter estimates of the peak velocity regression. ** $p < 0.01$; * $p < 0.05$; ~ $p < 0.1$; ns $p > 0.1$. For illustration purpose, error bars represent within-subject standard errors.

Overall, participants more often chose the seat located away from the emotional individual (“Away” and “Toward” respectively refer to the neutral and emotional actor side) ($F(1,16)=10.37$, $p=0.005$, $\eta^2_p=0.39$). Moreover, the level of intensity of the emotional display increased this tendency to avoid the emotional individual ($F(2.04,32.59)=6.85$, $p=0.003$, $\eta^2_p=0.30$, Greenhouse-Geisser corrected). Importantly however, the nature of the displayed emotion distinctively influenced participants’ choice (Emotion-by-Side interaction, $F(1,16)=14.90$, $p=0.001$, $\eta^2_p=0.48$): they significantly more often chose to sit away from the angry individual than next to him, but sat equally frequently away from as toward

the fearful individual (**See Figure 2b**). All other paired comparisons of the interaction Emotion-by-Side were significant (**See Table 1**). No other significant main effects or interactions were found (all $F_s < 2.10$, all $p_s > 0.10$, all $\eta^2_{ps} < 0.12$).

Proportion of choice (%)	Paired differences		t	ddl	p-value	Cohen's d
	Mean	95% CI				
AA - AT	6.08	[3.14, 9.02]	4.06	16	0.001	1.95
FA - FT	0.07	[-1.67, 1.81]	0.09	16	0.936	0.04
AA - FA	3.26	[1.65, 4.87]	3.97	16	0.001	1.25
AT - FT	-2.75	[-4.32, -1.18]	-3.42	16	0.004	-1.07
AA - FT	3.33	[1.35, 5.31]	3.30	16	0.005	1.27
AT - FA	-2.83	[-4.72, -0.95]	-2.95	16	0.009	-1.11

Table 1. Paired differences and statistics of the paired comparisons of the Emotion-by-Side interaction on choice proportions (%) in the action choice study. The abbreviations refer to the choice of the subjects with respect to the emotional actor: AngerAway: AA; AngerToward: AT; FearAway: FA; FearToward: FT; with “Away” referring to the opposite side of the emotional actor (i.e. side of the neutral actor) and “Toward” to the side of the emotional actor.

Impact of task-irrelevant emotional displays on movements' peak velocity. To better characterize the distinct influence of fearful and angry displays on action choices, we further investigated the action-decision process by continuously recording mouse-tracking data (custom-made Matlab program). We computed several kinematic measures (initiation times, movement duration, maximum deviation and peak velocity) using the Analyzer tool from the Mouse-Tracker software package (Freeman & Ambady, 2010). A parametric regression-based approach was adopted, consisting in regressing kinematic measures against the intensity of the displayed emotion (El Zein et al., 2015; Wyart, Myers, & Summerfield, 2015). For each analysis, a general linear regression model (GLM) was used where

emotion intensity was introduced as a trial-per-trial predictor of kinematic measures. The corresponding parameter estimates of the regression, reported in arbitrary units, were measured per participant, and then averaged across participants to produced group-level averages. We calculated the parameter estimates separately for our conditions of interest (Anger Away: AA, Anger Toward: AT, Fear Away: FA, Fear Toward: FT) and tested main effects on the corresponding intercepts. We also tested for a main effect of Emotion by comparing the Neutral condition to Anger and Fear pooled together.

We observed a significant Emotion-by-Side interaction ($F=6.81$, $p=0.02$, $\eta^2_p=0.30$) on peak velocity intercepts, thought to reflect choice confidence (Palser, Fotopoulou, & Kilner, 2015), showing that participants made quicker movements going toward fearful individuals than going away from them (FA vs FT: $t(16)=-2.61$, $p=0.02$, $d=-0.08$). The difference between AA and AT did not reach significance ($t(16)=1.34$, $p=0.20$, $d=0.08$) (**See Figure 2c**). No other paired comparisons (all $ts < 1.66$, all $ps > 0.12$, $d < 0.09$) or main effects were significant (all $Fs < 0.06$, all $ps > 0.81$, all $\eta^2_{ps} < 0.004$).

A summary of other kinematic measures indicates that i) threat-related displays (both anger and fear), as compared to neutral ones, significantly reduced the time required to launch a given action plan, indicating a speeded action selection mechanism when facing danger, and that ii) the selection process took place before movement initiation, as indicated by an absence of effects on the maximum deviation and its negative correlation with initiation time. For detailed analyses and statistics, please refer to the supplementary material.

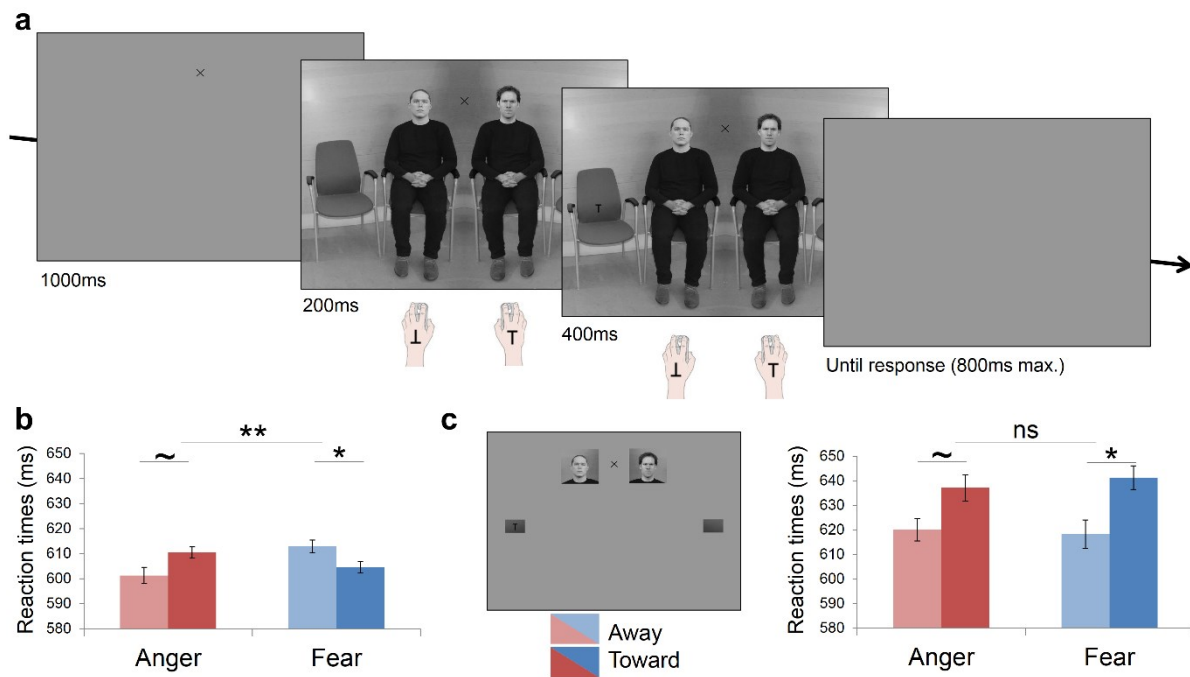


Figure 3. a,b) Spatial attention study. a) Time course of a trial where participants have to report the shape of the “T” appearing on either outer seat by pressing the corresponding key. The mapping between the responses and the keys was counterbalanced between participants. Please note that the pair of identities displayed on the stimuli was not used in this experiment and was selected for illustration purpose only, according to Radboud Faces Database permission. b) Emotion-by-Side interaction on the reaction times. c) Spatial attention control study. On the left, an example stimulus of the control study where the scene is covered by a grey mask in order to hide action-relevant information. On the right, the Emotion-by-Side interaction of reaction times. ** $p < 0.01$; * $p < 0.05$; ~ $p < 0.1$; ns $p > 0.1$. For illustration purpose, error bars represent within-subject standard errors.

Impact of task-irrelevant emotional displays on spatial attention. This spatial attention task builds upon the conceptual framework within which attention is a consequence of motor processes (e.g. the premotor theory of attention: Rizzolatti, Riggio, & Sheliga, 1994). Participants were presented with the same scenes as in the previous study but requested to report, as quickly as possible, the orientation of a target (upright or inverted “T”) appearing briefly on either outer seat (See Figure 3a). Overall, participants reported the orientation of the target significantly above chance ($m=75\%$, 95% CI [71, 79],

$t(23)=13.01$, $p<0.001$, $d=2.66$). Of interest here, attention biases were tested by performing an Emotion-by-Side-by-Level repeated-measures ANOVA on RTs, which revealed a significant Emotion-by-Side interaction ($F(1,23)=9.50$, $p=0.005$, $\eta^2_p=0.29$). Paired comparisons of interest (AA-AT and FA-FT) revealed that subjects were faster to discriminate the “T” when it appeared next to the fearful individual rather than away from him. In the case of anger, although the effect was in the predicted direction (i.e. trend for a quicker detection when the “T” appeared away from the angry individual) the comparison did not reach significance (See Figure 3b and Table 2). No other main effects or interactions were significant (all $F_s<2.7$, all $p_s>0.11$, all $\eta^2_{ps}<0.11$).

Reaction times (ms)	Paired differences		t	ddl	p-value	Cohen’s d
	Mean	95% CI				
AA - AT	-9.18	[-19.25, 0.89]	-1.79	23	0.087	-0.09
FA - FT	8.36	[1.13, 15.59]	2.26	23	0.033	0.08
AA - FA	-11.65	[-20.25, -3.05]	-2.66	23	0.014	-0.12
AT - FT	5.89	[-1.05, 12.83]	1.67	23	0.109	0.06
AA - FT	-3.30	[-12.61, 6.01]	-0.70	23	0.494	-0.03
AT - FA	-2.47	[-9.90, 4.96]	-0.65	23	0.522	-0.03

Table 2. Paired differences and statistics of the paired comparisons of the Emotion-by-Side interaction on RTs (ms) in the spatial attention study. Here, the abbreviations refer to the location of the “T”. Same abbreviations as in Table 1.

Impact of task-irrelevant emotional displays on spatial attention in the absence of action possibilities (spatial attention control study). Both the action and spatial attention tasks revealed differential impacts of fearful and angry expressions on action choice and attention allocation. To directly test whether the observed effects were related to the presence of action possibilities, as we originally hypothesized, we ran a final experiment where we removed the action-related context from the scene.

The design and the task were thus identical to the previous Spatial Attention study, except that, crucially, we superimposed a mask on the scene to hide any information susceptible to being associated with action opportunities. The only visible parts of the original scene were the faces of the two central individuals and the two locations where the “T” appeared on the outer seats (**See Figure 3c**). Participants reported the orientation of the target significantly above chance ($m=73\%$, 95% CI [69, 77], $t(24)=12.09$, $p<0.001$, $d=2.42$).

To test whether the Emotion-by-Side effect found in the original study was replicated in this setting, we performed a repeated-measures ANOVA on RTs with Emotion, Side as within-subjects factors, and Study as between-subjects factors. Of importance here, independent-samples t-tests indicated that participants from the original Spatial Attention Study and from the present Control Study did not differ on mean RTs (respectively $m=608\text{ms}$, 95% CI [569, 647]; $m=625\text{ms}$, 95% CI [589, 662]; $t(47)=0.66$, $p=0.51$, $d=0.19$) or accuracy levels (respectively $m=75\%$, 95% CI [72, 79]; $m=73\%$, 95% CI [70, 77]; $t(47)=-0.78$, $p=0.44$, $d=0.22$). Supporting our earlier postulate, the ANOVA revealed a significant Emotion-by-Side-by-Study interaction ($F(1,47)=7.72$, $p=0.008$, $\eta^2_p=0.14$). Contrary to the original study, the Emotion-by-Side interaction was no longer significant ($F(1,24)=0.97$, $p=0.33$, $\eta^2_p=0.04$), suggesting that removing action possibilities from the scene disrupted the influence of emotional displays on attention allocation (**See Figure 3c**). Importantly, a significant main effect of Side ($F(1,24)=4.73$, $p=0.04$, $\eta^2_p=0.16$) replicated a classical avoidance bias (e.g. Koster et al. 2006), such that the reaction times were decreased when the cue was presented away from the emotional individual. No significant main effect of Emotion was found ($F=0.08$, $p=0.78$, $\eta^2_p=0.003$).

Discussion

We conducted 3 experiments to assess the impact of task-irrelevant social threat displays on action and attentional responses. The first experiment revealed that angry and fearful expressions differentially shape the map of potential competing actions provided by the environment, by favouring the selection of actions that avoid angry and approach fearful individuals. The second study demonstrated that attention is allocated to the space of the scene corresponding to the endpoint of the action prioritized by anger and fear displays. Crucially, our third experiment confirmed this interpretation by revealing that the differential effect of anger and fear on attention allocation was disrupted when action possibilities were removed from the scene. Together, these findings demonstrate that, in a realistic context offering competing targets for action, action selection processes and associated attention allocation are influenced by threatening stimuli, accordingly to their social function.

Compared with existing stimulus-response compatibility paradigms that yielded discrepant results (i.e. both avoidance and approach tendencies to angry and fearful expressions depending on the context) (Krieglmeyer & Deutsch, 2013; Marsh, Ambady, & Kleck, 2005; Paulus & Wentura, 2016), our paradigm was ecologically valid (free choice task) and methodologically relevant (recording of kinematics). Our results revealed that the presence of task-irrelevant angry faces favoured the selection of avoidance responses, while the presence of fearful faces may favour the selection of approaching behaviours. Indeed, although approach tendency was not evidenced by participants' choices, their level of confidence in their choice, reflected by peak velocity (Palser et al., 2015), was higher when approaching fearful individuals. Thus, threat-related displays influence action-related decisions by shaping existing map of potential actions.

Building upon the idea that attention can be a consequence of motor processes (Rizzolatti et al., 1994), we further tested the impact of social threat on action responses using a task wherein participants had to discriminate the orientation of a cue appearing on either outer seat. Several studies have shown that planning an action facilitates (Baldauf & Deubel, 2010) and biases (Kirsch, 2015) the perception of visual cues located at the intended endpoint of that action (Fagioli et al., 2007; Wykowska et al., 2009). Therefore, if fearful and angry expressions drive the selection of distinctive targets for action, participants' attention should be allocated to the chosen seat. We showed that, participants were indeed quicker at detecting a cue appearing on the seats next to fearful displays, and tended to be faster, when it appeared away from angry individuals.

The differential effect of anger and fear observed in our action-related decisions and spatial attention paradigms is in line with our hypothesis that the perception of an angry (fearful) person would not only favour the selection of an action allowing to avoid (approach) that individual but also orient attention to the endpoint of these threat-prioritized actions. Although these findings do not allow drawing conclusions regarding the causal relationship between action selection and attention allocation, our third experiment, by using the same spatial attention paradigm while masking the action-related context, clearly demonstrated that removing action-related information disrupted differential effect of anger and fear on attentional allocation, and led to replicate classical attentional studies' findings whose paradigms also present bodiless emotional faces in contexts devoid of action opportunities (Koster et al., 2006).

The present results provide evidence that, in a realistic context offering competing targets for action, threat-related distractors determine attention allocation accordingly to their social function. These results are at odds with the prevailing view that attentional processes prioritize threatening information, irrespective of the associated behavioural response (Notebaert et al., 2011; Ohman & Mineka, 2001; Vuilleumier & Huang, 2009). The wealth of research demonstrating attentional biases

toward threat classically used stereotypical emotional faces, isolated from their bodies, and displayed on a plain background (Cisler & Koster, 2010). Here, by incorporating action opportunities to our design, we reveal that threat can bias both action- and attention-selection processes toward the most appropriate action possibility. In a similar vein, but using aversive auditory conditioning during an attentional cueing paradigm, a recent study demonstrated that when both threat and safety signals compete for attentional priority, attention is allocated to instrumental safety signals rather than to threat signals (Vogt et al., 2016). Thus, past research, by mainly focusing on threat-related attentional biases, has failed to investigate whether these biases relate to behavioural responses (Cisler & Koster, 2010). We suggest that ecologically valid paradigms are needed to better understand this relationship.

Angry and fearful faces differentially influenced both action- and attention-related decisions. Anger mainly favoured the selection of actions that avoided these individuals. This is consistent with the fact that angry faces, that enhance cues of strength and communicate the probability to be aggressed, (Sell et al., 2014) prompt observers to avoid them. Although some studies have shown that anger can be associated to approach behaviours, but mostly in the emitter (e.g. Krieglmeyer & Deutsch, 2013), our data indicate that angry faces primarily signal a direct threat to the observer and drive him to increase distance with the source of the threat (Sander et al., 2007).

Fear, as in the case of anger, is an arousing negative emotion that signals the presence of a potential danger in the environment (A. K. Anderson et al., 2003; Springer et al., 2007). Yet, contrary to anger, we observed that fearful individuals favoured the allocation of attention to the spatial area next to these individuals and higher confidence when approaching them. These findings are consistent with the fact that fearful faces were shown to enhance cues of vulnerability and affiliation (Hammer & Marsh, 2015) but also to prompt prosocial behaviours in both animals and humans (Dezecache, 2015; Hess, Blairy, & Kleck, 2000; Lorenz, 1966; Marsh, Kozak, & Ambady, 2007). Furthermore, affiliation has been suggested to be a primitive response to danger (Mawson, 2012), and grouping is an old

evolutionary strategy to cope with perceived risk of predation (Isbell, 1994). Our data thus highlight the potential prosocial function of fearful displays by showing that they encourage approach behaviours. Nevertheless, our design does not allow to clearly assessing why approaching fearful individuals may be the safest strategy. Future experiments would be needed to determine whether approaching fearful individuals is of self-preservative nature (a need for affiliation to alleviate one's own fear) or of prosocial nature (a desire to provide help) (Marsh et al., 2007; Dezechache et al., 2017).

Threat-related displays reduced the time required to initiate a given action plan, indicating speeded action selection when facing danger. We suggest that existing maps of potential actions are rapidly shaped through a modulation of the value associated with each competing option. The “affordance competition hypothesis” postulates that the brain forms multiple action plans in order to efficiently respond to environmental challenges, whilst gathering information to select the most appropriate according to the observer's current goal (Cisek, 2007). In the presence of threat, the emotional information likely modifies the value of each action plan, biasing the selection toward socially more adaptive behaviours. Even when emotional information is task-irrelevant, as in the everyday scenario of entering a subway car, such value modification must be very efficient and rapid so as to promote survival. Here, the action selection process seems to terminate before the onset of the movement (mean initiation time of 410ms), consistent with the idea of a very quick mechanism shaped by evolution (Thura & Cisek, 2014). Future experiments, using a “go-before-you-know” design to better follow the deliberation online (Gallivan, Bowman, Chapman, Wolpert, & Flanagan, 2016), as well as computational modelling (Lepora & Pezzulo, 2015), are needed to further specify the mechanisms underlying the prioritization of threat-specific actions.

To conclude, our findings strongly support that the presence of threat in the environment rapidly guides the selection of existing targets for action, and determines attention allocation toward the endpoint of the selected action. Further, we found that two negative emotional expressions, anger

and fear, distinctively impact action- and attention-related decisions, in accordance with their social meaning, namely aggression and affiliation respectively. We propose that these processes have been optimized through evolution to ensure survival.

Author contributions

EV, JLA and JG designed the study. EV developed stimuli, conducted the experiments and performed data analyses. EV, JLA and JG prepared the manuscript. All authors reviewed and approved the final manuscript.

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Competing financial interests

The authors declare no competing financial interests.

SUPPLEMENTARY INFORMATION

1. Stimuli

Our stimuli reproduced a realistic social environment and consisted of photographs depicting a waiting room with four seats, where the two middle seats were occupied by two individuals (a pair of females or males) and the two outer seats were empty. In order to build realistic controlled stimuli, we first ensured that each Female or Male individual was presented with the same Female or Male body, thus preventing the influence different bodies could exert on attention or action. To do so, each scene was the composite of one template Female or Male hemi-scene (photograph depicting either one Female or one Male sitting next to an empty seat) juxtaposed to its mirrored version, on which we superimposed faces.

Second, to minimize the potential influence of individuals' intrinsic facial features within each pair of Female or Male individuals, we used ten fixed pairs of identities controlled for gender as well as invariant trustworthiness and threat facial traits. To do so, we selected 20 neutral faces (10 Males) from the RadBoud Faces Database that showed the highest recognition rate in an emotion categorization task (El Zein, Wyart, & Grèzes, 2015 – results further confirmed by categorization post-tests showing recognition accuracy above chance in all three groups: all $t_s > 5.19$, all $p_s < 0.001$, all $d_s > 0.43$). We then converted the pictures to greyscale, presented them for 2000ms and ask 15 subjects (7 males, mean age: 27.3 ± 4.8 years) to rate them in terms of trustworthiness and threat on a continuous scale ranging from “not at all” to “very much”. These ratings were used to build fixed pairs by associating same sex identities that didn't differ significantly (all $t_s < 1.75$, all $p_s > 0.1$, all $d_s < 0.57$) on trustworthiness and threat ratings.

Using Adobe Photoshop CS3 (Adobe Systems, San Jose CA), we adapted the selected identities on the template photographs' Female or Male bodies. Faces varied in emotion (neutral, angry or fearful

expressions) and in intensity (4 levels of morphs for anger and fear, created from the neutral to the emotional expression using a simple linear morphing transformation), and were equalized in perceived emotional intensities (for details see El Zein et al., 2015)). The equalization was further confirmed by categorization post-tests showing main effects of intensity in all three groups (all $F_s > 8.88$, all $p_s < 0.001$, all $\eta^2_{ps} > 0.28$) but no other significant main effects or interactions (all $F_s < 4.06$, all $p_s > 0.06$, all $\eta^2_{ps} < 0.16$). In order to study the influence of Anger and Fear independently from each other and exclude emotion contrast effects (Paulus & Wentura, 2016), one actor of the pair always displayed a neutral expression while the other displayed either a neutral, angry or fearful expression. The identities, as well as the side of the actor expressing emotions, were fully counterbalanced.

2. Action-related decisions study

Impact of task-irrelevant emotional displays on movements' initiation time. We observed a main effect of Emotion ($F(1,16)=4.48$, $p=0.05$, $\eta^2_p=0.22$) indicating that participants took less time to initiate their movement in the presence of emotional displays. A regression of initiation time against emotion intensity further revealed a negative correlation (t-test against zero, $t(16)=-2.68$, $p=0.02$, $d=-0.65$) showing that the initiation time decreased when emotion strength increased. However, the Emotion-by-Side regression was not significant, neither when regressing it against intensity (all $F_s < 3.55$, all $p_s > 0.08$, all $\eta^2_{ps} < 0.18$) nor on the intercepts (all $F_s < 0.24$, all $p_s > 0.63$, all $\eta^2_{ps} < 0.01$). Thus, the time participants took to initiate their movements was not different when deciding to move away or toward the emotional individual, even when emotion intensity is accounted for.

Impact of task-irrelevant emotional displays on movements' duration. We observed a main effect of Emotion ($F(1,16)=11.87$, $p=0.003$, $\eta^2_p=0.43$) such that the movement duration was longer for emotional scenes compared to neutral ones. Moreover, a significant positive correlation was found between emotion strength and duration (t-test against zero, $t(16)=2.47$, $p=0.025$, $d=0.60$), showing that the duration increased when emotion strength increased. However, the Emotion-by-Side

regression revealed no significant effects, neither when regressing it against intensity (all $F_s < 2.87$, all $p_s > 0.11$, all $\eta^2_{ps} < 0.15$) nor on the intercepts (all $F_s < 1.94$, all $p_s > 0.18$, all $\eta^2_{ps} < 0.11$). Thus, the duration of the movements was not different between our conditions of interest, even when emotion intensity is accounted for.

Impact of task-irrelevant emotional displays on movements' trajectory. This type of analysis allows extracting deviations in the trajectories that are related to the evolution of the deliberation process. The principle is to time-normalize the data into a given number of time-steps using linear interpolation to get rid of the differences in length of the trajectories (in this study, we used the standard 101 time steps procedure implemented in Mouse Tracker). After time normalization, Mouse-Tracker can compute measures of spatial attraction such as the maximum deviation (MD). The MD of a trajectory is calculated as the largest perpendicular deviation between the actual trajectory and its idealized trajectory (a straight line between each trajectory's start and end points) out of all time-steps. The magnitude of the MD reflects the deliberation process: larger deviations suggesting a longer hesitation between the two choice alternatives (attraction toward both alternatives) compared to smaller ones. In our task, this measure was thus used as a marker of choice decisiveness and compared between our different conditions, with the hypothesis that actions which were specifically triggered by emotion displays would elicit stronger attraction and straighter trajectories than the opposite ones.

In order to assess whether the maximum deviation was impacted by the presence of emotional displays, we performed an Emotion-by-Side regression that revealed no significant main effect of Emotion ($F(1,16)=3.27$, $p=0.09$, $\eta^2_p=0.17$), such that the deviation of the movements was not different for neutral scenes when compared to emotional scenes. Furthermore, parameter estimates of the regression slope revealed no significant correlation between emotion strength and deviation (t-test against zero, $t(16)=-1.33$, $p=0.20$, $d=-0.32$).

The Emotion by Side regression with emotion strength revealed no significant main effects or interactions (all $F_s < 1.23$, all $p_s > 0.28$, all $\eta^2_{ps} < 0.07$) and neither did the intercepts (all $F_s < 0.83$, all $p_s > 0.38$, all $\eta^2_{ps} < 0.05$). To test whether the absence of effects could indicate that subjects started to move after they made their decision, so that the deliberation was already completed when movements were initiated, we performed a regression of MD against initiation time and found a significant negative regression (t-test against zero, $t(16) = -2.55$, $p = 0.022$, $d = -0.62$) such that MD was decreased when initiation time increased.

3. Emotion recognition post-tests

Methods

After each study, subjects completed two blocks of an Anger-Fear categorization task composed of 80 stimuli (10 pairs * 2 emotional expressions * 4 levels of morphs). They were presented with a grey screen for 1000ms, followed by the scene for 600ms. Subjects had to detect the emotion displayed by one of the two actors while fixating on the cross between the faces, and to report it by pressing the corresponding “Anger” or “Fear” keys. The mapping between the responses and the keys was counterbalanced between participants.

Results

Action-related decisions study. Two participants didn’t complete the post-test due to a technical problem. First, the overall accuracy revealed that subjects’ accuracy was significantly different from chance ($m = 64.8\%$, 95% CI [47.74, 81.85]; $t(14) = 6.39$, $p < 0.001$, $d = 0.43$). The Emotion-by-Level repeated measures ANOVA showed a significant main effect of Level ($F(3,42) = 23.81$, $p < 0.001$, $\eta^2_p = 0.63$) such that the accuracy increased with emotion intensity but no other effects were significant (all $F_s < 2.6$, all $p_s > 0.08$, all $\eta^2_{ps} < 0.16$).

Spatial Attention Study. The overall accuracy revealed that subjects' accuracy was significantly different from chance ($m=64.8\%$, 95% CI [59.3, 70.3]; $t(23)=-5.19$, $p<0.001$, $d=1.06$). We ran an *Emotion-by-Level* repeated measures ANOVA that revealed a main effect of Level ($F(3,69)=8.88$, $p<0.001$, $\eta^2_p=0.28$) such that the accuracy increased with emotion intensity, but no other effects were significant (all $F_s<4.06$, all $p_s>0.06$, all $\eta^2_{ps}<0.16$).

Spatial Attention Control Study. The overall accuracy revealed that subjects' accuracy was significantly different from chance ($m=65.5\%$, 95% CI [61.6, 69.4]; $t(25)=8.08$, $p<0.001$, $d=1.58$). We ran an *Emotion-by-Level* repeated measures ANOVA that revealed a main effect of Level ($F(3,75)=25.17$, $p<0.001$, $\eta^2_p=0.50$) such that the accuracy increased with emotion intensity. No other main effect or interaction were significant (all $F_s<1.41$, all $p_s>0.24$, all $\eta^2_{ps}<0.05$).

COMPLEMENTARY DATA: A pupillometry analysis

Introduction

Investigating physiological responses to threatening information permits to access the mechanisms they trigger in the observer. Amongst these responses, pupil dilation has been described as a sensitive measure of emotional arousal, namely the physiological activity associated to emotions. Indeed, numerous studies have demonstrated increased pupil dilation when exposed to arousing emotionally loaded stimuli, compared to neutral ones (Beatty, 1982; Bradley, Costa, & Lang, 2015; Bradley, Miccoli, Escrig, & Lang, 2008; Partala, Jokiniemi, & Surakka, 2000; Snowden et al., 2016; Van Steenbergen, Band, & Hommel, 2011).

The mechanism underlying this augmentation of pupil diameter would reflect increased sympathetic nervous activation in response to emotional information. Indeed, pupil diameter is determined by the activity of two components of the parasympathetic division, namely the parasympathetic one which regulates the constrictor muscle, and the sympathetic one which controls the dilator muscle. When aroused, the enhancement of the sympathetic activity would modulate the dynamic “push-pull” balance between the two components and favour an increase of pupil dilation (Steinhauer, Siegle, Condray, & Pless, 2004). Hence, pupil dilation offers to access individuals’ emotional states, with the advantage of neither soliciting participants during ongoing tasks nor being influenced by subjective reports biases.

Thus, within our experimental design, where participants have to make action-related decisions in response to threat-related displays, pupil diameter is susceptible to deliver interesting information regarding how arousing (threatening) angry and fearful facial expressions appear to the observer. Indeed, evolutionary theories posit that emotional displays convey information to observers, thereby serving an inter-personal function (Dezecache et al., 2013). It is notably argued that angry displays

signal a direct threat to the observer and convey cues of physical strength (Sell et al., 2014) whereas fearful displays do not themselves appear as threatening and convey affiliative signals (Hammer & Marsh, 2015). Hence, variations in pupil diameter could further corroborate these findings by showing that threat-displays can convey different signals to the observer and elicit different physiological responses. Along with studies on trauma-exposed individuals demonstrating that pupil diameter can scale to perceived threat (Fleming, Bandy, & Kimble, 2010; Kimble, Fleming, Bandy, Kim, & Zambetti, 2010), we hypothesize that angry displays would elicit a larger dilation than fearful ones because they are perceived by observers as an imminent threat directed toward themselves.

Moreover, pupil dilation could be informative regarding the type of action tendencies that are “naturally” favoured by each emotional display. Indeed, we posit that angry and fearful displays favour opposite adaptive motor responses, allowing the observer to reach safety either by avoiding the angry individual or approaching the fearful one (Vilarem et al., submitted). However, these reactions to danger could serve different motives which could possibly be reflected by pupil responses. For instance, avoidance of angry displays likely reflects the detection of a direct threat and the self-preservative drive to protect oneself from it. Thus, we hypothesize that this situation, where individuals decide to avoid a source of danger, would be characterized by a large pupil dilation which would reflect the degree of perceived threat and the motive to elude it. However, the case of fear is more ambiguous because fearful displays signal the presence of a danger while conveying cues of affiliation. Hence, approaching responses to fearful displays could either reflect self-preservative (a need for affiliation to alleviate one’s own fear) or prosocial (a desire to provide help) motives (Dezecache, Grèzes, & Dahl, 2017; Marsh et al., 2007). Both motives would be characterized by a large pupil dilation, as the literature has shown increased pupil diameter when aroused or when acting prosocially/empathetically (Leknes et al., 2012). However, if grouping decreases the state of fear by conferring social comfort, as evolutionary theories posit (Isbell, 1994), pupil dilation could be decreased during these approach behaviors.

Thus, in accordance with the evolutionary framework, we hypothesize that the factors Emotion (Anger or Fear) and Side (Away or Toward) would modulate pupil dilation. If approaching fear is associated to an increase in pupil dilation, we should observe an interaction between the Emotion and Side factors such that pupil diameter would be maximal when avoiding anger or approaching fear. However, if grouping decreases pupil dilation, the Emotion and Side effects should be additive, such that pupil diameter would be maximal for the most threatening situation, that is to say when participants decide to avoid the angry individual, and minimal for the least threatening situation, namely when participants decide to approach the fearful individual.

Methods

See Experiment 1 in Vilarem et al. (submitted) for details about the participants, the stimuli and the experimental procedure.

Data recording. After the training, the participants were positioned on the SR Research Head Support (chin and forehead rest) and were instructed to minimize head movements. Pupil diameter was measured continuously throughout the experiment using an Eyelink 1000 eye-tracking system, recording monocularly at a sampling rate of 250Hz. Calibration was achieved using a nine-point calibration grid, and performed three times (before the start of the main experiment, after 180 trials, and after 360 trials). Pupil dilation was also recorded during the post-test and calibrated once before the beginning of the task.

Data preparation. Blink artifacts were removed from the data using a custom interpolation method in which spline fitting was performed based on pupil diameter 200ms prior to blink onset, and 200ms after offset. Subsequently, high frequency components were removed (data smoothing) using a 50ms sliding window. Pupil measures were z-scored within trials, expressed relative to a pre-trial baseline period (–200 to 0ms relative to stimulus onset), and trimmed using cutoffs of ± 3 .

Data analysis. For each analysis, a general linear regression model (GLM) was used where emotion intensity was introduced as a trial-per-trial predictor of pupil dilation. The corresponding parameter estimates of the regression, reported in arbitrary units, were measured per participant, and then averaged across participants to produced group-level averages. In the main task, we performed an Emotion-by-Side regression, calculated the parameter estimates separately for our conditions of interest (Anger Away: AA, Anger Toward: AT, Fear Away: FA, Fear Toward: FT) and tested main effects on the corresponding intercepts. These GLMs were performed on a 600ms window around the peak and on a 600ms window locked to the response. In the post test, we only included the Emotion factor (no factor Side in the post-test) as a regressor, we calculated the parameter estimates of the regression separately for Anger and Fear, and tested main effects on the corresponding intercepts. We performed these GLMs on a 600ms window around the peak.

Results

Impact of task-irrelevant emotional displays on pupil dilation. A regression of peak pupil dilation against emotion intensity revealed no significant correlation (t-test against zero, $t(16)=1.13$, $p=0.28$, $d=0.28$) showing that pupil diameter was not modulated by emotion strength. The Emotion-by-Side regression revealed a significant main effect of Emotion ($F=5.38$, $p=0.03$, $\eta^2_p=0.25$) on the intercepts, driven by greater pupil dilation in response to Anger compared to Fear. We did not observe any other significant effects, neither on the intercepts (all $F_s<1.61$, $p_s>0.22$, $\eta^2_{ps}<0.09$), nor when regressing pupil dilation against intensity (all $F_s<1.37$, all $p_s>0.26$, all $\eta^2_{ps}<0.08$).

Impact of action choice on pupil dilation. A regression of response-locked pupil dilation against emotion intensity revealed no significant correlation (t-test against zero, $t(16)=1.05$, $p=0.31$, $d=0.25$) showing that pupil diameter was not modulated by emotion strength. The Emotion-by-Side regression revealed a significant main effect of Emotion ($F=5.87$, $p=0.03$, $\eta^2_p=0.27$) on the intercepts driven by a greater pupil dilation in response to Anger compared to Fear. We did not observe any other significant

effects, neither on the intercepts (all $F_s < 1.77$, $p_s > 0.20$, $\eta^2_{ps} < 0.1$), nor when regressing pupil dilation against intensity (all $F_s < 1.35$, all $p_s > 0.26$, all $\eta^2_{ps} < 0.08$).

Impact of task-relevant emotional displays on pupil dilation. A regression of pupil dilation against emotion intensity revealed a positive correlation (t-test against zero, $t(14) = 2.75$, $p = 0.02$, $d = 0.7$) showing that pupil dilation increased when emotion strength increased. The Emotion regression did not reveal any significant effects neither on the intercepts ($F(1,14) = 0.09$, $p = 0.77$, $\eta^2_p = 0.006$), nor when regressed with intensity ($F(1,14) = 0.002$, $p = 0.96$, $\eta^2_p < 0.001$).

Discussion

We recorded pupil dilation during a task where participants were making action choices in response to angry and fearful displays. Our results revealed that, in the action task, pupil diameter was increased in response to angry displays, compared to fearful ones, irrespective of the action choices, thereby likely reflecting enhanced arousal when facing anger.

The increased dilation in response to angry displays was consistent with our action choices data showing that anger favoured more avoidant responses than fear, but also with studies indicating that anger signals a direct threat to the observer, whereas fearful displays are not perceived as threatening (Said et al., 2010). Interestingly, this effect occurred despite the use of emotional stimuli which were equalized in perceived emotional intensities (see Methods in El Zein et al. 2015), thereby suggesting that differences in perceived emotional intensity did not account for differences in arousal. Rather, this effect seems to be underlain by the communicative function of angry and fearful displays and by the different signals they convey, respectively related to strength (Sell et al, 2014) and vulnerability (Hammer & Marsh, 2015).

However, no effects were observed regarding the type of action tendencies performed by the participants. One possible explanation would be that pupil dilation was influenced by the signals which

were relevant for accomplishing the task. Indeed, in the action-related decisions task, it seems that the nature of the emotion was the most relevant signal to track in order to make a decision, and pupil dilation was thus modulated by this information. However, in the categorization post-test, where the task demanded to categorize emotional displays, we did not observe any modulation by the nature of emotion but a modulation by the intensity of the signal, which might have been the most relevant signal to track in order to answer correctly. This could thus explain why we did not observe a modulation of pupil diameter by action choices.

Another explanation accounting for this absence of effect could be due to the structure of our task and the speed of pupil response. Indeed, pupil dilation is a slow response which peaks 1 second after a relevant event and is thus suited for slow tasks, or tasks in which meaningful events are well separated in time (Wierda, van Rijn, Taatgen, & Martens, 2012). However, our task was not a sequence of different events but a continuous presentation of a unique relevant event, namely the emotional information, which appeared at the onset of the stimulus and remained throughout the trial. The persistence of emotional information on the screen might have overcome other possible modulatory effects, such as the effects related to action choices occurring later in time. Response-locked analysis indeed revealed that the main effect of emotion on pupil dilation was sustained and was still observed after the response.

To conclude, the present work further corroborated the communicative function of emotional displays by showing that two threat-related facial expressions, namely anger and fear, elicit different physiological responses that may be related to their respective social functions.

COMPLEMENTARY ANALYSIS: A discrimination analysis

We examined visual performance on Experiment 2 and 3 in order to assess whether the presence of emotional displays, or the location of the cue regarding emotional displays, improved cue detection (accuracy) or discrimination (d-prime).

Spatial Attention Study

d-prime analysis. We ran two ANOVAs, one testing for a main effect of Emotion (Anger, Fear, Neutral) and one testing for an Emotion-by-Side interaction on d-prime scores. No significant effects were observed (respectively: $F(2,46)=0.55$, $p=0.58$, $\eta^2_p=0.02$; all $F_s<0.54$, all $p_s>0.47$, all $\eta^2_{ps}<0.02$).

Accuracy analysis. We ran two ANOVAs, one testing for a main effect of Emotion (Anger, Fear, Neutral) and one testing for an Emotion-by-Side interaction on d-prime scores. No significant effects were observed (respectively: $F(2,46)=0.68$, $p=0.48$, $\eta^2_p=0.03$; all $F_s<0.35$, all $p_s>0.56$, all $\eta^2_{ps}<0.02$).

Spatial Attention Control Study

d-prime analysis. We ran two ANOVAs, one testing for a main effect of Emotion (Anger, Fear, Neutral) and one testing for an Emotion-by-Side interaction on dprime scores. No significant effects were observed (respectively: $F(2,48)=1.27$, $p=0.29$, $\eta^2_p=0.05$; all $F_s<2.89$, all $p_s>0.102$, all $\eta^2_{ps}<0.11$).

Accuracy analysis. We ran two ANOVAs, one testing for a main effect of Emotion (Anger, Fear, Neutral) and one testing for an Emotion-by-Side interaction on dprime scores. No significant effects were observed (respectively: $F(2,48)=1.01$, $p=0.37$, $\eta^2_p=0.04$; all $F_s<2.09$, all $p_s>0.16$, all $\eta^2_{ps}<0.08$).

PART 2: Action and overt attentional responses to threat – A saccade study (Experiment 4)

This part will be presented as a draft of a manuscript that is currently in preparation:

Attention allocation predict the selection of safe action opportunities.

Attention allocation predict the selection of safe action opportunities.

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Abstract

When facing threat, reaching for safety appears as the most adaptive behaviour to ensure survival. Such reaction is likely to be accompanied by allocation of attentional resources toward its endpoint, so as to be performed efficiently. However, most of the studies investigating attentional responses to threat indicate that threat quickly attracts and captures attention, but do not provide evidence regarding subsequent behaviours. Recent findings from our team and others rather suggest that attention can be drawn to safety signals if participants are presented with a safe action opportunity. This study thus aimed at investigating both attention allocation and action responses to threat by recording saccadic activity while participants made a decision of action in response to threat-related facial expressions displayed within an environment providing safe action opportunities. Our results showed that, after being quickly allocated to the emotional face, attention is reoriented toward, and predict, the endpoint of the upcoming action. We propose that this effect is shaped by the presence, and the selection, of actions allowing to reach safety.

Introduction

Being able to accurately detect danger is crucial for survival and gives individuals an evolutionary advantage (LeDoux, 1996). Accordingly, threat-related attentional biases have been demonstrated in a large number of studies, using various paradigms (e.g. visual search paradigm, spatial cueing paradigm ...), stimuli material (e.g. photographs of spiders, angry faces, fear-conditioned shapes ...) and response modalities (eye or manual movements). Classically, these effects are reflected by faster and more accurate detection of threatening stimuli over non-threatening ones (e.g. Calvo et al., 2006; Eastwood et al., 2001; E. Fox et al., 2000; E. Fox, Griggs, & Mouchlianitis, 2007; Öhman et al., 2001; Pinkham et al., 2010; Preciado et al., 2017; Soares, Esteves, Lundqvist, & Öhman, 2009; Tipples et al., 2002). Indeed, threatening stimuli, even when neither physically-salient nor spatiotemporally task relevant (distractors), can capture covert (e.g. Yiend & Mathews, 2001) or overt attention (e.g. (Nissens, Failing, & Theeuwes, 2016) and alter performance of ongoing tasks (Ariga & Arihara, 2017; Fenske & Eastwood, 2003; Vuilleumier, Armony, Driver, & Dolan, 2001).

Altogether, these findings have established that attentional resources are quickly and efficiently exploited by threat-related stimuli. However, the question of the functionality of this early vigilance mechanism with regards to the elaboration of adapted behavioural responses arises. Indeed, fast identification of threat is as crucial for survival as the ability to adaptively respond to it in order to escape from danger. In sum, is there a relationship between attentional biases to threat and subsequent motor responses?

Insightful evidence can be provided by studies investigating the mechanisms following the early attentional capture toward threatening information. Numerous experiments have notably showed that biases away from threatening stimuli can arise consecutively to the initial orienting toward threat (Juth, Lundqvist, Karlsson, & Öhman, 2005; Mulckhuyse, Crombez, & Van der Stigchel, 2013; Schmidt,

Belopolsky, & Theeuwes, 2012). On the one hand, these effects have been described as avoidance responses occurring during later processing stages and following early attentional capture for threatening stimuli, according to the “vigilance-avoidance hypothesis” (Mogg, Bradley, Miles, & Dixon, 2004; Pflugshaupt et al., 2005). This pattern has been typically reported in anxious individuals and would allow to limit exposure to the threatening information by quickly reorienting attention away from it. It has been classically demonstrated using spatial cueing paradigms and characterized by faster manual reaction times in response to targets presented at opposite spatial locations of threat cues (Koster et al., 2006; Mogg & Bradley, 1999).

On the other hand, the avoidant responses observed in saccades tasks would result from the tight relationship between attention and motor programming. The premotor theory of attention indeed posits that salient information automatically trigger the planning of a saccade toward the stimulus (Rizzolatti et al., 1987). However, when the salient information has to be ignored, the saccade plan has to be suppressed, causing saccades to deviate away from the distractor once the suppression is fully completed (Rizzolatti, Riggio, Sheliga, 1994; Schmidt et al., 2012; Tipper, 2001; but see Wang & Theeuwes, 2014 for an alternative account). This effect has been characterized by short latencies saccades deviating toward the threatening stimuli whereas long latencies saccades deviate away from them (Mulckhuysen et al., 2013; Schmidt et al., 2012).

Alternatively, while previously cited experiments have investigated attention allocation to threat in the presence of other non-threatening stimuli, recent experiments have investigated attention allocation to threat in the presence of safety cues. This shift in paradigm is particularly interesting given that trying to reach safety is the most adaptive reaction in the face of threat.

Using a spatial cueing paradigm, Schmidt and colleagues (2017) demonstrated that safety cues, similarly to threat-conditioned cues, could capture attention. This effect was reflected by an interference of the execution of saccades when they were directed away from safety cues. Importantly

though, this effect was observed only when the time between stimulus and cue presentation was relatively long (i.e. 600ms). Also using a spatial cueing paradigm (with a 500ms delay between stimulus and cue presentation) but recording manual reaction times, another study showed that when instrumental actions permitting to reach safety were available, the associated safety cues were prioritized over threat signals (Vogt et al., 2016). Hence, it appears from these studies that when provided with action opportunities allowing to reach safety, and sufficient time, attention allocation can be oriented toward safety cues, even in the presence of threatening ones.

Further, previous experiments from our team suggest that attention allocation can be modulated by the presence of action possibilities in the scene (Vilarem et al., submitted). During three different behavioral tasks, we presented scenes representing a room with four seats, where the two outer seats were available while the other two were occupied by two individuals displaying emotional expressions (one was always neutral while the other was displaying a neutral, angry, or fearful expression). In the *action-related decisions task*, we assessed participants' natural action tendencies by asking them to make a mouse movement toward the seat on which they would like to sit; the second *spatial attention task* assessed attention allocation by asking participants to discriminate a cue appearing on one of the outer seats; the third *spatial attention control task* was identical to the second one, except that a mask was hiding the action-related context in order to assess whether the presence of opportunities for action were shaping attention allocation.

Interestingly, the first two tasks were congruent and showed that angry displays favoured avoidance responses (i.e. the seat away from the angry individual) while fearful displays facilitated approach responses (i.e. the seat next to the fearful individual), consistently with the aggressive and affiliative signals they respectively convey. Such emotion specific effects could be related to the findings described above, whereby selecting the seat away from an angry individual and next to a fearful one could be associated with reaching safety. Crucially, the third task gave insight about the nature of the

interplay between attention and action by showing that when opportunities for action were removed from the scene, the emotion specific effects disappeared in favour of a general threat attentional bias. These findings suggest that the presence of action opportunities shape attention allocation under threat.

However, our previous experiments did not provide any information regarding how attention is allocated over the time course of a trial. Particularly, they could not address whether the observed “action-related” attentional bias occurred early in time or whether it was the result of a reorienting of attention following classical biases toward threat. Thus, in order to address this question, we designed a task where participants had to make free choices of action in response to threat (same experimental design that Experiment 1 in Vilarem et al., submitted) while we were recording saccadic activity as a direct behavioural measure of attention allocation.

Investigating action choices with regards to saccades’ latencies and landing locations will allow investigating when and whether action selection influences attention allocation. Our findings (Vilarem et al., submitted) along with recent studies (Schmidt, Belopolsky, & Theeuwes, 2017; Vogt et al., 2016) suggest that actions allowing to reach safety should be favoured and might bias spatial attention before 600ms, and possibly before movement initiation, as our previous results suggest that action selection is completed at the time of movement onset (Vilarem et al., submitted). Finally, if action selection shape attention allocation, we should observe similar patterns on saccades’ latencies/directions and the proportion of choice.

Methods

1. Participants.

22 (8 males, mean age: 22.9 ± 3.2 years) participated in an action-related decision 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 licensed by the local research ethics committee (Comité de protection des personnes Ile de France III - Project CO7-28, N° Eudract: 207-A01125-48) and carried out in accordance with the Declaration of Helsinki. The participants provided informed written consent and were paid for their participation.

2. Stimuli.

The experimental design was identical to Experiment 1 in Vilarem et al. (submitted).

3. Experimental procedure and data analysis.

Experimental procedure. The procedure was identical to Experiment 1 in Vilarem et al. (submitted), except that participants were allowed to visually explore the scene. They were asked to fixate the central cross at the beginning of each trial and then requested to decide where to sit, and realize the movement to reach the seat, as soon as possible, while freely exploring the scene.

Saccadic activity was recorded monocularly (left eye for all subjects) at 1000Hz using an Eyelink 1000 (SR Research; Mississauga, ON, Canada) with a level desktop camera. A saccade was defined as the first time point at which the velocity exceeded $30^\circ/\text{s}$ and the acceleration exceeded $8000^\circ/\text{s}^2$. Subjects were stabilized on a chinrest during the experiment, and calibrated using a standard 9-point grid.

Data analyses. We excluded data from two participants due to outlier performance on movement accuracy (lower than the mean accuracy minus two standard deviations). Because high anxiety is

known to impact attention allocation to threat (for a review, see Grupe & Nitschke, 2013), we limited our sample to subclinical population and excluded one participant presenting a clinical anxiety score based on the State-Trait Anxiety Inventory (STAI) administered before the study. We therefore analyzed the data of 19 participants for this study. Participants' responses regarding the action choices were analyzed by calculating the proportion of trials in which they decided to sit next to the neutral or emotional individual and by running repeated measures ANOVAs with Emotion (Anger, Fear) and Side (away or toward from the emotional individual) as within-subjects factors. The data related to the saccadic behaviour were cleaned by excluding saccades data on incorrect trials and microsaccades (inferior to 1 degree of visual angle, see Martinez-Conde et al., 2009). We ran ANOVAs on the data related to saccades latencies and directions using Emotion and Side as within subject factors. In order to assess whether saccadic behaviour could be a trial-per-trial predictor of action choices, we performed logistic regressions including Saccade direction (away or toward emotion) and Emotion (anger or fear) as predictors, Choice (away or toward) as the dependent variable, and Subjects as random effects. Our scene was divided into 5 Regions of Interest (ROIs) (the cross area, each individual, each seat). Importantly, because our previous experiments have showed that emotion intensity is not a critical factor in our tasks, we have decided to pool all the intensity levels together in order to maximize the number of observations per condition of interest.

Results

Impact of emotional displays on action choices. Overall, participants more often chose the seat located away from the emotional individual ("Away" and "Toward" respectively refer to the neutral and emotional actor side), as revealed by a main effect of Side ($F(1,18)=47.33$, $p<0.001$, $\eta^2_p=0.72$). Importantly however, the nature of the displayed emotion distinctively influenced participants' choice (Emotion-by-Side interaction, $F(1,18)=6.97$, $p=0.02$, $\eta^2_p=0.28$): angry displays elicited more away responses than fearful ones, and fearful displays elicited more toward responses than angry ones. All

the paired comparisons of the interaction Emotion-by-Side were significant (**See Table 1**). The main effect of emotion was not significant ($F(1,18)=0.17$, $p=0.68$, $\eta^2_p=0.01$).

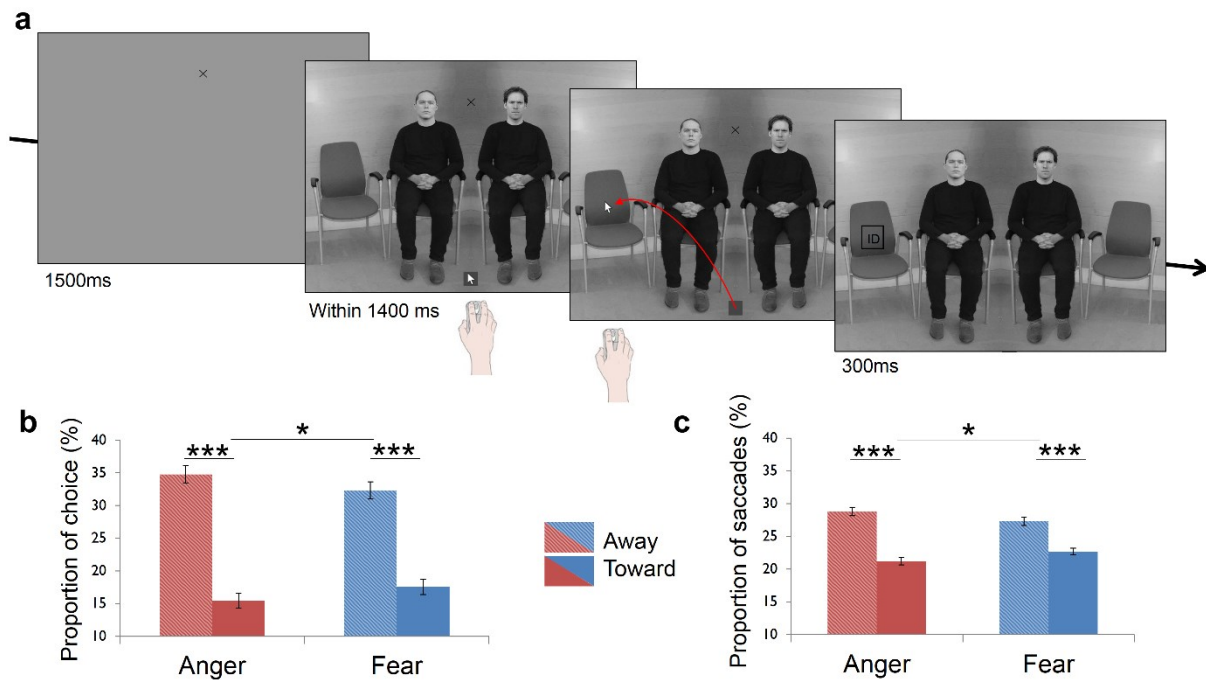


Figure 1. a) Time course of a trial where participants have to indicate where they would like to sit by moving their cursor from the bottom center to the chosen seat. The face of the participant appeared for 300ms after the offset of the movement. b) Emotion-by-Side interaction on the proportion of choice. c) Emotion-by-Side interaction on the proportion of second saccades landing sites. ** $p<0.01$; * $p<0.05$; ~ $p<0.1$; ns $p>0.1$. For illustration purpose, error bars represent within-subject standard errors.

Proportion of choice (%)	Paired differences		t	ddl	p-value	Cohen's d
	Mean	95% CI				
AA - AT	18.13	[12.56, 23.70]	6.84	18	<0.001	3.12
FA - FT	14.16	[9.40, 18.91]	6.26	18	<0.001	2.85
AA - FA	2.10	[0.43, 3.75]	2.64	18	0.02	0.39
AT - FT	-1.88	[-3.56, -0.21]	-2.36	18	0.03	0.35
AA - FT	16.25	[11.21, 21.28]	6.78	18	<0.001	2.97
AT - FA	-16.04	[-20.92, -11.16]	-6.90	18	<0.001	3.01

Table 1. Paired differences and statistics of the paired comparisons of the Emotion-by-Side interaction on choice proportions (%). The abbreviations refer to the choice of the subjects with respect to the emotional actor: AngerAway: AA; AngerToward: AT; FearAway: FA; FearToward: FT; with “Away” referring to the opposite side of the emotional actor (i.e. side of the neutral actor) and “Toward” to the side of the emotional actor.

Impact of emotional displays on saccadic activity. First, we analyzed the latency of the first saccades as an index of attentional attraction (Jiang, Won, & Swallow, 2014). Importantly here, we excluded saccades whose starting point was not on the fixation cross, as it was required by the task. Our data revealed that the latency of the first saccades, which was of 129ms on average (95% CI [116, 142]), was neither affected by the nature of emotional displays nor by the side where they were presented (all $F_s < 1.50$, $p_s > 0.24$, $\eta^2_{ps} < 0.08$).

Then, we explored the distribution of the landing saccades in order to better understand attention allocation over the time course of a trial. Using the ROIs approach, we observed that the first saccade was predominantly landing on the faces (89.67%, 95% CI [86.40, 92.94]), a small subset of saccades were directed toward the seats ROIs (1.44%, 95% CI [0.42, 2.46]) and the remaining subset was still into the cross ROI. Because saccades directed toward the seats were susceptible to be informative regarding action selection, and were too limited to be analyzed separately (data were missing for some

subjects who did not direct any first or second saccade toward the seats in some conditions), we pooled the saccades landing on the same sided face and seat and ran an Emotion-by-Side ANOVA on these proportion of saccades. We found that the first saccade was mostly directed toward the hemi-field with the emotional face ($m=53\%$, 95% CI [51, 56]; $F(1,18)=7.06$, $p=0.02$, $\eta^2_p=0.28$). But no other effect were significant (all $F_s<0.07$, $p_s>0.80$, $\eta^2_{ps}<0.004$).

The second saccade, which latency was on average of 492ms ([95% CI 437, 547]), was also mostly landing on the faces (88.28%, 95% CI [83.16, 93.39]) and in a lesser proportion on the seats (5.05%, 95% CI [0.36, 9.73]).¹ We observed that the second saccade was mostly directed toward the hemi-field with the neutral individual ($m=56\%$, 95% CI [54, 58]; $F(1,18)=36.35$, $p<0.001$, $\eta^2_p=0.67$). However, we found a significant Emotion-by-Side interaction ($F(1,18)=7.47$, $p=0.01$, $\eta^2_p=0.29$) such that there were more saccades away than toward anger, compared to fear. No main effect of emotion was observed ($F(1,18)<0.001$, $p=0.99$, $\eta^2_p<0.001$).

Impact of saccadic activity on the choice. In order to assess whether the interaction between Emotion and Side observed on the direction of the second saccade could significantly predict the choice in a trial-by-trial fashion, we performed logistic regressions. We compared three models: model 1 was modeling the main effect of saccade direction only, model 2 was modeling both main effects of saccade direction and emotion, and model 3 was modeling both main effects and the interaction between the direction of the saccade and emotion. The third model with the interaction term was better explaining the data than the two others (respectively for model 1 to 3: $AIC=359.2$, $AIC=361.1$, $AIC=358.7$) and revealed a significant interaction between the direction of the saccade and the nature of emotional displays (**see Table 2**)². This interaction term indicated that increased number of saccades away from

¹ Note that amongst the second saccades that landed on a face/seat ROI, 78.1% originated from the other face/seat ROI, 18.9% from the same face, and 0.03% from the cross ROI.

² Logistic model: $p(\text{away}) \sim \text{Saccade direction} + \text{Emotion (anger=1, fear=0)} + \text{Saccade direction} * \text{Emotion}$

the emotional individual in the anger vs. fear condition was associated to higher proportion of away choices, in line with the results observed on the proportion of choice.

Predictors	Odds ratio	95% CI	<i>p</i> -value
Intercept	0.23	[-0.85, 1.31]	0.007
Saccade direction	11.70	[10.08, 13.31]	0.003
Emotion	1.55	[0.88, 2.23]	0.202
Saccade direction * Emotion	0.34	[-0.67, 1.35]	0.035

Table 2. Summary of logistic regression analysis for variables predicting action choices.

Discussion

In this experiment, we studied the impact of social threat displays on action and attention using a task where participants were requested to freely choose a seat in a room where two individuals were already sitting, one displaying a neutral expression while the other either displayed neutral, angry or fearful facial displays. Beside the action choices that allowed to assess whether each of these threat-related displays favoured specific actions in the observer, we recorded saccadic behaviour in order to investigate the interplay between spatial attention and action selection in response to social threat.

First, our data on the proportion of choice replicated the results found in Vilarem et al. (submitted) with a differential impact of angry and fearful displays on action selection, as indicated by more avoidant actions in response to angry displays, compared to fearful ones, and more approach responses to the latter, compared with the former. This effect underlines that beyond their shared threat-relatedness, these emotions diverge with respect to the signal they send to the observer (Marsh et al. 2005). However, while we had found no difference between away and toward responses to fearful displays in the original task where participants were asked not to look at the faces, we observed

a significant difference in favour of avoidant responses under visual exploration conditions. This effect was underlain by a stronger general tendency to avoid emotional displays in this task compared to the original one where emotion processing was mostly implicit (independent-samples t-test on the proportion of away choices: $t(23.73)=5.16, p<0.001, d=1.68$). Hence, it might be hypothesized that the explicit processing of threat led to a stronger impact of threat on participants' choices, possibly because of the occurrence of emotion and valence categorization mechanisms. Supporting this interpretation, the possibility to explore the faces granted an increased sensitivity to emotional features, as revealed by higher accuracy in the categorization post-test in this task, compared to the original one ($t(32)=6.41, p=0.002, d=1.20$). Then, despite the difference found between anger and fear, it seems that the threat-relatedness of both emotional displays, which are generally categorized as negatively valenced, favoured avoidant responses in the observers.

In order to address the question of the interplay between attention and action raised by our previous findings (Vilarem et al., submitted), we analyzed saccadic activity as a direct measure of overt attention allocation. Our previous experiments suggested that attention was allocated toward the endpoint of the most chosen actions in response to angry and fearful displays, and indicated that this bias was "action-related", given its dependence upon the presence of action opportunities. However, these experiments did not provide evidence regarding the development of this effect. Thus, we analyzed the latency and the distribution of the landing saccades in order to understand when and how this "action-related" effect occurs.

Our data revealed that orienting of attention to faces occurred as early as 130ms and was preferentially directed toward emotional displays, thereby replicating superiority effects of emotional stimuli on attention demonstrated in saccades tasks (Mulckhuyse et al., 2013; Schmidt et al., 2012; Schmidt, Belopolsky, & Theeuwes, 2015). However, we did not observe faster saccades toward emotional displays, which is consistent with findings suggesting that distractor-related activity might be

strengthened by threatening information, resulting in more, but not per se faster, oculomotor capture (Mulckhuyse & Dalmaijer, 2016). We found no difference between angry and fearful displays nor on the latency neither on the direction of the first saccade, suggesting that this early pop-out effect was sensitive to the presence of emotional stimuli, but not to the nature of the threat-related signal.

However, we observed an emotional modulation on the direction of the second saccade. Saccades were predominantly directed away from the emotional individual but this effect was significantly more pronounced for angry displays, compared to fearful ones. Crucially, our data indicated that the landing site of the second saccade predicted the seat subsequently chosen by the subject, although the second saccade average latency preceded movement onset on average (respectively 492 and 505ms)

Thus, our data show that the first saccades were mostly directed toward the emotional individual while the second saccades were mostly directed away from the emotional individual. In the literature, such vigilance-avoidance pattern of attention allocation is generally reported in anxious individuals and is characterized by a quick vigilance toward threat cues, followed by an avoidance response at longer stimulus durations (Mogg et al., 2004; Pflugshaupt et al., 2005). This effect is classically interpreted as a mean for anxious individuals to identify danger (vigilance) while limiting exposure to it (avoidance). This latter avoidant response would serve the regulation of negative affect but also prevent habituation so as to maintain anxiety symptoms (Cisler & Koster, 2010).

However, given our results showing that the second saccade distribution pattern predict upcoming action choice, we propose that this avoidance-vigilance pattern could reflect early detection of threat, and the subsequent selection of a defensive behavioural response (e.g. fleeing). Hence, attention would first be captured by threatening information, due to its saliency and its ability to exploit attentional resources (Pessoa et al. 2012). In parallel, an action selection process would occur and be influenced by threat-related sensory information in order to select the most adaptive response. Indeed, according to the “affordance competition hypothesis”, the brain forms multiple action plans

whilst gathering information in order to select the most appropriate action in a given situation (Cisek, 2007). In the presence of threat, the emotional information acquired through the early attentional bias might modify the value of each action plan, biasing the selection toward socially adaptive behaviors (Vilarem et al., submitted). Once an action has been selected, the motor system would tune spatial attention toward the endpoint of the chosen action, consistently with previous theories and findings (Kirsch, 2015; Rizzolatti, Riggio, Dascola, & Umiltá, 1987) supporting that action selection can shape attention allocation. Then, we speculate that the avoidance effect following attentional capture would reflect the motivation to escape from threat in order to reach a safety place.

Another implication of this hypothesis is that this effect would be observed when sufficient time allows attention to be reallocated accordingly to action selection. This proposal is consistent with a recent saccade study that showed, using a spatial cueing paradigm, that cues of safety can capture attention, as reflected by slower saccades away from locations previously occupied by a safety cue, compared to threatening cues (Schmidt et al., 2017). However, this effect occurred only when enough time was available, that is when the time between the cue and the target was of 600ms (compared to 50ms) (Schmidt et al. 2017). In the same line, another study revealed that attention can prioritize signals of safety that allow to decrease future threat over threat signals, using a 500ms delay between the cue and the target (Vogt et al., 2016). Consistently with these findings, although using social stimuli, our data indicate that attention can be drawn to safety as early as 492ms, which is the average latency of the second saccade predicting action choice.

Hence, the present work proposes a description of the interplay between spatial attention and action selection in response to threat, within a realistic social environment. We posit that attention is first quickly attracted by emotion, providing sensory information that would guide action selection and favour one action plan over the others; the selected action would then bias spatial attention toward its endpoint. This mechanism would allow quick and appropriate responses when facing danger.

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PART 3: Action and covert attentional responses to threat – An EEG study (Experiment 5)

This part will present preliminary EEG data recorded during an action-related decisions paradigm. This ongoing work is realized in collaboration with Rocco Mennella.

Introduction

Experiments 1 to 4 suggest that anger and fear differently influence action selection in the observer, with angry displays consistently favouring avoidant responses, whereas selecting an adaptive action in response to fearful displays seems more ambiguous. In order to get a more comprehensive view of how and when emotional information can influence action selection, we recorded electroencephalography while participants were performing our action-related decisions task. Specifically, this experiment aimed at finding neural markers of action processes so as to uncover whether anger and fear differ in the way they shape action selection. Notably, markers of response conflict could allow investigating whether these threat-related displays generate competition between different action possibilities.

Of interest, the beta band activity has been shown to reflect motor processes, with decreased power during the preparation and execution of voluntary movements (Doyle, Yarrow, & Brown, 2005; Pfurtscheller, 1981; Pfurtscheller & Da Silva, 1999). Interestingly, recent studies have demonstrated that the amplitude of this desynchronization can also reflect parameters of the motor task such as the uncertainty about the endpoint of a motor response (Tzagarakis, Ince, Leuthold, & Pellizzer, 2010; Tzagarakis, West, & Pellizzer, 2015). Using reaching tasks where participants were cued with one or several possible target directions prior to movement execution, results indeed revealed that the reduction of power in beta-band activity was decreased in case of greater directional uncertainty (i.e. when several action possibilities were competing). Hence, following these findings, we hypothesize that fearful displays should elicit a weaker desynchronization compared to angry displays, given that fear appear to elicit more conflict between competing actions.

Response conflict can also be investigated by studying theta-band activity, as increases in theta power have been evidenced in tasks requiring to inhibit a prepotent motor response, as in Go-No go paradigms (Kirmizi-Alsan et al., 2006; Yamanaka & Yamamoto, 2010). Hence, an increased theta power

in response to no-go trials is proposed to reflect response conflict between two motor commands (Harper, Malone, & Bernat, 2014). Although our task differ from Go-No go tasks in the sense that participants were never instructed to withhold motor responses, we could hypothesize that competition between conflicting responses should be observed and modulate theta activity when participants do not perform their “preferred” response. Specifically, approach responses should elicit a greater synchronization in the case of angry scenes, but no clear predictions can be addressed for fearful scenes.

Thus, beta and theta power will be informative with regards to response selection processes and should help us getting a more complete picture of the data acquired in the previous experiments. However, it is important to note that the results presented in the following section are part of an ongoing work and will thus be considered and discussed with caution as they do not allow yet to draw firm conclusions.

Finally, additionally to oscillatory analysis, we wanted to address another question brought up by our previous experiments and investigate the motives associated with action choices. Indeed, our task allowed to study which signals were sent, and which response were favoured, by threat-related displays, but was not designed to access action motives. Although responses to anger were likely to reflect the self-preservative motive to protect oneself, responses to fearful displays could either reflect self-preservative or prosocial motives (Dezecache et al., 2017). Hence, we administered the Interpersonal Reactivity Index (IRI) that measures “reactions of one individual to the observed experiences of another” (Davis, 1980) in order to test whether action choices were influenced by individual differences on this trait. Precisely, we were interested in two subscales measuring “self-oriented” (“Personal distress”) and “other-oriented” (“Empathic concern”) feelings.

Materials and methods

1. Participants

30 (14 males, mean age: 24 ± 4.3 years) participated in an action-related decisions 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 licensed by the local research ethics committee (Comité de protection des personnes Ile de France III - Project CO7-28, N° Eudract: 207-A01125-48) and carried out in accordance with the Declaration of Helsinki. The participants provided informed written consent and were paid for their participation.

2. Stimuli

The experimental design was identical to Experiment 1 in Vilarem et al. (submitted), except that the number of stimuli was doubled in order to ensure statistical reliability for EEG analyses.

3. Experimental procedure

The experimental procedure was identical to Experiment 1 in Vilarem et al. (submitted).

4. Electrophysiological data recording and processing

Using a BioSemi headcap with active electrodes, the EEG was continuously recorded from 64 scalp sites, with CMS/DRL reference electrodes. The EEG signal was amplified using an ActiveTwo AD-box amplifier (BioSemi), low-pass filtered online (250 Hz) and digitized at 1000 Hz.

Pre-processing of the EEG signal was run in EEGLab (Delorme & Makeig, 2004). The signal was referenced offline to an average reference, down-sampled at 500 Hz, band-pass filtered between 1-32 Hz and epoched from 2s before to 3s after the face stimulus onset. Epochs were visually inspected and

discarded if containing muscular artifacts, and noisy electrodes were interpolated averaging the adjacent electrodes. Finally, blink artifacts were manually corrected using ICA.

With respect to the time-frequency analysis, a ‘multitapering’ approach was chosen (Slepian tapers, frequency range 4–32 Hz, four cycles per time window) in order to obtain power estimates between 4 and 32 Hz, using the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011) running on Matlab R2017a. Raw power was log-transformed before further analyses to normalize its distribution. For the analyses on theta band (4-7 Hz), for each trial the average power in the baseline from -0.49 to -0.2 sec was subtracted to minimize fluctuations in the raw power of the signal. Baseline subtraction (-0.3 to -0.1 sec) was also applied for the beta band (14-32 Hz); as far as alpha is concerned (8-12.5 Hz), we extracted an index of spatial attention (Belyusar et al., 2013), based on the hemispherical difference between homologous electrodes (i.e., P3 vs. P4). In particular, in trials in which the threatening face appeared on the left of the scene, the power at each right-hemisphere electrode was subtracted from its homologous on the left hemisphere (i.e., $\alpha_{\text{Left}} - \alpha_{\text{Right}}$). On the contrary, when the threatening face appeared on the right, the reverse subtraction was applied (i.e., $\alpha_{\text{Right}} - \alpha_{\text{Left}}$). Therefore, for 27 pairs of left/right electrodes we obtained a value that increases when attention is ipsilateral to the threatening face, and decreases when it is contralateral.

5. Statistical analyses

We excluded data from two participants due to poor EEG signal. Moreover, because high anxiety is known to impact behavioural responses to threat (for a review, see Grupe 2013), we limited our sample to subclinical population and excluded one participant presenting a clinical anxiety score based on the State-Trait Anxiety Inventory (STAI) administered before the study. We therefore analyzed the data of 27 participants for this study.

Behavioral data

Participants' responses regarding action choices were analyzed by calculating the proportion of trials in which they decided to sit next to the neutral or emotional individual and by running repeated measures ANOVAs with Emotion (Anger, Fear) and Side (away or toward from the emotional individual) as within-subjects factors. Importantly, because our previous experiments have showed that emotion intensity is not a critical factor in our tasks, we have decided to pool all the intensity levels together in order to maximize the number of observations per condition of interest. Additionally, we performed correlation between proportion of action choices and two subscales of the Interpersonal Reactivity Index (Davis, 1980), namely the "Personal distress" and the "Empathic concern" subscales.

EEG data

The same general linear regression model (GLM) was used for theta, alpha and beta bands, where the conditions of interest - emotion (anger, fear) and direction of the response (away, toward) - were introduced as trial-per-trial predictors of broadband EEG signals at each time point and electrode. Emotion intensity (from 0 for a neutral/emotionless expression to 7 for an intense fear/anger expression) was also taken in account, to control for possible effects of the strength of the displayed emotion. Thus, for each participant we applied the following GLM

$$EEG \sim AA + AT + FA + FT + AA * Int + AT * Int + FA * Int + FT * Int$$

where AA = Anger Away, AT = Anger Toward, FA = Fear Away, FT = Fear Toward and Int = emotional intensity. The time course of the parameter estimates of the regression, reported in arbitrary units, describes the neural 'encoding' of the relevant (emotion) information in both the situations where a response is produced away or toward the emotional face. Away vs. toward conditions were statistically contrasted within each emotion; we controlled for type 1 errors that come from multiple

comparisons across time points and electrodes using non-parametric cluster-level statistics (Maris & Oostenveld, 2007). As far as alpha asymmetry values are concerned, the cluster based correction was applied on 27 (i.e., number of pairs) instead of 64 electrode sites (27 pairs of homologous electrodes).

Source reconstruction analysis

For effects of interest, source analysis was performed using Brainstorm (Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011). A source model consisting of 15,002 current dipoles was used to calculate Kernel inversion matrices for each subject. Dipole orientations were constrained to the cortical mantle of a generic brain model taken from the standard Montreal Neurological institute (MNI) template brain provided in Brainstorm. A 3-shell forward EEG model was computed for each subject and a sLORETA algorithm using an identity noise-covariance matrix was employed to solve the inverse problem for each subject's parameter estimates.

Results

Behavioral data

Impact of emotional displays on action choices. Overall, participants more often chose the seat located away from the emotional individual ("Away" and "Toward" respectively refer to the neutral and emotional actor side), as revealed by a main effect of Side ($F(1,26)=18.12$, $p<0.001$, $\eta^2_p=0.41$). Importantly however, the nature of the displayed emotion distinctively influenced participants' choice (Emotion-by-Side interaction, $F(1,26)=12.96$, $p=0.001$, $\eta^2_p=0.33$): angry displays elicited more away responses, and fearful displays elicited more toward responses. The statistics of the paired comparisons of the interaction Emotion-by-Side are in **Table 1**. The main effect of emotion was not significant ($F(1,26)=0.48$, $p=0.50$, $\eta^2_p=0.02$).

Proportion of choice (%)	Paired differences		t	ddl	p-value	Cohen's d
	Mean	95% CI				
AA - AT	5.01	[2.76, 7.23]	4.57	26	<0.001	1.60
FA - FT	1.50	[0.13, 2.87]	2.25	26	0.03	0.71
AA - FA	1.64	[0.63, 2.67]	3.32	26	0.003	0.63
AT - FT	-1.86	[-2.94, -0.78]	-3.55	26	0.002	0.73
AA - FT	3.15	[1.54, 4.76]	4.01	26	<0.001	1.17
AT - FA	-3.36	[-4.95, -1.77]	-4.34	26	<0.001	1.29

Table 1. Paired differences and statistics of the paired comparisons of the Emotion-by-Side interaction on choice proportions (%). The abbreviations refer to the choice of the subjects with respect to the emotional actor: AngerAway: AA; AngerToward: AT; FearAway: FA; FearToward: FT; with “Away” referring to the opposite side of the emotional actor (i.e. side of the neutral actor) and “Toward” to the side of the emotional actor.

Impact of personality traits on action choices. To test the possible impact of individual differences in empathy on action choices, we entered the scores corresponding to the “Empathic concern” (EC) and “Personal Distress” (PD) subscales as covariates in the Emotion-by-Side ANOVA on the proportion of choices. We found a trend Emotion-by-Side-by-EC_scores interaction such as participants with higher EC scores tended to avoid more angry individuals and approach more fearful ones ($F(1,25)=3.58$, $p=0.07$, $\eta^2_p=0.13$). No other effects were significant (all $F_s < 1.85$, $p > 0.19$, $\eta^2_{ps} < 0.07$). The Emotion-by-Side-by-PD_scores led to no significant effects (all $F_s < 1.21$, $p_s > 0.28$, $\eta^2_{ps} < 0.05$).

EEG data

1. Beta band

The average of the parameter estimates for beta in the conditions of interest denoted the expected sustained response over motor areas, which lasted throughout the movement execution. Nonetheless,

when testing the difference between away and toward condition for anger and fear respectively, no significant differences were detected (i.e., all clusters with $p(\text{corr}) > 0.26$ in the time-window between 0 and 1.2 seconds). When focusing only on C3 electrode, at any time point the main effect of emotion (all $p_s(\text{uncorr}) > .08$) nor the interaction between emotion and direction (all $p_s(\text{uncorr}) > .15$) was significant between 0 and 1.2 seconds.

2. Theta band

The average of the parameter estimates for theta in the conditions of interest (Figure 1a) denoted a sustained frontocentral response, which lasted throughout the movement execution, compared to a shorter posterior response, presumably related to visual encoding of the stimulus. To investigate the apparent interaction between emotion and movement direction at frontocentral sites (Figure 1b), we contrasted away vs. toward responses in the two emotional conditions (anger and fear). The threshold for the initial paired t-tests was set at 0.05. The supra-threshold values were permuted 1500 times to identify the presence of significant clusters of a minimum of 3 electrodes, with alpha equal to 0.05. Based on visual inspection, the time-window for anger was set between 0.3 and 0.9 sec, and for fear between 0.3 and 1.4 seconds. The results are corrected for both the number of time points and electrodes and indicate a positive cluster ranging from 0.31 to 0.74 sec for anger, and a negative one for fear, from 0.45 to 1.3 sec. Both clusters are frontocentral, with the one for anger being slightly left-lateralized (Figure 1c). Overall, these results suggest that the AA and FT condition are respectively predictive of increased theta power at frontocentral scalp sites compared to AT and FA. To check for the effect of emotional intensity, we also plotted the interaction of this factor with each condition of interest, which overall showed parameter estimates very close to zero, suggesting negligible effect of emotional intensity on theta power.

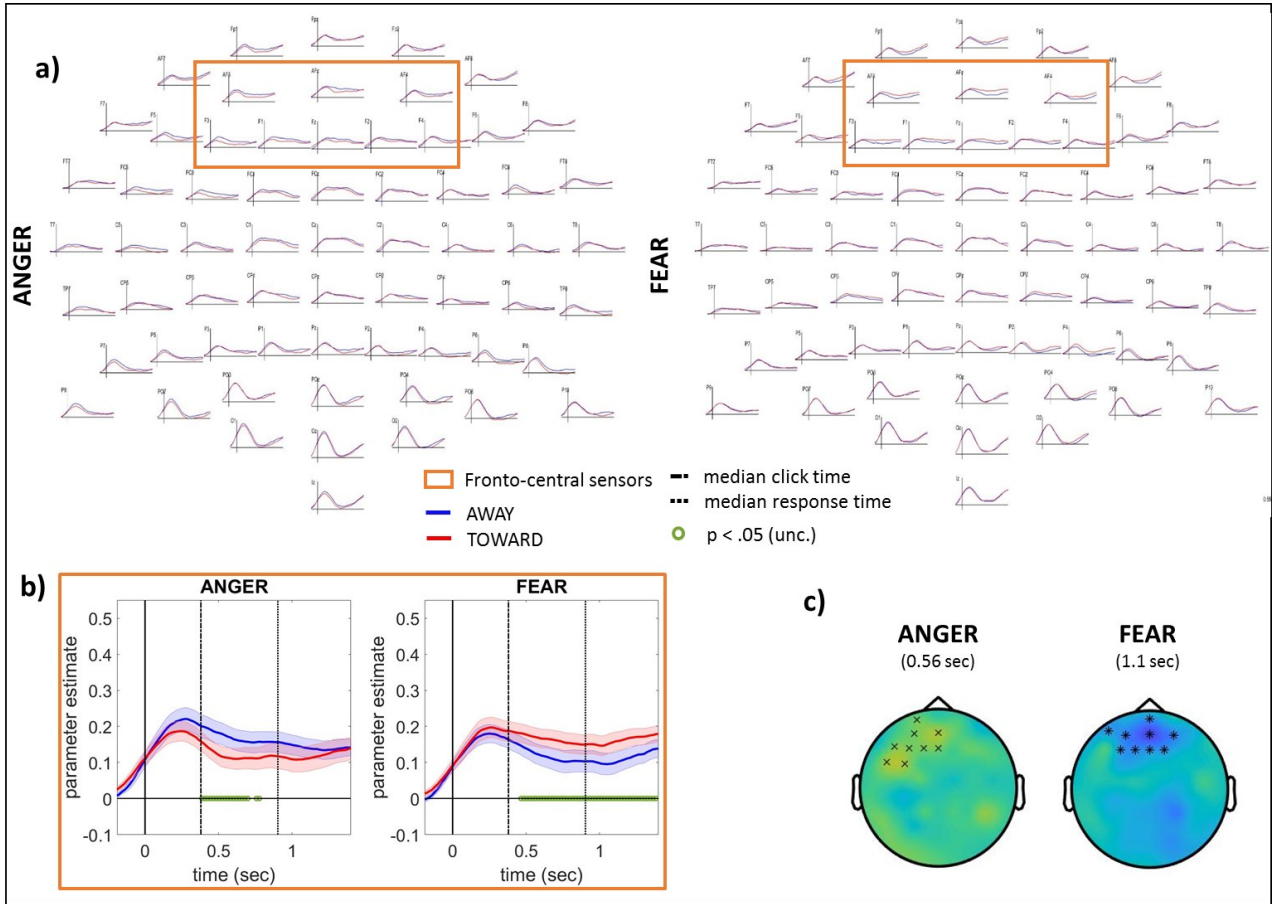


Figure 1. a) Average of the parameter estimates for theta in the conditions of interest. b) Away versus Toward contrast on the parameter estimates for each emotional condition c) Topographical representation of the Away versus Toward contrast for each emotional condition.

Based on these results, we wanted to test whether theta power and emotion significantly predicted the response choice at the behavioral level. Therefore, for each subject, the following logistic model was run to predict the choice at a trial-by-trial level:

$$p(AWAY) \sim THETA + EMOTION(anger = 1, fear = 0) + THETA * EMOTION$$

Figure 2a shows the average between subjects of the main effects and the interaction at frontocentral scalp sites. The main effect of emotion confirms the behavioral findings (i.e., anger increases the chance of an away response, compared to fear). We tested when and in which electrodes the main

effects of theta and the interaction between theta and emotion differed from zero, again using the cluster-based correction method (whole time window; -0.2 to 1.4 sec). It emerged that both effects are significant, with the interaction term indicating that increased frontocentral theta between 0.35 to 1.2 sec in the anger vs. fear condition was associated to higher chances to go away, in line with the results of the GLM (Figure 2b). Interestingly, source analysis on the parameter estimates of the interaction term suggested that the anterior cingulate cortex (ACC) is the plausible source of the interaction between theta band and emotion between 0.35 and 1.2 sec from stimulus onset (see Figure 2c).

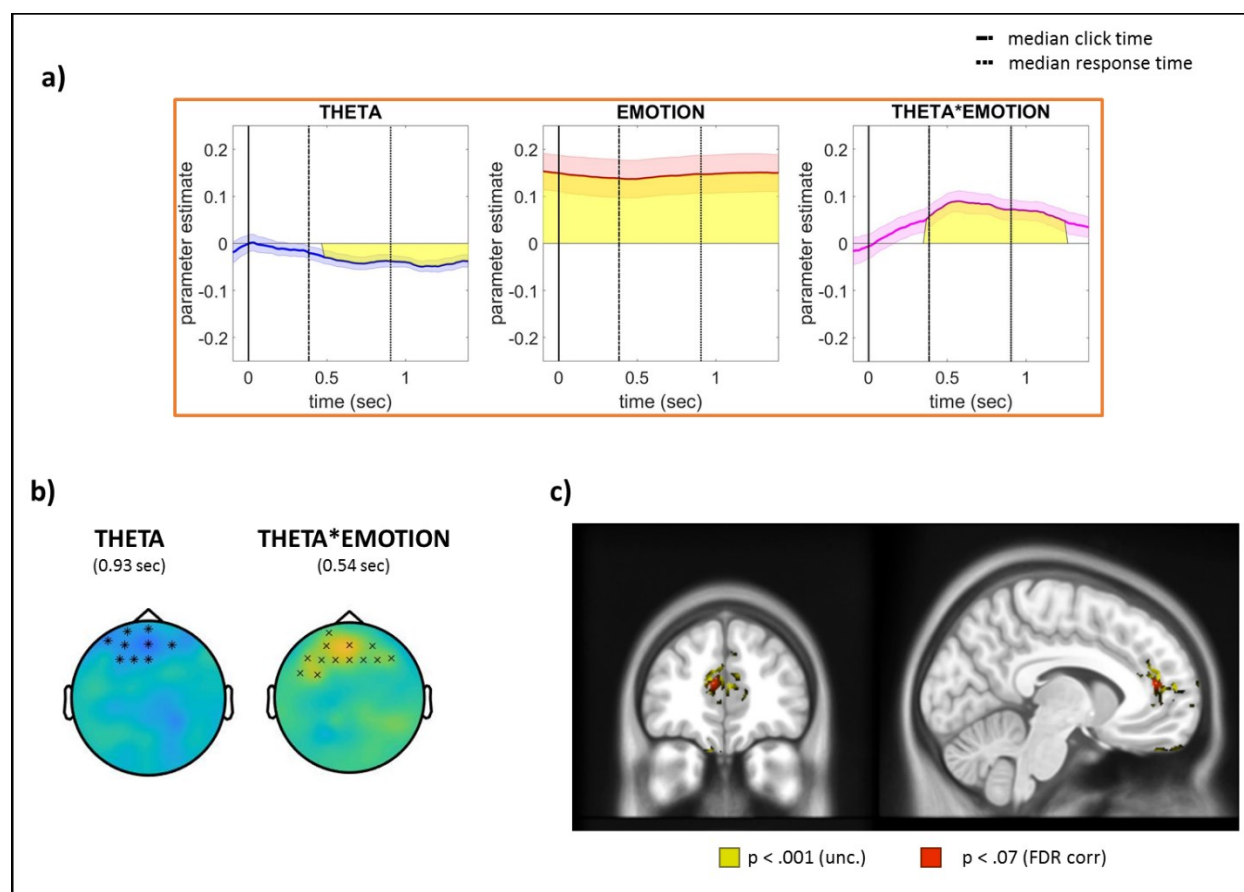


Figure 2. Results of the logistic model testing a predictive effect of theta power and emotion on action choices. a) Average between subjects of the main effects and the interaction on the parameter estimates of the logistic regression at frontocentral scalp sites. b) Topographical representation of the main effect and the interaction at frontocentral sites. c) Reconstructed source of the interaction between theta band and emotion between 0.35 and 1.2 sec.

Discussion

We conducted an experiment to assess the differential impact of angry and fearful displays on action selection processes. At the behavioural level, our experiment revealed that angry and fearful expressions were differing in the way they promoted actions in the observer, with greater avoidance of angry displays compared to fearful ones. At the neural level, we found increases in theta power when participants avoided angry and approached fearful individuals, as compared to the two other action choices.

The behavioural effects we found on action choices were replicating previous findings and revealed that anger favoured more avoidant responses than fear. This effect corroborates our previous results and suggests that angry displays indeed convey a different signal than fearful ones, precisely a more direct threat, which likely incites observers to increased avoidant behaviours. However, because past experiments did not provide any information regarding the motives underlying action choices, we administered a questionnaire measuring “self-oriented” and “other-oriented” feelings (IRI – Davis, 1980), as proxies for self-preservative and prosocial motives (Dezecache et al., 2017). Although marginally significant, the results tend to suggest that individual differences in experiencing feelings of compassion in response to unfortunate others, rather than feelings of personal distress, influence action choices in our task. This effect would be congruent with studies showing that prosociality and affiliation are common responses during exposure to danger (Sime, 1983), but future studies are needed to properly test this hypothesis.

However, the effects observed on the theta-band activity were opposite to what we had hypothesized. Indeed, increases in theta power are usually observed when deciding between conflicting responses, and are proposed to reflect the effort required to solve the competition (Mennella et al., 2017). This interpretation would imply that avoiding anger and approaching fear were the most effortful action choices. However, in the case of anger, our previous experiments revealed that participants

consistently “preferred” sitting away from the angry individual when asked to *freely* make action-related decisions (Experiments 1 and 4). It seems unlikely that participants would have repeatedly selected a more effortful action, while this strategy led to no particular benefit (no fulfilment of task demands, and no possible gains). In the case of fear, although our previous findings were discrepant with regards to its associated action choice, we could have expected increases in theta power associated to avoidant responses, given that fearful faces are related to approach behaviours in the literature (Hammer & Marsh, 2015). However, the opposite pattern was observed, with greater beta-band activity when participants were approaching fearful individuals. As of today, and to our knowledge, the theta-band activity literature does not provide an interpretation that could easily accommodate both our behavioural (past and present) and electrophysiological data.

The effect we observed on the theta-band activity appears to originate from the Anterior Cingulate Cortex, which is critically involved in performance monitoring and cognitive control (Botvinick, Cohen, & Carter, 2004). Notably, the ACC is proposed to monitor conflicts in information processing, and to inform cost-benefit analyses underlying action selection. However, its activity has either been shown to increase or decrease, when making an error or when making a choice between conflicting responses (Brown & Braver, 2007; Fukunaga, Brown, & Bogg, 2012; Magno, Foxe, Molholm, Robertson, & Garavan, 2006). The latter effect, along with findings showing that greater ACC activity is observed when participants make safe compared to risky choices (Fukunaga et al., 2012), would best fit our data. However, the early stage of these analyses and the amount of competing theories regarding ACC functioning (Ebitz & Hayden, 2016) encourages caution in the interpretation. Further analyses investigating the relationship between theta activity and behavioural markers of action selection should help us deepen our understanding of the observed effects.

DISCUSSION

Discussion of the findings

The work conducted in my Ph.D., including 5 experiments in healthy subjects, aimed at characterizing the relationship between attention and action under social threat. Experiment 1 assessed action selection in the presence of action opportunities; Experiment 2 assessed attentional biases in the presence of action opportunities; Experiments 3 assessed attentional biases within our threat-related experimental context in the absence of action opportunities; Experiment 4 assessed action selection in the presence of action opportunities jointly with overt attention allocation by recording saccadic behaviour; and Experiment 5 assessed neural correlates of action selection processes using electroencephalography.

These experiments led to the first conclusion that angry and fearful displays send different signals to the observer, respectively related to strength and vulnerability, hence corroborating evolutionary theories on the inter-personal function of emotional facial expressions. Further, these experiments showed that these threat-related displays distinctively influence both attention allocation and action selection as patterns of action choices and attention allocation revealed that anger favoured avoidance responses, and suggested that fear promoted approach behaviours, although this latter assumption has to remain cautious.

The use of multiple methodological approaches allowing to access “hidden” variables corroborated these different findings. In particular, they provided evidence regarding i) observer’s emotional states which corroborated that anger and fear convey different social signals (pupil dilation); ii) parameters of action selection which were insightful regarding the action decision-making process (kinematics); iii) and shifts of attention allocation which revealed that attention is first oriented to threat then

toward the endpoint of the chosen action (saccades). Finally, our experiments underlined the importance of considering the interplay between attention and action within ecologically valid contexts presenting key features of our natural environment, such as action opportunities.

1. Anger and fear: which signal and which response?

Angry and fearful facial expressions have been extensively studied in order to understand how they are perceived by observers, and how do observers react to these displays. According to the evolutionary framework, emotional displays have evolved in order to quickly and nonverbally communicate socially significant information to others, thereby serving an inter-personal function. Crucially, the stabilization of this communicative function entails that emotional signals have coevolved with observers' behavioural responses, so that these signals produce reactions that benefits both the emitter and the observer (Dezecache, Mercier, & Scott-Phillips, 2013; Scott-Phillips, 2008). The implication of this hypothesis is that behavioural responses of the observers are adapted to the social signals they are triggered by, and thus reflect the social function of the perceived emotional expression.

Emotions of anger and fear are negatively valenced expressions owing to their threat-relatedness. However, their associated facial expressions transmit different signals: while angry displays are themselves perceived as a direct threat, fearful displays warn the observers of an imminent threat (Sander, Grandjean, Kaiser, Wehrle, & Scherer, 2007). Moreover, studies have showed that the facial configuration of anger enhances cues of physical strength, increasing the observer's perceived probability to be aggressed and defeated (Sell et al., 2014). However, the facial configuration of fear appease social interactions and inhibit aggression by enhancing cues of vulnerability and affiliation (Hammer & Marsh, 2015). Hence, according to evolutionary theories, the signal conveyed by angry displays should favour avoidance responses in the observer whereas fearful displays could promote approach behaviours.

The case of Anger

Regarding behavioural responses to angry displays, our experiments demonstrated that anger promoted avoidant responses in the observer (attention allocation in Experiment 2, peak velocity in Experiment 1, action choices in Experiment 1,4,5). Moreover, in all our action-related decisions tasks, participants systematically reported more satisfaction after having avoided anger, suggesting that avoidance was the “preferred” response in the face of anger. Angry displays being perceived as a direct threat, avoidant behaviours were likely driven by a self-preservative motive to protect oneself from danger by increasing distance with the source of threat.

Although approach responses were always observed in a lesser proportion than away responses, this alternative action tendency might have been underlain by a drive to confront angry individuals (Bossuyt et al., 2014; Carver & Harmon-Jones, 2009; Wilkowski & Meier, 2010). Indeed, it has been proposed that perceiving an offending other can promote an effort to inflict pain or harm, and be associated with approach locomotion (Carver & Harmon-Jones, 2009). These behaviours have notably been related to dominance challenges, both in primates and humans (Mazur & Booth, 1998). These findings thus suggest that approach behaviours might have been driven in part by the motivation to approach angering social challenges in order to confront and overcome them (Wilkowski & Meier, 2010).

The case of Fear

The case of fear was less evident, given that some of our measures indicated that fearful displays favoured approach responses (peak velocity in Experiment 1, attention allocation in Experiment 2), some revealed competing responses between approach and avoidant responses (action choices in Experiment 1) and others suggested that fearful displays promoted avoidant responses (action choices in Experiments 4 and 5). Although less evidence was found in favour of avoidant responses, these

findings remain indecisive. One possible reason would be that fearful faces are ambiguous when they are paired with a direct gaze (Adams, Gordon, Baird, Ambady, & Kleck, 2003), and this ambiguity might have let different possible interpretations arose regarding the localization of the environmental threat (i.e. coming from the neutral individual's side, or from the fearful individual's side). Then, depending on the estimated location of danger, participants might have chosen different strategies, leading to mixed effects. Also, these results might be explained by the dual nature of fearful facial expressions, both related to threat and affiliation, which might have driven both avoidance and approach behaviours. Although avoidance of fear was probably driven by self-preservative motives (i.e. protect oneself from danger), approach behaviours could have been underlain both by self-preservative or prosocial motives. The former would reflect a need for affiliation to alleviate one's own fear, while the latter would reveal a desire to provide help, especially given that the combination of a distress cue with a direct gaze can signal a need for help (Marsh et al., 2007). In spite of recent evidence suggesting that grouping behaviors in the face of threat seem to be driven by self-preservative motives (Dezecache et al., 2017), our data suggest that feelings of compassion in response to unfortunate others could drive these behaviours (Experiment 5), although the effect only tended toward significance. Future studies could help better understand the motives driving action tendencies, by manipulating for instance the observer's state and testing how it affects action selection.

Anger versus Fear

Overall, our data suggest that angry and fearful displays send different information to the observer and distinctively influence action selection. Pupil dilation and action choices notably showed that angry stimuli were more arousing than fearful ones and that angry displays consistently promoted more avoidant behaviours than fearful displays, respectively.

These different levels of threat for the observer can be explained by the intrinsic facial configurations of fear and anger that convey distinct signals, consistently with previously cited studies. However, the

difference in perceived intensity could also be explained by the emotional displays' gaze direction. Indeed, it has been consistently showed that the perception of threat-related displays can be modulated by the gaze direction they have been paired with. Specifically, the detection of anger represents an immediate threat for the observer when paired with a direct gaze; by contrast, it is when paired with an averted gaze that fear marks the presence (and possibly the localization) of a threat in the environment (Sander et al., 2007). These combinations have been shown to be better recognized and judged as more intense than other combinations (Adams Jr & Kleck, 2003, 2005; Bindemann, Mike Burton, & Langton, 2008; El Zein et al., 2015; N'diaye, Sander, & Vuilleumier, 2009). A recent study has recently provided a mechanistic explanation by demonstrating that gaze direction enhanced the perceptual sensitivity to threat-signaling emotions (El Zein et al., 2015). Thus, because the emotional displays used in our tasks all displayed a direct gaze, anger might have been better recognized and perceived as more intense than fear, thereby explaining our effects.

However, this hypothesis is weakened by the fact that, on the one hand, our stimuli were carefully equalized in perceived emotional intensities, thus accounting for the difference in perceived intensity which might have resulted from pairing anger and fear with a direct gaze (see Methods in El Zein et al. 2015). On the other hand, the results of our categorization post-tests indicated that angry displays were categorized as accurately, and judged as intense, than fearful displays. Thus, it seems that the differences we observed were more likely explained by the different social signals that these displays convey, than by a difference in perceived emotional intensity. Our pupil dilation results further corroborate this interpretation by showing that the relevant information to track in our action-related decisions tasks seems to be the nature of the signal, and not its intensity.

2. Emotion and attention: extended span and increased perceptual sensitivity?

Numerous studies have demonstrated that emotional displays can quickly attract attention, but growing evidence suggest that emotional stimuli can also affect the perception of the environment,

and influence the quality of our perception. Regarding environmental monitoring, it has notably been shown that fearful stimuli, compared to angry and neutral stimuli, can enhance the detection of peripheral targets presented subsequently to an emotional display (Taylor & Whalen, 2014). This diffusion of attention to the environment is congruent with the suggested role of fearful expressions of maximizing sensory exposure in order to improve danger detection (Susskind et al., 2008). Regarding perceptual sensitivity, different studies have revealed that emotional or threat-related stimuli can enhance the visual processing of other information in the same location, with some studies showing that this enhancement is specific to low spatial frequencies, which preferentially convey emotion-related information and help locate the stimuli in space (Bocanegra & Zeelenberg, 2009; Phelps et al., 2006; Preciado et al., 2017; Song & Keil, 2013).

Following these findings, we could have hypothesized that threat-related facial expressions would have impacted on the perception of the cue in our spatial attention studies (Experiment 2 and 3), with fearful faces enhancing the *detection* of the target in the scene compared to angry faces, and emotional displays increasing the *discrimination* of the target compared to neutral displays. Moreover, we could also have expected such modulation to be stronger at the locations corresponding to actions' endpoints (away from anger, and toward fear), given that the spatial resolution of the visual system is proposed to be adjustable accordingly to planned actions (e.g. Kirsch 2015). However, we did not find any significant effects on accuracy or d-prime scores on our data (see Complementary analysis page 81).

The main difference between our studies and the previously cited ones, is that the cue was presented concomitantly with the faces, whereas the target was always presented subsequently to the emotional or threat-related stimulus in previous studies. The persistence of the faces on the screen might have increased the attentional load, and led attentional resources to be shared between the cue and the faces throughout the trial, thereby limiting these perceptual effects to occur. Future studies using the

same experimental design but making the cue appear after the scene could be ran in order to assess whether action selection in response to threat displays can also influence perceptual sensitivity.

3. Attention and action: a hierarchical relationship?

In the emotion domain, attention and action have often been studied separately. Studies investigating how threat-related stimuli can affect attention have established that they quickly attract attention, but little focus has been put on how these attentional biases relate to subsequent behaviours (see review by Cisler & Koster, 2010). Studies examining how threat-related stimuli influence motor processes have yielded discrepant results, and have rarely related action tendencies to preceding or following patterns of attention (Marsh, Ambady, & Kleck, 2005; Wilkowski & Meier 2010; Bossuyt et al. 2013; Enter et al. 2014; Hammer & Marsh 2015). However, the motor literature considers that attention and action are closely related mechanisms and studies them jointly (Rizzolatti et al. 1994). Notably, it has been shown that action planning can shape attention allocation and orient it toward action-relevant features (e.g. pertinent properties of an object, or endpoint of a selected action) (Fagioli et al. 2007; Wykowska et al. 2009; Kirsch 2015). Hence, in the face of threat, where fast detection and adaptive reaction are required, how do these mechanisms interact?

Here, we propose a model based on the literature and on our data, and speculate about the relationship between attention and action occurring in the face of threat and in the presence of action opportunities. We adopt the “affordance competition hypothesis” framework, developed by Cisek (2007) and validated by numerous empirical findings, both at the behavioural, computational and neural levels (Chapman et al., 2010; Cisek & Kalaska, 2005; Gallivan et al., 2016; Lepora & Pezzulo, 2015; Pezzulo & Cisek, 2016). This framework has been proposed as an alternative to the classical serial view which posits that the brain first gathers sensory information to build an internal representation of the world, independently of actions, makes a decision, computes an action plan and executes a movement. However, neurophysiological data argue against this modular viewpoint by demonstrating

that sensory and motor systems interact in action specification and selection processes (Kim & Shadlen, 1999; Platt, 2002). The “affordance competition hypothesis”, named after Gibson (1979) who first proposed the term “affordances”, was thus formulated to describe the constant competition between internal representations of the potential actions which give rise to behaviour.

This framework proposed that visual information is first transferred from the visual cortex to the parietal lobe, which then transforms it into representations of potential actions. These representations form a map of potential actions, which receives biasing inputs from regions collecting information for action selection. Different potential actions are then being simultaneously prepared until biasing inputs lead to the selection of one specific action. The representation of the chosen action is then strengthened, while the unchosen action representations are suppressed, as revealed by neurophysiological recordings in the dorsal premotor cortex (Cisek & Kalaska, 2005). The selected action is finally released into execution and provides visual and internal feedbacks.

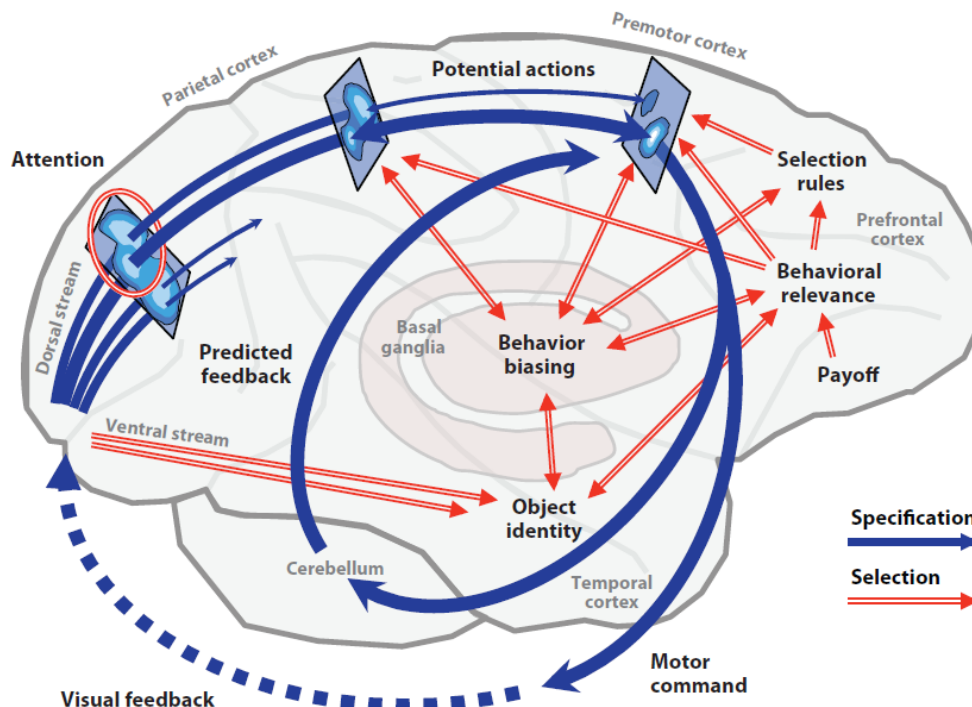


Figure 16. From Cisek & Kalaska (2010). Sketch of the affordance competition hypothesis in the context of visually-guided movement.

Considering our data in this framework (Figure 17), we suggest that in the context of our tasks, attention is first drawn to emotional faces, as evidenced by an increased proportion of first saccades directed toward the emotional individual (Experiment 4). In parallel, the presence of opportunities for action trigger the preparation of two action plans, directed toward each available seat (Cisek 2007). The acquisition of sensory information, and notably of emotion-related information, is going to modify the value of potential actions and bias action selection toward the most adaptive behaviour, as our action choices data suggest (Experiment 1,4,5). Our data might suggest that information about action value could transit notably through the anterior cingulate cortex. Then, once an action plan has been selected, the motor system is going to reorient spatial attention toward the endpoint of the chosen action, accordingly to the premotor theory of attention (Rizzolatti et al 1994). Our findings indeed suggest that shifts of overt (second saccades landing sites) or covert (reaction times) attention are congruent with action choices (respectively, Experiment 2 and 4). We believe that these attentional patterns are a consequence of action selection because removing action opportunities from the scene disrupted the emotion-specific effect, suggesting that the action-related context modulated the effect of emotion on attention (Experiment 3).

Our proposal is consistent with findings indicating that attention is quickly attracted by threat-related stimuli, but also with recent evidence revealing that, when both *sufficient time* and a *safe action opportunity* are available, attention can be directed toward safety cues (Vogt et al. 2016; Schmidt et al. 2017).

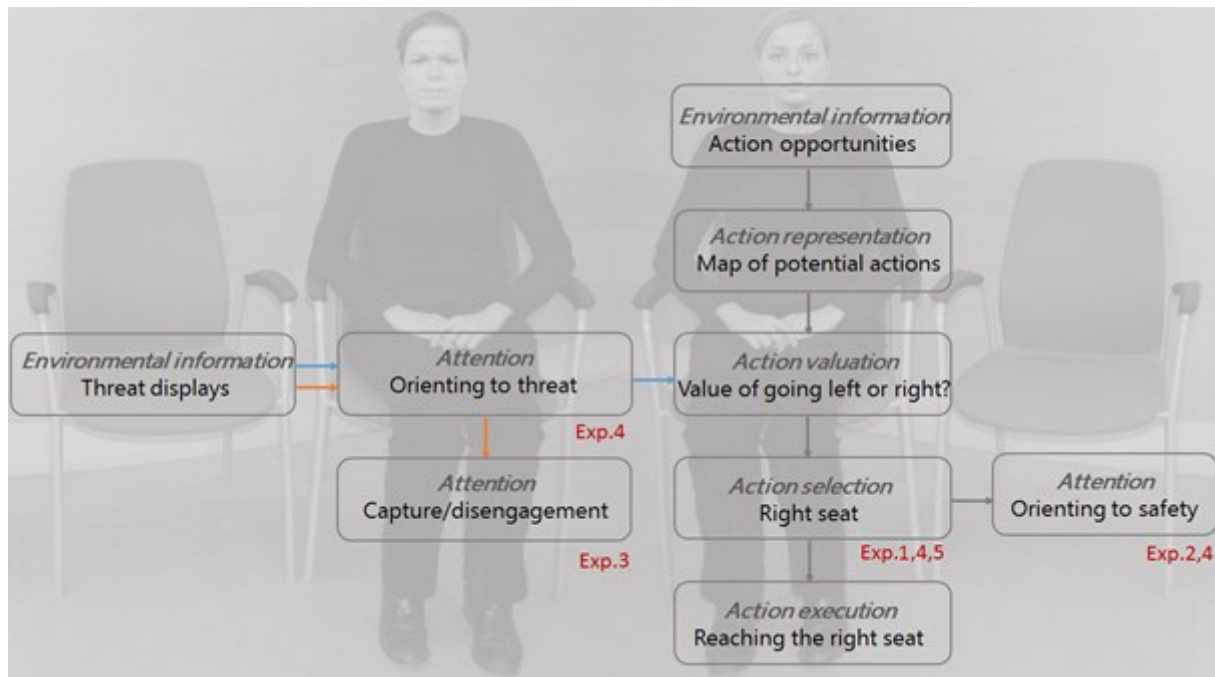


Figure 17. Sketch of a model accounting for the effects observed through 5 experiments on healthy subjects. It describes that when both emotional information and action opportunities are detected in the environment, the former is going to capture attention while the latter is going to prompt the formation of maps of potential actions. Then, sensory information, notably threat-related information in our experimental context, is going to bias action selection toward the most adaptive action (blue arrows). Action selection is then going to guide attention allocation toward the endpoint of the chosen action while the selected action is released into execution. We propose that in the absence of action opportunities, attention is going to be captured by threat-related stimuli, or directed away from it, in anxious individuals notably (orange arrows).

Limitations of the studies

The work conducted in my PhD presents several limitations that I will describe in the next paragraphs.

First, we have studied the interplay between attention and action in response to threat using independent experiments testing either one process or the other. Although two of our tasks aimed at addressing this question, with our spatial attention study without action opportunities (Experiment 3) testing attention allocation in the absence of action possibilities, and our saccade study (Experiment 4) investigating action selection while recording overt attention allocation, we did not conduct a study

where participants had to both select an action and detect a cue in the environment. The interpretation of our effects could have been strengthened by the use of dual tasks testing both attention allocation and action selection, because attentional and action responses could have been directly related to each other. Future studies will address this question in order to validate previous findings (see Perspectives section).

Second, our experiments focused on threat-related facial expressions because threatening contexts are particularly suited to study attention- and action-related mechanisms, due to their urgent nature. However, an open question is whether responses to positive stimuli share common features with responses to negative stimuli, or not. Notably, do approach behaviours toward positive stimuli are underlain by similar mechanisms than approach toward threat-related stimuli, like fearful displays. Although the response to this question could intuitively be negative, with regards to theories positing that positive stimuli are automatically associated to approach behaviours whereas negative stimuli are not (Bargh 1997), comparing these behaviours could help shed light on their respective motives.

Indeed, happy facial expressions are socially rewarding stimuli and are associated to approach and affiliative behaviours (Izuma, Saito, & Sadato, 2008; Spreckelmeyer et al., 2009); and research has shown that affiliation is also a common response during exposure to danger, even when people's life is directly at risk (Sime, 1983). However, while approaching happy individuals is likely driven by a self-oriented motive, approaching fearful individuals could be either of self-preservative, or prosocial nature (Dezecache et al. 2017). Then, comparing approach responses to both happy and fearful displays could have been informative to better understand the motives driving affiliative tendencies.

Third, in line with the previous criticism, our experiments did not allow to collect information regarding action tendencies' motives. However, understanding why a behaviour is expressed, and not only how, is crucial to better study complex social mechanisms. Because emotional displays were mainly implicit in our tasks, debriefing participants was not the ideal way to access their motivations (often,

participants were unaware of the presence of emotional displays). Alternatively, we could have selected our participants based on relevant personality traits susceptible to influence attention allocation or action selection in response to threat. Notably, social anxiety could have impacted both of these mechanisms, given that highly anxious individuals express hypervigilance to and avoidance of threat-related social information (Grupe & Nitschke, 2013). Otherwise, we could have manipulated the emotional or bodily state of the observer and test whether performance in our tasks were different before and after the manipulation. These different procedures would have developed our understanding of the observed behaviours.

Finally, the design of our task might have not been ideal to collect kinematic information regarding the unfolding of decisions over time. Indeed, we made the decision to use a paradigm in which participants were free to decide where they wanted to seat, with as few constraints as possible in order to exploit spontaneous tendencies. But the use of a “go-before-you-know” paradigm would have probably revealed effects on movements’ trajectories, although this behaviour might not be fully natural, and costly due to changes in ongoing courses of action.

Future directions

Future studies would be needed to address some open questions brought up by our experiments.

First, we plan on conducting a dual task in which both attention allocation and action selection could be tested. This would allow to directly relate attentional biases and upcoming motor responses. For instance, using the same experimental context than in our previous experiments (a scene with four seats and two individuals), we could conduct a task where participants are asked to freely choose a seat (or instructed to sit on a specific seat) but to withhold their movement while they make a

discrimination task. Or participants could be asked to choose a seat after having discriminating a cue in the environment. This would allow to measure in each subject the correlation between attentional biases and action choices, and to uncover the functional coupling between the two mechanisms.

Second, a task manipulating the state of the perceiver would help understanding action tendencies' motives. For instance, inducing stress (e.g. by randomly displaying an aversive sound) would allow measuring whether action choices are impacted by the manipulation, and better understanding the strategies that are deployed when facing threat. Notably, an increase in approach behaviours toward fearful individuals when participants are themselves in a state of fear would suggest that grouping behaviours are an adaptive response to threat (e.g. Dezechache et al. 2017).

Third, in order to further understand the relationship between action selection and emotional displays, and notably which action is favoured by angry or fearful facial expressions, we could conduct a Go-No go task (Fillmore, 2003). In this paradigm, participants are required to perform an action given certain stimuli and inhibit that action under a different set of stimuli, thereby permitting to measure action disposition by evaluating the effort required to inhibit a planned motor response. Accordingly, it has been shown that stronger action readiness is associated with more effortful motor inhibition in Go-No go tasks (Smith, Johnstone, & Barry, 2008). Then, on the one hand, this experiment would offer another way to relate threat-related displays and action choice, by measuring response conflict instead of free action choices. On the other hand, it would help us better understand our EEG findings, given that theta-band activity is also a marker of effortful motor inhibition.

CONCLUSION

The work conducted in this PhD focused on the interplay between attention allocation and action selection occurring in the face of threat, and in the presence of action opportunities.

The findings of our 5 experiments, and the model we propose, can be summarized using the everyday example that was developed throughout this manuscript: When we enter a subway car, looking for a seat, the presence of an angry individual will quickly capture our attention (Exp. 4) while our brain computes a map of potential actions leading to the different free seats. Action selection process will receive biasing inputs, notably carrying environmental information, and the presence of a potential danger will likely favour the selection of the seat farthest from the threat (Exp. 1,4,5). Then, attention will be directed toward the endpoint of this course of action, in order to facilitate motor behaviour toward the safe seat (Exp. 2,3). However, if an individual expresses fear, the safe seat might be the one closer to the fearful person, possibly depending on individual differences in reactivity to unfortunate others (Exp. 5).

Through this theoretical proposal, this work promotes the use of different methodological approaches (kinematics, pupillometry, saccades, EEG) that allowed tackling our question through different perspectives. By giving complementary information, the combination of techniques has been essential in developing our understanding of the mechanisms at play, although several questions remain open. Moreover, this work is also an opportunity to promote the use of ecologically valid experimental designs, especially when studying interaction with social environments. We believe using ecological paradigms has been crucial for our work, as they might have stimulate observers' spontaneous tendencies rather than dispositions formed during the execution of the tasks themselves. Recent technological developments (functional near-infrared spectroscopy, virtual reality ...) offer promising perspectives and will surely expand our knowledge regarding these complex social behaviours.

APPENDIX A: Post-tests in Experiments I to 5

1. Methods

After each study, subjects completed two blocks of an Anger-Fear categorization task composed of 80 stimuli (10 pairs * 2 emotional expressions * 4 levels of morphs). They were presented with a grey screen for 1000ms, then the scene appeared for 600ms. Subjects had to detect the emotion displayed by one of the two actors while fixating the cross between the faces and to report it by pressing the corresponding “Anger” or “Fear” keys. The mapping between the responses and the keys was counterbalanced between participants.

2. Post-tests’ performance

Action-related decisions study (visual fixation). Two participants didn’t complete the post-test due to a technical problem. The overall accuracy revealed that subjects’ accuracy was significantly different from chance ($m=64.2\%$, 95% CI [64.2, 64.2]; $t(14)=6.39$, $p<0.001$, $d=0.43$). We ran an *Emotion*Level* repeated measures ANOVA that showed a significant main effect of Level ($F(3,42)=23.81$, $p<0.001$, $\eta^2_p=0.63$) such that the accuracy increased with emotion intensity; but no other main effects or interactions were significant (all $F_s<2.21$, all $p_s>0.08$, all $\eta^2_{ps}<0.16$).

Action-related decisions study (visual exploration). The overall accuracy revealed that subjects’ accuracy was significantly different from chance ($m=76.5$, 95% CI [76.4, 76.5]; $t(18)=9.81$, $p<0.001$, $d=2.21$). We ran an *Emotion*Level* repeated measures ANOVA that revealed a main effect of Level ($F(3,54)=106.75$, $p<0.001$, $\eta^2_p=0.86$) such that the accuracy increased with emotion intensity; but no other main effects or interactions were significant (all $F_s<1.92$, all $p_s>0.18$, all $\eta^2_{ps}<0.1$).

Action-related decisions study (visual fixation and EEG). The overall accuracy revealed that subjects’ accuracy was significantly different from chance ($m=67.7\%$, 95% CI [67.7, 67.7]; $t(26)=13.45$, $p<0.001$,

$d=1.58$). We ran an *Emotion*Level* repeated measures ANOVA that revealed a main effect of Level ($F(3,78)=65.89, p<0.001, \eta^2_p=0.72$) such that the accuracy increased with emotion intensity; but no other main effects or interactions were significant (all $F_s<2.22$, all $p_s>0.09$, all $\eta^2_{ps}<0.08$).

Spatial Attention Study. The overall accuracy revealed that subjects' accuracy was significantly different from chance ($m=64.8\%$, 95% CI [64.7, 64.9]; $t(23)=-5.19, p<0.001, d=1.06$). We ran an *Emotion*Level* repeated measures ANOVA that revealed a main effect of Level ($F(3,69)=8.88, p<0.001, \eta^2_p=0.28$) such that the accuracy increased with emotion intensity; a trend toward a main effect of Emotion ($F(1,23)=4.06, p=0.06, \eta^2_p=0.15$) such that participants tended to be more accurate to categorize fearful expressions; but no *Emotion*Level* interaction ($F(3,69)=0.31, p=0.82, \eta^2_p=0.01$).

Spatial Attention Control Study. The overall accuracy revealed that subjects' accuracy was significantly different from chance ($m=65.5\%$, 95% CI [65.5, 65.5]; $t(25)=8.08, p<0.001, d=1.58$). We ran an *Emotion*Level* repeated measures ANOVA that revealed a main effect of Level ($F(3,75)=25.17, p<0.001, \eta^2_p=0.50$) such that the accuracy increased with emotion intensity; but no other main effects or interactions were significant (all $F_s<1.41$, all $p_s>0.24$, all $\eta^2_{ps}<0.05$).

3. Post-tests' influence on performance.

In order to assess whether the ability to recognize emotions in the post-tests was underlying our effects of interest (either main effect of Side, or interactions Emotion-by-Side), we ran these analyses again with categorization accuracies as covariates.

Action-related decisions study (visual fixation). The Emotion-by-Side-by-accuracy repeated-measures ANOVA on the proportion of choice yielded no significant effects (all $F_s<1.92$, all $p_s>0.19$, all $\eta^2_{ps}<0.13$)

Action-related decisions study (visual exploration). The Emotion-by-Side-by-accuracy repeated-measures ANOVA on the proportion of choice yielded a significant interaction between the main effect

of Side and the post-test accuracy ($F(1,17)=6.09, p=0.02, \eta^2_p=0.26$), such that the better the participants were in the post-test, the more they were avoiding to sit next to the emotional individual in the main task.

Action-related decisions study (visual fixation and EEG). The Emotion-by-Side-by-accuracy repeated-measures ANOVA on the proportion of choice yielded a significant interaction between the main effect of Side and the post-test accuracy ($F(1,25)=6.43, p=0.02, \eta^2_p=0.20$), such that the better the participants were in the post-test, the more they were avoiding to sit next to the emotional individual in the main task. Moreover, a significant triple interaction between Emotion and Side factors, and the post-test accuracy ($F(1,25)=4.63, p=0.04, \eta^2_p=0.16$) revealed that this effect was driven by angry scenes (correlation of accuracy with the difference score between AA and AT: $r=0.49, p=0.01$), no difference were found for fearful scenes ($r=0.24, p=0.22$).

Spatial Attention study. The Emotion-by-Side-by-accuracy repeated-measures ANOVA on the reaction times yielded no significant effects (all $F_s < 1.15$, all $p_s > 0.34$, all $\eta^2_{ps} < 0.05$)

Spatial Attention Control study. The Side-by-accuracy repeated-measures ANOVA on the reaction times yielded no significant effects ($F(1,23)=0.007, p=0.93, \eta^2_p < 0.001$).

APPENDIX B: Papers and scientific communications

Papers

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

Baltazar M., Hazem N., Vilarem E., Beauconsin V., Picq J.-L., Conty L. (2014) Eye contact elicits bodily self-awareness in human adults, *Cognition* 133(1), 120-127.

Abstract. Eye contact is a typical human behaviour known to impact concurrent or subsequent cognitive processing. In particular, it has been suggested that eye contact induces self-awareness, though this has never been formally proven. Here, we show that the perception of a face with a direct gaze (that establishes eye contact), as compared to either a face with averted gaze or a mere fixation cross, led adult participants to rate more accurately the intensity of their physiological reactions induced by emotional pictures. Our data support the view that bodily self-awareness becomes more acute when one is subjected to another's gaze. Importantly, this effect was not related to a particular arousal state induced by eye contact perception. Rejecting the arousal hypothesis, we suggest that eye contact elicits a self-awareness process by enhancing self-focused attention in humans. We further discuss the implications of this proposal.

Gamond L., Vilarem E., Safra L., Conty L. & Grèzes J. (accepted) Minimal group membership biases early neural processing of emotional expressions, *European Journal of Neuroscience*.

Abstract. Mere affiliation to a social group alters people's perception of other individuals. One suggested mechanism behind such influence is that group membership triggers divergent visual facial representations for in-group and out-group members, which could constrain face processing. Here, using EEG under fMRI during a group categorization task, we investigated the impact of mere affiliation to an arbitrary group on the processing of emotional faces. The results indicate that in and out-group members trigger differential event-related potential activity, appearing 150 ms after presentation of group membership information, which correlated with medial prefrontal fMRI activity. Additionally, EEG activity in the earliest stages of emotional processing (30-100ms after expression onset) dissociated unexpected group-related emotions (in-group anger and out-group joy) from expected ones and correlated with temporo-parietal junction fMRI activity. We discuss the possibility that such

dissociation may result from top-down influences from divergent representations for in-group and out-group members. Taken together, the present results suggest that mere membership in an arbitrary group polarized expectations which constrain very early neural processing of emotions.

Ioannou C., Vilarem E., Lefebvre A., Amsellem F., Delorme R., Chevallier C., Grèzes J. (in preparation)
Adolescents with autism can use implicit social threat to adapt their behaviour.

Abstract. Socio-communicative difficulties in autism spectrum disorders (ASD) have been investigated for years and the roots of these difficulties remain unclear. Inconsistencies in the results from emotion categorization tasks suggest that a generalized emotion processing impairment is unlikely to be the primary deficit in ASD, and that socio-communicative difficulties might exist independently of the ability to decode social signals. In this paper, we go a step further by testing the hypothesis that observed social difficulties in ASD are the consequence of a deficit in adapting and regulating behaviour in response to emotional signals. To do so, 28 ASD and 28 matched controls performed a free action choice task in the presence of task-irrelevant threat-related emotional displays and an emotion categorization task. The results revealed that TD and ASD adolescents adopted overall similar behaviours in the presence of task-irrelevant emotional displays: they chose actions that allowed them to avoid angry individuals more often and had longer reaction times to approach than to avoid fearful individuals. Furthermore, similarly to TD controls, ASD adolescents categorized emotional displays as fear or anger accurately. We discussed these findings in relation to the theories favouring preserved processing of social cues in ASD.

Posters

> Vilarem E., Armony J.-L., Grèzes J. (2017). Effects of social threat on attention and action-related decisions in a realistic social context. International Convention of Psychological Science (ICPS), Vienna, Austria.

> Vilarem E., Armony J.-L., Grèzes J. (2016). Effects of social threat on attention and action selection in a realistic social context. Société de Psychophysiology et de Neurosciences Cognitives (SPNC), Tours, France.

> Vilarem E., Armony J.-L., Grèzes J. (2016). Effects of threat-related facial expressions on attention and action selection in a realistic social context. European Society of Cognitive and Affective Neuroscience (ESCAN), Porto, Portugal.

- > Vilarem E., Armony J.-L., Grèzes J. (2016). Effects of social threat on attention and action-related decisions. Symposium on Biology of Decision-Making (SBDM), Paris, France.
- > Vilarem E., Armony J.-L., Grèzes J. (2015). Effects of threat-related facial expressions on spatial attention and action-related decisions in a realistic social context. Society for Social Neuroscience (S4SN), Chicago, United States of America.
- > Vilarem E., Armony J.-L., Grèzes J. (2015). Effects of threat-related facial expressions on spatial attention and action-related decisions in a realistic social context. Society for Neuroscience (SfN), Chicago, United States of America.
- > Vilarem E., Armony J.-L., Grèzes J. (2015). Effects of threat-related emotions on attention and action within realistic interaction context. Joint Action Meeting (JAM), Budapest, Hungary.
- > Vilarem E., Armony J.-L., Grèzes J. (2015). Effects of threatening facial expressions on attention and action-related decisions within realistic social context. Symposium on Biology of Decision-Making (SBDM), Paris, France.
- > Vilarem E., Armony J.-L., Grèzes J. (2015). Effects of threat-related emotions on attention and action within realistic social context. Journée ED3C, Paris, France.
- > Vilarem E., Armony J.-L., Grèzes J. (2014). Fearful and angry expressions elicit opposite spatial attention effects within realistic social contexts. Federation of European Neuroscience Societies (FENS), Copenhagen, Denmark.
- > Vilarem E., Grèzes J. (2014). Action-based decision-making about ambiguous social signals. Journée Ecole Doctorale Cerveau Cognition Comportement (ED3C), Paris, France.
- > Vilarem E., Gamond L., Safra L., Conty L., Grèzes J. (2013). Does my perception of your smile depend on our social relationship? Part 2: the fMRI study. International symposium on Vision, Action and Concepts, Lille, France.
- > Vilarem E., Gamond L., Safra L., Conty L., Grèzes J. (2013). Does my perception of your smile depend on our social relationship? Part 2: the fMRI study. New frontiers in social neurosciences, Journée IPSEN, Paris, France.

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Résumé

Les décisions d'action que nous prenons au quotidien nécessitent de considérer les affordances fournies par notre environnement, ainsi que les informations sociales susceptibles de guider nos décisions. Mais dans un contexte véhiculant à la fois des informations sociales potentiellement menaçantes et de multiples opportunités d'action, comme lorsque l'on entre dans une rame de métro en cherchant un siège, comment choisissons nous rapidement le siège où s'asseoir tout en évaluant la présence d'un danger potentiel ? Le travail réalisé au cours de cette thèse a visé à étudier les processus liés à l'action et à l'attention dans un contexte social réaliste doté d'opportunités d'action. Dans notre première étude, les choix spontanés d'action et les informations cinématiques ont révélé que les expressions de colère et de peur ont un impact différent sur la sélection d'action, et favorisent les actions permettant d'éviter les individus en colère et d'approcher les individus effrayés. La seconde étude a montré que l'attention peut être allouée vers la finalité des actions privilégiées par les expressions de colère et de peur. La troisième étude a démontré, de façon cruciale, que cet effet attentionnel disparaît lorsque les opportunités d'action sont retirées du contexte. De plus, l'activité saccadique enregistrée lors de la quatrième étude a permis d'explorer le développement de l'allocation attentionnelle, et a établi que l'attention était rapidement dirigée vers les visages émotionnels, puis réorientée vers la finalité de l'action choisie. Pour conclure, nos données suggèrent que l'action façonne l'attention en réponse à des signaux de menace et en présence d'opportunités d'action.

Mots Clés

Emotion, Action, Attention, Threat, Affordances.

Abstract

Everyday action decision-making entails to take into account affordances provided by the environment, along with social information susceptible to guide our decisions. But within social contexts conveying potentially threatening information and multiple targets for action, as when entering a subway car, how do we decide very quickly where to sit while gauging the presence of a potential danger? The work conducted during my PhD aimed at investigating action and attentional processes in a realistic social context providing action opportunities. In the first study, spontaneous action choices and kinematics revealed that threat-related angry and fearful displays impact people's free choice differently, i.e. favoured the selection of actions that avoided angry and approached fearful individuals. The second study further showed that attention was allocated to the space of the scene corresponding to the endpoint of the actions prioritized by those angry and fearful displays. Crucially, the third study evidenced that this effect disappeared when action opportunities were removed from the experimental context. Saccadic behaviour recorded in the fourth study allowed to access the development of attention allocation over time, and crucially revealed that attention was first quickly oriented toward threat before being directed toward the endpoint of the chosen action. Altogether, these findings suggest that action selection modulate attention allocation in response to social threat when embedded within realistic social contexts.

Keywords

Emotion, Action, Attention, Threat, Affordances.