Modulation of Gaze-oriented Attention with Facial Expressions: ERP Correlates and Influence of Autistic Traits

by

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AUTHOR'S DECLARATION

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Abstract

The direction in which another is looking at triggers a spontaneous orienting of attention towards gaze direction in the viewer. However, whether the facial expression displayed by the gazing individual modulates this attention orienting is unclear. In this thesis, the modulation of gaze-oriented attention with facial expressions was explored in non-anxious individuals at the behavioral level and at the neural level using Event-Related Potentials (ERP). In the gaze-cueing paradigm used, a dynamic face cue averting gaze and expressing an emotion was presented, followed by a lateral, to-be-localized target.

At the behavioral level, a faster response to targets appearing at the gazed-at location (congruent targets) than to targets appearing opposite to the gazed-at location (incongruent targets) was observed (Chapters 3-5). This so-called Gaze Orienting Effect (GOE) was enhanced with fearful, angry and surprised expressions relative to neutral and happy expressions and was driven by emotional differences in response speed to congruent targets (Chapters 3-5). These effects could not be attributed to better discrimination of those emotions when presented with an averted gaze (Chapter 2). These results confirm the impact of fear and surprise on gaze-oriented attention in non-anxious individuals and demonstrate, for the first time, a similar impact for angry expressions. All the emotions enhancing the GOE signal an evolutionary relevant stimulus in the periphery, are threat-related and carry a negative valence, which suggests that one of these attributes (or all combined) is driving the emotional modulation of gaze-oriented attention (surprise is treated like fear in the context of fearful expressions). In Chapter 4, the effect of the dynamic cue sequence on these GOE modulations was investigated. An emotional modulation of the GOE was found only when the gaze shift preceded the emotional expression, but not when the emotion was expressed before gaze shift or when expression and gaze shift were simultaneous. These results highlight the importance of using a sequence closer to real life situations (we usually orient attention before reacting to an object in the environment) in studying the modulation of the GOE with emotions.

At the neural level, we investigated the ERPs associated with gaze-oriented attention at target presentation and at cue presentation (Chapters 3 and 5). Confirming previous reports, the amplitude of a target-triggered P1 ERP component was larger in the congruent than in the incongruent condition, reflecting enhanced processing of gaze-congruent targets. In addition, cue-triggered ERPs previously observed in response to arrow cues, were investigated. An Early Directing Attention Negativity (EDAN) and an Anterior Directing Attention Negativity (ADAN) were found, indexing respectively attention-orienting to the cued location and maintenance of attention at the cued location. This is the first study to report both EDAN and ADAN components in response to gaze cues. These results show clear markers of attention orienting by gaze at the neural level, during both cue and target processing. Neither EDAN nor ADAN was modulated by emotion. The congruency effect on P1 was enhanced for fearful, surprised and happy faces compared to neutral faces in Chapter 3 but no differences between the emotions were found in Chapter 5. Thus, the emotional modulation of the brain processes involved in gaze-oriented attention is very weak and protracted or occurs mainly between target onset and response to target.

The relationships between participants' autistic traits and their emotional modulation of gaze-oriented attention were also investigated. Results showed a negative correlation with the GOE to happy upright faces and with the P1 congruency effect, which suggests that individuals with more severe autistic traits are less sensitive to the impact of social emotions like joy. The implication of these results for attention orienting in general and for individuals with Autism Spectrum Disorder is discussed.

Together, the findings reported in this thesis clarify the behavioral and neural processes involved in gaze oriented attention and its modulation by facial expression in addition to demonstrating a relationship between gaze oriented attention, its modulation with social emotions and autistic traits.

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As I am writing those lines, I am nearing the end of the journey I have started several years ago, when I moved to Canada to complete my PhD. Graduate school was an intense experience, punctuated with phases of intense excitation and phases of discouragement. But it was worth it because I have learnt tremendously and transformed into a more skilled and passionate researcher.

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Dedication

A ma famille et plus particulièrement, à mon Coeur d'Or de soeur, Marianne, à qui je dois tant. Même si le vide laissé par mon absence prolongée ne sera sans doute jamais comblé, je veux que tu saches que chacune des pages de cette thèse a été écrite en pensant a toi.

To my family and particularly to my Golden-Hearted sister, Marianne, to whom I am deeply indebted. Although I will never be able to compensate for the emptiness created by my long absence, I want you to know that I have written each page of this thesis with you in mind.

Table of Contents

List of Figures

List of Tables

List of Abbreviations

ADAN: Anterior Directing Attention Negativity

ADOS: Autism Diagnostic Observation Schedule

AG: Averted Gaze

ANOVA: Analysis of Variance

AQ: Autism Quotient

ASD: Autism Spectrum Disorder

Cond.: Condition

DG: Direct Gaze

EDAN: Early Directing Attention Negativity

EDD: Eye Direction Detector

ERP(s): Event Related Potential(s)

Expt(s): Experiment(s)

F: Frontal

FC: Fronto-Central

FT: Fronto-Temporal

FG: Fusiform Gyrus

GOE: Gaze Orienting Effect

ID: Intentionality Detector

PFC: Prefrontal Cortex

P: Parietal

PO: Parieto-Occipital

O: Occipital

RME: “Reading the Mind in the Eyes” test

RT(s): Reaction Time(s)

SD: Standard deviation

SE: Standard Error

STICSA: State-Trait Inventory for Cognitive and Somatic Anxiety

STS: Superior Temporal Sulcus

ToM: Theory of Mind

Chapter 1: General Introduction

A wealth of information can be extracted from others' faces, including static attributes such as gender and ethnicity, but also more transient clues about others' state of mind. For instance, the direction of others' gaze indicates the location within the environment where that person is focusing their attention and can inform us about their intention. Facial expressions, on the other hand, reflect what others feel and when combined with gaze direction, reflect what they feel toward the object they are looking at. Together, gaze and emotion cues allow us to quickly infer others' mental states about a specific object, which is particularly beneficial to predicting future behavior in a social context.

Research has shown that we orient our attention spontaneously toward another's gaze direction (Friesen & Kingstone, 1998), presumably to locate and identify their focus of attention. From an evolutionary perspective, it is sensible to assume that we orient faster and allocate more attention to a peripheral object if the detection of this object is potentially beneficial for our survival. As a result, many studies have also looked at the influence of facial expressions on gaze-oriented attention (see Frischen, Bayliss & Tipper, 2007 for a review). For instance, when we are attending to the face of another person, if an object evokes a look of fear in that person, that object is likely dangerous and it is important for us to attend to it fast. Many of these studies, however, have yielded quite discrepant results regarding the modulations of gaze-oriented attention by facial expressions. In addition, little is known about the neural basis of these possible modulations.

Gaze-oriented attention has been linked to mental state attribution abilities (Baron-Cohen, 1995) and has thus been a focus of investigation in clinical populations such as Autism Spectrum Disorder (ASD), which is characterized by social interaction deficits and impairments in mental states comprehension (5^{th} ed.; *DSM-V*; American Psychiatric Association, 2013). These deficits were initially thought to originate from abnormalities in processing social cues such as averted gaze or emotion, however a diminished ability to process either cues in isolation was never reliably shown in individuals with ASD (Nation & Penny, 2008; Jemel, Mottron & Dawson, 2006). Rather, recent experimental evidence suggests abnormalities in the combination of gaze and emotion cues in ASD (Uono, Sato and Toichi, 2009), which could be linked to their social deficits. Therefore, it appears crucial to investigate the mechanisms behind gaze and emotion integration in the general population so we can hope to comprehend how different these mechanisms are in the ASD population.

The purpose of this thesis was to determine the behavioral and brain correlates associated with the modulation of gaze-oriented attention with emotional faces in the general population. In addition, the possibility of a link between autistic-like traits and the ability to combine emotion and gaze cues was examined.

1.1 The role of gaze direction in social cognition

In the past fifteen years, Cognitive Neuroscience has witnessed a growing interest in gaze processing, previously neglected by the pioneering and influential cognitive model of face and person perception of Bruce and Young (1986). This interest stems from the now accepted view that gaze plays a fundamental role in social cognition and its development and may be at the core of social deficits exhibited by clinical populations such as ASD, as reviewed in this section.

1.1.1 Gaze direction discrimination: are you looking at me?

Others' gaze direction and duration can influence our perception of that person's social status, attractiveness and competence (see Kleinke, 1986 for a review). Additionally, gaze direction is particularly informative as to whether or not we are the focus of another's attention. In a social interaction, being looked at signals the engagement of our partner in the discussion while averted gaze signals a lack of interest for the topic, or preoccupation with other topics. Thus, it is not surprising that human beings are extremely sensitive to the direction of others' gaze. Newborns already show great interest in the eye region of the face (Maurer, 1985) and prefer to look at faces with opened than with closed eyes (Batki, Baron-Cohen, Weelwright, Connellan & Ahluwalia, 2000). In addition, neonates like faces with direct gaze better than faces with averted gaze (Farroni, Csibbra, Simion & Jonson, 2002).

In adults, direct gaze (DG) captures attention more than averted gaze (AG). Indeed, adults are more efficient in detecting faces with DG in an array of distractor faces with AG when contrasted with the opposite circumstance (detecting faces with AG in an array of distractor faces with DG) - a phenomenon known as "the stare in the crowd effect" (Conty, Tijus, Hugeville, Coelho & Georges, 2006; Senju, Hasegawa & Tojo, 2005; Von Griinau & Anston, 1995). Moreover, it takes participants longer to detect a lateral target presented along with a central face gazing straight ahead than when this face is gazing to the side or has closed eyes (Senju & Hasegawa, 2005). This effect disappears when a time lag is introduced between the face stimulus and the target, which suggests that faces with DG retain attention longer than faces with AG. However, faces with AG are also very informative in the context of a social interaction.

1.1.2 Averted gaze as an index of others' attention focus

Averted Gaze is a powerful, nonverbal signal allowing us to determine which location within the environment another actor is paying attention to and can help us direct our own attention toward this particular location. The ability to follow others' gaze, attend to the gazed-at object, and realize that others' thoughts are about this particular object are all crucial to social interaction. These abilities, referred to as *joint attention,* help determine what others have in mind and anticipate their future actions (see Mundy & Jarrold, 2010 for a review).

1.1.2.1 Joint attention

Joint attention can be initiated by means of eye gazing. Baron-Cohen (1995) postulated the existence of an innate module dedicated to gaze perception (the Eye Direction Detector, EDD) that would operate by detecting anything resembling eyes in the environment and by determining whether gaze is directed toward us or away from us. An EDD would play an essential role in the development of our understanding of others.

Joint attention is thought to rely on the integrity of an EDD and of another module, the intentionality detector (ID), which allows us to understand that every movement elicited by an external agent is a goal-directed movement (Baron-Cohen, 1995). Joint attention is thought to be an essential component of Theory of Mind (ToM), the ability to understand that others have mental states (e.g., beliefs, intentions, desires) and how they are instantiated. The eye region is thought to provide essential information about the mental states of others. Indeed, in the ToM test developed by Baron-Cohen, Wheelwright, Hill, Raste and Plumb (2001), adult participants have to identify, from among four possible choices, the label that best characterizes a picture corresponding to the eye region of a person with a particular mental state. This Reading-the-Mind-in-the-Eyes test (RME) was found to be successful in predicting ToM ability, showing the importance of the information located in the eye region to determine others' thoughts (Baron-Cohen et al., 2001).

As noted earlier, the ability to discriminate between direct and averted gaze is already present in neonates (Panel A of Figure 1). However, joint attention develops gradually during infancy. Gaze following, the capacity to orient one's attention to the direction indicated by another's gaze, emerges between 3 and 6 months of age (see Emery, 2000 for a review, panel B of Figure 1). At first, gaze following seems to rely on the movement associated with gazing faces but it quickly becomes more flexible and sensitive to the context in which the gazing face is observed, such as the expressed emotion (Frischen et al., 2007). It is between 9 and 14 months that joint attention arises, when infants realize that people around them look at what they think about (panel C of Figure 1). In addition, joint attention is a building block in the acquisition of a full ToM, at around 4-5 years of age. Indeed, the state of joint attention at 20 months of age has been shown to predict ToM ability at 44 months (Charman, Baron-Cohen, Swettenham, Baird, Cox & Drew, 2000, panel D of Figure 1).

A- Direct versus Averted Gaze (at birth)

B- Gaze Following (3-6 months)

C- Joint Attention (9-14 months)

D- "Theory of Mind" (4-5 years)

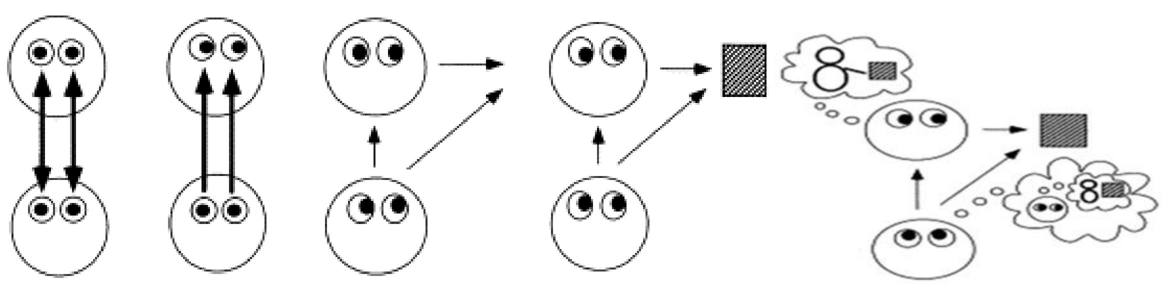

Figure 1: Joint attention and ToM development (adapted from Emery, 2000)

1.1.2.2 Joint attention and Autism Spectrum Disorder (ASD)

Individuals with ASD are impaired at social interaction, and show deficits in joint attention and ToM (Baron-Cohen, 1989). Indeed, difficulties in first-order and second order ToM tests (e.g., "X thinks Y" and “Z thinks X thinks Y”, respectively) have been observed in 5 year old children with ASD compared to typically developing children and children with Down Syndrome (Baron-Cohen, 1989). Children with ASD show signs of impairment in the cognitive abilities upon which ToM is predicated. They display little attention-sharing behavior and imitation during their social interaction (Sigman, Mundy, Sherman, & Ungerer, 1986; Charman et al., 2000). Moreover, contrary to typical toddlers, those with ASD have difficulty in acquiring the meaning of a novel word, when this word is referred to by means of eye gazing, indicating a failure to use joint attention to learn about their environment (Baron-Cohen, Baldwin & Crowson, 1997). Joint attention is clearly impaired in individuals with ASD who fail to spontaneously attend to the location attended to by another (e.g., Nation & Penny, 2008). Clinical deficits in joint attention are even part of the diagnostic assessment of children and adults with ASD (Autism Diagnosis Observation Schedule or ADOS: Lord, Rutter, Goode, Heembergen, Jordan, Mawhood, & Schopler, 1989). It has been suggested that joint attention never fully develops in individuals with ASD, leading to ToM deficits later in life (Baron-Cohen, 1989), as indicated by a decreased performance on the RME for individuals with ASD compared to typical individuals (Baron-Cohen et al., 2001).

In the laboratory, the attention orienting processes occurring during joint attention conditions have been investigated extensively using a variation of Posner’s original cueing paradigm (Posner, 1980). This so-called “gaze-cueing paradigm” is at the core of the present thesis and is reviewed below.

1.1.3 Attention orienting by gaze and the gaze-cueing paradigm

Posner (1980) described two types of mechanisms used to orient attention toward a stimulus in the environment. The first mechanism is called *overt* orienting and reflects our physical orientation toward the stimulus of interest by means of eye gazing for instance. The second mechanism is called *covert* orienting and is defined by the non-observable shift of our internal resources to the space occupied by the stimulus of interest. Covert orienting has been studied using cueing paradigms in which participants are presented with a cue followed by the onset of a lateral target. While maintaining their eyes fixated on the center of the screen, participants’ task is to respond to the target as quickly and as accurately as possible. The cueing effect, a faster response to the cued side compared to the uncued side, indicates that attention has been oriented covertly to the cued location.

In the gaze-cueing paradigm, central faces with averted gaze are used as cues. Such gaze cues yield both covert and overt orienting effects (Mansfield, Farroni & Johnson, 2003) although research has focused on the measure of covert attention as reflected by the so-called Gaze Orienting Effect (GOE). Specifically, participants show faster responses to targets appearing on the side looked at by face cues (gazed-at targets in congruent or valid trials) than to targets appearing on the side opposite to the direction of gaze (non-gazed-at targets in incongruent or invalid trials). The GOE is seen even when the trials in which a spontaneous saccade toward gaze direction occurred, are excluded (Mansfield et al., 2003). As reviewed by Frischen and colleagues (2007), the GOE is a robust phenomenon, which has been shown with various tasks (discrimination, localization and detection tasks). The GOE has also been shown with various cue stimuli such as schematic face drawings (e.g., Friesen & Kingstone, 1998), computerized faces (e.g., Tipples, 2005), face photographs (e.g., Langton & Bruce, 1999), drawings of animal faces or objects on which eyes were included (Quadflieg, Mason & Macrae, 2004) and even isolated eyes (Kingstone, Friesen, & Gazzaniga, 2000; Bayless, Glover, Taylor, & Itier, 2011).

Attention-orienting to gaze presents features of *exogenous* or automatic orienting (also called bottom-up/stimulus driven) seen in peripheral cueing paradigms where attention is reflexively attracted by a target presented in the visual periphery (Eriksen & Hoffman, 1974). Indeed, the GOE is seen as early as 100ms after cue onset, regardless of the predictive value of the cue. However, gaze-oriented attention also presents features of *endogenous* or voluntary orienting typically seen with centrally presented symbolic cues such as arrows. Unlike peripheral cueing but similarly to arrow cueing for instance, the GOE is still seen beyond 300ms and up to 700ms after gaze cue onset (Frischen et al., 2007). As a result, it has been suggested that gaze-oriented attention relies either on a combination of endogenous and exogenous attention, or on a totally different gaze-specific attention mechanism. Some of the results presented in this thesis help fuel this debate, which will be developed in the General Discussion.

The literature reviewed thus far focused on gaze-orienting studies using neutral faces. However, in real life, faces are rarely neutral. They typically express some form of emotion and different emotions reflect different appraisals of the object being looked at. In the next section I review briefly the current state of knowledge regarding the perception of facial expressions and how they might interact with gaze cues.

1.2 Integration of facial expression and gaze cues

Facial expressions indicate the emotion felt by another. They help us access others' mental states and adapt our own behavior to provide an appropriate response to our social partner. Scientists have been primarily concerned with finding a tangible way to categorize and measure facial expressions, which I discuss next.

1.2.1 Categorizing facial expressions

Using a discrete approach, Ekman & Friesen (1971) have identified six basic facial emotional expressions (happiness, sadness, surprise, fear, disgust and anger) that are universally and innately distinguished from one another (although see Jack, Garrod, Yu, Caldara & Schyns, 2012, for rejection of the universality account).

In the present thesis, we have focused on fear, anger, happiness and surprise. We chose these four basic emotions only, because including the six basic emotions would have led to too many conditions and would have increased the length of (already long) studies. Fearful and angry faces were selected because these emotions both signal the presence of a threat and it is therefore evolutionary relevant to attend to their object of focus (since it is dangerous). However, when looking away from an observer, fearful faces signal a direct threat while angry faces signal an indirect threat. Indeed, fearful faces signal a threat, not for the dangerous object they are looking at but for the individual expressing fear and for the observer of such individual, for whom the object could be dangerous as well. In contrast, angry faces signal a threat for the object (usually a person) to whom this emotion is directed more so than to the observer of the individual expressing anger (it is still dangerous for him as he could be the next target of the angry expresser). Surprised faces signal the presence of a novel and unexpected object which *could* be a threat (Fontaine, Scherer, Roesch & Ellsworth, 2007). Although surprised faces have been less studied than angry and fearful faces in the past, we believe that it is also evolutionary advantageous to attend to a *potentially* dangerous object to decide how to react to it. On the contrary, happy faces do not signal the presence of a threat and it is not critical for survival to attend to the object (the person) attended to by a happy person (although it might be socially relevant).

Although, in social cognition, most studies have tried to find behavioral and neural correlates associated with the perception of basic facial expressions, it is important to keep in mind that various dimensions are attached to basic facial expressions. According to the dimensional approach to categorizing emotions[1], fear, anger and surprise differ from happiness regarding their evolutionary relevance but also in regarding their valence. Indeed fear and anger carry a negative valence while happy carries a positive valence and surprise carries an ambiguous valence that is negative when presented with negative emotions and positive when presented with positive emotions (Neta & Whalen, 2010; Neta, Caroline-Davis & Whalen, 2011).

1.2.2 Attention to emotional faces and interaction with gaze direction

Because, they carry an important signal, facial expressions capture attention. For instance, in visual search tasks, where a target must be found among distractors, participants detect angry faces in a search array of neutral or happy faces faster than they detect neutral or happy faces in an array of threatening, angry faces (Eastwood, Smilek & Merikle, 2001; Fox, Russo & Dutton, 2002; Lipp, Price & Tellegen, 2009). This effect has been thought to reflect the preferential treatment of threat-related signals, an idea that has received considerable support from the literature (Ohman &Mineka, 2001; Ohman, Flykt & Esteves, 2001; Tipples, Atikson & Young, 2002; Fox & Damjanovic, 2006) and is thought to be linked to the evolutionary importance of detecting signals of threat.

This *threat superiority effect* is thought to rely on a complex neural network devoted to perceiving potential danger and reacting to it (e.g., Armony & LeDoux, 1999). The amygdala has been shown to play a critical role within this network, functioning as a "fear module" that enables fear to be perceived both in others and in ourselves (Aggleton & Young, 2000). This fear module should be activated when observing an angry person looking at us, because it can convey a direct threat to our safety (e.g., Lipp et al., 2009). In contrast, observing a person looking at us with a fearful expression is unlikely to activate the fear module because it would indicate that *we* are the threat and that we are not, ourselves, endangered. As a result, when investigating the threat superiority effect with a visual search paradigm, in which faces are presented with direct gaze, studies have used angry rather than fearful facial expressions. However, observing a fearful expression embedded in a face with averted gaze should activate a fear response,

[1] Fontaine et al. (2007) have described four dimensions, which, together, provide an adequate framework to describe others' facial expressions: valence (positive/negative or approach/avoidance), arousal (activation of sympathetic or parasympathetic system), potency (submission/dominance) but also unpredictability (novelty/permanence).

because, in that case, it signals the presence of a dangerous and thus potentially threatening object (e.g., snake, weapons) in the periphery and dangerous objects are known to activate the fear module (Fox, Griggs & Mouchlianitis, 2007). Those studies indirectly suggest an interaction between processing of gaze and processing of emotion.

This interaction is probable given the neuroimaging evidence that the brain networks involved in emotion and gaze processing overlap. Based on human neuroimaging and neuropsychology findings, and on monkey cell recording studies, Haxby, Hoffman and Gobbini (2000, 2002) proposed a model of face processing involving two separate streams, one devoted to the processing of invariant information such as facial identity within the fusiform gyrus and the other to the processing of changeable facial information such as emotion and gaze in the superior temporal sulcus (STS) region. Recent studies also show that the amygdala and the prefrontal cortex (PFC), both involved in processing emotions, are also involved in gaze processing (Itier & Batty, 2009; Nummenmaa & Calder, 2009 for reviews). In contrast, the insula and the limbic system are devoted to process emotional information specifically while the intraparietal sulcus is dedicated to process spatially directed attention that can be elicited by gaze signals (Haxby et al., 2000, 2002). Although these regions are known to interact with each other, it remains unclear to which extent and at what time this interaction occurs. Thus, in this thesis, the extent to which emotional processing interacts with processing of gaze-oriented attention was assessed at different stages of gaze-oriented attention, using event related potentials (ERPs) and behavioral measures.

1.3 Thesis Purposes

As reviewed above, the direction of another's gaze is important in social cognition. It allows us to determine whether we are likely to be approached or avoided and the perception of an averted gaze can direct our attention towards objects in the environment. In addition, perception of facial expressions mobilizes attention resources and informs us about the emotional state of others. Importantly, when combined with gaze direction, facial expressions allow us to make inferences about what others might think or feel regarding the attended object. Thus, combining emotion and gaze cues is essential to understand others' mental states and is at the basis of threat-related theories. Moreover, evidence from neuroimaging suggests an overlap in the brain regions involved in processing facial expressions and gaze direction. Evidence from neuroimaging combined with the threat related hypothesis suggests that attention orienting by eye gaze should be influenced by facial expression at the behavioral and at the neural level. As will be reviewed later however, the empirical evidence supporting an emotional modulation of gaze-oriented attention is mixed and is thus the focus of the present thesis.

Chapters 3, 4 and 5 all employed a gaze cueing paradigm. To increase the ecological validity of the studies, a dynamic face stimulus sequence was used, in which a face gazing straight ahead and displaying a neutral expression subsequently averted its gaze and expressed an emotion. In Chapter 3, we aimed at clarifying the behavioral correlates associated with the emotional modulation of gaze-oriented attention. In addition, we used Event-Related Potentials (ERPs) to determine the temporal stages involved in the neural processes of gaze-oriented attention and of its modulation by facial emotions.

As few studies have used dynamic gaze cueing paradigms, Chapter 4 empirically tested the influence of the type of dynamic stimulus sequence used on the emotional modulation of gaze-oriented attention. Three sequences were compared, in which emotion was expressed before, after, or concurrently with gaze shift.

As outlined at the beginning of this introduction, despite their deficits in social interaction, individuals with ASD show a preserved processing of isolated social cues (i.e., emotion and gaze direction). Thus, it has been suggested that the social interaction deficits observed in individuals with ASD could be due to their difficulty in combining gaze and emotion cues. In Chapter 5 we sought to investigate this hypothesis and explored the relationship between participants' autistic traits and their ability to combine gaze and emotion cues. Specifically, we aimed at determining how emotions influenced the behavioral and neural correlates associated with gaze-oriented attention in a population of mathematicians (with a wide range of autistic traits).

Before getting to the core of the thesis on the emotion modulation of attention orienting by gaze, I first explored whether processing of a particular facial expression differed depending on whether it was embedded in a face with direct or averted gaze. Several theories regarding the influence of gaze on emotion perception exist and Experiment 1, reported in Chapter 2, was designed to adjudicate between these theories and to determine the conditions under which gaze influences emotion perception.

Chapter 2: Does gaze direction influence emotion discrimination? (Experiment.1)[2]

2.1 INTRODUCTION

As reviewed in Chapter 1, during social interactions, we pay particular attention to others' facial expressions as they indicate their mental states (i.e., thoughts, beliefs, intentions) and enable us to predict their upcoming behavior. Eye gaze is another important facial feature in understanding others' intention. Our ability to discriminate between direct and averted gaze allows us to determine whether or not we are the object of others' attention and whether others' mental states are directed at us or at another object/individual in the environment (Kleinke, 1986). Given that gaze and emotion processing involve some common brain areas (refer to 1.2.2 for more details), it is likely that gaze direction analysis and emotion perception interact to some degree. In fact, many studies have shown that they do and that gaze direction influences emotion perception. However, these studies yielded inconsistent results and various theories have emerged to explain the observed impact of gaze on emotion discrimination (reviewed in Graham & LaBar, 2012).

According to the *direct gaze hypothesis*, the feeling of "being looked at" is such a powerful social signal that it enhances all aspects of face processing (Haley & Fessler, 2005; Bateson, Nettle & Roberts, 2006). Indeed, when faces are presented with direct gaze rather than averted gaze, gender is discriminated faster (Macrae, Hood, Milne, Rowe & Mason, 2002), face recognition is improved (Mason, Hood & Macrae, 2004 and Vuillermier, 2005) and if the face is attractive, activity in the ventral striatum, a brain area processing rewards, is increased (Kampe, Frith, Dolan & Frith, 2001). In addition, faces with a direct gaze capture attention more than faces with an averted gaze (See Senju & Jonhson, 2009 and Georges & Conty, 2008 for reviews). At the neural level, an enhanced activation in the amygdala for faces presented with direct gaze compared to faces presented with averted gaze was reported in two studies (George, Driver & Dolan, 2001; Kawashima, Sugiura, Kato, Nakamura, Hatano, Ito & Nakamura, 1999). In addition, using emotional faces, Wicker, Perrett, Baron-Cohen and Decety (2003) demonstrated stronger

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[2] This part of our work was presented at a local conference (Lassalle & Itier, 2012b). A full article presenting our results is in preparation.

activation of the STG for faces with straight gaze compared to faces with averted gaze, suggesting that processing of emotional faces is enhanced with direct gaze regardless of their emotion. However, no study to date has shown directly whether the speed and the accuracy of expression *discrimination* could also be enhanced with direct rather than averted gaze.

According to the *appraisal hypothesis*, gaze and emotion cues are used in combination, as a single source of information, and we interpret this information in terms of its relevance for our survival. Therefore this hypothesis targets threat-related emotions and does not make any specific predictions regarding emotions such as happiness, which does not impact survival. Perception of anger should be enhanced when expressed by a face with straight gaze, for instance, because it signals an imminent attack directed toward the observer. Similarly, a fearful face with averted gaze signals the presence of a threat in our close environment, and thus its treatment should be prioritized. Evidence for the appraisal hypothesis was provided by a study showing that angry faces are perceived as more angry when presented with direct gaze than when presented with averted gaze, and that fearful faces are rated as more fearful when presented with averted than direct gaze (Sander, Grandjean, Kaiser, Wherle & Scherer, 2007). Moreover, N'Diaye, Sander and Vuilleumier (2009) showed that angry faces with direct gaze and fearful faces with averted gaze yielded increased activation in brain regions devoted to processing emotion compared to angry faces with averted gaze and fearful faces with direct gaze, respectively.

The *shared neural hypothesis* was inspired by the motivational tendencies behind facial expressions and gaze direction. Some have suggested that fearful expressions signal avoidance for an observer, while happy and angry expressions indicate approach (Davidson, 1995; Harmon-Jones & Allen, 1998; Harmon-Jones & Sigelman, 2001; Harmon-Jones, 2003). Gaze also seems to activate the approach-avoidance system (Hietanen, Leppänen, Peltota, Linna-Aho and Ruuhiala (2008)). The shared neural hypothesis proposes that fearful expressions are better processed when embedded in faces with averted rather than direct gaze, while happy or angry expressions are better processed when presented in faces with direct rather than averted gaze, due to motivational tendencies elicited by gaze and emotion being congruent in those cases (Adams & Franklin, 2009). Evidence for this hypothesis stems from Adams and Kleck's work (2003, 2005), which showed that emotion recognition speed, accuracy and perceived intensity were increased for fearful and sad faces in the averted gaze condition compared to the direct gaze condition while they were increased for happy and angry faces in the direct gaze condition compared to the averted gaze condition. Adams, Gordon, Baird, Ambady & Kleck (2003) also found an increased amygdala activity for angry faces with averted compared to direct gaze and for fearful faces with direct compared to averted gaze, which the authors interpreted as reflecting the ambiguity associated with incongruent signals such as an angry face with averted gaze or a fearful face with direct gaze.

In the present experiment, we intended to adjudicate between these different hypotheses and we investigated whether the speed and accuracy with which facial expressions were discriminated were modulated by their gaze direction. Participants underwent two conditions, one in which they had to discriminate among fearful, surprised and neutral expressions (Condition FSN) and another in which they had to discriminate angry, happy and neutral facial expressions (Condition HAN). It is important to note that, although naturally ambiguous, the valence of surprise is influenced by the emotional context in which it occurs and surprise is perceived as carrying a negative valence when presented with another negatively valenced emotion (Neta & Whalen, 2010; Neta et al., 2011). Thus, when presented with fear, surprise takes a negative valence and should trigger the avoidance motivational system. Such a design allowed us to group avoidance emotions on the one hand and approach-related emotions on the other hand and to predict specific outcomes for each hypothesis[3].

According to the direct gaze hypothesis, emotion perception should be enhanced with direct gaze, regardless of the emotion. Thus, we should observe a main effect of gaze across both FSN and HAN Conditions, with better and faster discrimination of emotions for faces with direct gaze than for faces with averted gaze (Table 1a.). Alternatively, according to the appraisal hypothesis, there should be a main effect of gaze in Condition FSN such that both the perception of fear and surprise should be enhanced in the averted gaze condition compared to the direct gaze condition, as both emotions presented in the context of a fearful face signal the presence of a potential danger. However, in Condition HAN, there should be an enhanced processing of angry expressions with direct gaze (versus averted gaze) but no influence of gaze on the perception of happy faces (since a happy face is not relevant for survival, Table 1b.). Finally, if the shared neural hypothesis is true, we should also observe faster and more accurate emotion discrimination when both happy and angry faces are presented with direct gaze relative to averted gaze and when fearful and surprised faces are presented with averted gaze rather than direct gaze (Table 1c.).

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[3] Note that, although directly comparing all emotions in a single design would have been ideal, the current design was also chosen in preparation for the ERP experiment reported in Chapter 3, in which the number of trials required per condition precluded the direct comparison of the 5 emotions.

Table 1

Summary of the different hypotheses/predictions regarding the influence of gaze on emotion discrimination (DG=Direct Gaze, AG=Averted Gaze, RT= Reaction Time, A' measure of Accuracy)

Hypotheses	General rationale	Specific predictions for Experiment 1
a. Direct Gaze	Faster and more accurate for DG	-Main effect of gaze on RT: DG<AG for both HAN and FSN Conditions -Main effect of gaze on *A*': DG>AG for both HAN and FSN Conditions
b. Appraisal	-Relevance for survival so targeting threat related emotions like fear and anger (and possibly surprise in the context of fear) -No prediction for emotions like Happy	- FSN Condition: • Main effect of gaze on RT: AG<DG • Main effect of gaze on *A'*: AG>DG - HAN Condition: • Gaze by Emotion interaction on RT: DG<AG for Angry and no effect for Happy • Gaze by Emotion interaction on *A'*: DG>AG for Angry and no effect for Happy
c. Shared Neural	Motivational tendencies: approach vs. avoidance behavior	- FSN Condition • Main effect of gaze on RT: AG<DG • Main effect of gaze on *A'*: AG>DG - HAN Condition • Main effect of gaze on RT: DG<AG • Main effect of gaze on *A'*: DG>AG

2.2 METHODS AND RESULTS

2.2.1 Participants

Twenty-four subjects (11 females) were recruited at the University of Waterloo (20 to 25 years, mean =21.33, SD=1.20). As both anxiety and autistic traits are personality attributes known to impact the way in which emotion and gaze interact (Mathews, Fox, Yiend & Calder, 2003; Uono et al, 2009), they were assessed. Participants were recruited only if their anxiety trait was in the normal range, as measured by the State Trait Inventory for Cognitive and Somatic Anxiety [STICSA] scale (Ree, French, MacLeod & Locke, 2008), i.e., below the high anxiety STICSA score of 42 (mean= 31, SD= 4.70). Participants' autistic traits (indexed with the Autism Quotient [AQ] test, Baron-Cohen et al, 2001) were also assessed (mean=13.04, SD=4.35) and were below the threshold of 26 (above which participants are likely to be diagnosed with an Autism Spectrum Disorder (ASD) according to Woodbury-Smith, Robinson, Wheelwright & Baron-Cohen, 2005). Participants gave written consent and the study was approved by the Ethic Committee at the University of Waterloo.

2.2.2 Stimuli and procedure

2.2.2.1 Emotion recognition questionnaire (See Appendix A)

We selected 40 face pictures of eight different individuals (4 females) who expressed surprised, fearful, happy, angry and neutral expressions, from the MacBrain Face Stimulus Set (Tottenham, Hare, Millner, Gihooly, Zevin & Casey, 2009)[4]. Participants were presented with a print of all these faces on a paper questionnaire and had to select the emotion each of them expressed (among fear, surprise, neutral, happy and angry expression) and rate the intensity of that emotion on a 1 to 10 Likert scale (see Appendix A, for a sample). They took as long as they needed to complete this questionnaire. This initial questionnaire was used to ensure that participants were able to discriminate among the different expressions presented in a face with direct gaze. In addition, given that we used a smaller subset of identities and emotions than the MacBrain Face Stimulus Set and that faces were cropped to remove hair and external features (see next section), we wanted to compare our results to the validation of the original face database (Tottenham et al., 2009). Finally, in this questionnaire, we used static pictures of faces while, in the rest of this experiment, the faces were dynamic. Participants' emotion discrimination performance on this questionnaire served as a baseline for later performance when presented with dynamic faces looking straight ahead.

[4] Development of the MacBrain Face Stimulus Set was overseen by Nim Tottenham and supported by the John D. and Catherine T. MacArthur Foundation Research Network on Early Experience and Brain Development. Please contact Nim Tottenham at tott0006@tc.umn.edu for more information concerning the stimulus set.

2.2.2.2 Impact of gaze on emotion discrimination

The same 40 faces used for the emotion recognition questionnaire were used in the main experiment. The eye gaze of the faces was manipulated using Photoshop (Version 11.0). For each image, the iris was cut and pasted to the corners of the eyes to produce a directional leftward or rightward gaze in addition of the original straight gaze. An elliptical mask was applied to each picture so hair, ear and shoulders were not visible. The set of images was equated for contrast and luminance, using the SHINE toolbox (Willenbockel, Sadr, Fiset, Horne, Gosselin & Tanaka, 2010). All face photographs subtended a visual angle of 8.02° horizontally and 12.35 ° vertically, and were centrally presented on a white background.

Participants sat 67 cm in front of a computer monitor in a quiet, dimly lit and electrically shielded room, with their head restrained by a chin rest. They participated in two Conditions involving different emotions, run one after the other. In Condition FSN, fearful, surprised and neutral faces were presented, and in Condition HAN, happy, angry and neutral faces were presented. The order in which Conditions were presented was randomized across participants. Each trial started with a centered fixation cross (1.28° by 1.28° visual angle), that was presented randomly for 800, 900, 1000, 1100 or 1200ms. A neutral face with straight gaze was then shown for 500ms, followed by the same face expressing either a neutral, or an emotional expression. This second face looked rightward, leftward, or directly at the observer, and was presented for 500ms. This fast serial presentation provoked the perception of a face dynamically expressing an emotion and in averted gaze trials, also dynamically moving its eyes. Conditions FSN and HAN were programmed using Presentation software (Neurobehavioral Systems) and each consisted of 3 blocks of 96 trials separated by a self-paced break, resulting in 48 trials for each of the 6 experimental conditions. An experimental condition consisted of a combination of a particular gaze direction (averted [leftward and rightward averaged together] or direct) with a specific emotion (fear, surprise or neutral in condition FSN and happy, angry or neutral in condition HAN). There were an equal number of averted and direct gaze trials. The trial order was fully randomized within a block.

Following the dynamic face sequence, a vertical listing of three words (“fear”, “neutral”, “surprise” in the FNS Condition or “happy”, “angry”, “neutral” in HAN Condition) was presented in the center of the screen (see Figure 2 for an example). The positions of the words were randomized across participants in such a way that each emotion appeared at the center equally often across participants. Participants had to move the computer’s mouse from an initial lateral position (right or left: randomized across participants) to the correct word at the center of the screen as quickly and as accurately as possible. The selection slide remained until a response was made or for a maximum of 2000ms.This task was chosen to investigate the modulation of emotion discrimination with gaze direction and determine whether this modulation was in accordance with the direct gaze hypothesis, the appraisal hypothesis or the shared neural hypothesis (as outlined in the introduction and in Table 1).

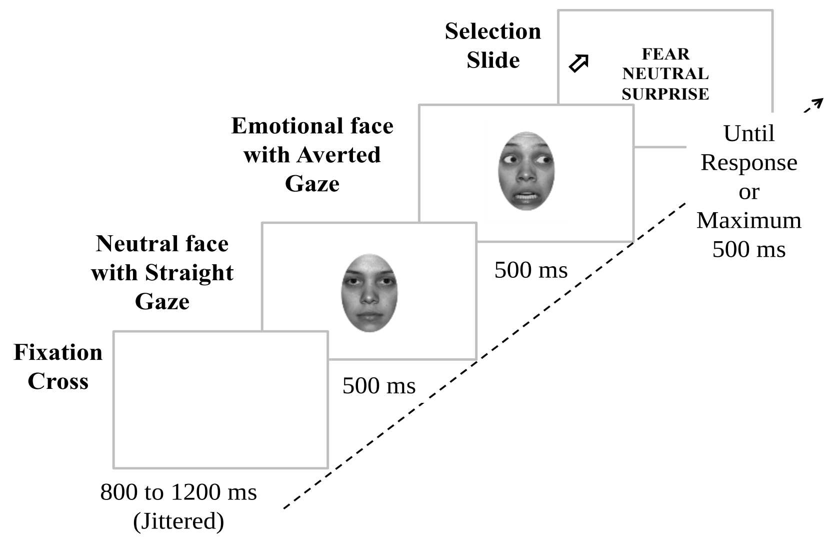

Figure 2: Example of a fearful, averted gaze trial of Condition FSN. The neutral word is at the center of the selection slide and the mouse initially placed on the left side (arrow).

2.2.3 Results and data analyses

2.2.3.1 Emotion recognition questionnaire

Response accuracy and intensity ratings were analyzed using a 5 (Emotion) by 8 (Face Identities) analysis of variance (ANOVA). The recognition rates for all emotions were above 80% and were slightly higher than those of the MacBrain Face Stimulus Set (Table 2). This was expected since only the faces with highest recognition rates were selected from the database and because only 5 emotion choices were given (compared to 7 choices in Tottenham et al., 2009). Although a main effect of Face Identity was found on emotion recognition rate (F=3.03, p=.02), pairwise comparison of the emotion recognition rate for the eight face identities revealed no recognition rate differences between the eight identities (p>.05). In accordance with Tottenham et al. (2009), there was no significant effect of identity on the intensity ratings (F=2.49, p=.15).

There was a main effect of emotion on the recognition rate (*F* (1.80, 37.70) =11.23, MSE=218.22, *p*<.01, η_p^2=.35), which was significantly higher for faces expressing happiness than anger (*p*=.02), surprise (*p*<.01) or fear (*p*<.01), while the recognition rate for neutral faces showed a trend toward higher recognition than fearful (*p*<.09) and surprised faces (*p*<.09) as seen in Table 2. This variability in the recognition rate of emotion is consistent with previous literature (e.g., Elfenbein & Ambady, 2003) in which happy expressions are accurately recognized and negative expressions are poorly recognized. The intensity ratings did not differ significantly across emotions (effect of emotion, *F* (1.47, 30.89) =1.77, MSE=4.99, *p*= .19, η_p^2=.08).

Table 2

Comparison of the mean proportion of correct emotion identification obtained for the questionnaire, the emotion discrimination task and the Tottenham and colleagues (2009) study (standard deviations in parentheses). DG= Direct Gaze, AG= Averted Gaze. FSN refers to the Condition in which fearful and surprised faces were used while HAN refers to the Condition in which happy, angry and neutral faces were used.

		Tottenham et al., 2009	Questionnaire	Emotion discrimination task	Emotion discrimination task
Experimental settings		DG	DG	DG	AG
		43 identities	8 identities	8 identities	8 identities
		7 emotions	5 emotions	3 emotions	3 emotions
		Static face	Static face	Dynamic face	Dynamic face
Accuracy (SD)	Happy	98 (.02)	100 (0.00)	98 (.04)	98 (.03)
	Neutral	91 (.06)	99 (.05)	FSN: 99 (.02)	98 (.03)
				HAN: 99 (.01)	99 (.02)
	Anger	90 (.15)	95 (.06)	97 (.04)	97 (.07)
	Surprise	81 (.13)	90 (.10)	90 (.07)	90 (.09)
	Fear	73 (.12)	83 (.20)	86 (.16)	87 (.15)

2.2.3.2 Impact of gaze on emotion discrimination

2.2.3.2.1 Accuracy

For each participant, the average response accuracy (proportion of hits) was computed separately for the Conditions HAN and FSN, for each emotion and each gaze direction (Table 2). A response was marked as incorrect if the mouse click occurred outside the zone of the monitor where the possible answers were located.

A', a measure of discrimination accuracy taking into consideration both the false alarm (F) and the hit rate (H)[5] was used. For each condition, the proportion of hits (H) was defined as the number of trials the correct word for the emotion presented was selected divided by the total number of trials for that condition. The proportion of False Alarms (F) was the number of time an incorrect word was selected divided by the total number of trials for that condition (e.g. selecting "neutral" when the face presented was a happy face). *A*' was analyzed using repeated measures ANOVA with facial expression (happy, angry, neutral or fearful, surprised, neutral) and gaze direction (direct or averted) as within subject factors, for each condition. Greenhouse-Geisser corrections were used when sphericity assumptions were violated. Significant effects were examined by means of Bonferroni-corrected paired comparisons.

A repeated measure ANOVA involving Facial Expression (happy, angry, neutral or fearful, surprised, neutral) and Gaze Direction (direct or averted) as the within-subject factors was performed for each condition. For FSN Condition, there was a main effect of Facial Expression (F (2, 46) =12.82, MSE=.02, p<.01, η_p^2=.36) with surprised and fearful faces being less accurately discriminated than neutral faces (p=.01 for both comparisons), as seen on Fig. 3[6]. There was neither a main effect of Gaze Direction (F (1, 23) =.01, MSE<.01, p=.91, η_p^2<.01), nor a Gaze Direction by Facial Expression interaction (F (2, 46) =.86, MSE<.01, p=.86, η_p^2<.01). For HAN Condition, there was a main effect of Facial Expression (F (2, 46) =4.12, MSE<.01, p=.02, η_p^2=.15) although Facial Expressions did not differ when using pairwise comparisons (Figure 3). However, the main effect of Gaze Direction and the Gaze Direction by Facial

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[5] Unlike the sensitivity measure *d'* originally proposed by signal detection theory, *A'* accepts F or H close to 0 or 1 and does not require many trials (Grier, 1971). The formula used was: A' = 0.5 + (H-F)*(1+H-F)/4*(H-F).

[6] Note that an *A'* of .05 reflects chance level. Thus all emotions were discriminated well above chance level.

Expression interaction were non-significant (F (1, 23) =2.09, MSE<.01, p=.16, η_p^2=.08 and F (2, 46) =2.10, MSE<.01, p=.13, η_p^2=.08 respectively).

We also compared neutral expressions using a repeated measure ANOVA involving Condition (HAN, FSN) and Gaze Direction (direct or averted) as within subject factors. The discrimination accuracy of neutral expressions did not differ between Conditions (F (1, 23) =.22, MSE<.01, p=.64, η_p^2=.01).

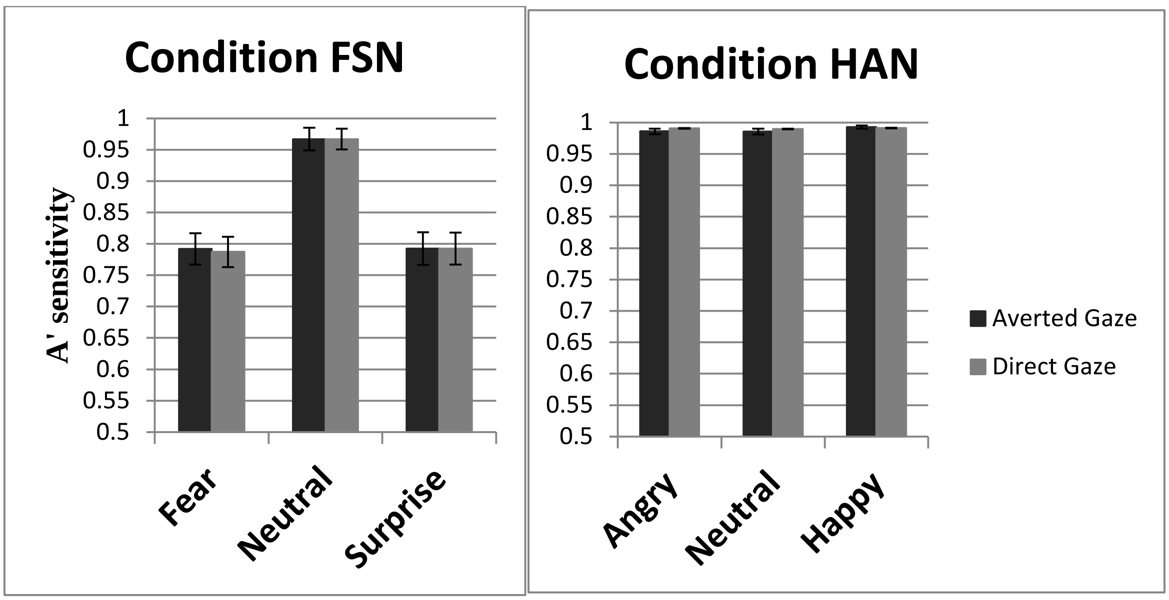

Figure 3: Discrimination accuracy (*A'*) for DG and AG in Condition FSN and HAN

2.2.3.2.2 Reaction Times

Reaction times (RTs) for each expression and gaze direction were calculated for every participant and for correct answers only. As was the case for *A'*, RTs were analyzed using a two way ANOVA with Facial Expressions and Gaze Direction as a within subject variables for each condition.

For FSN Condition, no effect was significant (Facial Expression, F (2, 46)=2.79, MSE=6903.73, p=.07, η_p^2=.11; Gaze Direction, F(1,23)=2.49, MSE= 1418.79, p=.09, η_p^2=.10; Gaze Direction by Facial Expression, F(2,46)=1.82, MSE=1002.71, p=.17, η_p^2=.07), although the RT for direct gaze faces tended to be shorter than RTs for averted gaze faces (574.62 vs 584.52 ms), as seen in Figure 4. For Condition HAN, there was neither a main effect of Facial Expression (F (2, 46)=4.48, MSE=12068.78, p=.21, η_p^2=.07), nor an interaction between Gaze Direction and Facial Expression (F (2, 46)=.82, MSE=4911.20, p=.82, η_p^2=.03) , but there was a main effect of Gaze Direction (F(1,23)=4.48, MSE=3463.88, p=.04,

η_p^2=.16) such that Facial Expressions with direct gaze (560.42 ms) were discriminated faster than Facial Expressions with averted gaze (581.18 ms).

To check that neutral expressions were responded to with the same speed in HAN and FSN conditions, a two way ANOVA was run, with Condition and Gaze Direction as within subject factors. Mean RTs to Neutral faces did not differ between Conditions (F (1, 23) =.43, MSE=885.81, p=.52, η_p^2=.02).

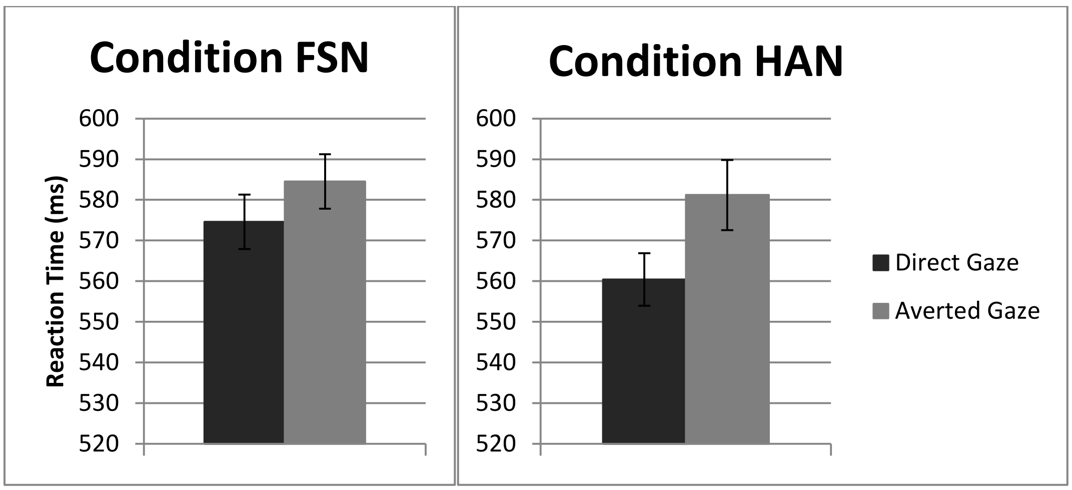

Figure 4: Response Speed (ms) for Direct Gaze and Averted Gaze in Condition FSN and HAN

2.3 DISCUSSION OF EXPERIMENT 1

The main goal of this experiment was to determine the impact of gaze on emotion processing in the general (non-anxious and non-autistic) population. Specifically, we wanted to adjudicate among three existing hypotheses regarding the impact of gaze on emotion discrimination: the direct gaze hypothesis, the appraisal hypothesis and the shared neural hypothesis. The experiment included one condition in which happy, neutral and angry facial expressions (HAN condition) were discriminated and another condition in which fearful, surprised and neutral expressions (FSN condition) were discriminated. In these two conditions, facial expressions were presented both with direct and averted gaze and were dynamic. In addition, participants filled in an emotion discrimination questionnaire featuring the same faces with direct gaze as in the actual experiment. This created a baseline for expression discrimination, which was comparable to most previous expression discrimination studies in the literature where faces are presented static with a straight gaze. We start by discussing the questionnaire and then the discrimination task (computerized experiment).

2.3.1 Emotion recognition in faces with direct gaze (questionnaire)

In accordance with previous studies (Tottenham et al., 2009; Calvo & Lundqvist, 2008; Palermo & Coltheart, 2004; Ekman & Friesen, 1976), we found that happy faces were better recognized than negative emotions such as fear and emotions with ambiguous valence such as surprise. This happy superiority effect could be due to the distinctiveness of the happy facial expression in which facial features are distinct from those of other emotions such as fear (Adolphs, 2002). The smile of happy faces is a particularly salient feature and might be sufficient to identify a face as happy (Leppänen & Hietanen, 2007). In contrast, fear and surprise have many similar features and tend to be confused with one another (Ekman & Oster, 1982). In addition, we might have a higher degree of familiarity with happy faces relative to faces expressing other emotions, because we interact with smiling faces on a regular basis. Furthermore, happy facial expressions are more rewarding for us than other emotions (Hare, Tottenham, Davidson, Glover & Casey, 2005). Finally, it has been shown that happiness and anger are more often expressed with direct gaze while fear and sadness are more often expressed with averted gaze (Argyle & Cook, 1976; Kleinke, 1986), which could potentially have elevated the recognition of happy and angry faces in this questionnaire since all faces were presented with a direct gaze.

2.3.2 Influence of gaze on emotion discrimination

In accordance with the results of the aforementioned questionnaire and previous studies, fearful and surprised expressions were less accurately discriminated than neutral expressions in the FSN session. However, in contrast with the results of the questionnaire and previous studies, happy facial expressions were not more accurately discriminated than angry or neutral facial expressions. The lack of "happy superiority effect" may be due to the smaller number of emotions to discriminate from in the HAN condition (three) compared to the questionnaire (five). Given that correct discrimination between emotions was very high, a ceiling effect seems to have been reached in the HAN condition, in which only easily distinguishable expressions were included.

Importantly, there was no overall effect of gaze on the accuracy of emotion discrimination in either Condition FSN or Condition HAN, which is in contrast with the prediction derived from all three previously outlined hypotheses. Indeed, the direct gaze hypothesis predicted better emotion discrimination accuracy with direct than averted gaze for all emotions. The appraisal hypothesis, on the other hand, predicted better emotion discrimination accuracy with averted than direct gaze for fear and surprise but better accuracy for direct than averted gaze for anger and no gaze difference for happy expressions. Finally, the shared neural hypothesis predicted better emotion discrimination with averted than direct gaze for fear and surprise but better discrimination for direct than averted gaze for both anger and happiness (Table 1).

In addition, there was no emotion effect on the speed of facial expression discrimination in the current experiment, contrary to what was found in previous studies (e.g., Calvo & Lundqvist, 2008; Palermo & Coltheart, 2004). However, in these two studies in which faster responses were found for emotional than neutral expressions, there were seven emotions to discriminate compared to three in each condition of the present experiment. Thus, the task was easier in the current experiment than in previous studies, which might explain why a quicker discrimination of happy faces was not found.

Recall that the appraisal hypothesis and the shared neural hypothesis predicted faster response with averted than direct gaze for fearful and surprised expressions and faster response for direct than averted gaze for anger. The shared neural hypothesis makes the additional prediction of a faster response for direct than averted gaze for happy expressions. In contrast, the direct gaze hypothesis predicts that emotions embedded in faces with direct gaze are responded to faster than emotions presented with averted gaze. In the HAN condition, emotions were discriminated significantly faster when embedded in faces with direct gaze than when embedded in faces with averted gaze, which is compatible both with the shared neural hypothesis and with the direct gaze hypothesis. However, this faster emotion discrimination response for faces with direct gaze was non-significant in FSN condition, which doesn't support fully the direct gaze hypothesis and is opposed to the prediction of the shared neural hypothesis. It could be that emotions are usually recognized faster when embedded in faces with direct gaze but this effect is attenuated for surprise and fear due to the incongruent motivational tendencies between direct gaze (indicating approach) and fear/ surprise (indicating avoidance). Alternatively, the reason why the gaze effect was more prominent in the session with happy and angry faces than in the session with fearful and surprised faces could be because happiness and anger are more commonly found in faces with direct gaze in natural settings (Argyle & Cook 1976; Kleinke, 1986).

Although our results fail to provide full support for either of the three hypotheses outlined in Table 1, they show for the first time a speed-up of emotion discrimination in faces with direct gaze compared to faces with averted gaze, (more apparent for happy and angry facial expressions than for fearful and surprised expressions), a result that partially support the direct gaze hypothesis. However, accuracy data did not support the direct gaze hypothesis, as emotion discrimination was equally high for direct and averted gaze directions, a result in contrast to a previous study reporting better discrimination for direct than averted gaze faces (Bindemann, Burton & Langton, 2008).

The lack of consistency between our results and the different hypotheses regarding the impact of gaze on emotion discrimination could be explained by results of recent studies suggesting that far from being obligatory, the interaction between gaze and emotion processing only occurs when certain conditions are met (Bindemann et al., 2008; Graham & Labar, 2007). Using a Garner interference paradigm, Graham and Labar (2007) showed that while expression judgments interfered with gaze judgments, gaze direction did not interfere with emotion recognition. They further showed that this interference emerged only in cases of low discriminability (e.g., when the intensity of the facial expressions to be discriminated was decreased). However, if low discriminability were the necessary condition for gaze and emotion to interact, we would at least expect an influence of gaze in the FSN Condition, given that fear and surprise are often confused with one another (Ekman & Oster, 1982). Since there was no impact of gaze neither on the speed of emotion discrimination nor on its accuracy, it is unlikely that low discriminability is a sufficient condition for emotion and gaze to interact. Another study suggested that gaze and emotion only interact when using a specific experimental setting (Bindemann et al., 2008). The authors could only replicate the results that motivated the shared neural hypothesis when they used the exact same stimuli and task as Adams and Kleck (2003). In addition, they showed that, even when the task and the stimuli were kept constant, the pattern of results found by Adams and Kleck disappeared when more than two emotions were presented in the same study, suggesting that Adams and Kleck's results were, in fact, an artifact of the experimental design due to the particular saliency of gaze when only two emotions were present. In the present study, there were three emotions in the design, which could explain why we did not observe an interaction between gaze and emotion perception.

2.4 CONCLUSION

Using a questionnaire with direct gaze faces displaying fearful, surprised, angry, happy and neutral expressions, a five-forced choice response system and unlimited response time, we found that happy facial expressions were discriminated better than the other facial expressions, in accordance with previous studies (e.g., Tottenham et al., 2009; Calvo & Lundqvist, 2008; Palermo & Coltheart, 2004; Ekman & Friesen, 1976). However, when using the same facial expressions presented dynamically in conditions involving only three emotions and a limited amount of time to respond, the discrimination accuracy for happy faces did not differ significantly from that of angry faces and no effect of emotion on response times was observed. These results indicate that the happy superiority effect is likely sensitive to experimental factors such as the number of emotions present, response time constraints and possibly dynamic presentation. In addition, we found that gaze did not impact emotion discrimination but impacted response speed, with faster response for direct than averted gaze faces (an effect that was more prominent in the HAN Condition than in the FSN Condition). These findings suggest that processing of gaze and facial expressions interact in complex ways that cannot be fully explained by the three main hypotheses tested here. In accordance with two previous studies (Bindemann et al., 2008; Graham & Labar, 2007), these results indicate that experimental conditions (e.g., number and type of emotions present in the design, task difficulty) play a role in whether gaze modulates emotion discrimination in a particular study.

2.5 IMPLICATION FOR THIS THESIS

In the remaining of this thesis, the influence of emotion on attention orienting to a gazed-at location will be investigated using the exact same pictures of facial expressions used in this chapter. In Chapter 3 we also used a similar design with FSN and HAN Conditions and the same dynamic face sequence. This first chapter allowed us to verify that emotions are discriminated with the same accuracy in the averted gaze and in the direct gaze conditions, with fearful and surprised expressions being the least well discriminated emotions, as generally reported. Thus, any increase in the gaze orienting effect (GOE) for these two emotions would unlikely be due to their lower recognition rates (as in this case a smaller GOE would be predicted), but rather to their emotional dimensions. Likewise, any reduction in the GOE for happy faces would not be attributable to lower recognition rate of happy faces. In addition, although emotions were shown to be discriminated faster in the direct gaze than in the averted gaze condition, the various emotions were not responded to differently in either gaze condition, ruling out the possibility that emotional differences found in the GOE paradigm (if any) would be linked to emotional discrimination per se.

Chapter 3: Fearful, surprised, happy and angry facial expressions modulate gaze-oriented attention: behavioral and ERP evidence (Experiment 2)[7]

3.1 INTRODUCTION

As outlined in Chapter 1 (section 1.1.2. and 1.2.3.), gaze direction is a crucial non-verbal cue, which we use to determine where, and to what others are attending. It can also direct the viewer's attention toward an object, a phenomenon called joint attention, which helps assess others' intentions and understand their behaviors and mental states (Baron-Cohen, 1995). Joint attention is typically studied using a gaze-cuing paradigm in which a central face cue with averted gaze is followed by a laterally presented target. Congruent trials in which the target appears at the gazed-at location are responded to faster than incongruent trials in which the target appears at the opposite side of gaze. The response time difference between congruent and incongruent trials reflects the orienting of attention toward gaze direction (Friesen & Kingstone, 1998). This robust GOE was shown for letter discrimination, target detection or localization tasks, for SOAs up to 700ms, and when the cue is non-predictive or even counter-predictive of the target location (for a review, see Frischen et al., 2007).

3.1.1 Influence of facial expressions on the GOE

Facial expressions are also important in social attention as they allow the observer to infer what an individual is feeling about an object. For example, a face with an averted gaze and expressing fear can communicate the presence of a danger located outside of the observer's attention focus. When gaze is averted, fearful faces provide additional information compared to neutral faces. This extra clue should incite faster orienting toward the looked-at object to speed up its localization and identification.

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[7] This is an Author's Original Manuscript of an article whose final and definitive form, the Version of Record, has been published in the *Social Neuroscience* in 2013 (copyright Taylor & Francis), available online at: http://www.tandfonline.com/ doi/full/10.1080/17470919.2013.835750. It has also been presented at one international conference and one national conference (Lassalle & Itier, 2011 and Lassalle & Itier, 2012a, respectively) and yielded an abstract in *The Canadian Journal of Experimental Psychology* and an abstract in the *Journal of Vision*.

Many studies have investigated whether emotions modulate attention orienting by gaze. A GOE increase with fearful compared to neutral and/or happy faces has been reported and interpreted as reflecting the evolutionary advantage to orient rapidly in the direction of a potential threat (Fox, Mathews, Calder, & Yiend, 2007; Graham, Kelland-Friesen, Fichtenholtz, & LaBar, 2010; Mathews et al., 2003; Pecchinenda, Pes, Ferlazzo, & Zoccolotti, 2008; Tipples, 2006; Putman, Hermans, & Van Honk, 2006; Bayless et al., 2011). However, some studies failed to report such a modulation (Fichtenholtz, Hopfinger, Graham, Detwiler, & LaBar, 2007, 2009; Galfano, Sarlo, Sassi, Munafo, Fuentes & Umilta, 2011; Hietanen & Leppänen, 2003; Holmes, Mogg, Monje Garcia, & Bradley, 2010). The lack of GOE modulation with fearful faces could be due to the use of short SOAs (e.g., Galfano et al., 2011 using 200ms SOA) as Graham and colleagues (2010) suggested that a minimum of 300ms was needed for a full gaze and emotion integration. It could also result from the use of a more difficult discrimination task rather than a localization task (e.g., Holmes et al., 2010). As the combination of gaze and emotion cues indicate where in the environment a danger might be, modulation of the GOE by fear might be seen more clearly with a localization task. Finally, this lack of GOE modulation by fear could originate from the use of static rather than dynamic facial expressions (e.g., Hietanen & Leppänen, 2003) since emotions are better processed when seen dynamically than statically (Sato & Kochiyama, 2004). Additionally, some studies have shown that the GOE enhancement for fearful compared to neutral or happy faces depended on participants' anxiety level (Fox et al., 2007; Matthews et al., 2003; Putman et al., 2006) while others reported such a modulation even in non-anxious participants (Bayless et al., 2011; Neath, Nilsen, Gittsovich & Itier, 2013). Thus, it remains unclear whether modulation of attention orienting by gaze with fear is limited to high anxious individuals or can be seen in the general population.

There are also inconsistent findings as to whether emotions other than fear modulate the GOE. Angry faces failed to enhance the GOE compared to neutral faces in most studies (Bayless et al., 2011; Fox et al., 2007; Hietanen & Leppänen, 2003). However, in these studies, fearful faces were always included. In one experiment in which fearful faces were not presented, angry faces enhanced the GOE compared with joyful and neutral expressions in high anxious individuals (Holmes, Richards, & Green, 2006). Although these results need to be extended to a non-anxious population, they suggest that the modulation of the GOE by emotions may rely on the relative rather than absolute valence of an emotion. That is, in the context of fearful faces, angry faces might not be perceived as negative enough to trigger a GOE enhancement.

Surprise has seldom been investigated in the gaze orienting literature but was recently shown to increase the GOE to the same extent as fear (Bayless et al., 2011; Neath et al., 2013). Fearful and surprised facial expressions share many facial features including eye widening (Gosselin & Simard, 1999), which contributes to their facilitation of gaze-oriented attention (Bayless et al., 2011). In addition, surprise's valence is ambiguous (Fontaine et al., 2007) but is interpreted negatively in the context of negative emotions such as fearful faces (Neta & Whalen, 2010, Neta et al., 2011). Finally, surprise signals the presence of an unexpected event, which could prompt faster orienting to determine whether it is a danger. In the present experiment, the modulation of the GOE by fearful, surprised, angry and happy facial expressions was investigated at the behavioral and neural level. Importantly, we used a similar design as in Chapter 2, i.e., an FSN Condition in which fearful, surprised and neutral faces were presented and a HAN Condition in which happy, angry and neutral faces were presented. We thus expected surprise to be perceived as fear, and anger not to be influenced by fear.

3.1.2 Event-related potentials (ERPs) indexing gaze-oriented attention

Event-related potentials (ERP) can track brain activity occurring before a response is made and thus help uncover the temporal dynamics of spatial attention orienting by gaze and its modulation by emotion. However, few ERP studies have focused on gaze orienting. Some studies have investigated the ERP correlates of attention at target presentation and shown that the amplitude of early visual components, P1and N1, was larger for targets preceded by congruent compared with incongruent gaze cues (Schuller & Rossion, 2001; 2004; 2005). These effects are thought to reflect the early facilitation of target visual processing, due to the enhancement of attention at the gazed-at location, and have also been reported for targets preceded by arrow cues (Eimer, 1997; Mangun & Hillyard, 1991). Other studies have focused on ERPs elicited by the cue. In arrow cuing studies, two components were shown to index two different attention stages (Nobre, Sebestyen, & Miniussi, 2000). The Early Directing Attention Negativity (EDAN) indexes the initial orienting of attention in the cued direction and reflects the increase of activity in cortical regions devoted to the processing of the cued location (Simpson, Dale, Luks, Miller, Ritter & Foxe, 2006) or the selection of aspects of the cue relevant for the accomplishment of the task (Van Velzen & Eimer, 2003). The Anterior Directing Attention Negativity (ADAN) indexes the holding of attention at the cued location and reflects the engagement of the fronto-parietal attention network in the control and redirection of attention in space (Praamstra, Boutsen, & Humphreys, 2005). Only a few studies have investigated these components in gaze cuing paradigms. Using schematic faces, one study found no evidence for EDAN or ADAN with gaze cues although they were both present with arrow cues (Hietanen, Leppänen, Nummenmaa, & Astikainen, 2008). In another study, using schematic eyes, an EDAN was found with arrow cues but neither with exogenous, nor with gaze cues (Brignani, Guzzon, Marzi & Miniussi, 2009). Using face photographs, another study reported evidence of an ADAN but not an EDAN component (Holmes et al., 2010), reflecting the shift of attention to the gazed-at location. It remains unclear whether these components can be found reliably in gaze cuing studies. So far, few ERP studies investigated the influence of emotion on spatial attention and all failed to show emotional modulations of the attention-related ERPs with gaze orienting (Fichtenholtz et al., 2007; 2009; Galfano et al., 2011; Holmes et al., 2010). However, no clear modulations of the size of the GOE with emotions were reported at the behavioral level in these experiments. To the best of our knowledge, no ERP study using the gaze orienting paradigm has yet reported emotional modulations of P1 and N1 components related to the target, or EDAN and ADAN components related to the gaze cue, in addition to modulations of the GOE.

3.1.3 Experiment 2: purpose and predictions

In the present ERP study we used a localization task and dynamic displays to investigate whether fearful, angry, happy, surprised and neutral expressions modulate the GOE and tracked the neural correlates of these modulations in a non-anxious population using ERPs. Given gaze cues are mainly used to orient attention toward a given location in the environment, we believed that the localization task, coupled with dynamic rather than static stimuli, would be one step closer to real-life situations and would reveal emotional modulations of the GOE previously not reported. To ensure a sufficient number of trials and to avoid a lengthy study, we ran two conditions separately, each including two emotions and a neutral expression. Fearful, surprised and neutral expressions were compared in Condition FSN while angry, happy and neutral expressions were compared in Condition HAN. Happy and angry facial expressions are considered approach-related emotions while fear and potentially surprise (in the context of fear) are avoidance-related emotions. This design allowed determining whether the emotional modulation of the GOE differed between emotions signaling approach and emotions signaling avoidance. Most importantly, it allowed testing the idea that anger can enhance the GOE compared to neutral faces when fear is not included in the design. At the behavioral level, in accordance with previous studies (Bayless et al., 2011; Neath et al., 2013; Holmes et al., 2006), we predicted that i] relative to neutral faces, the GOE would be larger for fearful and surprised faces and ii] angry faces would enhance the GOE compared to neutral and happy faces. Regarding ERP modulations, at target presentation, we expected to replicate the congruency effects on P1 and N1 components and predicted larger modulations of these effects for fearful, surprised and angry expressions compared to neutral expressions, reflecting an enhancement of the early visual processing of the target for these emotions. For ERPs recorded to the face cue, we hypothesized that the task and the dynamic face photographs used would help reveal the presence of EDAN and ADAN attention-related components. Given EDAN occurs between 200-300ms after cue onset (although sometimes EDAN extends to 400ms [Holmes et al., 2010]) and emotion and gaze cues seem to require more than 300ms to be fully integrated, we predicted no modulation of EDAN by emotion. In contrast, since ADAN occurs between 300-500ms during which the emotion and gaze cues are likely integrated, we anticipated it would show a larger modulation with fearful, surprised and angry expressions compared to neutral and happy expressions.

3.2 METHODS

3.2.1 Participants

Twenty-eight participants (14 females), all right handed, with normal or corrected-to-normal vision and no self-reported history of psychiatric or neurological illness, were recruited and tested at the University of Waterloo. They received $40 or course credits for their participation. Ten participants were excluded (5 different participants per condition) due to a lack of clear P1 component after visual inspection of the ERPs. This resulted in a final sample size of 23 participants (12 females) in Conditions HAN and FSN. Ages ranged from 19 to 27 years (Condition FSN: mean=21.4, SD=2.3; Condition HAN: mean=21.5, SD=2.5).

Participants were pre-screened based on their scores on the STICSA anxiety test (Ree et al., 2008) and only those whose trait anxiety scores were in the normal range, below the high anxiety score of 42, were tested (mean trait anxiety scores in Condition FSN=30.74, SD=6.76; Condition HAN=31.57, SD=7.08). Participants were also preselected on the Autism Quotient test (Baron-Cohen et al., 2001), which has been shown to modulate the GOE (Bayliss, di Pellegrino, & Tipper, 2005). Only participants whose autistic traits were below the threshold score of 26 (Woodbury-Smith et al., 2005) were selected (mean AQ scores in Condition FSN=16.09, SD=3.82; Condition HAN =15.61, SD=4.06). Age, AQ and STICSA scores did not differ significantly between the Conditions HAN and FSN. The study was approved by the University of Waterloo Research Ethics Board and all participants gave informed written consent.

3.2.2 Stimuli and procedure

The stimuli used were the exact same as in Chapter 2 (refer to Section 2.2.2. for a full description). All participants completed the two conditions one week apart. Condition FSN included fearful, surprised and neutral faces while Condition HAN included happy, angry and neutral faces. This design maximized the number of trials per experimental condition while diminishing fatigue effects that would have arisen in one single, lengthy experiment. The order in which the two conditions were run was counterbalanced across participants.

In both conditions, participants sat 67cm in front of a computer monitor in a quiet dimly lit and electrically shielded room with their head restrained by a chin rest. Each trial started with a centered fixation cross (1.28˚x 1.28˚ visual angle), presented randomly for 800, 900, 1000, 1100 or 1200ms. A neutral face with direct gaze was then shown for 500ms, followed by the same face expressing (or not) an emotion and with rightward, leftward or direct gaze, also presented for 500ms (Figure 5). This fast serial presentation provoked the perception of a face moving its eyes to the side and dynamically expressing an emotion (apparent motion). The target, a black asterisk (.85˚x .85˚), was then presented either on the right or on the left at a distance of 7.68˚ from the center of the screen. It remained on the screen until the participant responded or for a maximum of 500ms.

Conditions FSN and HAN were programmed using Presentation software (Neurobehavioral Systems) and each consisted of 11 blocks of 144 trials separated by a self-paced break, resulting in 88 trials for each of the 18 experimental conditions. An experimental condition consisted of a combination of a particular gaze direction (direct, rightward, and leftward) with a specific emotion and a target position (left or right). There were an equal number of congruent, incongruent and direct gaze trials. The trial order was fully randomized within a block with the eight face models appearing once for each condition.

Throughout Conditions FSN and HAN, subjects were instructed to maintain fixation at the central location. Twenty practice trials were run before starting each experiment and participants were told the direction of eye gaze was not predictive of target location. They were required to press the left key “C” on the keyboard with their left hand when the target was shown on the left and the right key “M” with their right hand when the target was presented on the right. They were asked to be as accurate and as fast as possible.

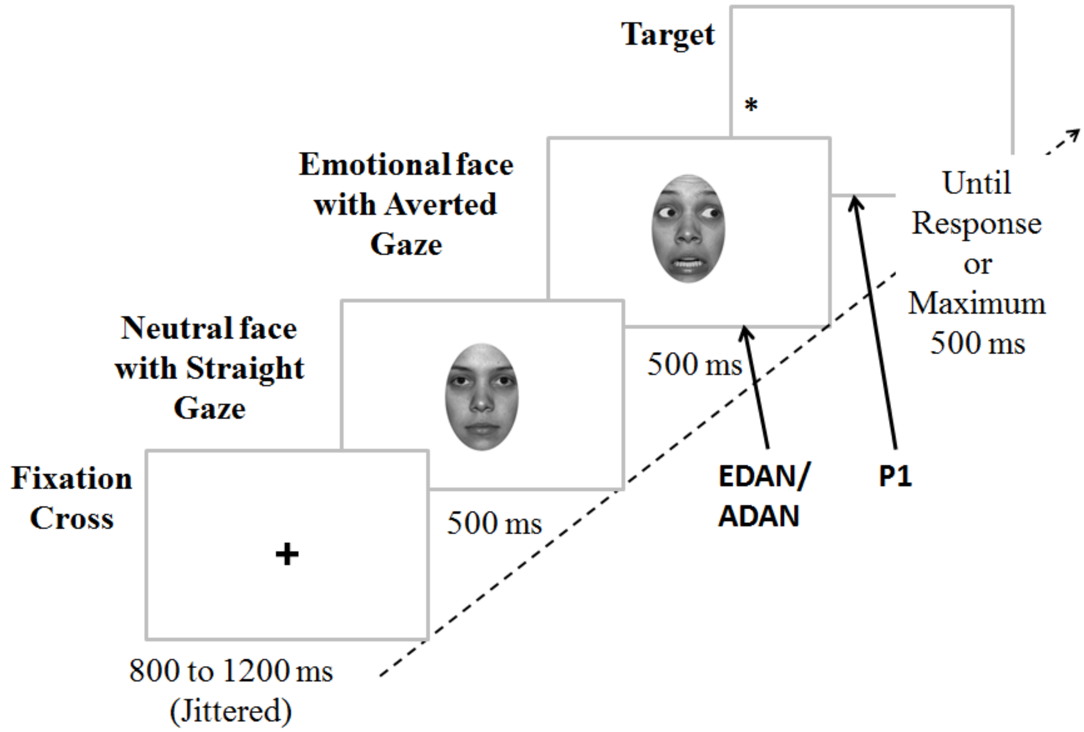

Figure 5: Procedure used with the example of an incongruent trial (target appearing in the direction opposite to gaze cue) and a fearful expression as used in Expt. 1. Arrows show at which stage the ERP components were measured (P1 at target presentation and EDAN/ADAN at cue presentation).

3.2.3 Electrophysiological recordings

The electroencephalogram (EEG) was recorded with an Active two Biosemi system using a 66-channel elastic cap (extended 10/20 system) plus 3 pairs of extra electrodes, for a total of 72 recording sites. Two pairs of ocular sites monitored vertical and horizontal eye movements from the outer canthi and infra orbital ridges (IO1, IO2, LO1, LO2); one pair was situated over the mastoids (TP9/TP10). EEG was recorded at a sampling rate of 516Hz. A Common Mode Sense (CMS) active electrode and Driven Right Leg (DRL) passive electrode serving as ground were used during acquisition. Offline, an average reference was computed and used for the analysis.

For the target analysis, EEG was epoched relative to a 100ms pre-target baseline up to 300ms post-target onset. For the cue analysis, EEG was epoched relative to a 100ms pre-gaze cue baseline up to 500ms post-cue onset. Data were band-pass filtered (0.01Hz - 30Hz). For each subject, trials with amplitudes larger than +/- 70µV recorded at any given time point on any channel but excluding eye movements, were first rejected before Independent Component Analysis (ICA) decomposition. This represented less than 10% of the total number of trials. ICA was then performed as implemented in EEGLAB (Delorme & Makeig, 2004), derived from all trials. ICA components reflecting major artifacts including ocular movements or electrode dysfunction were removed for each participant. After ICA decomposition, some more trials with extreme values (+/-50µV) were rejected if needed. ERPs were then computed for each subject and each condition. Across subjects, the average number of trials per condition after artifact rejection was 82±6 for Condition FSN and 83±5 in Condition HAN for P1 and between 140 and 160, for EDAN and ADAN.

3.2.4 Data analysis

3.2.4.1 Behavior

Responses were recorded as correct if the response key matched the side of the target appearance and if Reaction Times (RTs) were above 100ms and below 1200ms[8]. The remaining responses were marked as incorrect. Mean RTs for correct answers were calculated according to facial expressions and congruency, with left and right target conditions averaged together (an initial behavioral analysis revealed no effect of right or left targets). For each subject, only RTs within 2.5 standard deviations from the mean of each experimental condition were kept in the mean RT calculation (Van Selst & Jolicoeur, 1994). On average, less than 7.5% of trials were excluded per condition in each experiment.

It has been shown that a face gazing directly at the participant triggers slower response times than the same face looking to the side, especially when displaying a threatening facial expression (Fox et al., 2007; Georgiou, Bleakley, Hayward, Russo, Dutton, Eltiti & Fox, 2005; Mathews et al., 2003), which is consistent with the idea that different processes underlie the perception of direct and averted gaze (George et al., 2001). Because direct gaze seems to capture (and hold) attention to a larger extent than averted gaze (Senju & Hasegawa, 2005), we followed what has been done in previous gaze orienting studies (Bayless et al., 2011; Fox et al., 2007; Mathews et al., 2003) and analyzed direct gaze separately from averted gaze.

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[8] 1200ms would be 500ms of target presentation and 800ms of fixation cross.

For each experiment, error rates and RTs to averted gaze trials were analyzed separately using a mixed model ANOVA with Emotions (3: fearful, surprised neutral in Condition FNS and happy, angry, neutral in Condition HAN) and Congruency (2: congruent, incongruent) as within-subject factors and Condition Order as a between-subject factor[9]. When the Emotion by Congruency interaction was significant, simple main effects of emotion were conducted separately for congruent and incongruent trials, using the factor Emotion. RTs to direct gaze trials were analyzed using an ANOVA with Emotion as a within-subject factor and Condition Order as a between-subject factor.

3.2.4.2 ERPs

3.2.4.2.1 ERPs to targets

P1 peak was defined as the time point of maximum amplitude between 80 and 130ms after target onset[10], automatically selected within this time window for each subject and experimental condition. It was then verified by visual inspection. PO7/PO8 and O1/O2 were selected as the electrodes of interest based on data inspection. As P1 is maximal on the hemisphere contralateral to stimulus presentation, and to avoid unnecessarily complicated results, only the electrodes contralateral to the target side were analyzed, as done previously (e.g., Fichtenholtz et al., 2007, 2009). P1 amplitude and latency were analyzed using a 2(Electrodes: PO/O) by 2(Hemisphere: right or left) by 3(Emotions: fear, surprise, neutral or happy, angry, neutral) by 2(Congruency: congruent or incongruent) repeated measures ANOVA. Planned analyses were also carried out for each emotion separately.

3.2.4.2.2 ERPs to gaze cue

For this analysis, ERPs were computed time-locked to the gaze shift. Based on careful observation of the current data and previous reports (Hietanen et al, 2008; Holmes et al., 2010; Van Velzen & Eimer, 2003), the EDAN component was measured at posterior electrodes (averaged across P7 and PO7 on the

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[9] Although in Chapter 2, the two conditions were analyzed together, in one single omnibus analysis of variance, this was not possible in the present ERP study due to the rejection of different subjects in each condition after artifact rejection.

[10] N1 peak was defined as the peak of minimum amplitude between 115 and 205ms after target onset. However, N1 was in general wide and a clear peak could not be identified in more than half of the participants. Therefore N1 analysis was dropped.

left hemisphere and across P8 and PO8 on the right hemisphere) between 200 and 300ms while the ADAN component was measured at anterior electrode sites (averaged across F5, F7, FC5, FT7 for the left hemisphere and F6, F8, FC6, FT8 for the right hemisphere) between 300 and 500ms.

Given EDAN and ADAN are components characterized by more negative amplitudes for contralateral gaze cues compared to ipsilateral gaze cues, we investigated, for each hemisphere, whether amplitudes were more negative for face cues with gaze directed toward the contralateral side than for gaze directed toward the ipsilateral side[11]. For the left hemisphere, leftward gaze was the ipsilateral gaze condition and rightward gaze the contralateral gaze condition and inversely for the right hemisphere.

For both components, mean amplitudes for the ipsilateral and contralateral conditions were calculated for each of the three emotions and for each hemisphere. In each study, a 2(Hemisphere) by 2 (Gaze laterality: contralateral, ipsilateral) by 3(Emotion) repeated measure ANOVA was computed.

For all analyses, statistical tests (including behavioral analyses) were set at $\alpha<.05$ significance level and Greenhouse-Geisser correction for sphericity was applied when necessary. Adjustment for multiple comparisons was carried out using Bonferroni corrections.

3.3 RESULTS OF CONDITION FSN

3.3.1 Behavior

3.3.1.1 Direct Gaze Trials

Mean proportion of errors for direct gaze trials are shown in Appendix B (Table 5a). Analysis of errors revealed no main effect of Condition Order (F=.97, p=.34) or an interaction between Condition Order and Emotion (F=2.16, p=.13).

RT analysis to direct gaze trials revealed a main effect of Condition Order ($F(1, 21) = 8.59$, MSE=2376.88, $p<.01$, $\eta_p^2=.29$) such that the RTs were faster when Condition FSN was run second (294.87ms) than when it was run first (329.31ms). However, the Condition Order by Emotion interaction was not significant. In addition, as shown in Figure 6a, RTs recorded to direct gaze trials showed a main

[11] Note that, by definition, EDAN and ADAN are calculated for averted gaze trials only.

effect of Emotion ($F(1.31, 28.77)= 66.80$, MSE=75.95, $p<.01$, $\eta_p^2=.75$) with faster RTs for surprise and fear than for neutral ($p<.01$ for both comparisons).

3.3.1.2 Averted Gaze Trials

Mean proportion of errors for averted gaze trials are shown in Appendix B (Table 5b). The error rate analysis did not yield a main effect of Condition Order ($F=.37$, $p=.55$) or an interaction involving Condition Order. A main effect of Congruency was found (F (1, 21)=15.19, MSE=11.64, $p<.01$, $\eta_p^2= .42$) with more errors in the incongruent (7.04%) than in the congruent condition (4.78%). However, there was no main effect of Emotion ($F=1.53$, $p=.23$) or interaction between Emotion and Congruency ($F=0.1$, $p=.99$) on the error rate.

RT analysis to averted gaze trials yielded a main effect of Condition Order ($F(1, 21) =7.28$, MSE=4074.24, $p=.01$, $\eta_p^2= .26$) such that RTs were overall faster when Condition FSN was run after Condition HAN (mean= 287.65ms) than when it was run first (mean= 316.99ms). However no interaction involving Condition Order was significant. Specifically, the order in which Condition FSN was run did not interact with Congruency or Emotion. In addition, there was a main effect of Emotion ($F(2, 42) =4.43$, MSE=24.67, $p< .02$, $\eta_p^2 =.17$), with faster RTs to surprise than to neutral emotions ($p< .01$) and a tendency for faster RTs to fear than to neutral emotions ($p= .08$). Surprise and fear did not differ significantly. There was also a main effect of Congruency (F (1, 22) =44.19, MSE=226.80, $p<.01$, $\eta_p^2=.67$), reflecting faster RTs in the congruent than in the incongruent condition (Figure 6b). The Congruency by Emotion interaction was significant ($F(2, 44) =6.24$, MSE=17.81, $p< .01$, $\eta_p^2= .22$) due to a larger congruency effect for fear and surprise than for neutral emotions ($p< .01$ and $p=.02$ respectively; Figure 6c). The GOE (measured as the RT difference between incongruent and congruent conditions) did not differ significantly between fear and surprise. The congruent condition revealed a significant simple main effect of Emotion ($F(2, 44) = 8.28$, MSE=25.25, $p<.01$, $\eta_p^2=.27$), with faster RTs for surprise and fear (which did not differ) than for neutral ($p< .01$ for each comparison). There was no Emotion effect for the incongruent condition.

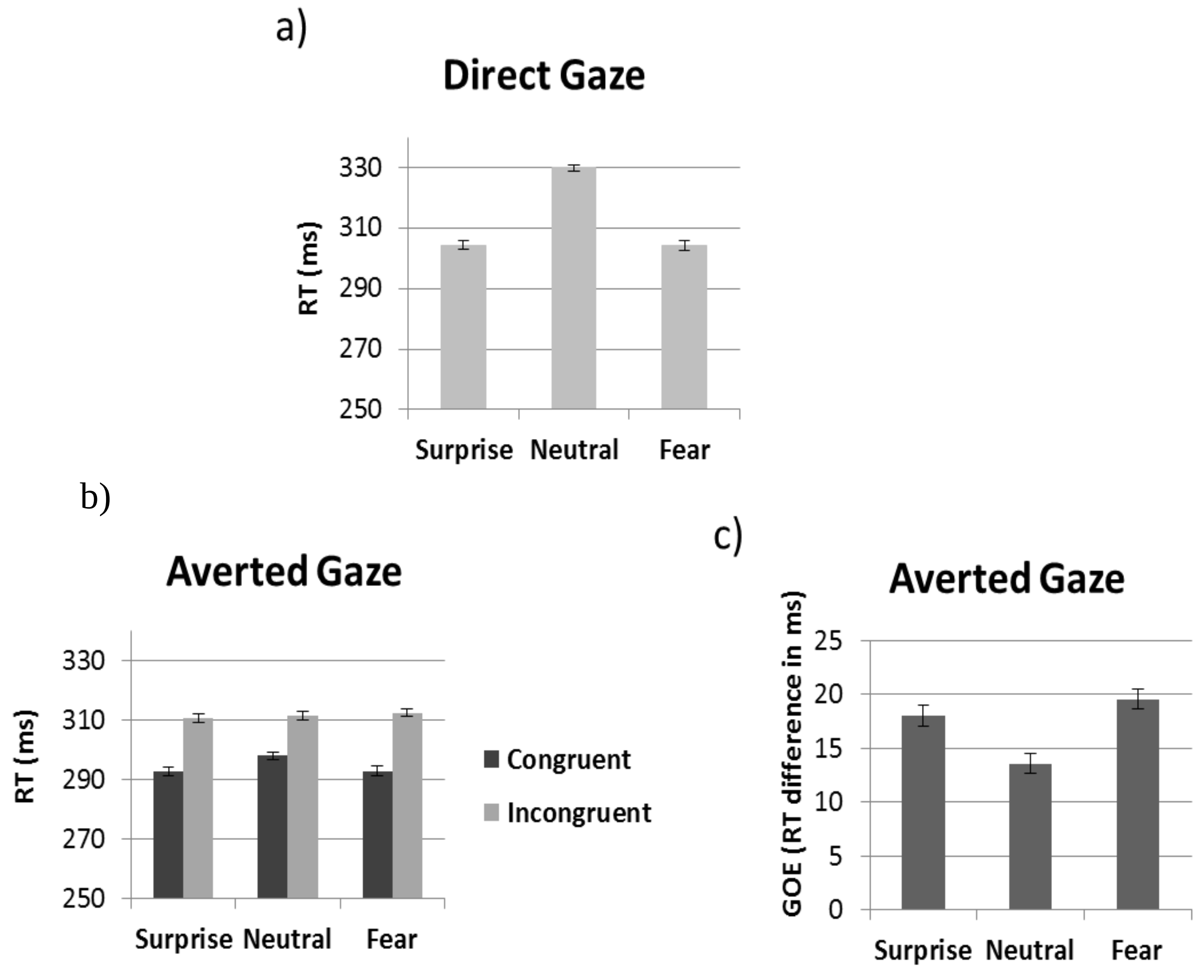

Figure 6: Behavioral results of Condition FSN. (a) Mean RTs to direct gaze trials. (b) Mean RTs to congruent and incongruent trials; (c) Mean gaze orienting effect (GOE) (RT incongruent –RT congruent) for each emotion; In all analyses, N=23 and error bars represent SE to the mean.

3.3.2 ERPs to targets

3.3.2.1 P1 Amplitude

P1 amplitude analysis revealed a main effect of Electrode ($F(1, 22) = 46.79$, MSE=5.96, $p < .01$, $\eta_p^2 = .68$) with larger amplitudes at O1/O2 than at PO7/PO8. A main effect of Congruency ($F(1, 22) = 5.19$, MSE=1.17, p=.03, η_p^2= .19) was due to larger amplitudes for the congruent than the incongruent condition. However, this effect was significant at PO7/PO8 (F(1, 22) =7.34, MSE= .86, p=.01, η_p^2= .25, Figure 7a and 7b) but not at O1/O2 sites, as revealed by a significant Congruency by Electrode interaction (F(1, 22) =7.51, MSE= .16, p=.01, η_p^2= .25).

Although no Congruency by Emotion interaction was found, planned analyses were performed for each emotion separately at PO7/PO8. The Congruency effect was present for surprise (F(1, 22) = 4.48, MSE= .67, p=.05, η_p^2= .17) and fear (F(91, 22) =6.40, MSE= .52, p= .02, η_p^2= .23) but not for neutral emotions as seen on Figure 7b.

3.3.2.2 Latency

A main effect of Congruency (F (1, 22) =6.24, MSE=38.21, p= .02, η_p^2= .22) was due to overall later P1 peak in the congruent than in the incongruent condition. In addition, the Congruency by Hemisphere by Emotion interaction was significant (F (2, 44) =4.34, MSE=32.12, p=.02, η_p^2= .17) but when the analysis was computed separately for each hemisphere, the Congruency by Emotion interaction was no longer significant for either hemisphere.

3.3.3 ERPs to gaze cues

3.3.3.1 EDAN

The analysis showed a trend toward a main effect of Hemisphere (F (1, 22) =3.63, MSE=9.99, p=.07, η_p^2=.14) with larger amplitudes in the right than in the left hemisphere. There was also a main effect of Gaze laterality (F (1, 22) = 10.76, MSE= .12, p<.01, η_p^2=.34) such that the amplitude was more negative for contralateral than ipsilateral gaze direction (Figure 8a, b). In addition, there was a main effect of Emotion (F (1.17, 25.65) = 16.38, MSE=1.15, p<.01, η_p^2=.43) such that fearful and surprised faces yielded more negative amplitudes than neutral faces as shown in Figure 8b (p< .01 for both). However, the Emotion by Gaze laterality interaction was not significant (F (2, 44) = .13, MSE= .07, p=.88, η_p^2<.01).

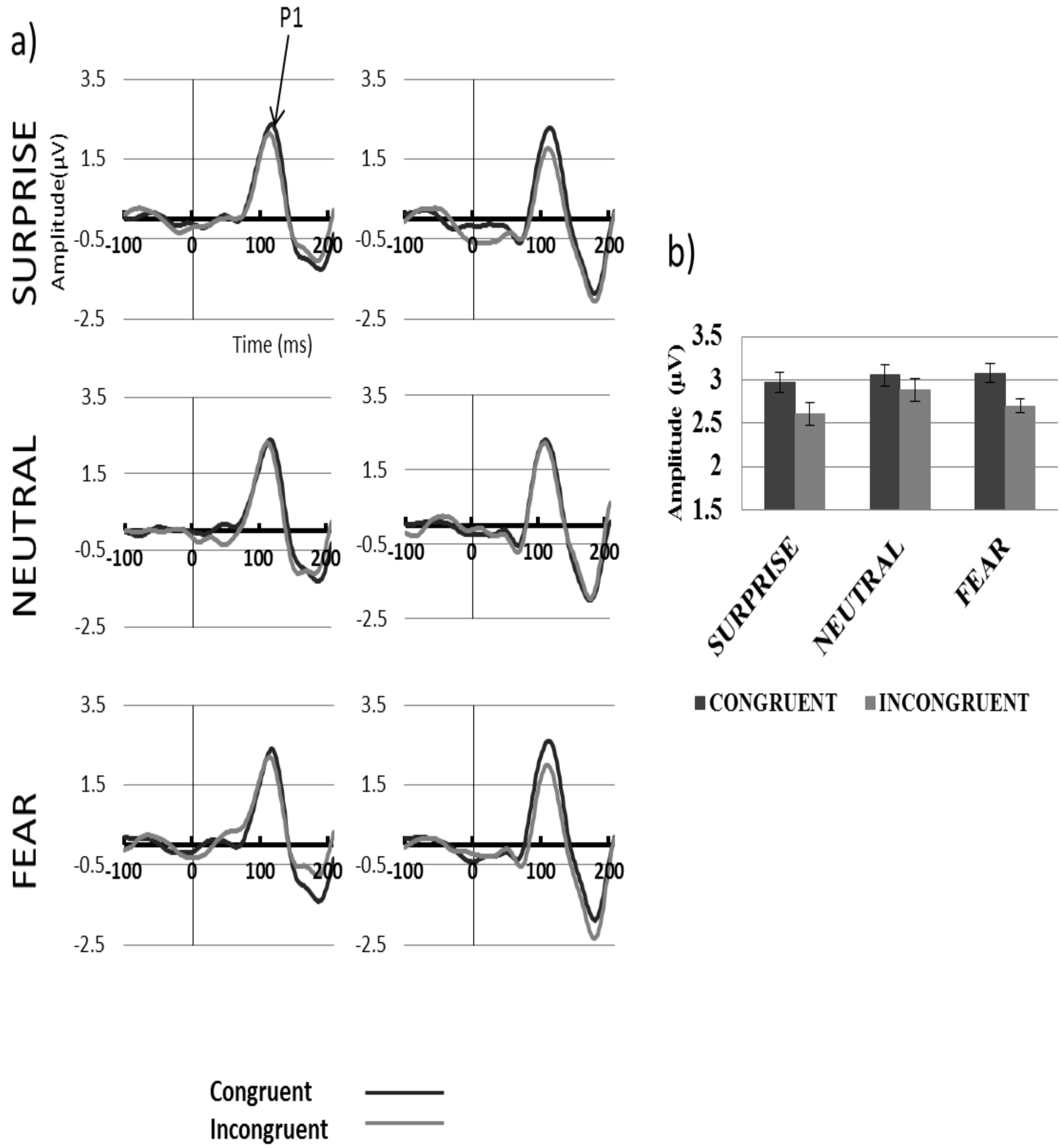

Figure 7: ERPs to the target in Condition FSN (a) ERP waveforms showing P1 component at electrodes PO7 (left hemisphere, left panels) and PO8 (right hemisphere, right panels) for each emotion (Fear, Surprise, Neutral: N=23). (b) Mean amplitudes for the congruent and incongruent conditions for each emotion.

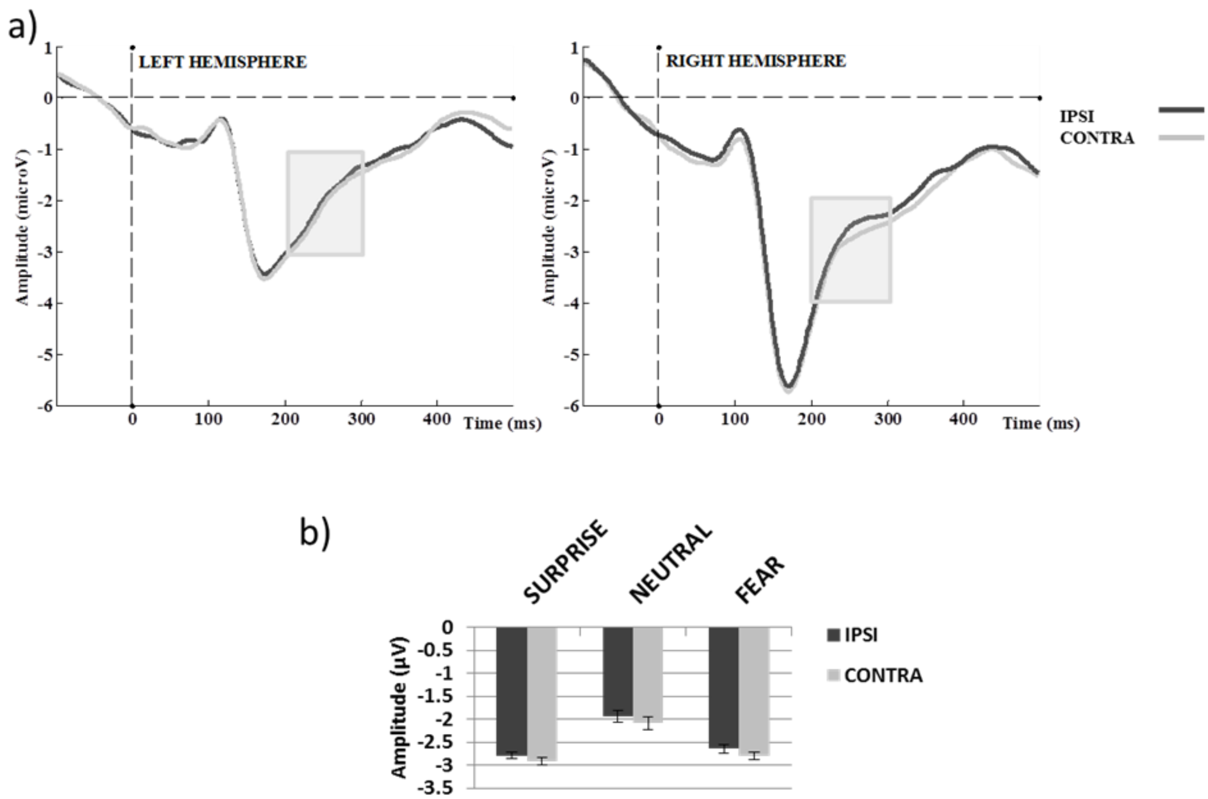

Figure 8: EDAN component to the face cue in Condition FSN (a) Effect of gaze laterality on the group ERP waveforms (averaged across emotions and electrodes). The grey zone marks the time limits of the analysis (200-300ms). (b) Group amplitudes for contra- and ipsilateral gaze directions for each emotion averaged across electrodes between 200 and 300ms.

3.3.3.2 ADAN

The analysis showed a main effect of Gaze laterality (F (1, 22) = 8.50, MSE=.17, p<.01, η_p^2=.28) such that the amplitude was less positive for the contralateral gaze compared with the ipsilateral gaze (Figure 9a, b). There was also a main effect of Emotion (F (1.72, 37.91) = 7.47, MSE= .25, p<.01, η_p^2= .25) such that surprised faces yielded larger amplitudes than fearful (p=.01) or neutral faces (p< .01) as shown on Figure 9b. No significant Emotion by Gaze laterality interaction was found (F (2, 44) =.80, MSE=.15, p=.80, η_p^2= .04). However, a Gaze laterality by Hemisphere interaction was present (F (1, 22) =7.07, MSE= .08, p= .01, η_p^2= .24) due to a Gaze laterality effect present in the left hemisphere (F (1, 22) =17.26, MSE= .11, p<.01, η_p^2= .44) but not in the right hemisphere (F (1,22)=.69, MSE= .14, p=.41, η_p^2= .03).

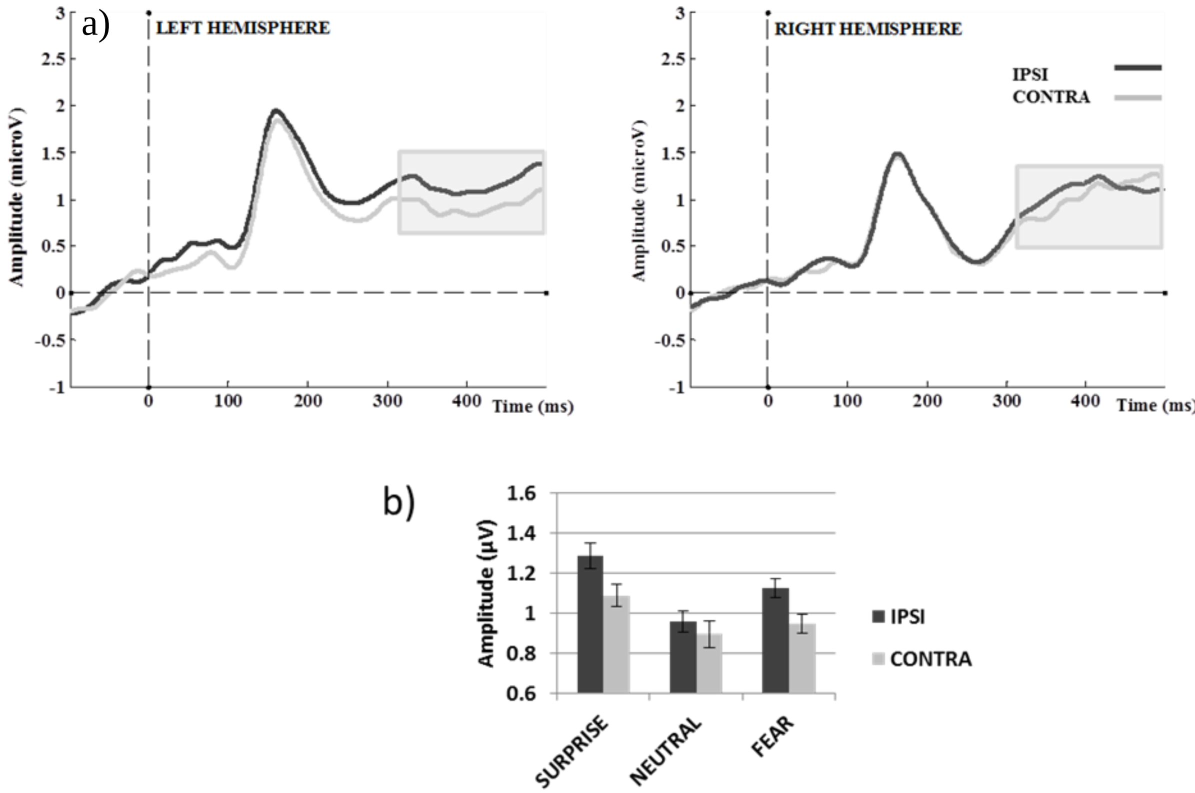

Figure 9: ADAN component to the face cue in Condition FSN (a) Effect of gaze laterality on the group ERP waveforms averaged across emotions and electrodes (F5, F7, FC5, FT7 for the left hemisphere, F6, F8, FC6, FT8 for the right hemisphere). The grey zone marks the time limits of the analysis (300-500ms). (b) Effect of gaze laterality on the average amplitude across ADAN electrodes between 300 and 500ms for each emotion.

3.3.4 Summary of Condition FSN

Participants were faster to respond to a gazed-at target than to a target located on the opposite side of the gazed-at location. This classic GOE was enlarged when the target was preceded by fearful or surprised compared with neutral faces. At target presentation, P1 amplitude showed a congruency effect at PO7/PO8 sites and planned comparisons revealed this effect was restricted to targets preceded by fearful and surprised expressions. At cue presentation, we found evidence for a gaze laterality effect, early at posterior sites (EDAN) and late at anterior sites (ADAN). Amplitudes were also larger for emotional than neutral faces between 200 and 300ms and this effect was less pronounced between 300 and 500ms. Finally, no Gaze laterality by Emotion interaction was found for EDAN or ADAN.

3.4 RESULTS OF CONDITION HAN

3.4.1 Behavior

3.4.1.1 Direct Gaze Trials

Mean proportions of errors are shown in Appendix B (Table 6a). No main effect of Condition Order (F=.05, p=.83) or an interaction between Condition Order and Emotion (F=.06, p=.95) were found for errors.

No effect of, or interaction with, Condition Order was found on the RT analysis. As shown on Figure 10a, RT analysis for direct gaze trials revealed a main effect of Emotion (F (2, 42) =93.96, MSE=75.17, p< .01, η_p^2= .82) with faster RT for angry and happy faces (which did not differ) when compared with neutral faces (both at p< .01).

3.4.1.2 Averted Gaze Trials

Mean proportion of errors are shown in Appendix B (Table 6b). No main effect of Condition Order (F=1.00, p=.76) or an interaction involving Condition Order were found for errors. A main effect of Congruency was found (F (1, 22) =7.92, MSE=16.05, p=.01, η_p^2= .27) with more errors in the incongruent (5.90%) than in the congruent condition (3.98%). However, there was no main effect of Emotion (F=2.73, p=.08) or an interaction between Emotion and Congruency (F=0.15, p=.96) on the error rate.

For RTs recorded to averted gaze trials, no main effect of Condition Order or interaction involving Order was significant. A main effect of Congruency (F (1, 21) = 43.24, MSE=207.83, p< .01, η_p^2= .67) reflected faster RTs in the congruent than in the incongruent condition (Figure 10b). In addition, the Congruency by Emotion interaction was significant (F (2, 42) =5.53, MSE=13.29, p<.01, η_p^2= .21) due to a larger GOE (i.e., larger congruent versus incongruent differences) for angry than for neutral (p< .01) and happy (p= .02) faces which did not differ significantly (Figure 10c). For congruent trials there was a simple main effect of Emotion (F (2, 42) =4.09, MSE=24.49, p=.02, η_p^2= .16) with faster RTs for angry faces compared with neutral faces (p=. 01); no other comparisons were significant. There was no emotion effect for the incongruent condition (Figure 10b).

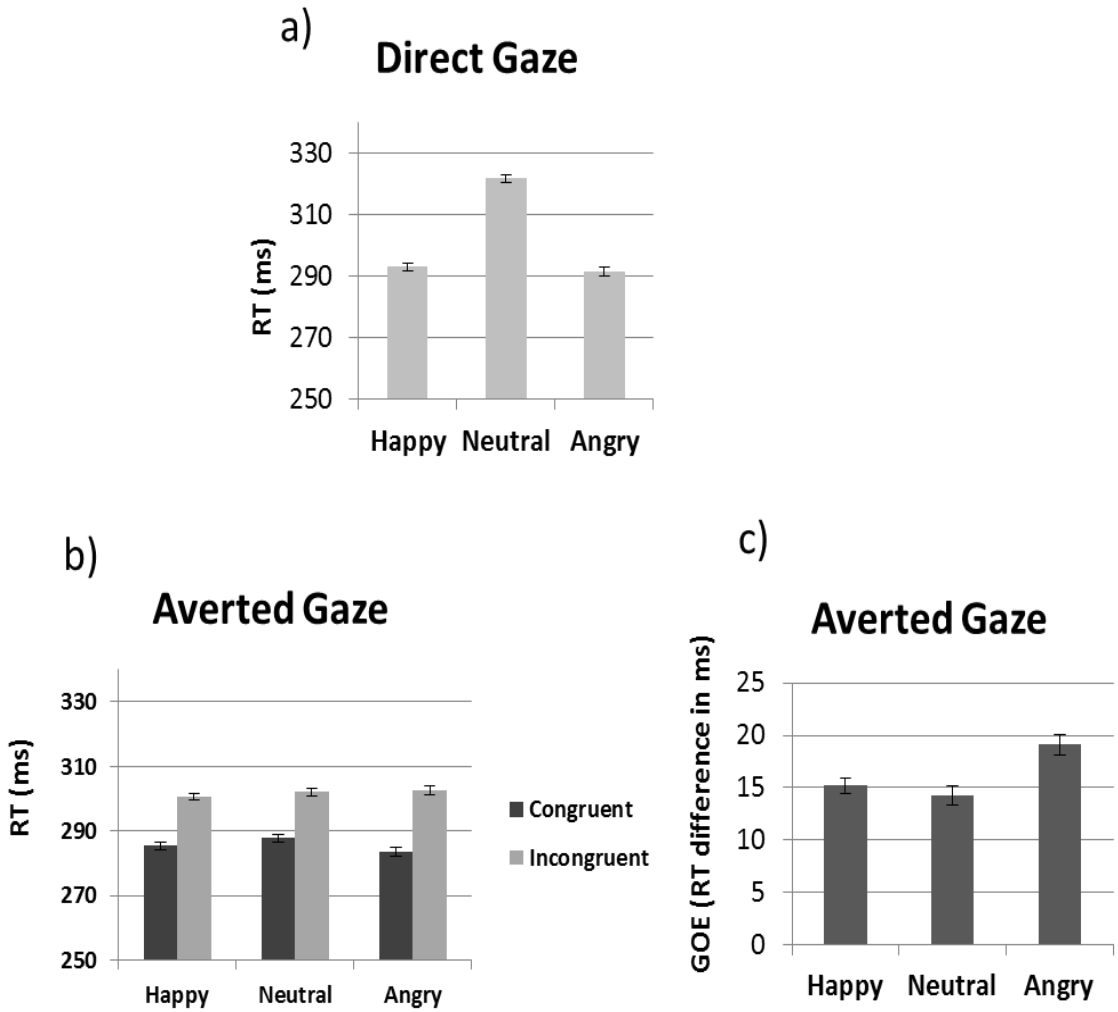

Figure 10: Behavioral results of Condition HAN. (a) Mean RTs for direct gaze trials; (b) Mean RTs for congruent and incongruent trials; (c) Mean gaze orienting effect (GOE) (RT incongruent – RT congruent) for each emotion. In all analyses, N=23 and error bars represent SE to the mean.

3.4.2 ERPs to the target

3.4.2.1 P1 Amplitude

We found a main effect of Electrode (*F* (1, 22) =22.46, MSE=19.63, *p*< .05, η_p^2= .51) with larger amplitudes at O1/O2 than at PO7/PO8, and a main effect of Emotion (*F* (2, 44) = 3.33, MSE=2.00, *p*< .05, η_p^2= .13) with overall larger amplitudes for targets preceded by happy than by angry faces (*p*< .01). Additionally, the expected congruency effect was found (*F* (1, 22) =4.20, MSE=1.73, *p*= .05, η_p^2= .16), with larger P1 amplitudes in the congruent than in the incongruent condition (Figure 11).

Planned analyses for each emotion revealed a main effect of Congruency for happiness (*F*(1, 22) = 6.42, MSE= .92, *p*= .02, η_p^2= .23) as well as a Hemisphere by Congruency interaction (*F*(1, 22) = 4.72, MSE=1.08, *p*= .04, η_p^2= .18) which was due to the congruency effect being present on the left (*p*= .02) but trending on the right hemisphere (*p*= .09). The congruency effect was not significant for the neutral or angry emotions (Figure 11 a, b).

3.4.2.2 P1 Latency

There was neither a main effect of Congruency (*F* (1, 22) =1.41, MSE=89.21, *p*=.25, η_p^2= .06) nor a Congruency by Emotion interaction (*F* (2, 44) =.59, MSE=63.87, *p*=.56, η_p^2=.03) on P1 latency.

3.4.3 ERPs to gaze cues

3.4.3.1 EDAN

A main effect of Hemisphere was found (*F* (1, 22) =6.93, MSE=11.18, *p*=.01, η_p^2=.24) with larger amplitudes in the right than in the left hemisphere. A main effect of Gaze laterality was also found (*F* (1, 22) = 9.25, MSE= .18, *p*<.01, η_p^2=.27) such that the amplitude was more negative for contralateral gaze compared with ipsilateral gaze direction (Figure 12a, b). In addition, there was a main effect of Emotion (*F* (1.25, 27.42) = 12.87, MSE=1.76, *p*<.01, η_p^2= .37) such that happy and angry faces led to more negative amplitudes than neutral faces as shown in Figure 12b (*p*<.01 for both). No significant interaction between Emotion and Gaze laterality was found (*F* (2, 44) = .28, MSE= .08, *p*=.63, η_p^2=.02).

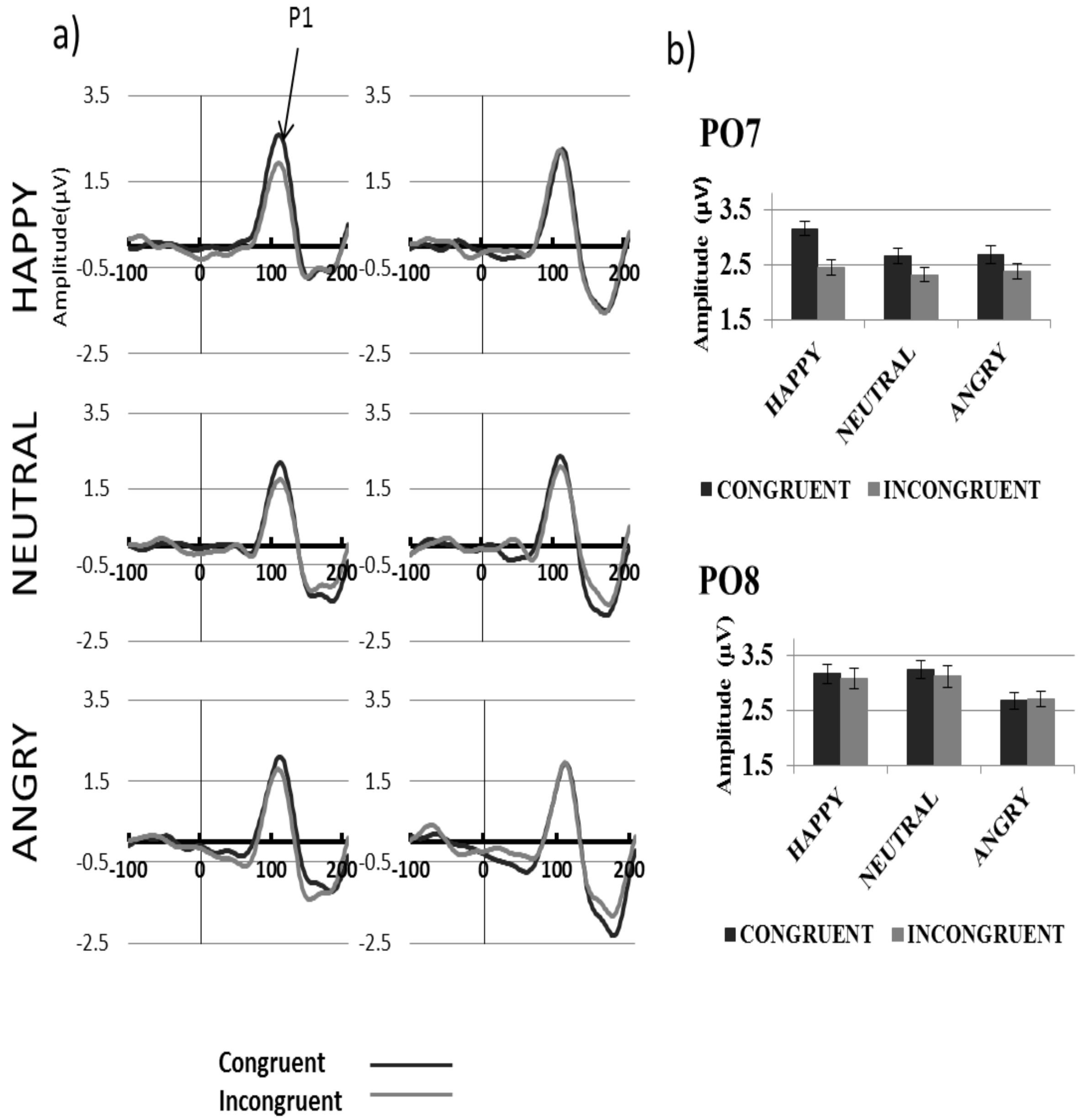

Figure 11: ERPs to the target in Condition HAN (a) ERP waveforms showing P1 component at electrodes PO7 (left hemisphere, left panels) and PO8 (right hemisphere, right panels) for each emotion (Happy, Angry, Neutral: N=23). (b) Mean P1 amplitudes for the incongruent and congruent conditions for each emotion: left hemisphere (PO7, upper panel) and right hemisphere (PO8, lower panel).

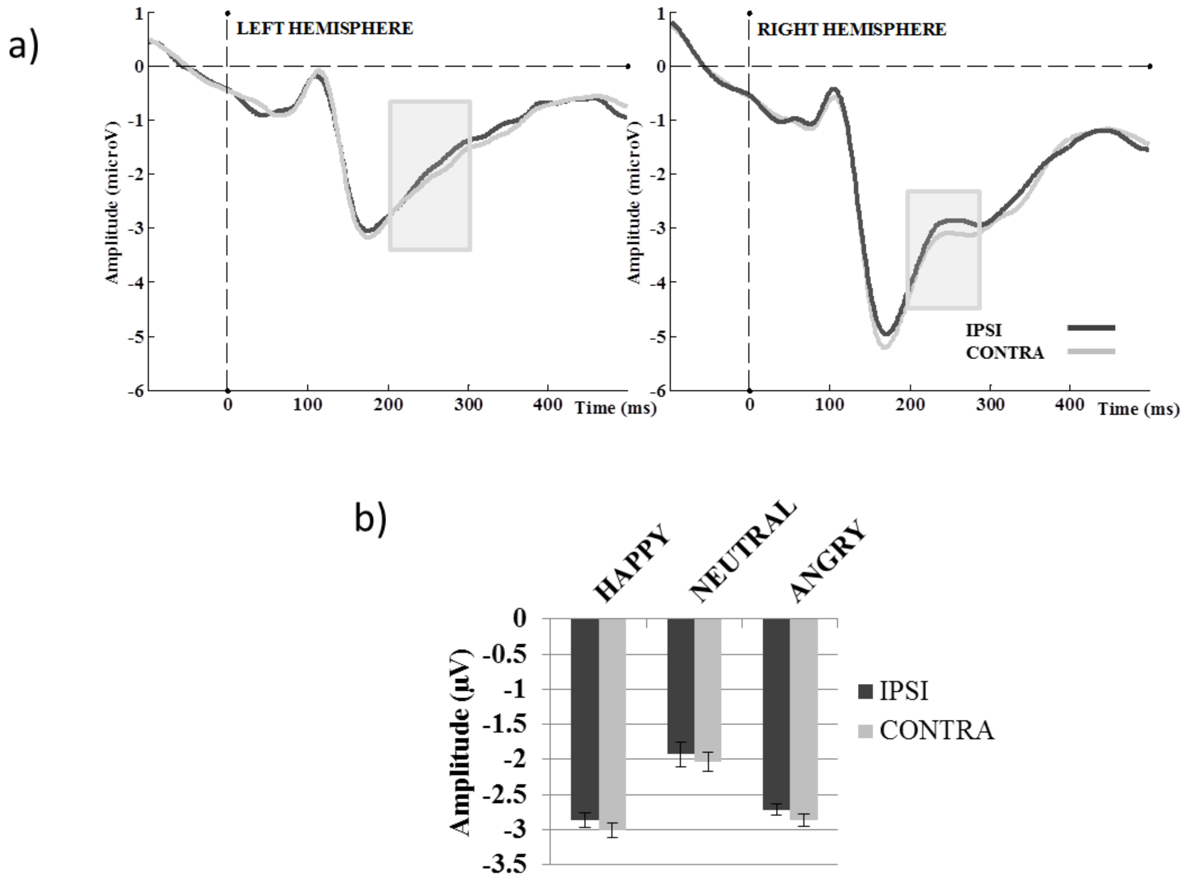

Figure 12: EDAN component to the face cue in Condition HAN (a) Effect of gaze laterality on the group ERP waveforms (averaged across emotions and across electrodes). The grey zone marks the time limits of the analysis (200-300ms). (b) Group amplitudes for contra- and ipsilateral gaze directions averaged across emotions and electrodes between 200 and 300ms.

3.4.3.2 ADAN

We found a main effect of Gaze laterality (*F* (1,22)= 7.07, MSE=.13, *p*=.04, η_p^2=.17) such that the amplitude was less positive for the contralateral gaze direction compared to the ipsilateral gaze direction as shown in Figure 13a and 13b. In addition, there was a main effect of Emotion (*F* (2, 44) =6.19, MSE=.49, *p*<.01, η_p^2=.22) such that happy faces led to larger amplitudes than neutral faces as seen on Figure 13b (*p*<.01). No Emotion by Gaze laterality interaction was found (*F* (2, 44) =.03 MSE=.10, *p*=.97, η_p^2<.01).

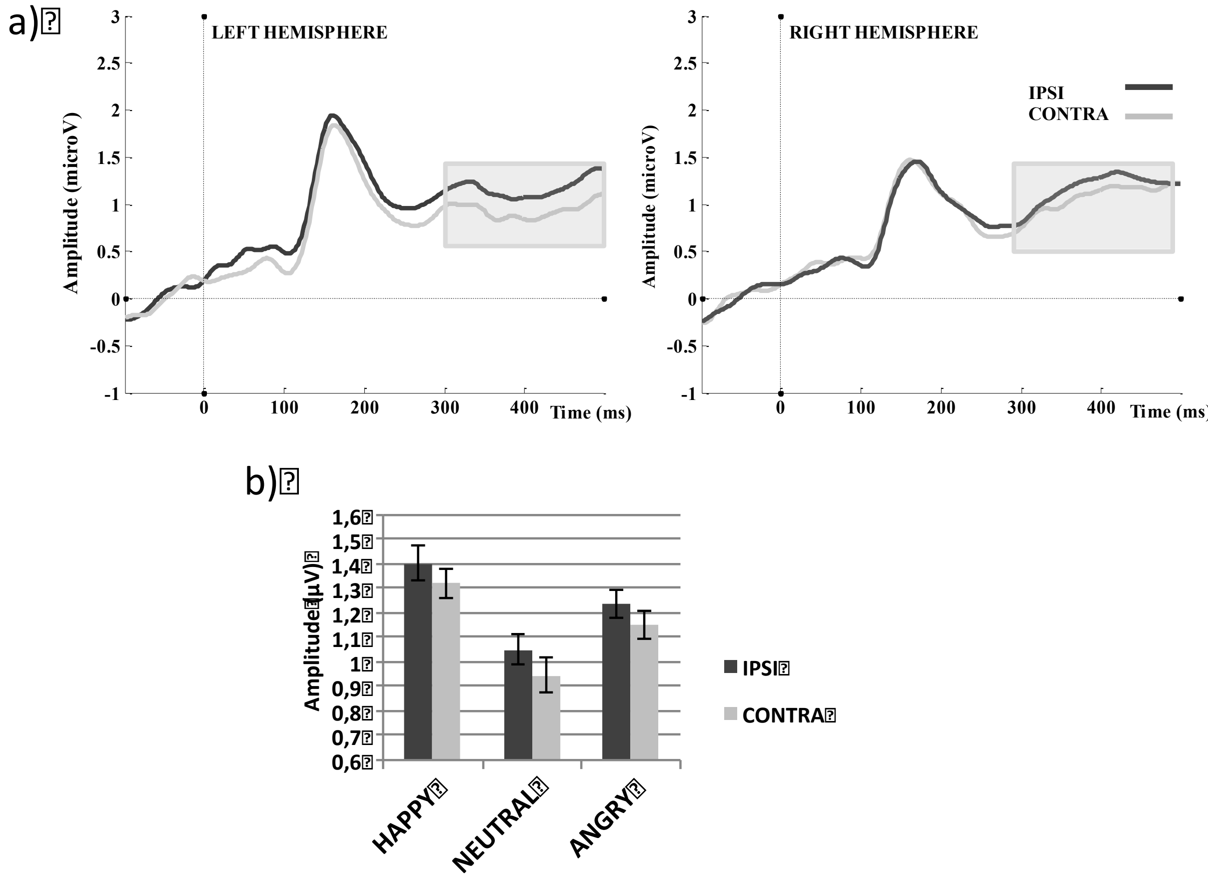

Figure 13: ADAN component to the face cue in Condition HAN (a) Effect of gaze laterality on the average ERP waveform (averaged across emotions and across electrodes). (b) Group amplitudes for contra- and ipsilateral gaze directions averaged across emotions and electrodes between 300 and 500ms.

3.4.4 Summary of Condition HAN

The classic GOE was found and was enlarged for targets preceded by angry faces compared to those preceded by neutral or happy faces. A congruency effect was found on P1 amplitude and there was a left lateralized enhancement of this effect when happy faces preceded the target. At cue presentation, amplitudes were more negative when the gaze was directed toward the contralateral than the ipsilateral hemifield at early latencies posteriorly (EDAN) and at later latencies anteriorly (ADAN). Larger amplitudes were also seen for emotional than neutral faces between 200 and 500ms although the effect was weaker between 300 and 500ms. However, no Gaze laterality by Emotion interaction was found for either of these two components.

3.5 DISCUSSION OF EXPERIMENT 2

Both RTs and scalp ERPs were recorded in two gaze-cuing conditions involving different facial expressions. We found that attention orienting was enhanced at gazed-at locations and that the size of this enhancement varied depending on the emotion expressed by the face cue. These behavioral and electrophysiological results are discussed in turn below.

3.5.1 GOE modulation by emotions

Our first goal was to establish the impact of anger, happiness, fear and surprise on attention orienting in the general, non-anxious population. Using dynamic stimuli, a localization task and a 500ms SOA, we observed faster RTs for the congruent compared to the incongruent conditions. This classic GOE (see Frischen et al., 2007 for a review) reflects the enhanced spatial attention allocation at the gazed-at location. Better accuracy was also found for congruent than incongruent trials, as previously reported (e.g., Graham et al., 2010). Most importantly, this GOE was enlarged when the cue displayed a fearful or surprised rather than a neutral expression and when it displayed an angry rather than a happy or neutral expression. This GOE enhancement was driven by faster reaction times for those emotions compared to neutral expressions in the congruent trials.

Numerous studies that investigated the modulation of the GOE with emotional faces focused on fear due to the intuitive advantage conferred by threat detection. Indeed, although fast attention orienting toward the direction of another's gaze is expected regardless of facial expression, orienting to an object eliciting fear should be even faster given the object being looked-at is likely a threat. In accordance with this idea and with previous studies, we found an increased GOE for fearful compared to neutral faces (Fox et al., 2007; Tipples, 2006; Graham et al., 2010; Mathews et al., 2003; Tipples, 2006; Neath et al., 2013). As outlined in the introduction of this chapter, failure by some studies to find such a GOE increase for fearful compared to neutral faces could be attributed to the use of a too short SOA (e.g., Galfano et al., 2011; Bayless et al., 2011), the use of a static rather than dynamic cue (e.g., Hietanen & Leppanen, 2003) or the use of a discrimination task rather than a localization task (e.g., Mathews et al., 2003 in low anxious; Holmes et al., 2010).

Surprised expressions have rarely been employed in gaze cuing experiments. One study reported larger GOE for surprised than angry and happy expressions, but not than neutral expressions (Bayless et al., 2011), possibly due to the use of a short SOA (200ms). In accordance with our results, a recent study reported a larger GOE for surprised than neutral faces (Neath et al., 2013). Interestingly, the magnitude of the GOE was similar for surprise and fear, as also found previously (Bayless et al., 2011; Neath et al., 2013). Both fearful and surprised faces are characterized by enlarged sclera size, which may make the gaze changes more salient and contribute to the increase in GOE (Bayless et al., 2011; Tipples, 2006). As seen with fear, rapid orienting toward an object looked at by a surprised face could also be highly beneficial for survival. Surprised faces signal the presence of a novel object but remain ambiguous regarding its valence. In the real world, surprise is transitory and is followed by another emotion (Fontaine et al., 2007). Given this subsequent emotion is uncertain, it could be advantageous for the viewer to orient faster toward the object eliciting surprise in order to determine whether it is dangerous. Alternatively, the GOE enhancement with surprise could be due to its negative valence in the context of fear. Indeed, surprise is perceived negatively when presented with negative emotions (Neta & Whalen, 2010; Neta et al., 2011). Relative rather than absolute valence might be important for an emotional modulation of the GOE, an idea that future studies will have to test.

Tiedens (2001) suggested that anger displays are used by expressers to be recognized as legitimate leaders since power is conferred to angry individuals. It could thus be advantageous to attend faster to whatever object made a powerful figure angry. Previous gaze orienting studies failed to show an enhancement of the GOE with anger (e.g., Bayless et al., 2011; Fox et al., 2007; Hietanen & Leppanen, 2003). This lack of result could be explained by the use of a too short SOA in some cases (e.g., Bayless et al., 2011). In other studies (Hietanen & Leppanen, 2003 [Exp.6], Bayless et al., 2011, Fox et al., 2007), fearful expressions were also present in the design and although localizing a conflict could be beneficial, it might be less so than localizing a danger. As a result, the effect of anger on the GOE could have been masked in experiments including fearful faces. One study in which fearful faces were not included did report an increase of the GOE with anger compared with neutral and happy faces, but only in high anxious participants (Holmes et al., 2006). The lack of effect reported in low anxious individuals in that study might be due to the use of a discrimination task. When using a localization task and a long enough SOA without fearful faces in the same design, we showed a GOE enhancement for angry relative to happy and neutral faces, in non-anxious participants (Condition HAN). Thus, like fear and surprise, anger can also enhance spatial attention orienting. Whether this enhancement is due to the task, the lack of fearful faces in the design, the SOA or all factors combined, will need to be addressed by future studies.

In contrast, joy never modulated the GOE in any study including the present one. From an evolutionary standpoint, there is no advantage to orient rapidly toward an object eliciting a smile, as this object is likely to be another non-threatening individual. Although important to signal a social interaction, a smiling face with averted gaze does not seem critical for immediate survival.

In addition to evolutionary relevance and relative valence of an emotion, eye sclera size has been linked to the modulation of the GOE with emotions and is larger in fearful and surprised faces compared to neutral faces (Bayless et al., 2011; Tipples, 2006). However, one study using similar faces as the ones used here found that sclera size was also larger for neutral than happy and angry faces (Bayless et al., 2011), making it unlikely that this was a critical factor in our results, given the larger GOE found for angry compared to neutral faces.

The amount of apparent motion also differs depending on the emotion expressed by the face cue. In the emotional conditions neutral faces with direct gaze changed to emotional faces with averted gaze, inducing apparent movement in gaze and in the rest of the face. Even when there was no gaze shift (direct gaze condition), the rest of the face moved. In contrast, in the neutral expression condition, neutral faces remained neutral and thus showed less apparent motion than emotional faces in the averted gaze condition and none in the direct gaze condition. However, movement didn't seem to be a critical factor in eliciting the GOE here, as happy expressions, which also contained movement, did not enhance the GOE compared to neutral faces. In contrast, in the direct gaze condition, it is impossible to disentangle whether emotional content or movement is driving the faster response for emotional relative to neutral faces as all emotions decreased the response times to targets compared to neutral faces. Future studies, using face inversion (which preserves movement but disrupts emotional processing), could help shed more light on this issue.

Importantly this GOE enhancement with fearful, surprised and angry facial expressions was found in the general, non-anxious, population. Previous studies showed that the GOE enhancement for negative emotions such as fear or anger was dependent on the anxiety or fearfulness of the participants (Putman et al., 2006; Tipples, 2006; Fox et al., 2007, Holmes et al., 2006; Mathews et al., 2003). In contrast, the present study showed a modulation of the GOE with fear, anger and surprise in non-anxious participants, replicating recent findings (Neath et al., 2013), and extending them, for the first time, to angry faces.

Thus, the emotion modulation of the GOE can be found in the general population when using dynamic stimuli and a localization task.

Finally, the GOE enhancement for the emotional faces reported here was due to faster RTs in the congruent condition rather than longer RTs in the incongruent condition, reflecting a facilitation of gaze-oriented attention for these emotions. Overall, these findings suggest that certain emotions boost gaze-oriented attention and that the degree to which an emotion influences spatial attention could depend on its relative evolutionary relevance, the fact that it signals threat or its negative valence.

3.5.2 ERPs to targets

Our second main goal was to find neural correlates of the modulation of gaze orienting by emotions using ERPs. P1, a component influenced by attention (Mangun, 1995), was investigated. In accordance with previous studies, P1 showed larger amplitudes for congruent than for incongruent trials (Hietanen et al., 2008; Schuller & Rossion, 2001, 2004, 2005), which reflected enhanced spatial attention allocation to gazed-at targets compared to targets that fell opposite to the gazed-at location.

Planned comparisons revealed that this congruency effect was restricted to targets following surprised and fearful faces in Cond. FSN and to right-sided targets following happy faces in Cond HAN. This is the first gaze cuing study showing a modulation of the congruency effect on P1 amplitude with emotion. Previous studies using shorter SOAs failed to observe this finding on P1 amplitude but also at the behavioral level (Fichtenholtz et al., 2007; Galfano et al., 2011), suggesting that when emotional faces are used, longer SOAs are required to influence the spatial attention network and the processing of the target, in accordance with previous research (Graham et al., 2010). Further supporting the idea that integration of gaze and emotion takes time, P1 was delayed in the congruent compared to the incongruent condition in Cond. FSN, whereas previous studies using only neutral faces reported a shorter P1 latency in the congruent compared to the incongruent condition (Hietanen et al., 2008; Schuller & Rossion, 2001, 2004, 2005) or simply didn't analyze P1 latency (Fichtenholtz et al., 2007, 2009; Galfano et al., 2011; Holmes et al., 2010).

The presence of a congruency effect on P1 for fearful and surprised but not neutral faces in the current study suggests that spatial attention resources were preferentially allocated to targets following these emotional faces, likely because they suggest a potential threat for the observer. The lack of congruency effect on P1 amplitude for targets following neutral faces contradicts previous findings (Schuller &

Rossion, 2001, 2004, 2005; Hietanen et al., 2008) but makes sense in this particular emotional context as objects observed with a neutral face are likely less important than objects looked-at by a fearful or surprised face.

In addition, while we observed an enhancement of the GOE for angry relative to happy and neutral faces, the congruency effect on P1 was only enhanced for right targets preceded by happy faces (i.e., only in the left hemisphere). This might reflect the anticipation of a positive item, which has been linked to left hemispheric activation (Davidson & Irwin, 1999). Anticipation could also explain why anger did not modulate the congruency effect on P1 amplitude, as in this case the outcome is ambiguous (Carver & Harmon-Jones, 2009). Although not significant, there was a tendency for the P1 congruency effect to be localized to the right hemisphere for targets following fearful and surprised faces (Figure 7a), which is also consistent with the hypothesis of a lateralized P1 congruency effect linked to the anticipation of the outcome depending on the valence of the face cue.

Alternatively, this emotional modulation of the P1 congruency effect could reflect later stages of emotional processing of the cue interacting with the visual processing of the target. Indeed, it was recently argued that emotions for which the diagnostic feature is in the bottom part of the face (like mouth for happiness) activate the left hemisphere while emotions for which the diagnostic feature is located in the top half of the face (like eyes for fear and surprise) activate the right hemisphere preferentially (Prodan, Orbelo, Testa, & Ross, 2001).

Overall, the attention effect on early visual processes related to the target was enhanced for surprise and fear, and for happiness in the left hemisphere, possibly reflecting contamination by later processing stages of the preceding facial expression or the anticipated valence of the target. Future studies will have to disentangle between those hypotheses.

3.5.3 ERPs to the gaze cues

Our final goal was to establish the temporal stages involved in the emotional modulations of gaze-oriented attention during cue presentation. It was suggested that the processes at play in gaze-oriented attention are similar to those involved in arrow-oriented attention (e.g., Brignani et al., 2009). Thus, the two stages of attention, orienting toward a cued location and holding attention at that location, indexed respectively by EDAN and ADAN components in arrow cuing paradigms, were expected. The present study is the first to report both EDAN and ADAN components in a gaze cuing paradigm. Hietanen and colleagues (2008) found EDAN and ADAN with arrow but not gaze cues while Holmes and colleagues (2010) found no evidence for EDAN with gazing faces but did find an ADAN component. These discrepant results could be due to the use of different experimental parameters. We used face photographs presented dynamically while Hietanen and colleagues (2008) used static schematic face drawings. In addition, we used a target localization task, not a target discrimination or a detection task as used previously by Holmes and colleagues (2010) and Hietanen and colleagues (2008) respectively. Although the GOE was shown regardless of the task for neutral faces, smaller congruency effects were seen with discrimination compared with detection or localization tasks due to their higher cognitive demands (Friesen & Kingstone, 1998). The choice of the task was based on the idea that, in real life, we most often use eye gaze to localize the source of the emotion before discriminating it. Our results are consistent with studies suggesting that attention orienting by gaze and arrows may recruit similar neural networks (e.g. Brignani et al., 2009) although to be conclusive, prospective studies will need to directly compare EDAN and ADAN components to arrow and gaze cues in the same paradigm. It is also important to note the larger gaze laterality effect at ADAN than at EDAN. This suggests that although attention orienting starts around 200ms after gaze shift (EDAN), it is maximal between 300-500ms of cue processing (ADAN).

As expected, EDAN was not modulated by emotion given it occurs between 200-300ms after gaze cue onset, whereas emotion and gaze cues seem to require more than 300ms to be fully integrated. In addition, in accordance with Holmes and colleagues (2010), we did not observe an emotional modulation of ADAN, suggesting that emotion does not modulate gaze-oriented attention before 500ms after gaze onset.

Incidentally, we found that for faces with averted gaze, amplitudes at posterior sites were larger for facial expressions relative to neutral faces between 200 and 300ms (EDAN). This effect is in line with the literature reporting an enhancement of ERP components with all emotions regardless of their valence between those latencies, and likely reflecting general emotional arousal (see Vuilleumier & Pourtois, 2007 for a review). At anterior sites, between 300 and 500ms (ADAN), amplitudes were also enhanced, albeit less strongly, for surprise and happiness relative to neutral faces, likely reflecting more complex emotional appraisal (Vuilleumier & Pourtois, 2007).

3.5.4 Temporal dynamics of gaze-oriented attention and its modulation by emotion

Overall, we showed that in a gaze cuing paradigm, just like in arrow cuing studies, orienting of attention by gaze and holding of attention at gazed-at location could be indexed by EDAN and ADAN components.

The first response to emotions was seen between 200-300ms after face cue onset (EDAN) during which attention orienting processes just began. Between 300 and 500ms after cue onset (ADAN) emotion processing continued while attention orienting was fully expressed. Thus, both emotion and gaze-oriented attention processes occurred during the cue presentation but the emotional effect was larger earlier on while attention orienting was maximal later on, suggesting a slight temporal difference between these processes.

The integration of gaze and emotion occurred even later. Emotional expressions began to influence gaze orienting only at target presentation, as seen by modulations of the congruency effect on P1 for targets preceded by happy, surprised and fearful expressions. As P1 occurred on average around 100ms after target onset, emotional modulation of attention thus started around 600ms after cue onset. However, the emotional modulation observed at this stage was weak and lateralized. It also differed from the emotional modulation of gaze-oriented attention observed at the behavioral level (with larger GOE for angry, fearful and surprised faces relative to neutral faces). The emotional modulation of gaze-oriented attention thus occurred between the P1 and the motor response, i.e., between 600ms and 800ms after cue onset (given an average of 300ms response times) and varied as a function of emotions. That is, fear and surprise increased attention to the target (P1) and increased the behavioral GOE (compared to neutral faces). In contrast, happiness increased attention to the target but did not increase the behavioral GOE while anger did not modulate attention to target but did increase the GOE. We thus conclude that fear and surprise modulate attention processes earlier than does anger. We also suggest other processes occur between target-triggered P1 and the behavioral responses that would account for the emotional modulation of the GOE with anger and the lack thereof with happiness. Alternatively, it is possible that emotions start modulating attention processes before target onset, but in incremental ways that would be individually too weak to be picked up by ERPs such as EDAN or ADAN. In this view the behavioral response would be the result of the integration of these multiple neural processes occurring between the presentation of the cue and the motor response.

3.6 CONCLUSIONS

In the present ERP study involving a dynamic display of facial expressions and a target localization task, we showed that the gaze orienting effect was enhanced for fearful and surprised faces compared to neutral faces and for angry faces compared to neutral and happy faces, in a sample of non-anxious individuals. We also presented evidence for an emotional modulation of the gaze congruency effect on P1 ERP component recorded to the target. Finally, we were able to find ERP correlates of spatial attention orienting during gaze cue presentation (EDAN and ADAN components) although at these stages, attention was not yet modulated by the emotion of the face cue. Modulations of gaze-oriented attention by emotions arose later, starting weakly on P1 and being seen more clearly on the GOE. These effects were different depending on the emotion, with seemingly earlier modulations for fear and surprise than for anger. Together, these findings suggest that the modulation of spatial attention with emotion in gaze cuing paradigms is a rather late process, occurring between 600 and 800ms after face cue onset.

In the next chapter of this thesis, I focused on behavior alone and investigated the effect of the type of dynamic sequence used on the modulation of the GOE by emotions.

Chapter 4: Emotional modulation of attention orienting by gaze depends on cue sequence (Experiment 3)[12]

4.1 INTRODUCTION

In Chapter 3, we saw that the GOE was modulated by fearful, angry and surprised expressions in non-anxious participants, when a localization task, a 500ms SOA and a dynamic face stimulus were used. However, given that the modulation of gaze-oriented attention with emotions is a small effect (around 4-6ms on average in Chapter 3), it is likely sensitive to experimental parameters, which could explain the lack of consistent results across previous gaze-cueing studies. For instance, the way in which a face cue is presented is an important methodological difference between studies. A few studies have used static face presentations (Hietanen & Leppänen, 2003 [Exps.1-4]; Holmes et al., 2006 [Exp.3]; Hori, Tazumi, Umeno, Kamachi, Kobayashi, Ono & Nishijo, 2005) and none of them showed a modulation of the GOE with emotional faces. Other studies have used dynamic facial stimuli, which are known to enhance the perception of emotions (e.g., Sato & Kochiyama, 2004). However, the sequence chosen for the dynamic face cues varied substantially across these studies. The parameters associated with a particular sequence might have influenced the way in which the emotion was processed, and, in some cases, facial expressions might not have been processed well enough to modulate gaze orienting.

Some studies have used dynamic stimuli sequences in which the emotion was expressed first, before gaze aversion (Hietanen & Leppänen, 2003; Mathews et al., 2003[Exps. 5 and 6]; Galfano et al., 2011). Among these studies, only Matthews and colleagues (2003) showed an enhancement of the GOE with fearful faces, but this effect was restricted to high anxious participants. Such null results could be due to a lack of ecological validity (i.e., in real life, most often, people react to a stimulus after localizing and evaluating it). In addition, given that facial expressions remain constant throughout the stimulus presentation while gaze shifts abruptly, processing of gaze signals might be prioritized over emotion processing. Finally, eye size varies depending on the emotion expressed by the face. The eyes are wide-open in fearful and surprised faces and are squinted in angry and happy facial expressions. Given that

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[12] This part of our work was presented at a national conference (Lassalle & Itier, 2012b) and yielded an abstract in The Canadian Journal of Experimental Psychology. A full article presenting our results is in preparation.

gaze is more salient in large eyes than in squinted eyes, the way in which eye gaze is processed could be influenced by the facial emotion.

Other studies have adopted a dynamic stimulus display in which gaze and emotion were changed simultaneously such that a frame showing a neutral face with direct gaze was immediately followed by a frame showing an emotional face (of same identity) with averted gaze (Holmes et al., 2010; Tipples, 2006; Chapter 3) or by a succession of frames representing the face gradually shifting its gaze and expressing an emotion (Bayless et al., 2011; Fichtenholtz et al., 2007; 2009; Putman et al., 2006; Uono et al., 2009). Some of these studies showed a modulation of the GOE with facial expressions (Chapter 3; Tipples, 2006; Putman et al., 2006; Bayless et al., 2011, Uono et al., 2009) but others did not (Fichtenholtz et al., 2007; 2009; Holmes et al., 2010). Although more ecologically valid, this stimulus sequence still presents the low level confound mentioned earlier: the size of the eyes varies with the expressed emotion (e.g., wide eyes for fear, squinted eyes for happiness).

The last type of dynamic facial cue used was a display in which the gaze was averted first, before emotion onset. When using such a stimulus, Graham and colleagues (2010) observed a modulation of the GOE with fearful faces in an unselected population (i.e., participants' anxiety was not assessed) and Neath and colleagues (2013) reported a larger GOE for fear and surprise than neutral faces across a developmental non-anxious population. This stimulus sequence makes the most sense in terms of ecological validity since one would need to foveate toward an environmental stimulus before reacting to it. In addition, it allows the effect of the gaze shift to be independent from eye aperture.

The extent to which differences in these dynamic cue sequences influence the modulation of gaze-oriented attention by facial expressions is unknown and some of the null findings reported in the literature might be driven, in part, by the sequence used. In the present studies, involving only non-anxious participants (to avoid any confound due to anxiety), we investigated whether the modulation of the GOE by various facial expressions (neutral, fearful, happy, angry, surprised) was influenced by the dynamic cue sequence used. We had three conditions, one in which the face cue expressed an emotion before averting its gaze (Condition 1), one in which the cue averted its gaze before expressing an emotion (Condition 2), and finally one in which both emotion and gaze changed at the same time (Condition 3). We predicted that the emotional modulation of the GOE would be largest in Condition 2 given the likely more ecological nature of this sequence. We were also interested in clarifying whether this emotional modulation of the GOE was due to emotional faces (modulating the GOE) being responded to faster than neutral faces in the congruent condition (*facilitation* of engagement to the gazed-at location) or slower than neutral faces in the incongruent condition (*inhibition* of disengagement) or both. The enhancement of the GOE by certain emotion was due to both a facilitation of engagement and an inhibition of disengagement for emotional relative to neutral faces in Putman and colleagues (2006). However, emotional faces that modulated the GOE facilitated engagement but did not inhibit disengagement compared to neutral faces in Chapter 3, a result we hoped to replicate in the present experiment.

In Chapter 3, we reported an enhancement of the GOE for fearful and surprised expressions compared to neutral expressions, as well as an enhancement of the GOE for angry expressions compared to neutral and happy expressions (recall that there were two separate conditions with different emotions in each). Fearful and angry faces have a negative valence and both signal threat, while happy faces have a positive valence. The valence of surprise, although inherently ambiguous (Fontaine et al., 2007), is negative in the context of negative emotions like fear and also perceived as signaling threat (Neta & Whalen, 2010; Neta et al., 2011). We thus interpreted the GOE findings as driven by the negative valence and/or the communication of an environmental threat. The increased GOE found for anger was only reported once before (Holmes et al., 2006 [Exp.3]). Interestingly in both designs, anger was tested without fear. We thus hypothesized that when fearful faces were present in the design, the threat-related modulation of the GOE by anger might be attenuated compared to when angry faces were presented with just happy or neutral faces as in Chapter 3 and in Holmes and colleagues (2006). We tested this hypothesis in the present experiment by including all five emotions in each cue sequence condition. If the presence of fearful emotions in the design is the reason why anger did not modulate the GOE in previous studies, we expected to see an increased GOE for fearful and surprised faces but not for angry faces. If the GOE was also modulated by anger, we would conclude that other factors were responsible for the previously reported null findings and that the GOE is indeed increased by negative and threat-related emotions.

We also hoped to clarify the cost and benefit pattern for neutral faces, using a dynamic sequence. Some early gaze-cueing studies (using neutral faces) reported that, in addition to faster responses to congruent than to incongruent targets, the congruent targets were also responded to faster than targets preceded by a face with direct gaze (used as a non-directional cue), reflecting a *benefit* in engaging attention in the gazed-at direction (Friesen & Kingstone, 1998; Hietanen, 1999; Langdon & Smith, 2005). However, whether the incongruent condition is responded to more slowly than the direct gaze condition remains unsettled: this *cost* in disengaging attention from the gazed-at location (towards the actual target presentation) was found by some studies (Hietanen, 1999; Langdon & Smith, 2005) but not by Friesen & Kingstone (1998). Determining whether there is a disengagement cost in gaze-cueing could potentially shed light on the nature of the gaze orienting effect. Indeed, non-predictive peripheral or exogenous cueing (refer to section 1.1.3. for details) is thought to be associated with a pattern of benefit without cost (Posner & Snyder, 1975) while both cost and benefit of similar magnitude are observed in predictive symbolic cueing (Posner, 1980). Similarly with arrow cueing, we predicted to find both a cost and a benefit with gaze cueing. Indeed, EDAN and ADAN, two cue-triggered ERP components typically found in arrow cueing, were also present in a gaze cueing experiment (Chapter 3), suggesting arrow and gaze cueing could rely on similar spatial attention mechanisms.

4.2 METHODS

4.2.1 Participants

In each experimental condition, 18 students from the University of Waterloo were included (Table 3). They all ranged from 18 to 28 years of age. Participants had no self-reported history of psychiatric or neurological illness, were all right handed and had a corrected-to-normal vision.

As in Chapters 2 and 3, only participants scoring below 42 on the trait anxiety scale (STICSA: Gros, Antony, Simms, & McCabe, 2007) were included in the final analysis. Mean anxiety score and age did not differ between the 3 groups as measured by independent t-tests. Participants were either paid $10 or received a course credit for their participation in the study. The experimental procedure was approved by the Ethics Research Board of the University of Waterloo and all participants gave written informed consent.

Table 3

Demographics of the participants for the three conditions (F= female, M= male, SD into brackets)

Measures	Condition 1	Condition 2	Condition 3
Number of subjects	18 [10F, 8M]	18 [9F, 9M]	18 [9F, 9M]
STICSA score	30.83 (5.66)	30.39 (6.14)	30.50 (4.93)
Age (years old)	21.6 (1.82)	21.7 (2.68)	19.80 (1.44)

4.2.2 Stimuli and procedure

These stimuli were identical to those used in Chapters 2 and 3 (see section 2.2.2 for a full description).

Similarly to Experiments 1 and 2 (Chapter 2 and 3 respectively), participants performed Experiment 3 in a quiet, medium-lit and electrically shielded room and sat 67 cm away from the computer screen. A chin rest and a head restraint were used to keep the viewing distance of the monitor constant and minimize participants' movements.

Each condition was programmed using Presentation software (Neurobehavioral Systems) and consisted of 5 blocks of 240 trials each. Within a block, each of the 8 identities was presented 30 times in a different condition (one emotion; fear, surprise, neutral, anger and happiness combined with a gaze direction; direct, rightward or leftward, and a target position; left or right). The trials were randomized within a block. Each trial started with a fixation cross (1.28˚ by 1.28˚ of visual angle) presented randomly for 800, 900, 1000, 1100 or 1200ms at the center of the screen. Subsequently, a dynamic face (8.02˚ by 12.35 ˚ of visual angle) sequence was presented centrally for a total of 1000ms. The trial ended by the presentation of a target, consisting of a black asterisk (.85˚ by .85˚ of visual angle) that was presented on either side of the monitor, 7.68˚ from the center, for a maximum of 500ms. The face sequence differed between the three experiments (Figure 14). In Condition 1 (emotion followed by gaze shift), the sequence was composed of a neutral face with direct gaze presented for 200ms followed by the same face displaying one of the five possible expressions for 300ms. The emotional face then averted its gaze to the left or right and this last frame lasted 500ms. In Condition 2 (gaze shift followed by emotion expression), the initial neutral face with direct gaze was presented for 500ms before the onset of the gaze shift. The same neutral face with averted gaze was then presented for 200ms followed by the same gazing face now expressing an emotion for 300ms. In Condition 3 (gaze shift and emotion occurring concurrently), the initial neutral face with direct gaze was also presented for 500ms, followed by the emotional face with averted gaze for 500ms[13]. Thus, for all three conditions, the stimulus onset asynchrony (SOA) between the onset of gaze shift and the appearance of the target was always 500ms and the entire dynamic facial

[13] Note that the stimulus sequence used in Condition 3 of this study is identical to the stimulus sequence used in Chapter 3. However, Conditions FSN and HAN presented in Chapter 3 included only three facial expressions while there were five different facial expressions included in the design of Condition 3 (and Conditions 1 and 2).

sequence (before target onset) was always 1000ms (Figure 14). The instructions were the same as in Chapter 3.

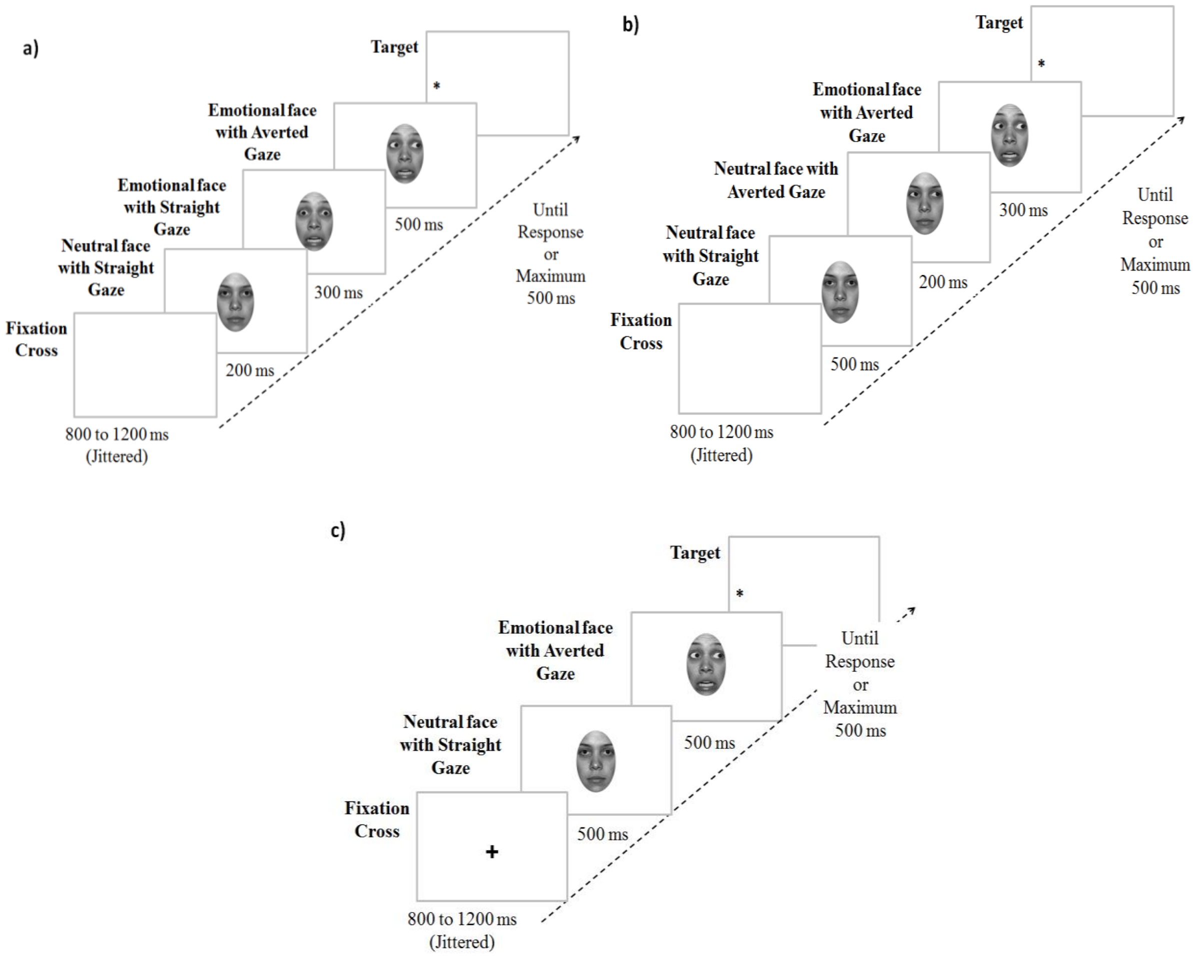

Figure 14: Trial Sequence for a) Condition 1: Emotion, then Gaze, b) Condition 2: Gaze, the Emotion, c) Condition 3: Gaze/ Emotion simultaneous

4.3 DATA ANALYSES

Responses were recorded as correct if the response key matched the side of the target appearance and if reaction times (RTs) were within 100-1200ms. The remaining responses were marked as incorrect. For each experiment, mean response times for correct answers were calculated according to facial emotions (happy, angry, neutral, fearful and surprised) and congruency (congruent, incongruent, straight gaze), with left and right target averaged together. For each subject, only RTs within 2.5 standard deviations from the mean of each condition were retained for that participant's mean RT calculation (Van Selst & Jolicoeur, 1994). This resulted in the exclusion of less than 8% of the trials, on average for each of the Conditions 1, 2 and 3 (Appendix C: Table 7a, 7b and 7c, respectively).

4.4 RESULTS

4.4.1 Overall analysis including congruent/ incongruent/ direct gaze trials and cost-benefit analysis for neutral faces

Trials were analyzed using a mixed design analysis of variance with Condition (1, 2, and 3) as a between subject variable and Emotion (fearful, angry, surprise, happy, and neutral expressions) and Congruency (congruent, incongruent, and direct gaze targets) as within subject variables.

There was a main effect of Congruency (F (1.77, 90.37) =135.74, MSE=253.31, p<.01, η_p^2=.73) such that a faster response was observed in congruent trials than in incongruent and direct gaze trials. In addition, this analysis yielded a significant interaction between Emotion, Congruency and Condition (F (11.94, 304.42) =3.95, MSE=64.53, p<.01, η_p^2=.13). Each Condition was thus analyzed separately. A main effect of Congruency was found in all 3 conditions (Condition1] F (2,34)=31.73, MSE=138.46, p<.01, η_p^2=.14; Condition 2] F(2,34)=113.10, MSE=325.81, p<.01, η_p^2=.87; Condition 3] F(1.83,31.12)=36.15, MSE=58.87, p<.01, η_p^2=.65) and Congruency interacted with Emotion in all three conditions (Condition 1] F(8,136)=2.82, MSE=48.16, p<.01, η_p^2=.14; Condition 2] F(8,136)=12.34, MSE=49.39, p<.01, η_p^2=.43; Condition 3] F(3.90,66.29)=21.25, MSE=46.89, p< .01, η_p^2=.56).

In Condition 1, targets were localized faster in congruent trials than direct gaze and incongruent trials for all emotions except anger, for which congruent targets were only localized faster than incongruent targets (Figure 15). In addition, direct gaze trials were responded to faster than incongruent trials for happy and surprised expressions. In Condition 2, congruent targets were localized faster than direct gaze targets and incongruent targets for all emotions. In addition, incongruent targets were also detected faster than direct gaze targets for neutral, angry and fearful faces. In Condition 3, congruent targets were localized faster than incongruent targets for all emotions except neutral. In the neutral condition, congruent and incongruent targets yielded similar RTs and were detected faster than direct gaze targets. In addition, direct gaze targets were detected faster than incongruent targets significantly for happy and fearful faces.

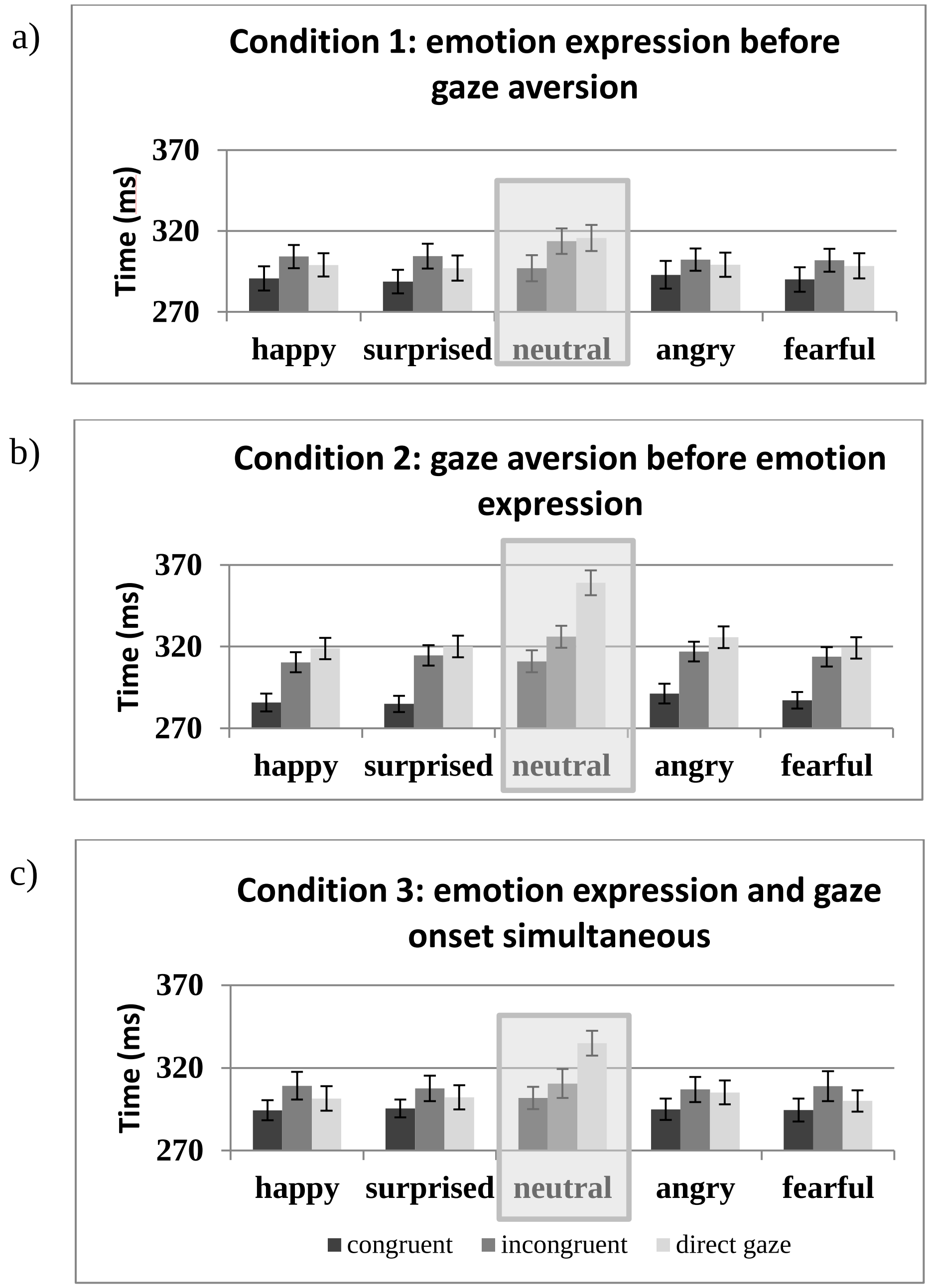

Figure 15: RTs (ms) to targets following happy, surprised, neutral, angry, and fearful faces in congruent, incongruent and direct gaze trials for a) Condition 1, b) Condition 2, c) Condition 3. The shade of grey surrounds the RTs to neutral faces as they are the target of the cost-benefit analysis.

4.4.2 Influence of facial expressions on attention to direct and averted gaze

As mentioned earlier in this thesis, faces with direct gaze are known to capture attention more than faces with averted gaze, especially when they display a threatening emotion (see section 3.2.5, second paragraph). Thus, we also analyzed direct gaze trials separately from averted gaze trials, as done in Chapter 3.

4.4.2.1 Direct gaze analysis

Trials preceded by faces with direct gaze were analyzed using a mixed analysis of variance with Condition (1, 2, and 3) as a between subject factor and Emotion (fearful, surprised, happy, angry and neutral expressions) as a within subject factor. There was a main effect of Condition (F (1, 2) =3.85, MSE=4479.44, p= .03, η_p^2=.13) such that slower responses were observed in Condition 2 than in Condition 1. There was also a main effect of Emotion (F (4, 204)=117.61, MSE=80.25, p< .01, η_p^2=.70) such that all emotional faces were responded to faster than neutral faces, and fear and surprise were responded to faster than anger. Finally, there was an interaction between Emotion and Condition (F (4.68, 119.36) =5.61, MSE=138.56, p< .01, η_p^2=.18). Although each Condition analyzed separately displayed an Emotion effect (Condition1] F(4, 68)=18.04, MSE=60.52, p<.01, η_p^2=.52; Condition 2] F(4,68)=49.41, MSE=108.06, p<.01, η_p^2= .74; Condition 3] F(4, 68)=54.03, MSE=72.16, p<.01, η_p^2= .76) such that targets preceded by emotional faces were responded to faster than targets preceded by neutral faces (p<.01 for each emotion in each condition), this effect of Emotion was largest in Condition 3 and smallest in Condition1 (Figure 15, direct gaze trials).

4.4.2.2 Averted Gaze Analysis

4.4.2.2.1 GOE analysis

For the analysis of averted gaze trials, we focused on the GOE (RT incongruent trials- RT congruent trials), using a 3(Condition: 1, 2, and 3) by 5(Emotions: happy, surprised, neutral, angry, fearful) repeated measure analysis of variance.

The GOE showed a main effect of Condition (F (1, 2) =6.97, MSE=563.46, p<.01, η_p^2=.22) and was larger in Condition 2 than in Conditions 1 and 3 (p<.01 for both comparisons, Figure 16). Conditions 1 and 3 did not differ. It is important to note that this effect of Condition was due to the added difference of the congruent and the incongruent trials as neither incongruent trials, nor congruent trials exhibited an effect of Condition when analyzed separately (p= .86 and p= .55 respectively).

In addition the GOE showed a Condition by Emotion interaction (F (8,204) =3.76, MSE=36.56, p< .01, η_p^2= .13) and was thus analyzed for each Condition separately. This analysis revealed a main effect of Emotion on the GOE only for Condition 2 (F (4, 68) = 7.59, MSE=72.74, p< .01, η_p^2=.31) but not for Conditions 1 or 3 (F (4, 68) =1.84, MSE=91.52, p=.13, η_p^2=.10 and F (4, 68) = 2.01, MSE=51.24, p=10, η_p^2=.11, respectively). The effect of emotion on the GOE for Condition 2 was due to a larger GOE for angry, fearful and surprised expressions compared to neutral ones (p<.05 for all comparisons). In addition, the GOE for happy faces was not significantly different from the GOE for neutral faces but it was also not significantly different from the GOE for fearful, angry and surprised faces (Figure 16).

4.4.2.2.2 Influence of facial expressions on engagement and disengagement

For Condition 2, we analyzed congruent and incongruent trials separately to determine the influence of facial expressions on engagement and disengagement components. There was a main effect of Emotion on both congruent and incongruent trials (F (4, 68) =32.20, MSE=66.24, p<.01, η_p^2=.65 and F (4, 68) =13.34, MSE=47.13, p<.01, η_p^2=.44, respectively), reflecting faster RTs for emotional than for neutral expressions in both types of trials. As seen on Figure 15 (congruent and incongruent trials), This difference between emotional and neutral faces seemed, however, more pronounced in the congruent than in the incongruent condition for fearful, angry and surprised faces, resulting in a GOE enhancement for those facial expressions compared to neutral expressions when the RT difference was computed. In contrast, engagement and disengagement were equally facilitated for happy faces relative to neutral faces, resulting in a lack of significant GOE difference between happy and neutral expressions.

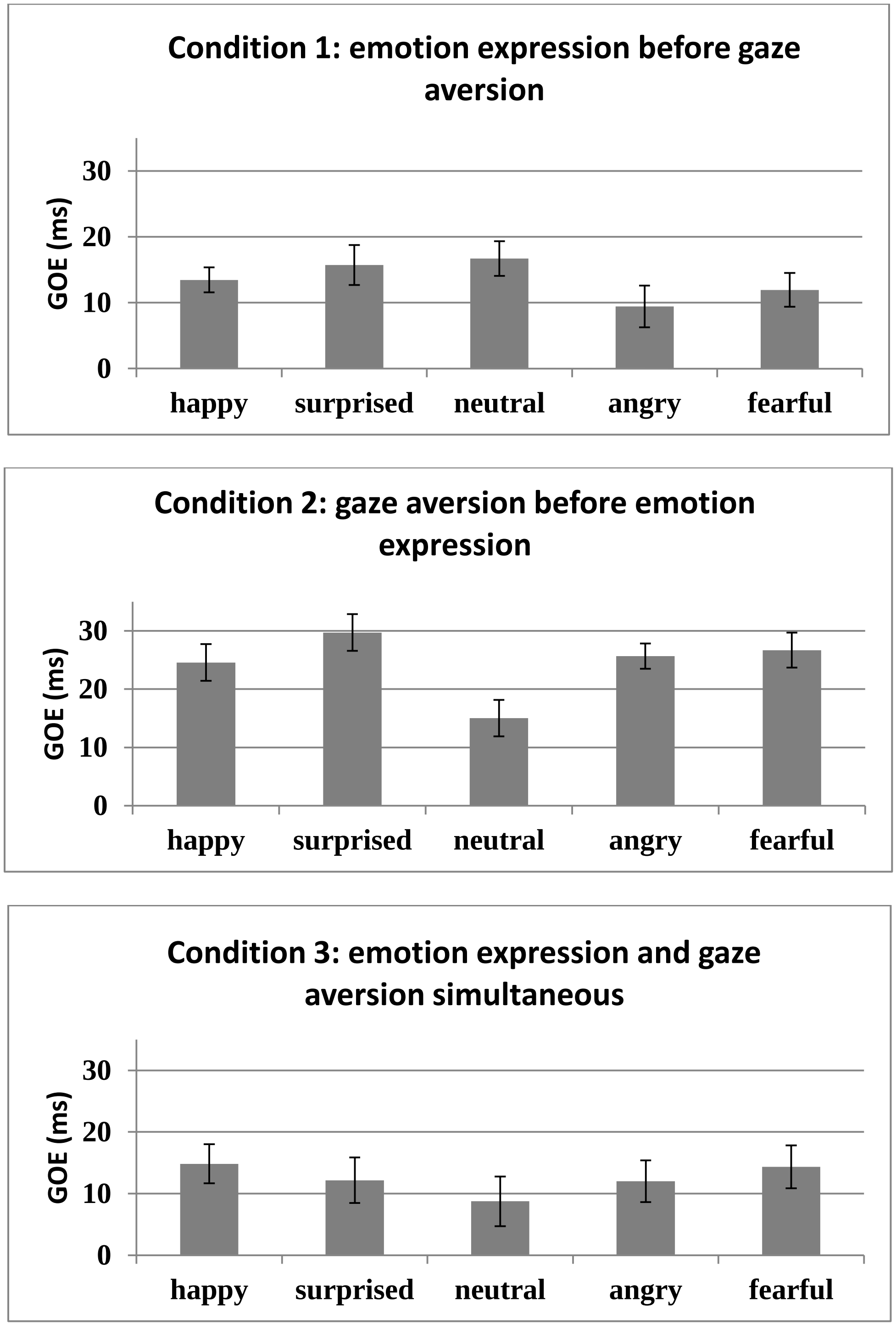

Figure 16: GOE (ms) for happy, surprised, neutral, angry and fearful facial expressions in a) Condition 1 b) Condition 2 c) Condition 3

4.5 DISCUSSION OF EXPERIMENT 3

Previous research using gaze cuing paradigms has yielded inconsistent results regarding the modulation of the Gaze Orienting Effect (GOE) with facial expressions. The present study explored the idea that these observed discrepancies could be due, at least in part, to the type of cueing stimuli used. To test this hypothesis, we employed dynamic face cue sequences in which gaze aversion followed (Condition 1), preceded (Condition 2) or occurred concurrently with the facial expression (Condition 3).

These stimulus sequences differ in term of their ecological validity. Imagine the following scenario. You are studying at the library, with a friend facing you. Upon hearing an unusual noise, you look to the side and notice a snake coming out of a book. Since you are afraid of snakes, you express fear. Although your friend is wearing earplugs, from looking at you he can infer immediately that something dangerous is present at the location you are looking (as in Condition 2). However, if you first expressed fear and then averted your gaze (as in Condition 1), your friend could think that he scared you and that you are now fleeing away. If you had expressed fear and looked away at the same time (as in Condition 3), the signal would be ambiguous for your friend as he would not know whether the threatening stimulus occurred in front of you or in your periphery. As such, the stimulus sequence presented in Condition 2 is the most ecologically valid (usually, you react to something after it enters your visual field). The stimulus sequence presented in Condition 3 is ambiguous (you could, in principle, react to something *while* you are focusing your attention on it, although it would be ambiguous for the observer) and the stimulus sequence presented in Condition 1 is the least ecologically valid (how could you react to something that you are not yet attending to?).

In addition, in Condition 1, the size of the eyes differs depending on which emotion is expressed by the face (e.g., wide opened eyes for fear and squinted eyes for happiness) and gaze is more salient in faces with enlarged eyes (as with fear), which could have facilitated an enhancement of the GOE with certain emotions like fear. However, it is unlikely because the GOE is actually not enhanced by facial expressions in Condition 1. Although more ecologically valid, the stimulus sequence presented in Condition 3 (and in Chapter 3) also presents this eye size confound, as the gaze shift is not independent of the eye size associated with a particular facial expression. The stimulus sequence used in Condition 2, however, circumvents this eye size confound (the gaze shift occurs independently of the size of the eyes associated with a particular facial expression). These various types of cue stimuli have not been directly compared in past research and, with this experiment, we aimed at determining the extent to which differences in the cue sequence influences the modulation of gaze-oriented attention by facial expressions.

4.5.1 Impact of stimulus sequence on gaze oriented attention and its modulation with facial expressions

In all three conditions, participants exhibited a GOE. However, this GOE was largest in the more ecologically valid condition (Condition 2), and reflected the combined effects of a faster response to congruent targets and a slower response to incongruent targets in Condition 2 compared to Conditions 1 and 3. The use of a more ecological stimulus sequence (Condition 2) could thus potentiate attention to gaze by both enhancing engagement to the gazed-at location and hindering disengagement from this location.

Our main goal was to determine which cue sequence would enable the congruency effect to be influenced by emotions. Only in Condition 2, in which the cue averted its gaze before expressing an emotion, did we find an enhancement of the GOE with angry, fearful and surprised facial expressions compared to neutral expressions. Thus, the type of cue used in this Condition 2 seems best suited to study the impact of emotions on gaze-oriented attention. It is more naturalistic as in real settings one tends to react to a stimulus after orienting towards it. It is also possible that the short presentation of an emotion in that sequence (300ms compared to 800ms in Condition1 and 500ms in Condition 3) enabled a particular sensitivity to the expressive face. Finally, in Condition 2, the gaze shift is independent of facial expression so it is not confounded by the differences of eye aperture between the various emotions (Graham et al., 2010).

The eye size has been shown to enhance the gaze orienting effect to some extent (Bayless et al., 2011; Tipples, 2006), so we expected to find an enhanced modulation of the GOE with emotions in which the sclera was enlarged (fear and surprise) in Conditions 1 and 3. Indeed, in those conditions, the gaze shift was confounded with the eye aperture associated with emotion (as it occurred after or together with the emotion onset). Fearful and surprised faces are characterized by wide open eyes so it is easier to process a change in the gaze direction with those emotions compared with happy faces, for which the eyes are squinted. On the contrary, we found that the GOE was only modulated in Condition 2 where the gaze shift occurred in a neutral face and thus was not confounded by eye aperture. Our results suggest that eye aperture is not a critical factor in the modulation of gaze-oriented attention with emotional faces. In accordance with those results, other studies in which the cueing stimulus consisted of a facial stimulus averting its gaze before expressing an emotion also yielded a modulation of the GOE with emotions (Graham et al., 2010; Neath et al., 2013).

The lack of GOE modulation by emotions when gaze was averted after or simultaneously with emotion onset (Condition 1 and Condition 3 respectively) is consistent with most studies in which similar designs have been used (Fichtenholtz et al., 2007; 2009; Galfano et al., 2011; Hietanen & Leppänen, 2003; Holmes et al., 2010; Mathews et al., 2003). The fact that a modulation of attention to gaze with emotions was observed in Chapter 3 is interesting. Indeed, the exact same sequence as in Condition 3 was used in Chapter 3 except that only three emotions were included in each condition (fear, surprise, neutral for the FSN condition and happy, angry, neutral for the HAN condition). This suggests that the affective context in which an emotion is presented might influence its ability to impact attention to gaze. Using a similar sequence to Condition 3 (a neutral face with straight gaze immediately followed by a frame showing the emotional face with averted gaze or by a succession of frames representing the face gradually shifting its gaze and expressing an emotion), several authors (Putman et al. 2006; Tipples et al., 2006; Uono et al., 2009) found an enhancement of the GOE with fearful faces relative to neutral faces. However, their results are difficult to interpret because high anxious participants were included and it has been shown that anxiety influences the way in which emotion modulates gaze-oriented attention (Mathews et al., 2003; Putman et al., 2006; Tipples, 2006).

Our findings are crucial for future experiments that will investigate the impact of emotion on the gaze orienting effect. Indeed, if researchers are interested in the role of emotional gaze in social interaction, it will be in their best interest to use the more ecologically valid cue sequence that was used in Condition 2, which conclusively shows that gaze can be modulated by emotion in a non-anxious population. However, we acknowledge several limiting factors in this experiment which future studies will have to address. First, it will be important to use a different non-directional cue than a face with direct gaze, which includes some facial movement to determine whether some of the observed effects were due to the lack of movement in our direct gaze neutral condition. Second, it will be important to test the influence of the presentation time of facial expression on attention to gaze, as, despite a constant SOA of 500ms, this parameter differed between our three conditions, with the emotion being expressed for 800ms in Condition 1, for 300ms in Condition 2 and for 500ms in Condition 3. It will also be crucial to determine whether or not the time elapsing between the last change in the stimulus sequence and the target onset is an important factor, as it varied between experiments in the present study (500ms for Condition 1 and Condition 3 but 300ms for Condition 2). Finally, it will be important to determine the affective context in which one emotion could enhance the GOE compared to neutral faces. Indeed, even though we used the exact same experimental design in Condition 3 as used in Chapter 3, we failed to show a statistically significant enhancement of the GOE with fearful, surprised and angry faces compared to neutral faces in Condition 3 while a significantly larger GOE for fearful, surprised and angry faces compared to neutral faces was found in Chapter 3.

4.5.2 Enhanced GOE for fear, surprise and anger: facilitation of engagement or inhibition of disengagement?

In Condition 2, angry, surprised and fearful faces modulated the GOE to the same extent demonstrating that anger can modulate the GOE when presented in a gaze-cueing experiment in which fearful expressions are included. This result is in contrast with the idea presented in Chapter 3 according to which the GOE modulation by angry faces would be attenuated when fearful faces are included in the gaze cueing experiment. Indeed, angry faces indicate a more indirect threat than fearful faces (see section 1.2.1 for more details). The GOE was enhanced by anger even when fearful faces were included in the gaze cueing experiment, which suggests that all emotions carrying a negative valence and indicating a threat can enhance the GOE.

We were interested as well in whether the modulation of the GOE by fearful, angry and surprised faces in Condition 2 was due to facilitation of engagement or to inhibition of disengagement for those emotions relative to neutral faces. Interestingly, all emotional expressions yielded faster, responses than neutral expressions, both in the congruent and in the incongruent condition. This suggests a facilitation of both engagement and disengagement. The enhancement of the GOE for fear, surprise and anger compared to neutral was due to a relatively larger facilitation of the response to congruent targets than of the response to incongruent targets, for these emotions, compared to neutral faces. On the contrary, happy faces facilitated equally the response to congruent and incongruent targets compared to neutral. Thus, happy faces, contrary to angry, fearful and surprised faces, failed to significantly modulate the GOE, compared to neutral faces. These results suggest that the facilitation of the response to targets for emotional faces is slightly attenuated in the incongruent compared to the congruent condition. In other words, both the engagement and the disengagement component are facilitated for emotional relative to neutral expressions. However, for fearful, surprised and angry faces, the engagement component is more facilitated than the disengagement component while for happy faces; the engagement component is equally facilitated than the disengagement component. As a result, the GOE is enhanced for all emotional but happy faces relative to neutral faces.

4.5.3 Traditional cost and benefit analysis for gaze-oriented attention to neutral faces

In Conditions 2 and 3, when the facial expression was neutral, targets preceded by faces with direct gaze were responded to slower than both congruent and incongruent targets. These results are consistent with Senju and Hasewaga (2005) who, using faces with neutral expressions, showed an enhanced dwell time for faces with direct gaze compared to faces with averted gaze due to the attention capture generated by the feeling of being looked-at. In addition, these results suggest the presence of a benefit (faster RT for congruent than direct gaze trials) in attention orienting to gaze without cost (slower RT for incongruent than direct gaze trials) in disengaging attention from the gazed at location, which is in accordance with Neath and colleagues (2013) who used the exact same sequence as Condition 2 in a developmental population. However, this is in contrast with previous studies that used neutral faces and reported both benefits and costs (Hietanen, 1999; Langdon & Smith, 2005). It is possible that these discrepancies are due to the fact that apparent movement occurred in our neutral stimulus with averted gaze but not in our neutral stimulus with direct gaze while none of their stimuli exhibited movement. Since we wanted to use dynamic stimuli to reflect ecological conditions, this limitation was difficult to overcome as a face always start as a neutral face with direct gaze and changes more or less depending on the condition.

However, the results of Condition 1, in which responses were only faster for congruent targets than for targets following faces with direct gaze, are in line with those of Friesen and Kingstone (1998) who also only found a benefit (no cost) when using neutral stimuli. It is unclear why the different experiments presented here yielded different results regarding costs and benefits. There might be an influence of the context of the stimulus sequence used in a particular experiment, as the neutral stimulus was exactly the same across the three experiments (1000ms of face with straight gaze in the non-congruent condition and 500ms of face with straight gaze followed by 500ms of face with averted gaze in the congruent and incongruent condition). Thus, the response to direct gaze trials preceded by neutral faces could be sensitive to the context (i.e., the stimulus sequence used for emotional and gazing faces) of a particular experiment. Moreover response to neutral direct gaze trials was faster in Condition 1 than in Condition 2. Thus, the neutral face with direct gaze captured attention more in the context of the stimuli sequence of Condition 2 than in the context of the stimuli sequence of Condition 1, resulting in a slowed response to the target. Contrary to Condition 1 in which the last change occurred 500ms before target onset, the last change occurred 300ms before the onset of the target in Condition 2, acting as an immediate warning. The proximity of this warning sign with the appearance of the target could potentiate its impact and the absence of such a warning could lead to a failure to prepare to disengage attention from the central face looking straight ahead.

Jonides and Mack (1984) described a good non-directional cue as being just as informative as a directional cue regarding the forthcoming target onset. They argued that the only differing feature between non-directional and directional cues should be that directional cues indicate a location while non-directional cues do not. The non-directional cue should not involve additional processes compared with the directional cue. Thus, using a face with direct gaze as a non-directional cue is problematic. Indeed, as outlined above, the feeling of being looked at is known to capture attention and trigger specific processes. In addition, when cueing stimuli are dynamic the directional gaze cues contain movement while the neutral gaze cues do not. Rather than using a problematic neutral condition, Jonides and Mack (1984) urged researchers to avoid using such a condition whenever possible. The cost-benefit analysis might thus be of limited validity when using dynamic gaze cues.

4.6 CONCLUSION

The impact of cue sequence on the emotion modulation of gaze-oriented attention was investigated across three conditions. In Condition 1, emotion was expressed before gaze aversion while it was expressed after gaze aversion in Condition 2 and concurrently with gaze aversion in Condition 3. Our results show that emotions only influence attention orienting to gaze when the sequence reflects naturalistic conditions and when the emotion is presented independent of eye aperture (Condition 2). This is important because previous studies used these types of cuing interchangeably and yielded apparently inconsistent results. Future studies using this specific stimulus sequence (gaze shift followed by emotion expression) should be able to shed more light regarding the mechanisms at play in the influence of emotions on the GOE.

In accordance with Chapter 3, the results of Chapter 4 suggest that the GOE is potentiated when negatively valenced emotions are expressed by the face (i.e., fear, surprise in the context of fear and anger) and provide evidence for a facilitation of the engagement component involved in the modulation of attention to gaze with certain facial expressions.

Finally, a traditional cost and benefit analysis revealed the presence of a benefit in engaging attention to the gazed-at location with no cost in disengaging attention from the gazed-at location, which suggest similarities between gaze-cueing and peripheral (automatic) cueing but not symbolic (arrows) cueing. We also noted that neutral faces with direct gaze tended to capture attention compared to neutral faces with averted gaze and were less dynamic. For these reasons, in Chapter 5, the direct gaze condition was no longer included.

Chapter 5: Do autistic traits influence gaze-oriented attention to happy and fearful faces? (Experiment 4)[14]

5.1 INTRODUCTION

In Chapter 3, the behavioral and neural correlates underlying the modulation of gaze-oriented attention with facial expressions in the general population were uncovered. At the behavioral level, it was shown that the GOE was enhanced for fearful and surprised faces relative to neutral ones and for angry faces relative to neutral and happy faces. At the ERP level, although ERPs indexing attention to gaze at cue (EDAN and ADAN) and target (congruency effect on P1) onset were present, only the congruency effect on P1 was modulated with emotions. In Chapter 4, facial expressions with a negative valence (fearful, angry, and surprised) were also shown to enhance the GOE but only when using a dynamic face cue averting its gaze before expressing an emotion. Using such face cue sequence in Chapter 5, the possibility of a relationship between autistic traits and the modulation of gaze-oriented attention with emotions was investigated in the general population.

As indicated in Chapter 1 (section 1.1.2.), individuals with ASD exhibit a clinical deficit in joint attention (Nation & Penny, 2008) that has been linked to their later lack of theory of mind (ToM) abilities and to their social skills deficit (Baron-Cohen, 1995). However, whether joint attention also varies as a function of autistic traits in typical individuals is unclear. Social skills and other autistic-like traits can be indexed in typical individuals using the Autism-Spectrum Quotient (AQ) questionnaire (Baron-Cohen, Wheelwright, Skinner, Martin & Clubey, 2001), and one study showed a negative correlation between AQ scores and the GOE (Bayliss et al., 2005), indicating that the more an individual exhibits autistic traits, the less she orients attention towards gaze direction. That study, however, tested only neutral faces and it remains unknown whether the GOE could be modulated by facial expressions differentially depending on typical individuals' autistic traits. This question is pertinent given the recent evidence that, contrary to typical individuals, those with high functioning ASD do not exhibit an enhanced GOE for fearful faces compared to neutral faces (Uono et al., 2009). To orient their attention, people with ASD

[14] This part of our work was presented at a local conference and at an international conference (Lassalle & Itier, 2012d, Lassalle & Itier, 2013). It yielded an abstract in the Journal of Vision. A full article presenting our results is in preparation.

might thus not integrate gaze and emotions to the same extent as typical individuals, which could explain their lack of ToM and their social skills deficit.

The present experiment explored the link between one's AQ score and one's propensity to use gaze signals to orient attention– an indicator of joint attention– in the general population, and whether this relationship varied with the facial expression of the cue. We also investigated whether the ERP correlates of attention to gaze reported in Chapter 3 (e.g., EDAN, ADAN, P1) were differentially modulated by gaze and emotion cues depending on the autistic traits exhibited by typical individuals. Finally, using inverted faces in addition to upright faces, we investigated whether the emotional modulation of the GOE was driven by the actual emotional content of the face, as inversion is known to disrupt facial emotion recognition (e.g., Derntl, Habel, Windischerberger, Robinson, Kryspin-Exner, Gur & Moser, 2009), or by other factors such as facial movement driven by the unequal change in configuration of the facial features (the eyes going from neutral to wide open or squinted, the mouth moving to an O shape or to a large smile, etc.). Given that Uono and colleagues (2009) showed that individuals with ASD were impaired at modulating the GOE with fearful faces, only fearful and happy faces were used.

Based on previous literature, on results of Chapters 3 and 4 and on the threat hypothesis, we expected to find the classic GOE and its enhancement with fearful expressions for both RTs and ERP components. We also expected a Congruency by Orientation interaction reflecting the general decrease in GOE with inversion as previously reported (Langton & Bruce, 1999; Hori et al., 2005; Kingstone, Friesen & Gazzaniga, 2000; Graham et al, 2010; Bayless, Glover, Taylor & Itier, 2011). Importantly, we expected a three-way interaction between Orientation, Congruency and Emotion, reflecting a larger decrease of the GOE with inversion for fearful faces. Although we did not use neutral faces here, happy faces have been shown to elicit a GOE similar to that of neutral faces (Chapter 3). Thus, if the larger GOE for fear than happy faces seen with upright faces was due to the emotional content of the face, we expected a larger inversion effect on the GOE for fearful than happy faces. This three-way interaction would suggest that the GOE is driven by the emotional content of the face rather than by low level features such as apparent motion or feature shape. Lastly, according to previous research, we expected that the overall GOE would negatively correlate with the AQ score, such that the higher the autistic trait scores, the smaller the GOE (Bayliss et al., 2005). Based on Uono and colleagues (2009), we also expected to see an even larger negative correlation between the AQ score and the GOE for fearful faces compared to happy faces. Finally, we also hoped to see a similar correlation with the ERP components indexing attention orienting.

5.2 METHODS

5.2.1 Participants

Three hundred and forty-six (346) students from the faculty of mathematics of the University of Waterloo (UW) were pre-screened based on the completion of three questionnaires for which they received $5 and a chocolate bar. One questionnaire quickly assessed emotion recognition abilities; the second assessed participants' trait anxiety; the third questionnaire was the Autism-Spectrum Quotient (AQ) test (Baron-Cohen et al., 2001). The pre-screening phase is described in more detail later. As we wanted a wide range of AQ scores, participants were recruited in the mathematic department because previous research has shown that individuals with high AQ scores are more prevalent in scientific disciplines than in humanities disciplines such as Psychology (Baron-Cohen et al., 2001), a finding confirmed by our preliminary survey. Unfortunately, recruiting in the Math department biased the gender enrolment, with more males being recruited and tested than females.

To be invited to participate in the EEG experiment, participants i) had to score above chance level for each emotion displayed in the emotion recognition questionnaire, ii) had to score below the high anxiety score of 42, iii) had to be free of neurological or psychiatric illness.

Of the 224 math students who met the questionnaires' criteria and were eligible, 78 participated in the EEG study. Eight participants were rejected, one for inconsistent scoring on the AQ questionnaire which was administered twice by mistake and seven because of too few trials per condition after artifact rejection for one or several of the ERP components measured. The final sample included 70 participants (21 females), all right handed, with normal or corrected-to-normal vision and no self-reported history of psychiatric or neurological illness. Participants were between 18 and 29 years old (mean=20.91 years, SD=2.12), had anxiety scores in the normal range (mean=33.77, SD=6.07) and AQ scores ranging from 7 to 37 (mean=21.30, SD=7.46). Participants were tested in the Psychology department at UW and received $20 for their participation. The study was approved by the UW Research Ethics Board, and participants gave informed written consent.

5.2.2 Pre-screening phase

In the pre-screen phase, participants completed the emotion recognition questionnaire described in Chapter 2 (section 2.2.2 and Appendix A). However, in the present experiment, participants were not asked about the intensity of the perceived emotion. Participants had to recognize each of the 5 presented emotions above chance level to qualify for the EEG study. We verified that our participants could recognize emotions to make sure that the way in which they modulated the GOE with emotions cannot be attributed to an inability to recognize certain emotions.

As in previous chapters, participants' trait anxiety was assessed using the STICSA and only students whose trait anxiety scores were below the high trait anxiety score of 42 were selected to participate in the study as high trait anxiety has been shown to modulate the influence of emotions on the GOE (e.g., Putman et al., 2006; Fox et al., 2007; Mathews et al., 2003).

The third pre-screening questionnaire was the Autism-Spectrum Quotient (AQ) test developed by Baron-Cohen and colleagues (2001) and used as a quick screening tool for ASD in clinical and research settings. An AQ score above 26 indicates 80% likelihood for the participant to fall within the autism spectrum (Woodbury-Smith et al., 2006). The AQ is a questionnaire comprising five different subscales of ten questions each, assessing areas of different behaviors in the ASD population: i) social skills, ii) attention to details, iii) attention switching, iv) communication (the higher the score, the lower the communication ability) and v) imagination. A high AQ score indicates a pattern of high attention to details, low social skills, little communicative and imaginative abilities and difficulty with attention switching.

5.2.3 EEG experiment

5.2.3.1 Stimuli and procedure

The same photographs as the emotion recognition assessment were used in the EEG study except that individuals displayed only fearful and happy expressions.

Faces were preprocessed in the same manner as in Chapter 3.

Participants sat 67cm in front of a computer monitor in a quiet, dimly lit and electrically shielded room, with their head restrained by a chin rest. Each trial started with a centered fixation cross (1.28˚x 1.28˚

visual angle), presented alone for a jittered amount of time between 800 and 1200ms. A neutral face with straight gaze was then shown for 500ms before the same neutral face was presented with a rightward or leftward gaze for 200ms. It was then followed by the presentation of the same face with averted gaze and expressing either happiness or fear for 300ms (Figure 17). As in previous chapters, this sequential presentation induced the perception of a face moving its eyes to the side and dynamically expressing an emotion (via apparent motion). The face was presented upright or inverted (rotation of 180˚). A black asterisk target (.85˚x .85˚) was then presented on either side of the fixation cross at a 7.68˚ eccentricity and remained on the screen until the response or for a maximum of 500ms. The initial fixation cross remained on the center of the screen for the entire trial time and was thus superimposed on the face.

The experiment was programmed using Experimental Builder software (SR Research) and consisted of 10 blocks of 128 trials separated by a self-paced break, resulting in a total of 1280 trials, with 80 trials for each of the 16 basic conditions. A condition consisted of a combination of a particular emotion (happy, fearful) with a specific orientation (upright, inverted), a particular gaze direction (rightward, leftward) and a congruency type (congruent, incongruent). There were an equal number of congruent and incongruent trials and trial order was fully randomized within a block. Given the numerous limitations associated with using direct gaze trials as the control condition and outlined in Chapter 4, there were no direct gaze trials in Experiment 4.

Throughout the experiment participants were instructed to maintain fixation on the central cross and to remain still. Fixation on the cross was ensured using an eye-tracking device (Eyelink 1000), which was calibrated between each block. Twenty practice trials were run before the start of the first block and participants were told the direction of eye gaze was not predictive of target location. They were required to press the keyboard left key “C” when the target was shown on the left and the right key “M” when the target was presented on the right, using both hands. They were asked to be as accurate and as fast as possible.

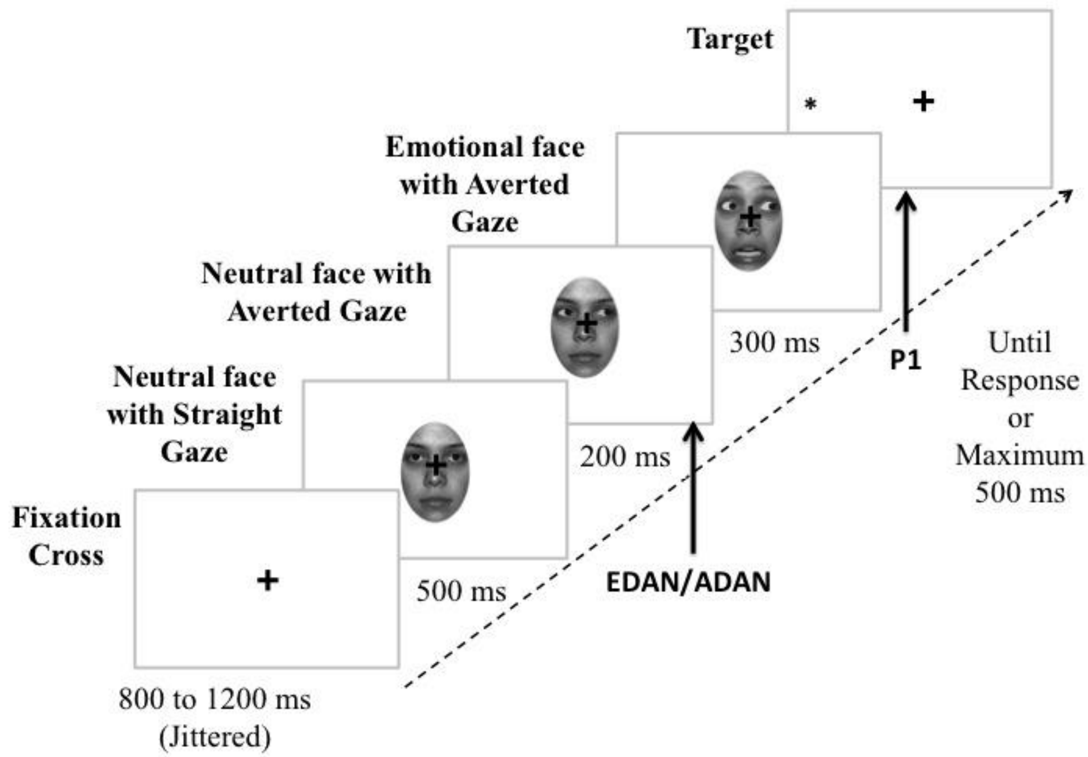

Figure 17: Example of an incongruent trial in which the cue expresses fear. The arrows indicate the stage at which the ERP components are being measured (EDAN/ADAN when the cue is presented and P1 when the target is presented).

5.2.3.2 Electrophysiological recordings

EEG recording and preprocessing was conducted in the exact same manner as in Chapter 3 (refer to section 3.2.3 and 3.2.4).

5.2.4 Data analysis

5.2.4.1 Reaction times (RTs)

RTs were preprocessed in the same manner as in previous experiments resulting in the exclusion of 7% of the trials.

Mean RTs were analyzed using a 2 (Emotions: fearful, happy) by 2 (Congruency: congruent, incongruent) by 2(Orientation: upright, inverted) repeated measures Analysis Of Variance (ANOVA). When the Emotion by Congruency interaction was significant, further analyses were conducted separately for congruent and incongruent trials, using the factor emotion and orientation. To determine if there was a link between autistic traits and attention orienting, Pearson correlations were computed between the GOE for each emotion and each orientation and i) the total AQ score and ii) the score obtained on each of the four AQ subscales.

5.2.4.2 ERP to targets (P1)

ERPs were time-locked to the onset of the lateral target (-100ms to +500ms epoch). Based on previous literature and data inspection, we selected PO7/PO8 and O1/O2 as the electrodes of interest for P1 analysis. Only the side contralateral to the target was analyzed.

We defined P1 as the peak of maximum amplitude between 70 and 130ms after target onset, using an automated procedure. Individual data were then inspected to check that the correct peak was measured and manual peak measures were performed if necessary. P1 amplitudes and latencies were analyzed using a 2(Orientations: upright or inverted) by 2(Congruency: congruent or incongruent) by 2(Emotions: fear or happy) by 2(Electrodes: Parietal-Occipital or Occipital) by 2(Hemisphere: right or left) repeated measures ANOVA[15].

5.2.4.3 ERPs to gaze cue (EDAN/ADAN)

ERPs were time-locked to the onset of the gaze shift (-100ms to +500ms epoch). Recall that, due to the sequence used, the first 200ms reflected the processing of a neutral face with averted gaze and that, by 300ms after gaze shift, the face expressed an emotion and the recordings thus corresponded to the processing of an emotional face with averted gaze.

In accordance with Chapter 3 and after inspection of the current data, measurement for the EDAN component was made at posterior electrodes (P7, P8, PO7, PO8) between 200 and 300ms while measurement for ADAN component was made at anterior electrode sites (F5, F6, F7, F8, FC5, FC6, FT7,

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[15] Note that because the target was analyzed only on the side contralateral to target presentation (for clarity), the hemisphere factor can also be thought of as a left/right target position factor.

FT8) between 300 and 500ms. For each component, the mean amplitude across the defined time window was averaged across the electrodes for a given hemisphere.

For each hemisphere we tested whether amplitudes were more negative for gaze directed toward the contralateral side than for gaze directed toward the ipsilateral side, which would indicate the presence of EDAN or ADAN components. Mean amplitudes for the ipsilateral and contralateral conditions were calculated for each emotions and hemisphere and analyzed using a 2(Orientation) by 2(Emotion) by 2(Hemisphere) by 2(Gaze laterality: contralateral, ipsilateral) repeated measure ANOVA.

For all analyses (EDAN/ADAN, P1, behavior), statistical tests were set at $\alpha<.05$ significance level. Greenhouse-Geisser correction for sphericity was applied when necessary. We adjusted for multiple comparisons using Bonferroni corrections.

5.2.4.4 Correlations with AQ

Pearson correlations were also performed to evaluate, across the population, the link between autistic traits (as assessed by AQ scores) and the GOE (the overall GOE, the upright GOE, the happy upright GOE, happy inverted GOE, fearful upright GOE, and fearful inverted GOE). When a significant/trending correlation was found, it was investigated further, using a correlation between the scores at the different subscale of the AQ (imagination, communication, social skills, attention switching and attention to details) and the variable of interest to investigate which autistic traits were most involved in this effect. We also used Pearson correlation to evaluate the link between autistic traits and the ERPs associated with gaze oriented attention (EDAN, ADAN, congruency effect on P1). In addition to the overall correlation, correlations were also performed for each condition outlined above (upright, inverted, happy upright, happy inverted, fearful upright, fearful inverted). When a significant/trending correlation was found, we investigated it further using a correlation between the scores at the different subscale of the AQ and the variable of interest to investigate which autistic traits were most involved in this effect. Only significant effects are reported unless otherwise stated.

5.3 RESULTS

5.3.1 Behavioral Results

A main effect of orientation (*F* (1, 69) =74.98, MSE=35.96, $p< .01$, $\eta_p^2= .52$) was due to longer RTs for inverted (mean= 321.77ms, SE=3.73) than upright faces (mean= 317.39ms, SE=3.83). The main effect of congruency (*F* (1, 69) =250.58, MSE=223.79, $p< .01$, $\eta_p^2= .78$) reflected faster responses to gazed-at (congruent) targets compared to non-gazed-at (incongruent) targets (Figure 18a). This congruency effect was larger in the upright (mean GOE = 22.63ms, SE=1.46) than the inverted (mean GOE = 17.39ms, SE=17.39) condition (Figure 18b) as revealed by a significant orientation by congruency interaction (*F* (1, 69) =22.64, MSE= 42.40, $p< .01$, $\eta_p^2= .25$). An emotion by congruency interaction was also present (*F* (1, 69) =14.31, MSE=29.88, $p< .01$, $\eta_p^2= .17$) due to a larger GOE for fearful faces (mean=21.76ms, SE=1.41) compared to happy faces (mean=18.27ms, SE=1.23) (Figure 18b). A separate analysis for the congruent and incongruent conditions showed a significant effect of emotion in both conditions (*F* (1, 69)= 4.70, MSE=23.75, $p= .03$, $\eta_p^2=.06$ and *F* (1,69)= 12.04, MSE=29.00, $p<.01$, $\eta_p^2=.15$, respectively). This emotion effect was due to slightly faster RTs for fearful (mean=308.94ms, SE=3.82) than happy faces (mean= 310.21ms, SE=3.77) in the congruent condition and to slightly longer RTs for fearful (mean=330.70ms, SE=3.84) than happy faces (mean=328.47ms, SE=3.90) in the incongruent condition, making the incongruent-congruent difference in RT larger for fearful than happy faces. The three-way interaction of orientation by congruency by emotion was not significant (*F*=1.90, $p= .17$).

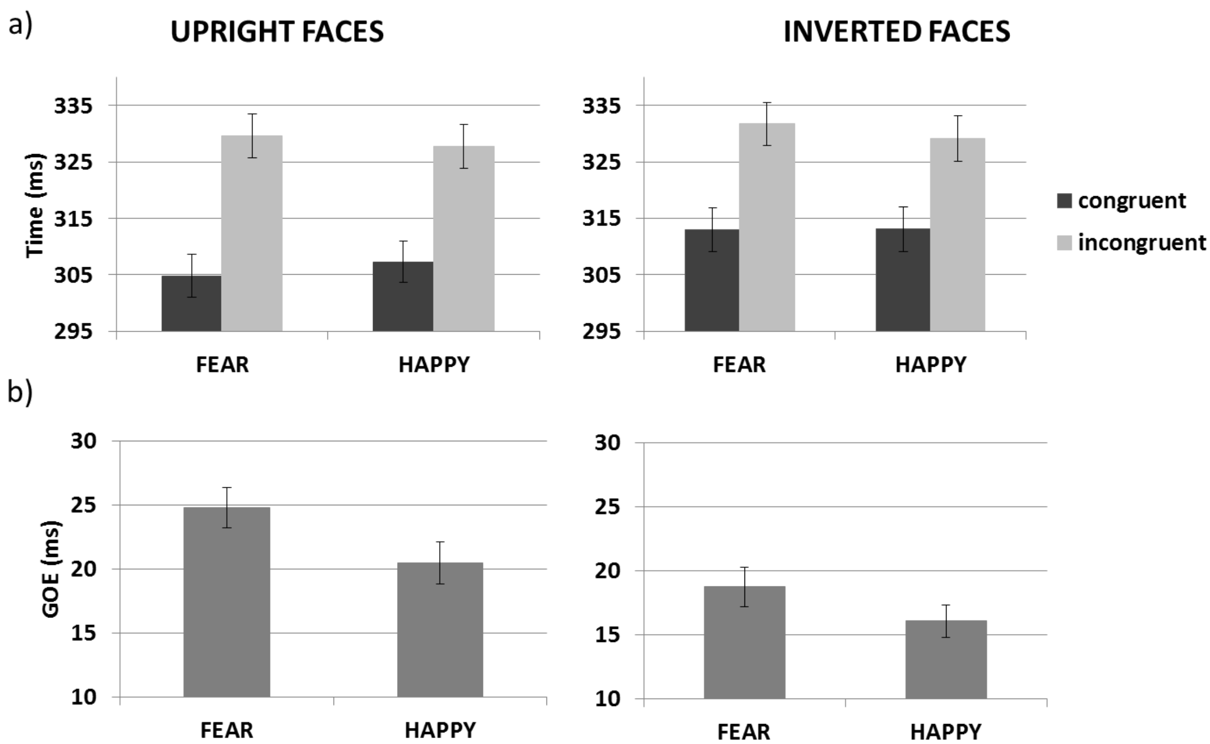


Figure 18: Behavioral results. (a) Mean RTs to face cues presented in the upright condition (left panel) and in the inverted condition (right panel). (b) Mean GOE for fearful and happy faces. N=70 and error bars represent SE.

5.3.2 ERPs Results

5.3.2.1 ERPs to the target

The average number of trials per condition for P1 component was 67.77 (SD= .06).

5.3.2.1.1 P1 component

The analysis of P1 amplitude showed the expected main effect of congruency (F (1,69) =4.22, MSE= .71, p= .04, η_p^2= .66) with larger amplitude in the congruent than in the incongruent condition (Figure 19). In addition there was a main effect of hemisphere (F (1, 69) =12.07, MSE=26.57, p< .01, η_p^2= .15) with larger amplitudes in the right than in the left hemisphere, as well as a main effect of electrode (F (1,69)=18.89, MSE=18.58, p< .01, η_p^2= .22) with larger amplitudes at occipital than at parieto-occipital sites. No other effect was found.

P1 latency analysis yielded a main effect of electrode (F (1, 69)= 4.81, MSE=932.42, p= .03, η_p^2= .07) and an electrode by orientation interaction (F (1, 69) =6.20, MSE=56.75, p =.02, η_p^2=.08) such that latencies were longer at O1/O2 than at PO7/PO8 sites but only in the upright condition (F(1,69)=6.31, MSE=58.12, p=.01, η_p^2=.08). No main effect of congruency was found and a significant orientation by congruency interaction (F (1, 69) =4.92, MSE=46.18, p= .03, η_p^2= .07) was due to a congruency effect (longer latency in the congruent than in the incongruent condition) reaching significance in the inverted condition only. No congruency effect was found for upright faces.

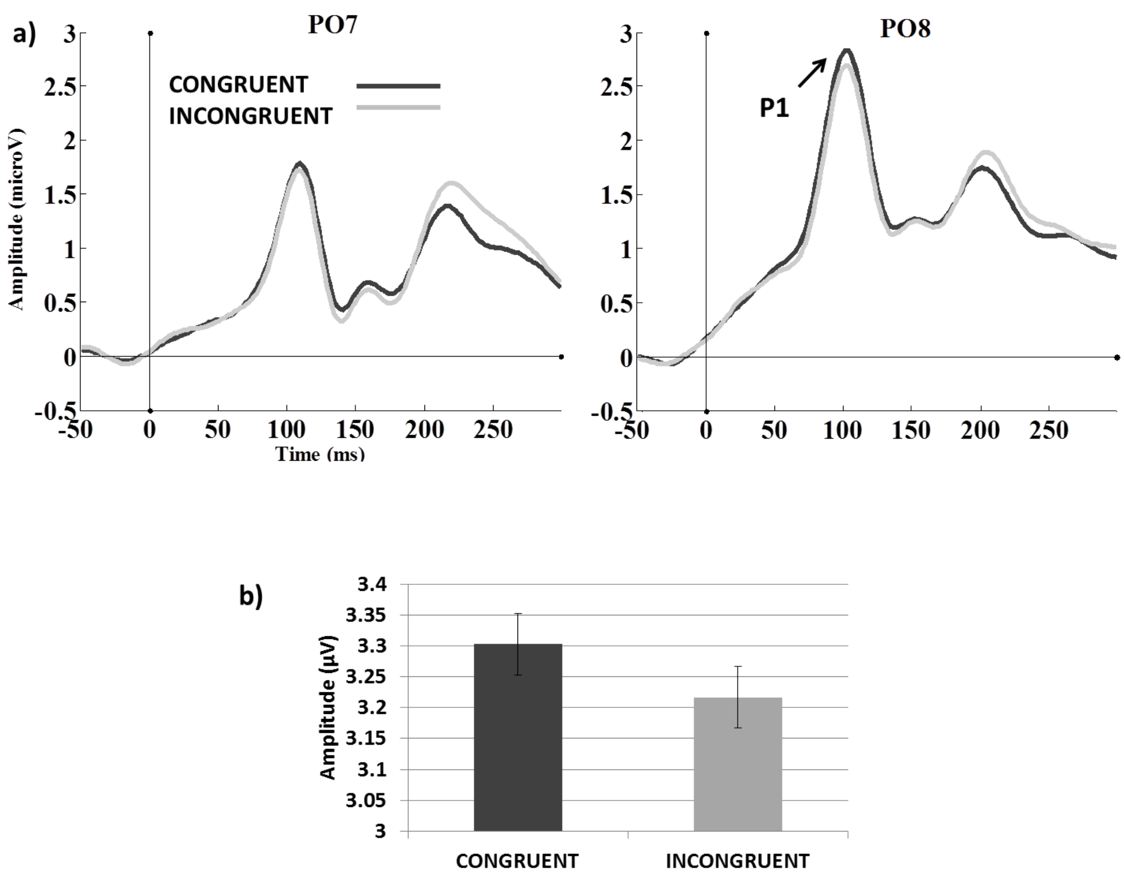


Figure 19: Target-triggered ERPs (a) ERP waveforms featuring the P1 component at PO7 (left hemisphere, left panel) and PO8 (right hemisphere, right panel) for the congruent and the incongruent conditions (waveform averaged across emotions and orientations, N=70). (b) Mean P1 amplitudes to congruent and incongruent targets (waveform averaged across emotions and orientations)

5.3.2.2 ERPs to the gaze cue

ERPs were time locked to the onset of gaze shift (which happened with a neutral face) and thus included the onset of facial expression 200ms later. The average number of trials per condition for EDAN/ADAN components was 132.43 (SD=1.01).

5.3.2.2.1 Early Directing Attention Negativity (EDAN)

A main effect of hemisphere (F (1, 69) =7.36, MSE=21.11, p< .01, η_p^2=1.00) was due to more negative amplitudes in the right than the left hemisphere. As expected, there was a main effect of gaze laterality (F (1, 69) =8.99, MSE= .85, p< .01, η_p^2= .12) such that amplitudes were more negative when the gaze cue was directed toward the contralateral side than when it was directed toward the ipsilateral side (Figure 20). However, this laterality effect interacted with hemisphere (F (1,69)=4.40, MSE= .85, p= .05, η_p^2= .07) and with orientation (F (1,69)=5.41, MSE= .71, p= .02, η_p^2= .07) such that it was only present in the right hemisphere (F (1,69)=10.89, MSE= .97, p< .01, η_p^2= .14) and in the upright condition (F (1,69)=12.65, MSE= .88, p< .01, η_p^2= .16). There was no significant main effect of, or interaction with, emotion.

5.3.2.2.2 Anterior Directing Attention Negativity (ADAN)

Analysis of ADAN revealed a main effect of orientation (F (1, 69) =17.74, MSE=8.83, p< .01, η_p^2= .21) such that larger amplitudes were observed for the upright than for the inverted condition. The expected effect of gaze laterality was also significant (F (1, 69) =6.39, MSE=2.95, p= .01, η_p^2= .08) with less positive amplitudes in the contralateral than in the ipsilateral condition (Figure 21). No effects of, or interaction with, emotion were found.

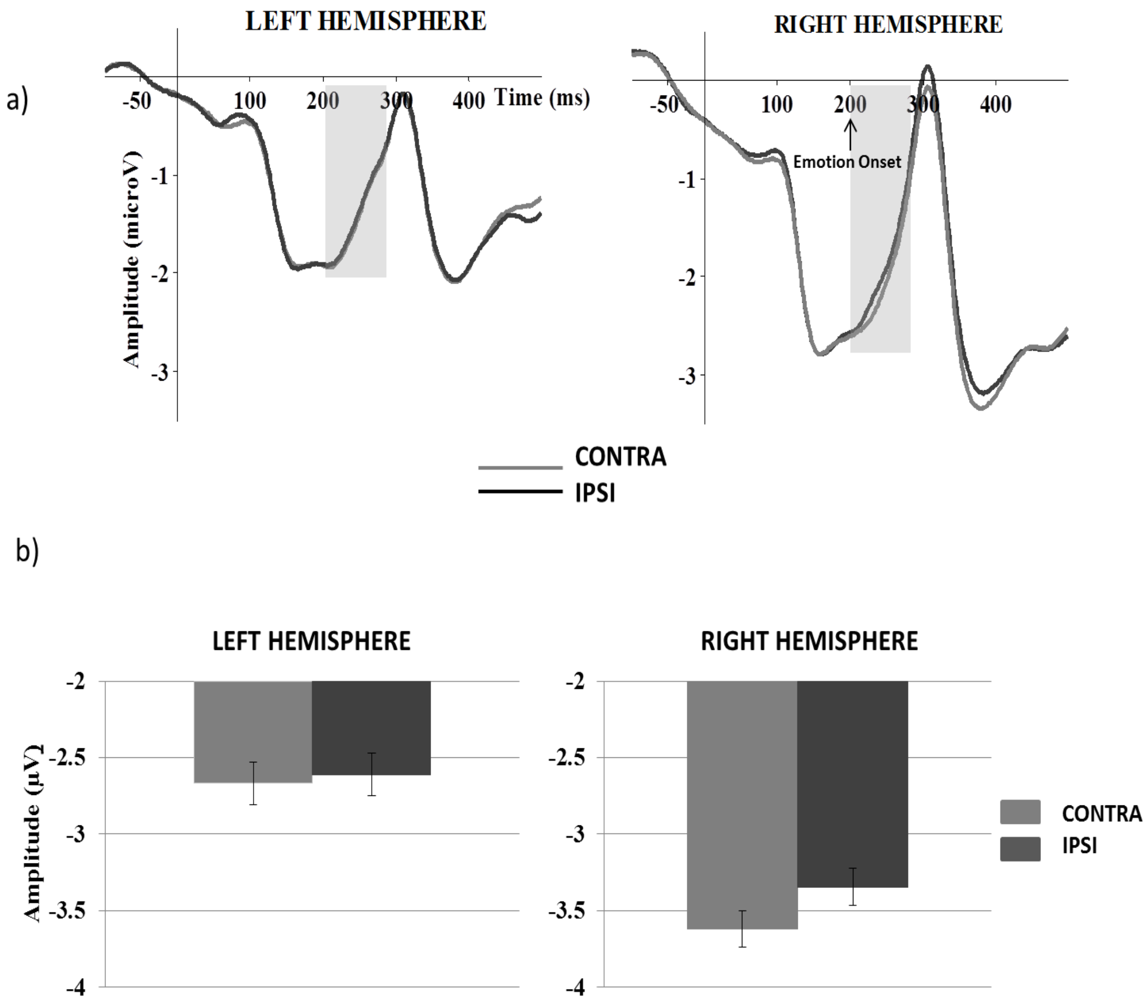
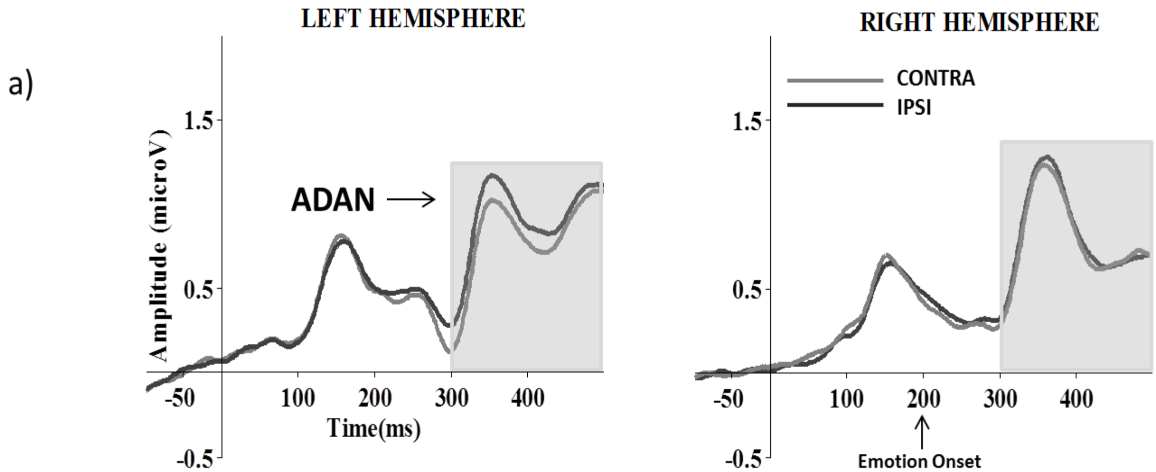


Figure 20: First cue-triggered ERP: EDAN. (a) ERP waveforms for contralateral (contra) and ipsilateral (ipsi) gaze cues (averaged across orientation, emotions and electrodes: P7 and PO7 for the left hemisphere, P8 and PO8 for the right hemisphere). The grey zone indicates the time limits of the analysis (200-300ms). (b) Mean amplitudes for contralateral (contra) and ipsilateral (ipsi) gaze directions, between 200 and 300ms, for each hemisphere (averaged across orientation, emotions and electrodes: P7 and PO7 for the left hemisphere, P8 and PO8 for the right hemisphere).



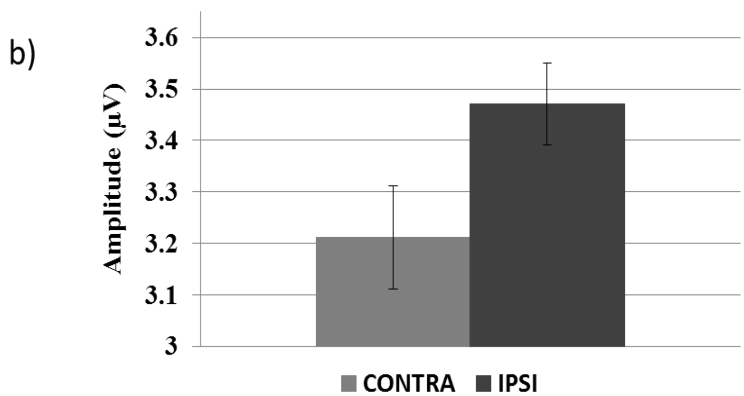


Figure 21: Second cue-triggered ERP: ADAN. (a) ERP waveforms for contralateral (contra) and ipsilateral (ipsi) gaze cues (averaged across emotions, orientation, and electrodes: F5, F7, FC5, FT7 for the left hemisphere, F6, F8, FC6, FT8 for the right hemisphere). The grey zone marks the time limits of the analysis (300-500ms). (b) Mean amplitudes for contralateral (contra) and ipsilateral (ipsi) gaze directions between 300 and 500ms averaged across emotions, orientation, hemispheres and electrodes (F5, F7, FC5, FT7, F6, F8, FC6, FT8).

5.3.3 Correlation between attention orienting and the AQ score

As seen in Figure 22, there was a trending negative correlation between AQ scores and the GOE for happy faces in the upright condition (r (70) = -.23, *p*= .06), reflecting a decrease in the GOE for happy upright faces as AQ scores increased. When the AQ sub-scales were analyzed separately, significant correlations were found between the scores on the “attention to detail” and “imagination” subscales of the AQ and the GOE for happy faces (r (70)=-.29, *p*= .02 and r (70)=-.28, *p*= .02, respectively). Thus, the less detail-oriented and the more imaginative a person is, the larger the GOE for happy faces. No other correlations were significant at the behavioral level.

As seen in Figure 23, for ERPs, there was a trending negative correlation between the AQ score and the congruency effect on P1 amplitude (r (70) = -.21, *p*= .07). In addition, scores on the social skills and the communication subscales of AQ were also mildly correlated with the overall congruency effect on P1 amplitude (r (70) = -.23, *p*= .06 and r (70) = -.22, *p*= .06 respectively). The trending negative correlation between the congruency effect on P1 amplitude and the overall AQ score was restricted to the upright condition, when upright and inverted faces were analyzed separately (*r* (70) = -.22, *p*= .06). Thus, the more social skills and communication abilities a person has, the larger the congruency effect on P1, particularly in the upright condition.

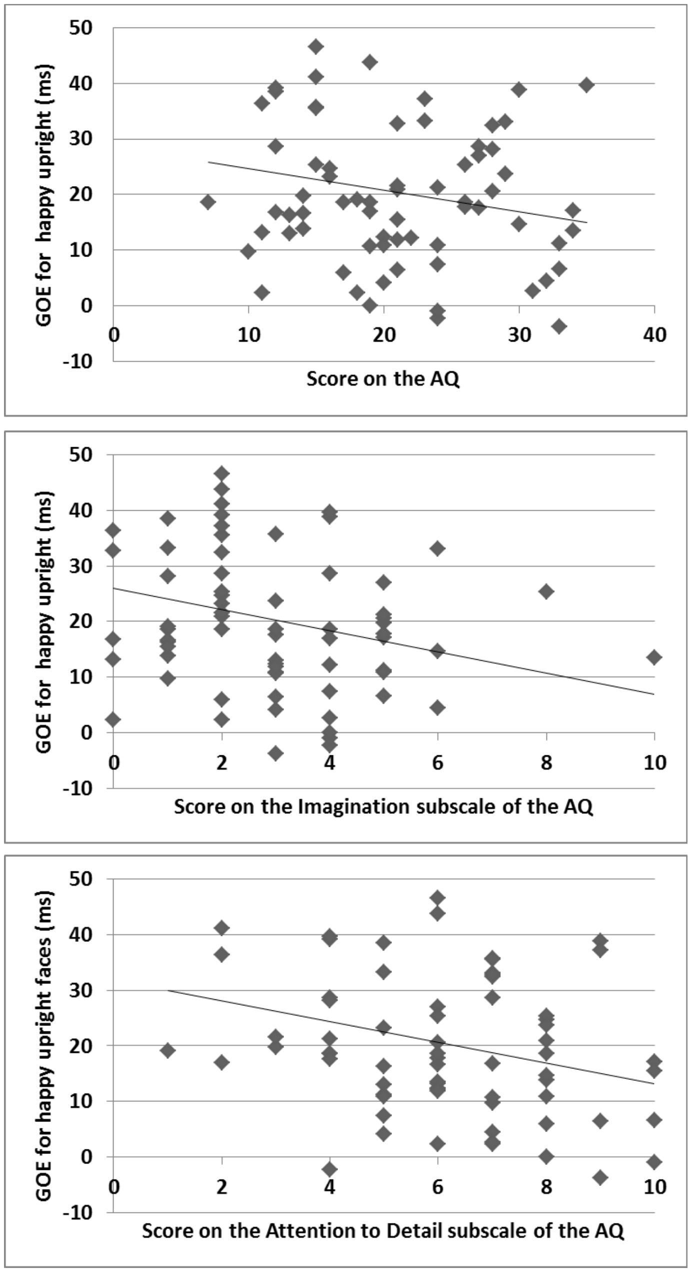


Figure 22: UPPER PANEL: correlation between participants' AQ scores (on the x-axis) and their GOE for happy upright faces (on the y-axis). MIDDLE PANEL: correlation between participants' scores on the Imagination subscale of the AQ (x-axis) and the GOE for happy upright faces (y-axis). LOWER PANEL: correlation between participants' scores on the Attention to Detail subscale of the AQ (x-axis) and the GOE for happy upright faces (y-axis)

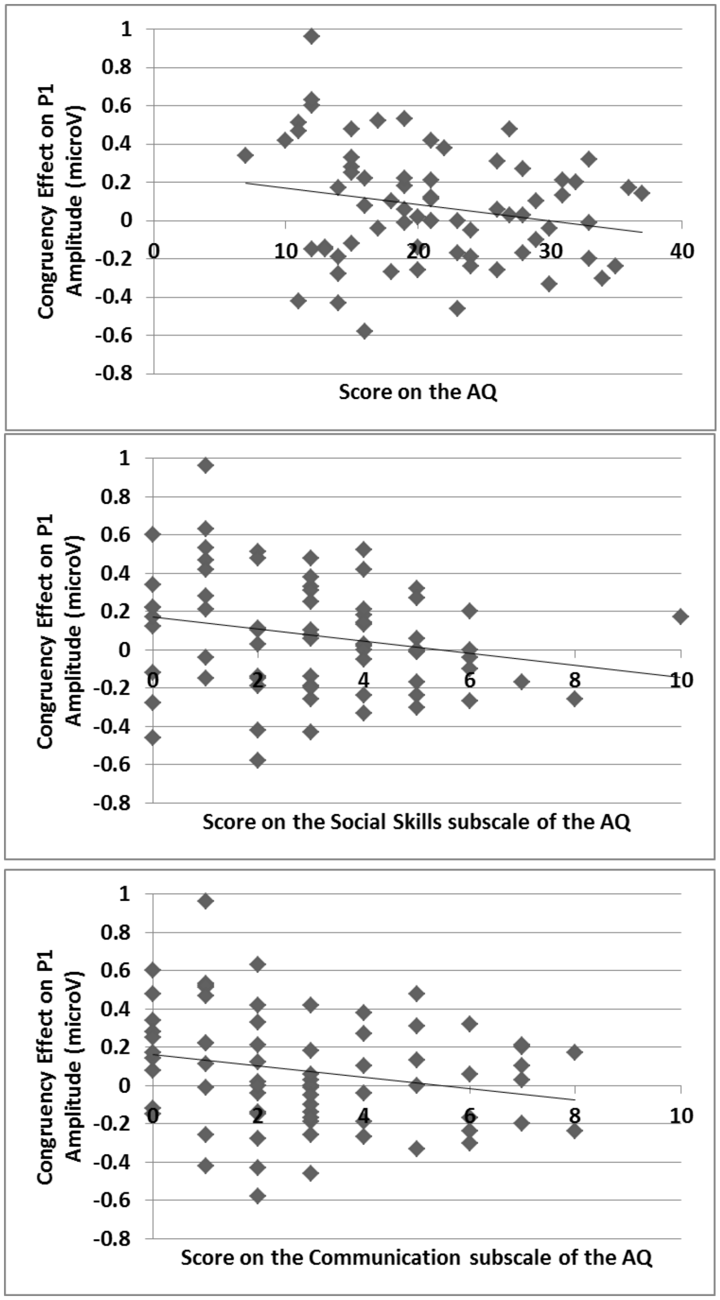


Figure 23: UPPER PANEL: correlation between participants' AQ scores (on the x-axis) and their congruency effect on P1 amplitude in microvolts (on the y-axis). MIDDLE PANEL: correlation between participants' scores on the Social Skills subscale of the AQ (x-axis) and their congruency effect on P1 amplitude in microvolts (y-axis). LOWER PANEL: correlation between participants' scores on the Communication subscale of the AQ (on the x-axis) and their congruency effect on P1 amplitude in microvolts (on the y-axis).

5.4 DISCUSSION OF EXPERIMENT 4

We investigated the behavioral and ERP correlates of the modulation of attention to gaze with fearful and happy faces, using a localization task. We used a sequence in which the facial expression occurred after the gaze shift, for three reasons. First, it seems ecologically valid as in real life we tend to orient our gaze toward a stimulus before reacting to it. Second, the gaze shift is not confounded by the difference in eye aperture between happy and fearful expressions (i.e., eyes are squinted for happy expressions and enlarged for fearful expressions). Third, results from Chapter 4 showed an enhanced modulation of the GOE when this stimulus sequence was used compared to other stimulus sequences. Again, the GOE and its modulation by emotion were investigated, and cue-triggered, as well as target-triggered ERPs, were measured. We also examined the relationship between these measures and one's Autism Quotient (AQ) score, indexing autistic traits.

5.4.1 Influence of facial expressions on the GOE

At the behavioral level, we found the traditional gaze orienting effect (GOE) with faster responses to congruent than to incongruent trials (Driver, Davis, Ricciardelli, Kidd, Mawell, & Baron-Cohen,1999; Friesen & Kingstone, 1998). In addition, the GOE was larger with fearful than happy faces in this non-anxious sample, reproducing previous findings (Bayless et al., 2011; Neath et al., 2013). Interestingly, the enhancement of the GOE for fearful faces compared to happy faces was due both to a faster localization of the targets in the congruent condition and to a slower localization of targets in the incongruent condition, for fearful faces compared to happy faces. This suggests both a facilitation of the orienting response and an inhibition in disengaging attention from the cued location, for fearful faces, compared to happy faces.

5.4.2 Influence of inversion on the GOE

Two main types of information are present within a face. Local and configural information rely respectively on isolated features and on feature arrangement within a face (Rhodes, 1993, Tanaka & Farah, 1993). Face inversion is known to disrupt face configuration and force a feature-based processing (Bartlett & Searcy, 1993; Yin, 1969; Tanaka & Farah, 1993). Face identification is diminished in inverted faces compared to upright faces, an effect known as the face inversion effect (Valentine, 1988). In addition, previous studies have shown that gaze discrimination is altered in inverted faces (Jenkins &

Langton, 2003; Schwaninger, Lobmaier & Fischer, 2005; Senju & Hasegawa, 2006) and that the gaze-cueing effect is diminished and sometimes even abolished with inversion (Langton & Bruce, 1999; Hori et al., 2005; Kingstone et al., 2000; Graham et al., 2010; Bayless et al., 2011 [but see Tipples, 2005]). In line with these results, we found a smaller GOE for inverted than upright faces, reflecting the decreased efficiency of gaze cues when presented in inverted faces. Our results suggest that integrity of face configuration contributes to the GOE.

Using inverted faces, we also wanted to determine whether the observed enhancement of attention to gaze with fearful compared to happy faces was due to a difference in the emotional content of the face or to a difference in the *amount of movement* between fearful and happy faces. The amount of movement refers to the apparent movement driven by the change from a neutral to an emotional expression. The difference in apparent movement between the two emotions is thus driven by a differential amount of configural change (eyes wide open for fear and squinted for joy, mouth rounding for fear and a big smile for joy etc). That movement would be identical between upright and inverted faces. In contrast, inversion impacts emotion discrimination (e.g., Derntl et al., 2009). If facial expression identification is critical for an emotion to modulate the GOE, we would expect to observe a larger GOE for fearful compared to happy faces in the upright but not, (or less so) in the inverted condition given that fearful and happy expressions would be discriminated from one another less accurately in inverted faces than in upright faces. However, the three-way interaction between Congruency, Emotion and Orientation was not significant. Given that the enhancement of the GOE with fearful expressions relative to happy expressions was preserved with inversion, emotion identification does not seem to be a critical factor in the emotional modulation of the GOE. Rather, another factor, possibly a difference in the amount of movement associated with fearful and happy faces, could drive the larger GOE for fearful than happy faces Alternatively, the larger GOE for fearful than happy faces might be driven by local cues such as eye size which is identical in both orientations (fearful eyes are always more open than happy eyes, regardless of orientation) but is larger in fearful than happy faces.

5.4.3 Modulation of ERPs to targets by gaze and emotion cues

At target presentation, in agreement with previous studies, P1 amplitude to targets was enhanced in the congruent condition compared to the incongruent condition (Schuller & Rossion, 2001, 2004, 2005; Hietanen et al., 2008; Chapter 3). This congruency effect on P1 amplitude is thought to reflect the enhancement of visual processing at the cued location (Hopf & Mangun, 2000). However, this congruency effect did not differ between fearful and happy expressions. In Chapter 3 we found a larger congruency effect on P1 to targets preceded by fearful as well as by happy faces compared to targets preceded by neutral faces. Although we did not compare this congruency effect directly between fearful and happy conditions (recall that FSN and HAN conditions were analyzed separately), these results suggested that both fearful and happy faces yielded a similar congruency effect (except for the lateralization found for happy faces). The present results are thus in line with those of Chapter 3.

Results for the P1 latency, however, were inconsistent with previous findings. Using a neutral face cue, some studies found an earlier P1 in the congruent condition compared with the incongruent condition (Schuller & Rossion, 2001, 2004, 2005), while using emotional face cues, we showed a delayed P1 latency in the congruent compared to the incongruent condition in Chapter 3, which was thought to reflect additional time linked to the integration of gaze and emotional cues, itself impacting the processing of the target. Similarly, in the present study, a delayed P1 for congruent targets compared to incongruent targets was found, however only when the face was inverted. The reason why upright faces did not yield a similar delay here as in Chapter 3 is unclear but could be related to the different sequence used between the two ERP studies.

5.4.4 Modulation of cue-triggered ERPs

We were also interested in investigating the two cue-triggered ERPs, EDAN and ADAN, indexing respectively attention orienting to the cued location and attention holding at the cued location. Hietanen and colleagues (2008), comparing schematic neutral face cues and arrow cues, found evidence for EDAN and ADAN with arrow cues but not with gaze cues. However, using emotional faces and a discrimination task, Holmes and colleagues (2010) showed the presence of ADAN (but not EDAN), while Chapter 3 using emotional faces and a localization task found evidence for both ADAN and EDAN. In the current experiment, we also used a localization task (which we believe is more relevant than a discrimination or a detection task, in gaze cuing studies, given that the cue indicates a location in the environment) and emotional face cues, although with a different cue sequence than in Chapter 3. We replicated the findings of Chapter 3 regarding the presence of EDAN and ADAN in response to emotional gaze cues, and, similarly, the lack of a modulation of these components by emotion.

Thus attention-orienting to gaze seems to involve attention stages comparable to those reported in attention orienting to arrow cues, which are identifiable using ERPs (EDAN, ADAN, P1). However, despite emotional modulation of the GOE behaviorally, none of these ERP components were sensitive to the type of emotion tested. Because a neutral face condition was not employed in the present experiment[16], we cannot claim that emotions did not influence the processes at all. In fact, a comparison between the P1 congruency effects presented here and those obtained in Chapter 3 suggests that emotions influenced gaze-oriented attention at target level, but similarly for fearful and happy expressions. These results indicate that emotion needs to be processed for more than 400ms (delay between the onset of emotion -300ms before target onset- and P1 occurring 100ms after target onset) to modulate attention to gaze. According to this idea, the brain processes involved in attention to gaze would be modulated by emotion possibly during target presentation or afterwards, between 100ms and 300ms after target onset, at which time the behavioral response occurs. Alternatively, it is possible that emotion influences brain processes devoted to gaze-oriented attention continuously but weakly and that this modulation is not detectable with scalp ERPs.

5.4.5 Influence of autistic traits

We found a trend toward an inverse correlation between the size of one's GOE for happy faces and one's score on the autism-spectrum quotient (AQ) such that higher levels of autistic traits and lower levels of social skills were associated with smaller GOEs to happy facial expressions. This finding was contrary to what we expected initially. Given the lack of enhancement of the GOE by fearful faces for autistic individuals reported by Uono and colleagues (2009), we expected an inverse relationship between autistic traits and the size of the GOE to fearful faces, not happy faces. Our result suggests that individuals with high autistic traits process happy upright faces (and not fearful upright faces) differently than individuals with low autistic traits.

A smile is often directed at someone and thus a happy face looking away can suggest the person is looking at a pleasurable object or at another individual. Fear in contrast, is rarely directed at another

[16] The reason why neutral faces were not used in Experiment 4 is that, with gaze-then-expression sequence, a comparison between emotional faces and neutral faces is confounded, because emotional faces express fear or surprise 300ms before target onset while neutral faces do not change. Thus, there would be an added warning sign that the target is coming for emotional relative to neutral faces.

individual and rather reflects the presence of a danger in the environment. The lack of correlation between AQ scores and the GOE for fearful faces suggest individuals with high AQ and low AQ are similarly sensitive to fearful gaze, likely because of its threat related implication. Individuals with high AQ do not have as much incentive as individuals with low AQ to look in the direction indicated by a smiling face because it indicates the presence of a social interaction and social interactions are not as interesting or rewarding for them as they are for individuals with low AQ. This idea is in line with current research suggesting a diminished reward value of happy facial expression in individuals with ASD (who would score high on the AQ) compared to typical individuals (Sepeta, Tsuchiya, Davies, Sigman, Bookheimer & Dapretto, 2012). In the AQ test, the Imagination subscale indicates "the faculty or action of forming new ideas, or images or concepts of external objects not present to the senses". The significant inverse correlation we found between the score on the Imagination subscale of the AQ and the GOE for happy upright faces could be due to the fact that a certain amount of "imagination" is required for participants to associate the faces presented in experimental conditions (i.e., grey-scale pictures presented on a computer monitor, averting their gaze and expressing an emotion) with real faces that could send social signals in a natural context (i.e., happy faces smiling to another, fearful faces reacting to a danger in the environment), especially for happy faces, since participants are alone, in a closed room.

Interestingly, the inverse relationship between AQ and the GOE for happy faces was found only for upright faces, in which facial configuration is not altered. Since the integrity of facial configuration is important for emotion recognition, the emotional content of happy faces seems to be important in this trending correlation with the AQ score. This idea is consistent with the significant correlation between scores on the Attention to Detail subscale of the AQ and the GOE for happy upright faces. Indeed, this correlation suggests that individuals who are less detail-oriented (more focused on global information) have an increased GOE for happy faces. When perceiving a face, if individuals are more focused on global than local information, they tend to focus on the configuration rather than on the features, which would make it easier to access the emotional content of the face (relying on configural information). Further studies should compare populations with and without ASD on their gaze orienting response to happy gazing faces to shed more light on this phenomenon.

Our findings also indicated an inverse relationship between the congruency effect on P1 and the AQ score: higher levels of autistic traits were associated with a reduction in the congruency effect on P1, particularly in the upright face condition. The negative correlation between the congruency effect on P1 and the AQ score is in line with Bayliss and colleagues (2005) who found a negative correlation between the GOE and the AQ score. However, the correlation between autistic traits and the size of the congruency effect on P1 is only trending so caution should be applied in interpreting these results until they are replicated. Interestingly, we also found a significant negative correlation between the congruency effect on P1 amplitude and scores on the social skills or communication subscales of the AQ, such that participants with more communicative abilities and social skills had a larger congruency effect on P1 amplitude. Given that gaze-oriented attention is an experimental proxy for joint attention, the present results could contribute to explaining the neural mechanisms involved in the clinical deficits of joint attention and ToM observed in individuals with ASD, impaired at social interactions and communication (Okada, Sato, Murai, Kubota, & Toichi, 2003; Dawson, Toth, Abbott, Osterling, Munson, Estes & Liaw, 2004). Future studies will need to extend these results, comparing the target-triggered ERPs of individuals with and without ASD in gaze cueing experiments.

In sum, autistic traits appear to influence the neural responses to gaze-oriented attention and our attention allocation to happy gazing faces. This suggests that the deficit in joint attention observed in ASD could have its roots in deficits occurring at an early stage of brain processing of attention to gaze. It also suggests that the information carried by a happy face looking away is not as interesting for individuals with high AQ than for individuals with low AQ due to its social content.

5.5 CONCLUSION

The results of this experiment confirm an enhancement of attention to gaze with fearful faces compared with happy faces in a non-anxious sample. They also demonstrate that the GOE is disrupted with inversion but that the larger GOE for fearful than happy faces is preserved in inverted faces suggesting that i] configural information is critical for the GOE, and ii] the emotional modulation of the GOE relies more on the movement associated with particular emotions or in the difference in the aspect of the eye for different emotions than on the emotional content of a face per se. At the brain level, a congruency effect on P1 amplitude was found at target onset, and EDAN and ADAN were present at cue onset, in agreement with Chapter 3. However, none of these ERP components were modulated by emotion in Experiment 4.

Importantly, the degree to which one’s attention is oriented by happy faces depends on his or her autistic traits with high AQ individuals showing less sensitivity to happy faces than individuals with low

AQ. Thus, autistic-like traits influence the way social signals are processed. Moreover, the congruency effect on P1 amplitude was dependent on one's AQ: it was larger in individuals with low AQ than in individuals with high AQ. This result indicates less attention allocation to the gazed-at direction in individuals with high AQ than in individuals with low AQ, which is in line with the deficit of joint attention observed clinically in individuals with ASD.

Future studies will have to replicate the observed influence of AQ on the brain processes devoted to attention and on the allocation of attention resources to faces signaling a social interaction. They will also have to investigate this phenomenon in ASD population to determine its contribution to their observed deficits.

Chapter 6: GENERAL DISCUSSION

6.1 Results overview

In order to make sense of others' behaviors, we rely heavily on non-verbal facial cues such as gaze direction and facial expressions. Successful interactions necessitate not only proper "reading" of these cues in isolation (i.e., being able to recognize and interpret various facial expressions and gaze directions), but also their integration. Indeed, a particular emotion (e.g., fear) has a different meaning when it is embedded in a face with direct gaze (e.g., your social partner is afraid of you) than when it is embedded in a face with averted gaze (e.g., your social partner is afraid of an object in the periphery that might be dangerous for you as well). The way in which we combine gaze and emotion cues to orient our attention toward a specific location in the environment was investigated in this thesis.

First, in Chapter 2, we tested the impact of gaze direction on emotion discrimination. Our results showed that fear and surprise are the least well-discriminated emotions, as typically reported, regardless of gaze direction. Although responded to faster when presented with direct than averted gaze, fearful, angry, happy, surprised, and neutral expressions yielded similar response times when combined with a given gaze direction and accuracy did not vary with gaze direction.

In Chapters 3, 4, and 5, the influence of facial expressions on gaze-oriented attention was investigated, using gaze-cueing paradigms. In addition, Chapters 3 and 5 used ERPs to track the neural correlates of these attention-orienting effects. In Chapter 3 we found an enhanced GOE for fearful and surprised expressions relative to neutral expressions and for angry expressions relative to neutral and happy expressions. We were able to demonstrate these effects in a non-anxious sample while it had been previously shown in highly anxious participants. In addition, we showed that the typical congruency effect on P1 amplitude recorded to the target was modulated by emotion and we found for the first time in a gaze cueing experiment, the presence of attention-related ERPs recorded to the cue, EDAN and ADAN.

In Chapter 4, we investigated whether the interaction between emotion processing and gaze-oriented attention occurred regardless of the order in which gaze and emotion cues were presented. We found that the GOE for fearful, angry and surprised facial expressions was enhanced relative to neutral expressions only when aversion of gaze preceded emotion expression.

This sequence was thus used in Chapter 5, in which the relationship between autistic-like traits and emotional modulation of gaze-oriented attention was investigated, in the normal population. In accordance with previous results, the GOE was larger for fearful than happy expressions. The GOE was also attenuated by inversion, although similarly for both emotions, suggesting that its emotional modulation relied more on local than global information. Similarly to Chapter 3, we found a congruency effect on P1 amplitude at target onset and the presence of EDAN and ADAN at cue onset. These attention-related ERPs were not modulated differently by fearful and happy faces. Importantly, a larger GOE with happy facial expressions was observed in more imaginative and less detail-oriented individuals, and the congruency effect on P1 amplitude to targets following upright faces was also larger in individuals with more social skills and communicative abilities. These results suggest that autistic-like traits impact gaze-oriented attention to social emotions at the brain and behavioral levels.

In the next section, we outline the precise contributions of the results presented throughout this thesis (and summarized above) in understanding attention to gaze and its modulation by facial expressions.

6.2 Contributions of our work

6.2.1 Facial expressions influence gaze-oriented attention

6.2.1.1 The GOE is modulated by facial expressions even in non-anxious participants

In accordance with previous studies (e.g., Friesen & Kingstone, 1998), participants showed a GOE in all three gaze-cueing studies presented in this thesis (Chapters 3-5), despite changes in stimuli sequences and in the nature/number of emotions included in the design. These results confirm that the GOE is a robust phenomenon that can be replicated.

A modulation of the GOE with facial expressions was observed in Chapter 3, Chapter 4 (Cond. 2) and Chapter 5, when a dynamic face cue, a 500ms SOA and a localization task were used. This is an important finding because several studies failed to report an emotional modulation of gaze-oriented attention (Hietanen & Leppanen, 2003; Fichtenholtz et al., 2007, 2009; Galfano et al., 2011; Holmes et al., 2010). This lack of GOE modulation could be due to the use of SOAs shorter than 300ms (e.g., Galfano et al., 2011 used 200ms SOA) as Graham and colleagues (2010) suggested that it was the minimum SOA required for a full integration between gaze and emotion cues. The use of a discrimination task might also account for some of these null findings (e.g., Holmes et al., 2010), as it is harder (Posner, 1980) and less ecologically valid than a localization task. Since the combination of gaze and emotion cues indicate where in the environment the object eliciting one's facial expression is located, a localization task seems more adequate than a discrimination task. Finally, the use of static rather than dynamic facial expressions (e.g., Hietanen & Leppänen, 2003) could have prevented a modulation of gaze-oriented attention with emotions, as emotions are better processed when seen dynamically than statically (Sato & Kochiyama, 2004).

In addition, it was previously unclear whether the modulation of the GOE with emotion was dependent on participants' anxiety/fearfulness traits (Fox et al. 2007; Mathews et al., 2003; Putman et al., 2006; Holmes et al., 2006 [Exp.3]) or was also present in non-anxious participants (Bayless et al., 2011; Neath et al., 2013). Our findings (Chapters 3; 4 [Cond. 2]; 5) confirm that non-anxious participants exhibit an emotional modulation of the GOE when parameters such as a dynamic face cue and a localization task are used. The presence of a modulation of gaze-oriented attention with emotions in our non-anxious samples suggests that this phenomenon is not driven by anxiety and could play a role in everyday social interactions in the general population.

6.2.1.2 The GOE is enhanced for fearful, surprised and angry facial expressions

It was expected that emotions signaling a threat in the environment, like fear, would enhance the GOE compared to neutral expressions. Indeed, there is an undeniable evolutionary advantage to orienting faster toward a location looked-at by a fearful face, indicating a danger, than to a location looked-at by a neutral face. In accordance with this idea and with many previous studies (Fox et al., 2007; Graham et al., 2010; Mathews et al., 2003; Pecchinenda et al., 2008; Tipples, 2006; Putman et al., 2006; Bayless et al., 2011; Neath et al., 2013), we found that the GOE was enhanced for fearful expressions compared to neutral expressions (Chapters 3 and 4 [Cond.2]) and compared to happy expressions (Chapter 5 but see Chapter 4 [Cond.2]). A happy face with averted gaze signals the presence of a rewarding object, often a person, in the periphery. Thus, it is not as evolutionarily relevant to attend to the location looked at by a happy face as it is to a location attended by a fearful face, although it is definitely socially relevant.

We also observed an enhanced GOE for surprised expressions compared to neutral expressions (Chapters 3 and 4 [Cond.2]). Only two previous gaze-cueing studies included surprise in their design (Bayless et al., 2011; Neath et al., 2013) and only one found an enhancement of GOE for surprised compared to neutral expressions (Neath et al., 2013). Our replication of this finding, using the same design as Neath and colleagues (Chapter 4 [Cond.2]) as well as a different design (Chapter 3), is thus important. Surprise is somewhat of an outlier among basic facial expressions because it has an ambiguous valence (neither positive nor negative) and it is usually a short-lived emotion, replaced by a positive or a negative expression (Fontaine et al., 2007). In fact, it has been shown that the interpretation of surprise depends on the context: it is perceived as negative when presented with negative expressions, but as more positive when presented with positive expressions (Neta & Whalen, 2010; Neta et al., 2011). In both Chapters 3 and 4, negative facial expressions were more numerous than positive facial expressions and thus it is likely that surprised faces were interpreted as witnessing a negative, maybe threatening event. This would explain the larger GOE for surprised than neutral faces found and the fact that this effect was as large as for fearful faces.

Finally, we found an enhancement of the GOE with angry expressions compared to neutral (Chapters 3 and 4 [Cond.2]) and happy (Chapter 3) expressions. Most previous studies in which angry faces were tested did not report a modulation of the GOE by anger (e.g., Bayless et al., 2011; Fox et al., 2007; Hietanen & Leppänen, 2003). We noticed one exception in which anger increased the GOE of anxious participants (Holmes et al., 2010). As this study was the only one that did not include fearful faces in its design, we hypothesized, in Chapter 3, that the presence of fearful faces might mask potential effects of anger on the GOE. Angry faces with averted gaze do not *necessarily* signal a danger in the periphery, but rather, a confrontation between the angry person and someone else and it could be argued that attending to a conflict is less evolutionarily advantageous than attending to a danger (as signaled by a fearful face with averted gaze). However, and for the first time, we found an enhancement of the GOE for angry relative to neutral faces in an experiment also including fearful faces (Chapter 4 [Cond. 2]). Together with the findings reported for surprise, our results suggest that the GOE is increased by threat signaling expressions (anger, fear, and surprise in the context of fear). The null findings reported for anger in previous studies might be due to experimental factors such as the SOA or task used. Our result of a larger GOE with angry than neutral faces in a non-anxious sample is thus a novel and important finding. Importantely, our results suggest that the modulation of the GOE for emotional faces relative to neutral faces is driven by a true facilitation of attention orienting in congruent trials rather than by an inhibition of attention disengagement in incongruent trials (Chapters 3 and 4).

The evolutionary hypothesis and the threat-related hypothesis are similar as it is the threat related content of the sequence that makes fast attention orienting evolutionary relevant (the fearful face expresses a danger I should attend to as quickly as possible for my safety). However, threat-related expressions are also negative in valence and it is thus impossible, with the current emotions used, to know which of the two dimensions influence the GOE (surprise taking a negative valence in the context of fearful expressions). In contrast, sad faces are also negative in valence but do not signal threat and thus might be useful to use in future studies. Intuitively however, it seems unlikely that sad faces would orient our attention faster than neutral faces. Although this needs to be verified experimentally, intuition thus favors the threat-related hypothesis.

6.2.1.3 In dynamic displays, facial cue sequence matters

Among studies that have investigated the impact of emotions on gaze-oriented attention using a dynamic display, some have used a face cue in which the emotion was changed before the gaze onset (e.g., Mathews et al., 2003) while other studies have used a face cue in which the gaze was averted before emotion expression (e.g., Graham et al., 2010). Yet other studies have used a face cue averting its gaze and expressing an emotion simultaneously (e.g., Tipples, 2006). The various face cue sequences used by previous studies might have played a role in the discrepant results reported in the literature in regard to the modulation of the GOE by emotions. Chapter 4 is the first study to directly compare these three cue sequences in a single design and to show that the cue sequence actually influences the modulation of the GOE by emotions quite dramatically (Table 4). Specifically, a GOE modulation with facial expressions was observed only when gaze shift preceded emotion expression (Cond. 2) but not when emotion was expressed before gaze shift (Cond. 1) or when both occurred simultaneously (Cond. 3). Chapter 5 and other studies using a sequence in which the face cue shifted gaze before expressing an emotion (Graham et al., 2010; Neath et al., 2013) also showed an emotional modulation of the GOE, confirming the reliability of this finding. These results are in line with our intuition that most of the time, in real life, we need to first look at an object before we can react to it. In contrast, Cond. 1 sequence is rarely[17] found in real life and violates the typical order in which an observer expects to witness events while Cond. 3

[17] In real life situations involving more than just the visual modality, we could potentially observe someone reacting to a noise in the distance, and then looking around to determine where this sound occurred and what triggered it.

sequence is ambiguous. However, this last sequence was used in Chapter 3, in which we did observe an emotional modulation of the GOE with facial expressions. This discrepancy might be due to the number of emotions presented (five in Chapter 4 [Cond.3], three in each condition of Chapter 3) and to the fact that participants were screened for autistic traits in Chapter 3 but not in Chapter 4. We come back to these points in sections 6.2.2.4 and 6.2.3.

In addition to being more ecologically valid, Cond. 2 sequence has the advantage of yielding a gaze shift independent of the eye aperture associated with a particular emotion (fearful faces have typically larger eye size than neutral or happy faces) since it occurs before emotional expression. Bayless and colleagues (2011) actually measured the eye size of their stimuli and found that it was largest in fearful faces, followed by surprised faces, neutral faces, angry faces and smallest in happy faces. When the emotion expression precedes or is concurrent with gaze aversion, it is confounded with the eye aperture and any increase or reduction in the GOE with fearful or surprised faces could be due to a better processing of gaze itself because of eye size. This confound was present in Chapter 3 in which gaze and emotion changed simultaneously. However, eye size alone can't explain the emotional modulation of the GOE observed in Chapter 3 because, otherwise, we would have found a larger GOE for neutral than angry faces in condition HAN (as neutral faces were found to have a larger eye sclera than angry faces, given that we used similar stimuli as Bayless and colleagues [2011]), while the opposite was found. It seems important that future studies investigating the emotional modulation of the GOE use a sequence in which gaze shits before emotion is expressed. It would also be important to experimentally test our intuition that the sequence presented in Cond.2 is indeed perceived as the most ecological among the three sequences used in Chapter 4 and verify that this is also the intuition of naïve participants.

6.2.1.4 Influence of "emotional context" on the GOE modulation with emotions?

Interestingly, as seen on Table 4, fearful faces enhanced the GOE compared to happy faces in Chapter 5 but not in Chapter 4 (Cond. 2). Given the exact same sequence was used in both (gaze shifted before emotion expression), sequence alone cannot explain these discrepant findings. The number and types of emotions included, however, differed across these studies, which we will refer to as the *emotional context* of an experiment. Thus, it is possible that the emotional context in which a facial expression is presented determines whether it enhances the GOE compared to happy faces. As another example, Chapter 3 and Chapter 4 (Cond.3) also used the same face cue sequence (gaze aversion and emotion expression simultaneous) and the same emotions (fearful, angry, happy, neutral surprise). However, all emotions were presented together in Chapter 4 (Cond.3) while they were presented across two separate conditions in Chapter 3 (FSN and HAN Conditions). Critically, no modulation of the GOE with emotions was observed in Chapter 4 Cond.3 while a modulation of the GOE with emotions was observed in both conditions in Chapter 3, clearly showing that the emotional context in which facial expressions are presented influences whether they modulate the GOE (Table 4).

Table 4

Summary of the GOE modulations with facial expressions (Fearful:F, Happy:H, Angry:A, Surprised:S, Neutral:N) across Chapters 3- 5. The experiments which comparison suggests an influence of the face cue sequence on the GOE modulation with emotions are highlighted grey. The experiments which comparison suggests an influence of the number/types of emotion (emotional context) included in the design are circled in black. In all Chapters, participants were non-anxious.

	Included emotions	**Sequence 1**: emotion *before* gaze	**Sequence 2**: emotion *after* gaze	**Sequence 3**: emotion *together with* gaze
Chapter 3 (8<AQ<26)	-Cond. FSN: F, S, N -Cond. HAN: H, A, N			F, S> N A> H, N
Chapter 4 (AQ not monitored)	H, A, N, F, S	Cond.1: No modulation	Cond.2: F, A, S>N	Cond.3: No modulation
Chapter 5 (7<AQ<37)	F, H		F>H	

This idea of emotional context is in accordance with Wieser & Brosch (2012) who suggested that the way an emotion is perceived partly depends on which other emotions are included in the experimental design. For example, a neutral face is judged as sadder when following a happy face than when following another neutral face (Russell & Fehr, 1987) and, as mentioned earlier, the valence attributed to surprise is congruent with the valence of the contextual expressions (Neta & Whalen, 2010; Neta et al., 2011). In light of those results, we postulate that the way in which we process an emotional face cue is affected by the emotions expressed in preceding trials. This perceptual modulation might, in turn, influence the impact of emotional faces on gaze-oriented attention.

We recently designed a new study to test this hypothesis of GOE modulation with emotional context in which the magnitude of the GOE associated with fear will be compared, in the same subjects, between blocks in which fearful faces are presented with just happy, angry or surprised expressions. If the GOE for fear differs across blocks, this will indicate that the type of emotion present in the design influences the way a particular emotion is understood.

6.2.2 Gaze-oriented attention can be reliably tracked at various stages.

If the magnitude of the GOE is quite small (between 8 and 30ms across studies), its emotional modulation is even smaller (5ms on average in this thesis) and influenced by the experimental design (i.e., SOA, face cue sequence, possibly number/type of emotions included). In addition, the GOE is only an indirect measure of gaze-oriented attention, as it reflects processes that occurred after cue presentation as well as during and after target presentation. Event Related Potentials (ERPs) can be used to track these processes directly when they take place. In Chapters 3 and 5, we demonstrated that ERPs could reliably index the stages involved in attention orienting to gaze.

Importantly, the experiments presented in Chapters 3 and 5 are the first gaze cueing studies to report the presence of both attention-related EDAN and ADAN components recorded to the cue, despite variations in the paradigms used, which attests to the reliability of these findings. EDAN indexes attention-orienting to the gazed-at location, while ADAN, occurring later, reflects holding of attention at a gazed-at location. Previously, these components had been reliably shown only with symbolic cues (e.g., Praamstra et al., 2005). A study contrasting gaze and symbolic cueing, found the presence of EDAN and ADAN for arrow cues but not for gaze cues (Hietanen et al., 2008). However, the gaze cues were embedded in overly schematic pictures of faces, a stimulus that might not have been realistic enough to elicit the same processes as gaze perceived from face photographs. Using pictures of real emotional faces in a discrimination task, Holmes and colleagues (2010) showed the presence of ADAN but not EDAN in a gaze cueing paradigm. The fact that we observed both ADAN and EDAN when using pictures of real emotional faces and the more ecologically valid localization task, suggests that task might impact the processes recruited for gaze-oriented attention. We argue that a localization task is more ecologically valid as one usually orients toward a location before assessing what is present at that location. In any case, our results suggest that similar attention stages, as revealed by these two ERP components, can be seen in both symbolic and gaze cueing paradigms. The finding of EDAN/ADAN presence for arrow cues but not gaze cues led some to argue that eyes are special in engaging attention and rely on a different attention-orienting mechanism than arrows (e.g., Hietanen et al., 2008). The presence of both components for gaze cues reported in this thesis questions this assumption. Given that EDAN and ADAN are characteristic of symbolic cueing known to rely on voluntary or endogenous attention (see section 1.1.3), our results suggest that the early stages of gaze cueing might also rely on endogenous attention. This idea is in accordance with previous evidence demonstrating similarities between arrow and gaze cueing (see Frischen et al., 2007 for a review). However, caution is required given arrow and gaze cues were not compared in a single experiment in this thesis. Future studies will need to compare the ERPs elicited by both types of cueing in the same experiment for more conclusive evidence of similarities and differences in the processes engaged by arrow and gaze cueing.

In addition to cue-triggered ERPs, we also investigated the modulations of the P1 component triggered by the presentation of targets as a function of gaze congruency and preceding emotion cue. In accordance with previous findings (Schuller & Rossion, 2001, 2004, 2005), P1 exhibited larger amplitudes in the congruent condition than in the incongruent condition, across two different experiments. Planned comparisons revealed that this effect was found for targets preceded by emotional faces but not by neutral faces, a finding interpreted as reflecting an effect of the emotional context in which neutral faces were presented. Overall, this P1 congruency effect indicates an enhancement of visual processing at the cued location (Hopf & Mangun, 2000). However, we did not find an earlier P1 latency in the congruent compared to the incongruent condition, as reported previously with neutral face cues (Schuller & Rossion, 2001; 2004; 2005). Instead, using emotional faces, we showed that P1 occurred later in the congruent than in the incongruent condition (although in Chapter 5 this effect was restricted to inverted faces). This was the first report of a congruency effect on both P1 amplitude and latency in gaze cueing experiments using emotional faces. The reliability of these effects (especially latency) will thus have to be assessed by future studies.

No emotional modulation of EDAN and ADAN was found in either study, suggesting that, at the brain level, gaze-oriented attention is not modulated by emotion in the first 500ms after gaze shift. In contrast, emotion modulates the P1 congruency effect compared to neutral faces but the emotional modulations of the congruency effect on P1 (for happy, fearful and surprised faces) do not yet reflect the emotional modulation of the GOE seen at the behavioral level (for fearful, surprised and angry faces). Thus, we conclude that, in both studies, further emotional modulation of the neural processes associated with gaze-oriented attention occurs between the P1 (~100ms after target onset) and the behavioral response (~300ms after target onset), that is, between 600-800ms after gaze cue onset (which always occurred 500ms after gaze cue onset), which is fairly late.

6.2.3 Autistic traits influence gaze oriented attention and its modulation by facial expressions

Beside social interaction deficits, individuals with Autism Spectrum Disorder (ASD) exhibit deficits in communication and imagination as well as an extreme attention to details and a difficulty disengaging from activities they are intensely focused in (Baron-Cohen, 2000). However, the severity of those symptoms is highly heterogeneous in the ASD population and the new Diagnostic and Statistical Manuals of Mental Disorder (5th ed.; DSM-V; American Psychiatric Association, 2013) recognizes ASD as a continuum ranging from low-functioning ASD to high functioning ASD. This continuum even extends to the general population: people exhibit more or less autistic traits and these autistic traits can be assessed using the Autism Quotient (AQ- Baron-Cohen et al., 2001) that comprises questions encompassing the five domains particularly impaired for individuals with ASD (social skills, communication, imagination, attention to details, attention switching). It is believed that individuals studying mathematics, computer science or engineering have on average higher scores on the AQ than individuals in other disciplines (Baron-Cohen et al., 2001).

In addition to the symptoms listed above, ASD is characterized by clinical deficits in Theory of Mind (ToM) and joint attention (JA). However, individuals with ASD do not seem to exhibit deficits in processing social cues such as gaze and emotion tested in isolation (Nation & Penny, 2008; Jemel et al., 2006). Social cues are thus perceived by individuals with ASD but not used adequately to determine intentions of others. In line with this idea, the size of the GOE was shown to be inversely correlated to participants' AQ score in the general population, suggesting a relationship between the autistic traits and the ability to use gaze cues to direct attention (Bayliss et al., 2005). In addition, it was observed that, contrary to neurotypicals, individuals with ASD do not show a larger GOE with fearful faces compared to neutral faces (Uono et al., 2009). This finding suggests that individuals with ASD also have difficulty modulating gaze-oriented attention with fearful facial expressions. Given that individuals with high AQ show a decreased GOE and individuals with ASD (who score high on the AQ) do not modulate the GOE with fearful faces, in Chapter 3, we selected participants who scored below the cutoff, to avoid the confound potentially associated with high AQ (high likelihood to be clinically diagnosed with ASD).

However, we were interested in how differences in AQ score influence gaze-oriented attention and its modulation by emotional faces. Thus, in Chapter 5, we opted for the opposite approach and included participants with a wide range of AQ scores. We recruited participants in the Mathematic department of the University of Waterloo in order to include individuals with high AQ scores (which are difficult to find among psychology students). Based on Uono and colleagues (2009), we predicted that the AQ score would be inversely correlated with the GOE for fearful faces (the higher the AQ score, the smaller the GOE for fearful faces). In contrast, we observed a trending inverse correlation between participants' AQ score and their GOE for *happy* upright faces (but not fearful upright faces) such that the more pronounced the autistic traits, the smaller the GOE for happy upright faces. Specifically, we found that the GOE for happy upright faces was inversely correlated with the "imagination" and "attention to detail" subscales of the AQ such that the less imaginative and the more detail-oriented a person, the smaller her GOE for happy upright faces. Given that a happy face looking away is often smiling at somebody, this result could suggest that individuals with high AQ scores are less inclined to attend to a location where a social interaction occurs than individuals with low AQ scores (i.e. with better social skills), probably because social interaction is not as rewarding for them (Sepeta et al., 2012). To be motivated to look in the direction indicated by a happy face, you need to be quite imaginative as you have to be able to picture a possible social interaction, despite being in a confined laboratory, witnessing pictures of faces on a computer screen, which could explain the relationship between imaginative abilities and the GOE to happy faces. In addition, to determine that a happy face signals a social interaction, you also have to access its emotional content, a skill that depends on global/holistic processing as opposed to featural processing (focused on details), which probably explains why less detail-oriented individuals have a higher GOE for happy faces.

It is noteworthy that in Chapter 4 Cond. 2, in which, in contrast to Chapters 3 and 5, no GOE enhancement for fearful and angry faces relative to happy faces was observed, participants' AQ was not monitored. In accordance with the results of Chapter 5, if the participants of Chapter 4 Cond. 2 had an exceptionally low AQ score (which could be possible given participants in that study were recruited among psychology students), they would also have an exceptionally large GOE for happy faces. An enlarged GOE for happy faces due to participants' low AQ could have masked differences between the GOE to angry/fearful faces and the GOE to happy faces. This idea remains, of course, speculative.

In addition, in Chapter 5, at the ERP level, we found a trend toward an inverse correlation between the congruency effect on P1 and the AQ score such that the more intense the autistic traits, the smaller the congruency effect on P1 to target following upright faces. More precisely, we found a significant inverse correlation between the congruency effect on P1 amplitude and the score on the "social skills" and the "communication" subscales of the AQ such that the higher the social skills and the communication ability, the larger the congruency effect on P1 amplitude. As P1 indexes the allocation of attention resources to the gazed-at side, this suggests that individuals with good communication abilities and social skills (as indexed by the AQ) use gaze cues to direct their attention more than individuals with poor communication and social skills. In addition, if the brain mechanisms involved in gaze-oriented attention are similar to those involved in joint attention, the present results could contribute to explaining the neural mechanisms involved in the clinical deficits of joint attention and ToM, observed in individuals with ASD (Okada et al., 2003; Dawson et al., 2004). Future studies will need to extend these results, comparing the target-triggered ERPs of individuals with and without ASD in gaze cueing experiments.

It is noteworthy that most studies investigating gaze-oriented attention in an ASD population (infants or adults) reported a similar gaze cueing effect in typical and in autistic individuals (Kylliainen & Hietanen, 2006; Vlamings, Stauder, Van Son & Mottron, 2005; Chawarska, Klin & Volkmar, 2003; Swettenham, Condie, Campbell, Milne & Coleman, 2003; Senju, Tojo, Dairoku & Hasegawa, 2004; Greene, Colich, Iacoboni, Zaidel, Bookheimer & Dapretto, 2011), despite a clear clinical deficit of joint attention observed in individuals with ASD (Mundy & Crowson, 1997). These results are somewhat inconsistent with Bayliss and colleagues (2005), who found an inverse correlation between AQ and the GOE such that the higher the AQ score (closer to those of ASD participants), the smaller the GOE. However, these results are in line with the findings we report in Chapter 5, in which we did not find a correlation between participants' AQ score and their overall GOE, supporting the idea that individuals with high AQ (resembling those with ASD[18]) don't show a GOE deficit. Instead of a behavioral deficit in gaze-oriented attention (as measured by the overall GOE), individuals with high AQ show a deficit in mobilizing their

[18] Approximately one third of the participants included in Expt. 4 scored above the cut-off of 26 (which indicates an. 80% likelihood of being clinically diagnosable with ASD).

brain processes devoted to allocating spatial attention to gaze (as measured by the congruency effect on P1) and in modulating gaze-oriented attention with social emotions (as measured by the GOE to happy faces).

It is currently unclear why deficit in mobilizing brain processes devoted to allocating spatial attention to gaze cues do not translate into a GOE deficit in individuals with high AQ. Possibly, the GOE, an indirect measure of gaze-oriented attention, is not sensitive enough to reflect gaze-oriented attention deficits present in individuals with high AQ because those deficits are too subtle and variable. Alternatively, individuals with high AQ could use compensatory mechanisms to make up for differences in the way their brain processes gaze-oriented attention. The reason why a joint attention deficit was previously observed in individuals with ASD (who exhibit a high AQ) while a gaze-oriented attention deficit was not is also unclear. Possibly, the GOE is actually not an adequate behavioral proxy for joint attention. After all, joint attention involves more than just orienting to the direction indicated by others' gaze. It also involves "shared attention", an intense focus of the social partners on each other that is usually apparent with social partners glancing back at each other after looking at the object (Moore & Dunham, 1995). Needless to say, this condition is not realized in laboratory settings, since participants are interacting with a face presented on a computer screen, have a non-relevant object to look at (an asterisk) and do not have the possibility to glance back at the picture after looking at the object, since it already disappeared. To study joint attention in a more ecologically valid way, recent neuroimaging studies have used face-to-face interaction (e.g., Redcay. Dodell-Feder, Mavros, Kleiner, Pearrow, Triantafyllou, Gabrieli & Saxe, 2012). Although technically challenging, these studies could provide insights as to whether gaze-oriented attention is an adequate proxy for joint attention.

Alternatively, it could be that individuals with high AQ (resembling those with ASD) are not impaired at joint attention per se but at integrating gaze signals with other social signals like facial expressions. Indeed, in real life, joint attention never occurs on blank faces but always on expressive faces, and if our social partner wants to direct our attention to some object, she will use many cues in combination, not just averting one's gaze. In fact, individuals with better social skills might be more sensitive to others' gaze when it is associated with a facial expression, indicating a special relevance for the looked-at object. In line with this idea we showed that individuals with high AQ do not modulate gaze-oriented attention with happy faces in the same way individuals with low AQ do. Whether this modulation deficit is restricted to happy faces or is present for other social emotions as well remains to be investigated. However, caution needs to be applied in interpreting these results, given that our correlations are only trending even though our sample size is quite large and that a difficulty integrating fearful emotion (not happy emotion) with gaze cues was previously observed in individuals with ASD (Uono et al., 2009).

To explain these inconsistencies and the discrepancies between findings of a joint attention deficit and findings of an intact GOE in individuals with ASD, future studies will need to clarify to which extent we actually investigate joint attention when using gaze-cueing paradigms and how to modify the design of these gaze-cueing experiments to study joint attention more ecologically. In addition, upcoming experiments will need to disambiguate whether joint attention actually entails, more than a response to gaze cues, a response to the integration of social cues like gaze and emotion.

6.3 Limitations of our work

6.3.1 Using faces with straight gaze as a control condition in gaze cueing paradigms

When defining attention orienting to peripheral and symbolic cues, Posner (1975, 1980) described a control condition in addition to the congruent and the incongruent conditions. The control condition consisted of a target preceded by a non-directional cue (a double arrow for symbolic cueing and a flashed square in a central location for peripheral cueing). Faster RTs in congruent than in control trials were thought to reveal a benefit in engaging attention to the cued location while slower RTs in incongruent than in control trials were thought to reveal a cost in disengaging attention from the cued location. When a cost and benefit analysis was used in cueing experiments, peripheral cueing yielded a cost-less benefit (Posner & Snyder, 1975), while predictive symbolic cueing yielded both costs and benefits (Posner, 1980). As a result, cost-less benefit and benefit-with-cost were thought to be the hallmark of exogenous and endogenous attention, respectively.

Previous gaze cueing experiments, using a face with direct gaze as the non-directional cue for the control condition, showed a cost-less benefit, as in peripheral cueing (e.g., Friesen & Kingstone, 1998). In line with these results, when applying a cost and benefit analysis to faces with a neutral expression, we also found a cost-less benefit (Chapter 4), which provides evidence for the involvement of exogenous rather than endogenous attention in gaze-cueing, in contrast with the evidence presented in section 6.2.2. However, caution is necessary because, in fact, both congruent and incongruent targets were responded to faster than targets following neutral faces with direct gaze (Chapter 4: Cond. 2 & 3 but not Cond.1), suggesting that faces with direct gaze are dwelled on more than faces with averted gaze. In accordance with this idea, faces with direct gaze were shown to capture attention more than faces with averted gaze (Senju & Hasegawa, 2005), a finding that has been attributed to the powerful approach signal entailed by faces with direct gaze (while faces with averted gaze signal avoidance). In addition in this thesis, neutral faces with direct gaze were static stimuli while neutral faces with averted gaze were dynamic stimuli (gaze direction is changed). Thus, faces with direct gaze do not appear to be an ideal control for faces with averted gaze because the two differ on more than one dimension (non-directionality versus directionality (gaze), approach versus avoidance, and static versus dynamic).

To avoid the confounds associated with using faces with direct gaze as a control condition, in this thesis, we followed the recommendation of Jonides & Mack (1984) to drop the control condition when it differed from the test condition on other dimensions (here approach versus avoidance, static versus dynamic) than the one of interest (directionality versus non-directionality). Similarly to other gaze-cueing researchers (e.g., Bayless et al., 2011; Fox et al., 2007; Mathews et al., 2003), in Chapters 3 and 4, we analyzed the direct gaze condition separately from the congruent and the incongruent conditions (in Chapter 5, we did not include a direct gaze condition). Instead of applying a cost and benefit analysis, we used, like others, the Gaze Orienting Effect (GOE: difference between RTs to congruent and incongruent trials) as an index of gaze cueing magnitude, the RTs to congruent targets as an index of attention engagement to the gazed-at location and the RTs to incongruent targets as an index of disengagement from the gazed-at location.

Diverse attempts have been made to overcome the static versus dynamic confound of faces used as a control stimulus, some using faces crossing their eyes (e.g., Bayless et al., 2011) and others faces opening their eyes (e.g., Langdon & Smith, 2005). Unfortunately, because faces with crossed eyes are rarely seen in natural settings, and thus surprising, they differ from a face with averted gaze on the familiarity/weirdness dimension and are not processed the same way (Hietanen & Yirttimaa, 2005). Faces opening their eyes to the front seem to be better suited as control conditions for faces opening their eyes to the side (although the approach versus avoidance confound does not disappear). Interestingly when using such a control condition, Langton and Smith (2005) showed that gaze cueing was associated with a pattern of cost-less benefits at SOAs shorter than 300ms but with a pattern of benefit-with-cost at longer SOAs. This shows that conclusions of studies applying a cost and benefit analysis can change dramatically depending on the control condition they use. Future studies, interested in shedding light on the costs and benefits associated with gaze-cueing to neutral faces (so it can be compared to peripheral and arrow cueing as well as across different emotions) will need to find an appropriate control condition.

6.3.2 Using neutral expressions as a control for emotional expressions

In gaze cueing experiments, *facilitation* of engagement of attention to gaze is defined as a faster response to congruent targets for the test condition than for the control condition while *inhibition* of the disengagement of attention from the gazed-at location is defined as a slower response to incongruent targets in the test condition than in the control condition. In Chapters 3 and 4, neutral faces were used as the control for emotional faces. Although neutral faces are an appropriate control when the gazing face cue is static, it is not anymore when the gazing face cue is dynamic, as the neutral face doesn't differ only on the dimension of interest (emotion versus non-emotion) but also on another important dimension: movement. In a dynamic display, a neutral gazing face changes to an emotional gazing face in the test condition, inducing perceived movement, while no change is seen in the control condition, as the face remains still. This results in more apparent movement for the emotional (gaze shift plus emotion change) relative to the neutral face (gaze shift only in the case of neutral averted gaze conditions and no movement at all in the case of neutral direct gaze). In Chapter 3, using neutral faces as a control for emotional faces, we observed that the enhancement of attention to gaze for fearful, surprised and angry expressions relative to neutral expressions was due to facilitation of engagement but not to an inhibition of disengagement. That is, in congruent trials, RTs were faster for emotional than neutral faces while in incongruent trials; no RT difference was seen between emotional and neutral faces. In contrast, in Chapter 4 Cond.2, while a similar facilitation of response was seen for congruent trials, responses in incongruent trials were also facilitated for emotional expressions relative to neutral faces, although not as much. This facilitation of disengagement seen in Chapter 4 Cond.2 but not in Chapter 3 could be due to the difference in sequence used. Indeed, in Chapter 3, the last change in the sequence occurred 500ms before target onset, for both neutral and emotional faces with averted gaze (gaze shift for neutral faces and both gaze shift and emotion expression for emotional faces). In contrast, in Chapter 4 Cond.2, the last change occurred 500ms before target onset when the cue was a neutral face with averted gaze (gaze shift) but only 300ms before target onset when the cue was an emotional face with averted gaze (emotion expression). In this case, the occurrence of the last change closer to target onset in the emotional than in the neutral condition could act as a warning sign and facilitate response to target in emotional compared to neutral faces, regardless of congruency.

Given that no gaze-cueing study so far has reported a modulation of the GOE with happy relative to neutral faces, in Chapter 5 we used happy faces as the control condition in order to avoid the confound associated with the difference of movement between emotional and neutral faces. When doing so, we observed that the enhanced GOE for fearful compared to happy faces was due to both a facilitation of engagement and to an inhibition of disengagement for fearful faces compared to happy faces (i.e. faster RTs in congruent trials but slower RTs in incongruent trials, for fearful than happy faces). However, using happy faces is not an ideal control condition either, because happy faces differ from fearful faces on many dimensions (e.g., familiarity, rewarding value, accuracy with which it is discriminated as outlined in Chapter 2). This represents an important limitation of Chapter 5.

Instead of using a neutral face or another emotional face as the control condition, future studies using dynamic face cues could use a control condition changing from a neutral to a calm face so there is a slight change in configuration between the gaze aversion and the emotional expression[19]. In addition, previous studies have shown that neutral faces are not always perceived as emotionally neutral (e.g., Thomas, DeBellis, Graham & LaBar, 2001) and that calm faces might be a better baseline condition (Tottenham et al., 2009). Future studies, using a face changing its expression from neutral to calm as a control condition for a face changing its expression from neutral to emotional could avoid the movement confound associated with using neutral faces as a baseline when the face cue is dynamic.

6.3.3 Context and target relevance

In the series of gaze-cueing experiments presented in this thesis, we have used a localization task. We argued that it is more relevant than a discrimination task, given that we usually use gaze cues as an indication of the location of the environment that is being attended. This implies that we believe in

[19] Since Tottenham et al. (2009) report that participants can distinguish between a neutral and a calm face with a satisfying level of accuracy, it indicates that the configuration of calm face is different enough from neutral face to be recognizable. They define a neutral face as “plain, alert face like passport photo, neither negative nor positive” and a calm face as “similar to neutral, almost bordering on pleased or slightly happy, maybe daydreaming, person looks very serene, less threatening than neutral faces”.

providing a relevant context (i.e., a task that reflects what we actually use gaze cues for) to observe the processing of gaze cues in an ecologically valid manner.

Interestingly, however, we kept the aspect of the target constant (a small black asterisk), regardless of the emotion expressed by the preceding face cue. When the face cue is neutral, it is not very important because we don't expect the looked-at object to be anything special. However, when the face cue expresses an emotion, fear for example, we expect that it is looking at a frightening object. The finding that, instead, it is looking at a black asterisk is quite odd because it is *emotionally incongruent*. Emotional incongruence is a barrier to ecological validity: over time, if I see that an individual repeatedly expressing fear while looking at a black asterisk, I might stop paying attention to the signal she sends me because they are obviously not accurate. Instead, if I see this individual repeatedly looking to the side while expressing fear in response to seeing a snake, I might pay close attention to the signals she sends me because they are accurate and might inform me of a danger. Most studies investigating the emotional modulation of gaze-oriented attention did not take into consideration the emotional congruence between target and gaze cue. As social neuroscientists, we tend to endorse the discrete approach to understanding emotions and think of the six basic facial expressions in terms of the muscles they activate, often ignoring the impact of context on the processing of facial expressions. However, recent evidences are challenging this view and re-claiming the impact of context on the way we perceive an emotion (Hassin, Aviezer & Bentin, 2013; Wieser & Brosch, 2012). More specifically, emotional congruence between target and cue has been shown to play a critical role in gaze cueing experiments. Indeed, recent studies showed that the emotional modulation of the GOE with fearful faces was conditional on the emotional congruence between target and cue (Friesen, Halvorson & Graham, 2011; Kuhn & Tipples, 2011; Dawel, McKone, Irons, O'Kearney & Palermo, 2013).

However, although future behavioral studies will need to take into consideration the emotional congruence between target and cue, it was not as relevant, in the present thesis. Indeed, in Chapters 3 and 5, we measured target-triggered ERPs, P1 and N1. P1 and N1 happen to be very sensitive to low-level differences like spatial frequency. Thus, it was critical that the aspect of the target remained constant regardless of the emotion expressed by the preceding face cue. In addition, since we were interested in the influence of sequence on the emotional modulation of the GOE in Chapter 4 and wanted to compare our results to the other experiments presented in this thesis, we kept the aspect of the target identical to Chapters 3 and 5. Nevertheless, it is to be noted that, despite the use of a simple asterisk as a target, we did observe an emotional modulation of gaze-oriented attention with emotion in most of the gaze-cueing studies presented in this thesis, which shows that, although target relevance potentially plays a role, it is not essential for emotions to modulate the GOE.

6.4 Conclusion

In this thesis, we investigated the behavioral and brain correlates associated with gaze-oriented attention and its modulation with various emotions. We made a conscious effort to get one step closer to everyday life situations by using dynamic face cues and a localization task. We showed an enhancement of the GOE with fearful, surprised, and for the first time, angry faces in three gaze-cueing experiments involving non-anxious participants. These effects were mostly driven by a true facilitation of attention during congruent trials and were most likely due to the implied threat conveyed by these emotions. We demonstrated for the first time that these effects are greatly impacted by the cue sequence used, with gaze shift preceding emotion expression yielding maximal results. Findings also suggest that the way an emotion impact gaze-oriented attention depends, in part, on the emotion(s) it is paired with. We also showed that attention orienting could be reliably tracked using ERPs and that cue-triggered components previously reported in arrow cueing paradigms were seen reliably in gaze cueing paradigms. Emotion seems to modulate only later stages of processing, including target-triggered P1, and occurs rather late, between 600-800ms post-cue onset. Finally, the GOE and its neural correlates are mildly sensitive to autistic traits in the normal population, possibly reflecting a diminished sensitivity to social emotions like happiness in individuals with high autistic traits.

The modulation of gaze-oriented attention with emotions seems to be a subtle effect, which depends on many experimental parameters (e.g., sequence, emotional context, etc…). The field is in its infancy (the first study reporting a GOE appeared only 15 years ago) and there are still many unanswered questions regarding this effect that future studies will need to address. Although, I am most interested in exploring the link between Autism Spectrum Disorder and the modulation of GOE with facial expressions, the evidence regarding a possible link between AQ score and the modulation of gaze-oriented attention with emotions are presently quite weak. Extensive investigation of the mechanisms involved in the emotional modulation of gaze-oriented attention in neurotypicals is needed before we can hope to learn anything about ASD, using this paradigm.

Appendix A: Sample Items from the Emotion Recognition Questionnaire

Instructions: Please, circle the answer to the question. For the scale, be aware than one is xtremely low intensity and 10 is extemely high intensity.

What is the emotion expressed by the face?
-fear
-happiness
-anger
-surprise
-neutral

How intense is the emotion expressed on a 1 to 10 scale?
1 2 3 4 5 6 7 8 9 10

What is the emotion expressed by the face?
-fear
-happiness
-anger
-surprise
-neutral

How intense is the emotion expressed on a 1 to 10 scale?
1 2 3 4 5 6 7 8 9 10

What is the emotion expressed by the face?
-fear
-happiness
-anger
-surprise
-neutral

How intense is the emotion expressed on a 1 to 10 scale?
1 2 3 4 5 6 7 8 9 10

Appendix B: Error Rates Chapter 3 (Experiment 2)

Table 5

Mean error rates obtained in Condition FSN for averted gaze trials (a) and direct gaze trials (b)

a)

Errors (%) for direct gaze trials	Mean (SD)
Surprise	4.82 (4.87)
Neutral	6.47 (6.79)
Fear	5.95 (5.95)

b)

Errors (%) for averted gaze trials		Mean (SD)
Surprise	congruent	4.92 (5.73)
	incongruent	7.24 (5.38)
Neutral	congruent	5.04 (4.52)
	incongruent	7.26 (5.69)
Fear	congruent	4.40 (4.77)
	incongruent	6.77 (5.90)

Table 6

Mean error rates obtained in Condition HAN for averted gaze trials (a) and direct gaze trials (b)

a)

Errors (%) for direct gaze trials	Mean (SD)
Happy	3.71 (3.94)
Neutral	5.33 (5.07)
Angry	3.16 (3.19)

b)

Errors (%) for averted gaze trials		Mean (SD)
Happy	congruent	3.65 (2.49)
	incongruent	5.48 (4.69)
Neutral	congruent	4.57 (3.61)
	incongruent	6.25 (5.00)
Angry	congruent	3.71 (2.97)
	incongruent	5.95 (5.39)

Appendix C: Error Rates Chapter 4 (Experiment 3)

Table 7

Mean error rates obtained in Condition 1 (a), Condition 2 (b), and Condition 3 (c)

a)

Condition 1	Happy	Surprised	Neutral	Angry	Fearful
Congruent	5.44	7.06	6.32	7.21	6.18
Incongruent	6.91	6.62	9.71	7.94	8.68
Direct gaze trials	7.94	7.79	7.21	7.79	7.06

b)

Condition 2	Happy	Surprised	Neutral	Angry	Fearful
Congruent	4.44	7.06	6.67	4.72	4.17
Incongruent	7.78	9.86	9.31	7.50	9.72
Direct gaze trials	6.39	5.14	11.11	5.83	5.69

c)

Condition 3	Happy	Surprised	Neutral	Angry	Fearful
Congruent	3.75	2.64	5.97	4.86	3.33
Incongruent	5.42	4.31	5.56	5.42	7.08
Direct gaze trials	3.89	5.83	4.58	4.86	4.58

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