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**The Interaction between Visual Attention and
the Processing of Visual Emotional Stimuli in
Humans: Eye-Tracking, Behavioural and
Event-Related Potential Experiments**

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Abstract

Past research has shown that the processing of emotional visual stimuli and visual attention are tightly linked together. In particular, emotional stimuli processing can modulate attention, and, reciprocally, the processing of emotional stimuli can be facilitated or inhibited by attentional processes. However, our understanding of these interactions is still limited, with much work remaining to be done to understand the characteristics of this reciprocal interaction and the different mechanisms that are at play. This thesis presents a series of experiments which use eye-tracking, behavioural and event-related potential (ERP) methods in order to better understand these interactions from a cognitive and neuroscientific point of view.

First, the influence of emotional stimuli on eye movements, reflecting overt attention, was investigated. While it is known that the emotional gist of images attracts the eye (Calvo and Lang, 2004), little is known about the influence of emotional content on eye movements in more complex visual environments. Using eye-tracking methods, and by adapting a paradigm originally used to study the influence of semantic inconsistencies in scenes (Loftus and Mackworth, 1978), we found that participants spend more time fixating emotional than neutral targets embedded in visual scenes, but do not fixate them earlier. Emotional targets in scenes were therefore found to hold, but not to attract, the eye. This suggests that due to the complexity of the scenes and the limited processing resources available, the emotional information projected extra-foveally is not processed in such a way that it drives eye movements.

Next, in order to better characterise the exogenous deployment of covert attention toward emotional stimuli, a sample of sub-clinically anxious individuals was studied. Anxiety is characterised by a reflexive attentional bias toward threatening stimuli. A dot-probe task (MacLeod et al., 1986) was designed to replicate and extend past findings of this attentional bias. In particular, the experiment was designed to test whether the bias was caused by faster reaction times to fear-congruent probes or slower reaction times to neutral-congruent probes. No attentional bias could be measured. A further analysis of the literature suggests that subliminal cue stimulus presentation, as used in our case, may not generate reliable attentional biases, unlike longer cue presentations. This would suggest that while emotional stimuli can be processed without awareness, further processing may be necessary to trigger reflexive attentional shifts in anxiety.

Then the time-course of emotional stimulus processes and its modulation by atten-

tion was investigated. Modulations of the very early visual ERP C1 component by emotional stimuli (e.g. Pourtois et al., 2004; Stolarova et al., 2006), but also by visual attention (Kelly et al., 2008), were reported in the literature. A series of three experiments were performed, investigating the interactions between endogenous covert spatial attention and object-based attention with emotional stimuli processing in the C1 time window (50–100 ms). It was found that emotional stimuli modulated the C1 only when they were spatially attended and task-irrelevant. This suggests that whilst spatial attention gates emotional facial processing from the earliest stages, only incidental processing triggers a specific response before 100 ms. Additionally, the results suggest a very early modulation by feature-based attention which is independent from spatial attention.

Finally, simulated and actual electroencephalographic data were used to show that modulations of early ERP and event-related field (ERF) components are highly dependent on the high-pass filter used in the pre-processing stage. A survey of the literature found that a large part of ERP/ERF reports (about 40%) use high-pass filters that may bias the results. More particularly, a large proportion of papers reporting very early modulations also use such filters. Consequently, a large part of the literature may need to be re-assessed.

The work described in this thesis contributes to a better understanding of the links between emotional stimulus processing and attention at different levels. Using various experimental paradigms, this work confirms that emotional stimuli processing is not ‘automated’, but highly dependent on the focus of attention, even at the earlier stages of visual processing. Furthermore, the uncovered potential bias generated by filtering will help to improve the reliability and precision of research in the ERP/ERF field, and more particularly in studies looking at early effects.

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Declaration

I declare that this thesis was composed by myself, that the work contained herein is my own except where explicitly stated otherwise in the text, and that this work has not been submitted for any other degree or professional qualification except as specified.

(David J. Acunzo)

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Chapter 1

Introduction

The purpose of the work presented in this thesis is to better understand the relationships between the processing of visual emotional stimuli and visual attention. Past research has shown that these two processes (or classes of processes) are tightly linked together. In particular, emotional stimuli processing can modulate attention, and, reciprocally, the processing of emotional stimuli can be facilitated or inhibited by attentional processes. However, our understanding of these interactions is still limited, and much work remains to be done to fully understand which brain structures are involved and the different mechanisms at play. Details on the time course of these processes and their interaction, extent and limits are still under much scrutiny, as well as how they are affected by motivation, social situations, personality, pathologies, etc.

The following sections of the present chapter briefly outline key concepts, providing the background necessary to appreciate the subsequent chapters. The typologies of visual attention are first introduced, followed by a brief presentation on emotional stimuli and their processing. Finally, a general introduction on the core of the topic, namely the interaction between emotional stimulus processing and attentional processes, is provided before introducing the content of the subsequent chapters. Reviews more specific to the research questions addressed are provided in the following chapters.

1.1 Visual attention

Visual attention is the feature of the visual system that enables us to select and ignore parts of the incoming flux of visual information. Because the amount of information is

so large and our brain has only a limited computational capacity (see e.g. Broadbent, 1982), selecting the most behaviourally relevant parts of the information for further processing is a necessity.

The study of visual attention goes a long way back. After a hundred years of research impassionating psychologists and neuroscientists, the definition by James (1890, pp. 403–404) applied to visual attention still holds true today:

Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others [...].

Although intuitively easy to grasp, attention is a concept difficult to formalise as it is difficult to measure in a straight-forward manner. The large amount of research that has been carried out for a century, however, have given us insights on the characteristics of visual attention and some of its brain mechanisms. In particular, it has been found that there are different types of visual attention, each of which can be studied separately.

1.1.1 Overt and covert attention

Visual attention can be split into *overt* and *covert* attention. Overt attention is defined by the position of the eyes. An overtly attended location in the visual field is a location directly looked at, falling in the fovea of the eye. This aspect of visual attention may be the most straight-forward one to define and measure, as it is measurable using an eye-tracker (see Section 2.1.1) and is reducible to two (or three) variables, namely the spatial coordinates on the visual field (or visual world).

Since von Helmholtz (1896), it is known that one can pay attention to objects situated in the periphery of the visual field, and not only the fovea. Von Helmholtz used a printed sheet of paper in the dark, briefly illuminated by an electric discharge. “[He] found [himself] able to choose in advance which part of the dark field off to the side of the constantly fixated pinhole [he] wanted to perceive by indirect vision. Consequently, during the electrical illumination, [he] in fact perceived several groups of letters in that region of the field. [...] The letters in other parts of the field, however, had not reached perception, not even those that were close to the point of fixation” (from the English translation of the 2nd edition of von Helmholtz 1896 by Nakayama and Mackeben,

1989). A covertly attended location is an attended location that does not fall in the fovea. Since there is no behaviour associated with shifts of covert attention, indirect measures are needed. Measures of covert attention include the difference in reaction time or accuracy at discriminating between targets situated in an attended *versus* unattended location of the visual field. Discrimination accuracy will be higher and reaction time will be shorter in attended than unattended locations. More indirect behavioural measures such as contrast sensitivity have also been used (Carrasco, 2006).

A functional link between overt and covert attention has long been suspected. In particular, the idea that (oculo-)motor commands could affect visual information was proposed by von Helmholtz (see Moore et al., 2003). More recently, Rizzolatti et al. (1987) proposed, with the “premotor theory of attention”, that spatial covert orienting is generated by a weaker activation of the same networks involved in the generation of eye movements. While physiological work indeed found neural circuits involved in both covert and overt orienting, there is also evidence for the existence of separate dedicated networks for both orienting modes (Awh et al., 2006).

The experiment presented in Chapter 2 deals with overt attention, whilst those in Chapters 3 and 4 consider covert attention.

1.1.2 Endogenous and exogenous attention

Voluntary and involuntary shift of attention are also distinguished. One can decide where to look, or what to pay attention to: in this case attention is called *endogenous*, sustained or voluntary. When the shift of attention is triggered by a stimulus, it is said to be *exogenous*, transient or reflexive.

From a neuroscientific point of view, covert attention is understood as a top-down signal coming from attentional networks to the visual cortices (see Desimone and Duncan, 1995; Raz and Buhle, 2006). Several cortical and subcortical structures are involved in these networks. Voluntary shifts of attention to behaviourally relevant targets at expected locations and reorienting to behaviourally relevant targets appearing at unexpected locations are thought to be mediated by two distinct frontoparietal networks: a dorsal network, involving the frontal eye field and the intraparietal sulcus, and a frontal network involving the temporoparietal junction and ventral frontal areas of the right hemisphere (see e.g. Corbetta and Shulman, 2002; Vossel et al., 2012). Subcorti-

cal structures such as the superior colliculus (Robinson and Kertzman, 2002) and the pulvinar nucleus (Petersen et al., 1987) are also involved in attentional orienting and are thought to be part of these attentional networks. Attentional signals are sent to visual areas, modulating the processing of visual information. Neural activity thought to be involved in perceptual processing is altered, as well as subjective perception (Carrasco, 2006). More specifically, attention is typically understood as a signal enhancing the signal-to-noise ratio of the neurons in the visual cortices (and maybe even the lateral geniculate nuclei, see O'Connor et al. 2002). The mechanism often suggested for visual attention is the enhancement of neural representation of the attended location (or feature, see Section 1.1.3) through a modulation of the gain of sensory neurons (Luck et al., 1997; Desimone, 1998; Hillyard et al., 1998). Scalp recordings suggest that the earliest modulations by attention occur approximately at 100 ms in extra-striate areas, and the activity in the striate cortex is modulated from 140 ms by delayed re-entrant feedback from higher areas (Martínez et al., 1999; Noesselt et al., 2002). Recently, however, it has been argued that the visual information can be modulated earlier (Kelly et al., 2008). This will be discussed in further detail in Chapter 4.

Endo- and exogenous attention can be studied separately, and it has been found that they have different characteristics. For instance, they have a different time course: shifts of exogenous attention are faster (100–120 ms) than endogenous (around 300 ms) (Carrasco, 2011), and they affect perception and brain activity in a different manner (Pestilli et al., 2008).

Variants of the Posner paradigm (Posner, 1980) have been extensively used in cognitive psychology and neuroscience for the study of attention. Endogenous attention is often studied by instructing the participant to pay attention to a certain part or feature in his visual field, as done in Chapter 4. Exogenous attention to a particular location in the visual field can be triggered by the onset of a stimulus at that particular location, as intended in Chapter 3.

1.1.3 Spatial and non-spatial attention

A large portion of the research on visual attention has studied spatial attention, i.e. locations of the visual field that are attended *versus* unattended. But attention can be focused on other dimensions or features, such as colour, motion direction or orientation, and also objects (Scholl, 2001). In the real world, dimensions are often con-

founded (e.g. we attend to a particular object with particular features at a particular location), but in an experimental setting, it is possible to disentangle these components and analyse their mechanisms.

Spatial and feature-based attention have been proposed to reflect two sides of the same coin, and were unified under the ‘feature-similarity gain model’ (Treue and Martinez Trujillo, 1999). This model states that the response of neurones will see their gain increased or decreased, reflecting how much similarity they share with the features of current behavioural interest. Therefore, when attending a particular motion direction, all the neurones of the visual field whose preferred direction is the attended one will see their gain increased. When attending a particular motion direction at a particular location, all neurones of the visual field whose preferred direction is the attended one will still see their gain increased, but the ones in the attended location will be increased even more. This model therefore considers spatial attention as one of the many kinds of visual attention, and feature-based attention as sharing similar mechanisms to spatial attention. Spatial and feature-based attention are typically viewed as fairly independent processes with little or no interaction between one another, with separate neural systems and different cognitive processes controlling both types of attention. See Carrasco (2011) for a review of the characteristics of feature-based attention and its similarities and differences with spatial attention.

Chapter 4 deals with spatial and feature-based attention.

1.2 The cognitive neurosciences of emotion

The modern study of visual emotional stimulus processing is part of a larger field studying the relations between cognition and affect. Traditionally (until the mid-twentieth century), cognition, affect and conation (i.e. will) were considered as distinct parts of the mind and were largely studied separately. The New Look movement of the forties and fifties is often cited as when the hypothesis that emotion and cognition could influence each other was first considered (see e.g. Fox 2008 for more details on the history of the study of emotion-cognition interactions). The cognitive neuroscience of emotion has now embraced this view, and many studies focus on how perception and cognition are altered by affect, and *vice versa* (see e.g. Vuilleumier et al. 2003a). This is the approach taken in the present thesis. Here, the influence of the affect gener-

ated by a visual stimulus on attention (a function traditionally labelled as cognitive) is examined, and *vice versa*.

Emotional stimuli are stimuli that are important for survival of the individual. They can be considered as stimuli that are behaviourally relevant in most cases (because they are so critical for survival). Negative stimuli include stimuli signalling the presence of danger or threat, such as an angry or fearful face, or a snake. Positive stimuli may include food, sexually relevant stimuli or babies.

Emotional stimuli generate an emotional response, which is generally characterised by an excitation of the autonomous nervous system that can be measured with skin conductance, heart beat, blood pressure, or pupil dilation (see e.g. Balconi et al., 2009). Another way to characterise emotional stimuli is through appraisal, i.e. subjective ratings from individuals. For instance, each stimulus from the International Affective Picture System (IAPS, Lang et al., 2008), commonly used in emotion research, has been rated by individuals along several dimensions, including the commonly used “valence” (from negative to positive) and “arousal” (low to high). A highly emotional image will have a valence far from zero and a high arousal value.

1.3 Attention and emotional stimuli

The processing of (visual) emotional stimuli has been closely studied in conjunction with attentional processes. From an evolutionary perspective, it has been proposed that emotional stimuli should be processed preferentially, because a failure to quickly detect and react to such important stimuli would be a threat to survival. Attentional biases to emotional stimuli would therefore constitute an evolutionary advantage. Indeed, many studies have found that emotional stimuli are processed preferentially. For example, in an attentional blink paradigm, the second target will be less likely to be missed if the stimulus is emotional (Anderson and Phelps, 2001). Similarly, when participants are presented with an emotional image concurrently with a neutral image, participants will preferentially observe the emotional image (Calvo and Lang, 2004). These kinds of experiments, however, may not reflect real-life situations, in which stimulus complexity is much higher, and where the information to be processed is part of a visual scene containing multiple items. The experiment presented in Chapter 2 deals with this exact question.

A large amount of clinically-oriented research has been focusing on high anxiety subjects (clinical and non-clinical). This population has the particularity of having a larger bias to negative, and more particularly fear-laden, stimuli. The dot-probe paradigm (MacLeod et al., 1986) has been used to investigate which aspects of attentional processing are affected by emotional stimuli in anxious populations (Bar-Haim et al., 2007). This paradigm consists of presenting a pair of stimuli concurrently (one neutral, one emotional), followed by a target at the location of one or the other stimulus. Attentional bias to emotional stimuli is measured as the difference in reaction time to the target when presented at the location of the emotional *minus* the neutral cue. A dot-probe experiment was conducted in an attempt to replicate past research. This experiment is described in Chapter 3.

While the idea that emotional stimuli can modulate attention is not disputed, the idea that attention can inhibit emotional processing is slightly more contentious. Some theories propose that emotional stimuli are processed somehow “automatically”, i.e. independently from attentional resources. Neuroimaging data indeed supports the view that emotional processes (or a subset of them) may be less dependent on attentional resources than non-emotional stimulus processing (Vuilleumier et al., 2001, 2002). However, the automaticity of emotional stimulus processing has been put into question, with experimental evidence showing that attention away from emotional stimuli does impair their processing and that the limited processing resources also apply to emotional stimuli (Pessoa et al., 2002b; Holmes et al., 2003; Yates et al., 2010).

Related to this view that emotional processing is independent from attention is the idea that emotional information is processed quickly in the brain. Zajonc (1980) proposed that emotional information is treated prior to cognitive processing. This view found some support in neuroanatomical data, with the discovery of a subcortical route that is responsible for emotional auditory conditioning in mice (LeDoux, 1998, chap. 6). The existence of an equivalent subcortical pathway in humans has been proposed. Projections from the retina to the superior colliculus would enable a route to the amygdala bypassing the supposedly slower geniculo-striate pathway. This view is supported by neuropsychological (Morris et al., 1999; Pegna et al., 2005) and neuroimaging data (Morris et al., 1999; Garrido et al., 2012), and is often mentioned to justify experimental results compatible with emotional stimulus processing being fast or independent from attention (Dolan and Vuilleumier, 2003; Öhman, 2005). However, both the existence of this pathway and its implication in emotional stimulus processing has been

criticised (Pessoa and Adolphs, 2010), and this question remains open. What is clear, however, is that there is some evidence that emotional information is processed early, but issues of replication and contradicting results make it difficult to draw conclusions (see Section 4.2.3). This theme will be developed in more details in Chapter 4, where the event-related potentials (ERP) were studied at very early latencies for emotional and neutral stimuli.

1.4 Contents of the thesis

This thesis will present experimental work on human subjects, using eye-tracking, behavioural and ERP methods, carried out to explore aspects of the interactions between emotional processing and attention mentioned above.

Chapter 2 explores how overt attention is driven by emotional items when embedded in a complex visual scene. Eye-tracking offers the advantage of investigating how visual scenes are explored most naturally by humans, i.e. through saccadic eye movements. Past work has investigated eye movements driven by emotional scenes and showed a strong bias toward emotional content. No study, however, has explored how the eye could be driven by emotional items embedded in a larger picture. It was found that while emotional items hold attention, they do not attract it.

Chapter 3 presents an attempt at replicating a dot-probe experiment, using a group of high anxiety *versus* a group of low anxiety participants. The dot-probe task has been successful at measuring attentional biases in high anxiety participants. It is an interesting paradigm, as it can be adapted to answer many research questions. No effect was found in the experiment, but possible reasons for this failed replication attempt are discussed.

Chapter 4 describes a series of three ERP experiments. ERP is complementary to behavioural methods, as it enables researchers to study the timecourse of visual and cognitive processing in the brain as the task is performed. These experiments explored the hypothesis that facial expression generates very early modulations (< 100 ms). Visual stimulus processing was studied under various attentional conditions. It was found that emotional stimuli modulated the C1 only when they were spatially attended and task-irrelevant. The results also suggest a very early modulation by feature-based attention which is independent from spatial attention.

In the course of this series of ERP experiments, a potential bias due to raw data high-pass filtering was found, which could have generated false positive results in previous works. Chapter 5 details the characteristics of this bias, focusing on the early visual component C1. Artificial and real ERP data from the experiments described in Chapter 4 were used for the demonstration.

Finally, Chapter 6 discusses the results of the studies conducted as a whole, attempting to clarify the contribution of the current thesis. Ideas for future related projects are also outlined.

Chapter 2

Overt Attention and Emotional Items in Visual Scenes^{*†}

2.1 Introduction

2.1.1 Eye movements and eye-tracking

Most of cognitive psychology and cognitive neuroscience studying attention has focused on covert attention, often asking participants to look at a fixation point. However, in natural conditions, because of the drop in visual accuracy away from the fovea, we freely move our eyes to look at objects of interest. The study of eye movement therefore arguably allows one to study attention shifts in their most “natural” form.

Humans explore their visual environment through saccadic eye movements. They hold a *fixation* on a location for a few hundreds of milliseconds, then generate a *saccade* to a new location. Typically, about two or three saccades are generated each second. Both the task performed by an individual and the content of an explored scene influence eye movements. Yarbus (1967, p. 174) showed how, given the same scene, different tasks lead to different parts of the scene being explored. It is obvious that someone will explore a different part of a scene if they are asked to look for clouds, as opposed

^{*}This chapter is an adaptation of Acunzo and Henderson (2011), provided in Appendix B.

[†]Part of the work described in this chapter was carried out for the obtention of the MSc degree in Neuroinformatics (Acunzo, 2008). More specifically, the main experiment was carried out for the MSc, while the control experiment and the writing of the paper were performed after obtention of the MSc degree.

to pedestrians. Inversely, it has been observed that visual features in a scene constitute a predictor of fixation location during scene exploration. Computational models have been developed in order to predict the location of fixations, most of them relying on local features (the most well-known of all is the saliency-based model by Itti and Koch, 2000), although some incorporate more global features (see e.g. Torralba et al., 2006). While it appears that humans preferentially fixate on objects (Nuthmann and Henderson, 2010), there is still debate to which extent semantic information drives eye movements in scenes (see Section 2.1.2).

Eye movements can be measured using an eye-tracker. The eye-tracker used (SR Research Eyelink 1000, shown in Fig. 2.1) relies on the use of an infra-red camera directed towards the eyes of the participant, and on image processing techniques enabling the extraction of the position of the pupil. An infra-red light, also directed toward the participant, generates a reflection on the cornea (corneal reflection) that can easily be extracted using some thresholding method on the image. For a given eye position, a two-dimensional vector between the centre of the pupil and the corneal reflection can be measured. Using a calibration procedure where the position of the corneal reflection and the pupil positions of the participant, and the location looked at are both known, one can calculate fitting parameters enabling inference of the position fixated on the screen for any eye position within a certain range.



Figure 2.1: Eye-tracker used for the experiment presented in this chapter. With this type of eye-tracker, the head of the participant is fixed using a chin and forehead rest. The position of the eyes is measured using an infra-red camera and light, through the semi-reflective glass in front of the participant's face.

2.1.2 Overt attention and emotional stimuli

Eye-movement research has shown that emotional stimuli attract overt attention (Calvo and Lang, 2004; Nummenmaa et al., 2006, 2009; Alpers, 2008). In these studies, participants were peripherally presented two images while their eye movements were recorded. When an emotional image was presented concurrently with a neutral image, the probability of the first fixation landing on the emotional picture versus the neutral one was significantly higher. It was also shown that participants fixated the emotional image for a longer time. In Nummenmaa et al. (2006), even when explicitly instructed to attend to the neutral image, participants first fixated on the emotional image. Finally, a more recent study (Nummenmaa et al., 2009) examined saccade latency when participants were instructed to look either left or right when a distractor image was presented on each side. It was found that saccade latency was delayed when the image opposite to the instructed direction was emotional. Saccade trajectories were also modulated by surrounding emotional content: when participants were instructed to saccade vertically whilst presented with distractor images on the sides, the saccade curved away from emotional images. In Becker and Detweiler-Bedell (2009), participants were instructed to passively look at an array of four faces while their eye move-

ments were recorded. Interestingly, the authors found that participants avoided looking at the threatening face as early as the first saccade, suggesting an early evaluation of the face valence and bias of subsequent eye movements.

These results suggest that eye movements are modulated by emotional content within the visual field in an unconscious and automated manner. This is consistent with paradigms looking at covert attention, which suggest that emotional stimuli can modulate attention even when they are task-irrelevant (Bar-Haim et al., 2007).

However, the research discussed above used particular viewing conditions. First, the stimuli used usually contained a small number of independent images or items. Because the items were independent (i.e. content and location were unrelated), an independent ‘emotional gist’ could have been extracted for each item. Additionally, the items were often presented extrafoveally while the participant was fixating a dot in the centre of the screen. This low initial foveal load might have facilitated the emotional processing of the extrafoveal images. Finally, the high frequency of emotional stimuli, together with the low variance of semantic content and the few possible locations where items could be displayed, may have eased the task of the participants by increasing their expectation for emotional stimuli. Despite previous research showing that attention and eye movements are modulated by extrafoveal emotional content under these particular conditions, it is unclear whether these effects would remain under more natural conditions where perceptual and foveal load is high and where objects are part of a whole scene.

To answer this question, a paradigm initially developed to assess the effects of semantic gist violation on eye movements (Loftus and Mackworth, 1978) was adapted. Participants’ eye movements were recorded while viewing scenes in which one target object did not fit with the rest of the image (e.g., an octopus in a farm). Interestingly, items violating the gist do not seem to generate any semantic ‘pop-out’ effect, but do hold attention longer than non-violating items (de Graef et al., 1990; Henderson et al., 1999; Gareze and Findlay, 2007; Castelhana et al., 2009; Võ and Henderson, 2009; Rayner et al., 2009; but see Loftus and Mackworth, 1978; Becker et al., 2007; Underwood and Foulsham, 2006; Underwood et al., 2008)

For this study, a set of stimuli consisting of pairs of realistic scenes was developed. Each pair consisted of two photographs, which solely differed by a target item: in one condition, this item had a neutral valence, in the other, it had an emotional (positive

or negative) valence. Participants were asked to try to remember those images for a subsequent memory test while their eye movements were recorded. Additionally, scenes were horizontally flipped, so that the target item was presented on the left or right side of the initial fixation point. Target item position (left or right) and valence (neutral or emotional) were then the conditions of the 2×2 within-participant design.

According to previous research on eye-movements and emotional stimuli, the hypothesis that emotional items would be fixated earlier than neutral targets was made. However, the absence of influence by semantic information in visual scenes on attracting eye movements in a portion of the literature (de Graef et al., 1990; Henderson et al., 1999; Gareze and Findlay, 2007; Castelhana et al., 2009; Vö and Henderson, 2009; Rayner et al., 2009) suggests that emotional information would not have such an influence. Additionally, the hypothesis that emotional targets would be fixated earlier if located on the left-hand side of the initial fixation point was tested. Previous research suggests laterality effects, with a right hemisphere advantage to process emotional stimuli (see e.g., Keil et al., 2004; Calvo and Nummenmaa, 2007; Calvo and Avero, 2008). In particular, in the context of eye-movement research, Alpers (2008) used the same paradigm as Calvo and Lang (2004) and reported that the effects of the emotional content on the first fixation observed in previous experiments were present only when the emotional picture was presented in the left hemifield. Finally, the hypothesis that participants would fixate the emotional targets for a longer time than the neutral ones was made, as both the literature on emotional stimuli (Calvo and Lang, 2004 and replications) and scene perception (de Graef et al., 1990; Henderson et al., 1999; Gareze and Findlay, 2007; Castelhana et al., 2009; Vö and Henderson, 2009; Rayner et al., 2009) would suggest.

2.2 Methods

The procedure and stimuli was approved by the University of Edinburgh Department of Psychology Ethics Committee.

2.2.1 Participants

Sixteen participants (10 female) took part in the experiment, most of whom were students in the University of Edinburgh recruited through an internal university website. All participants reported normal or corrected-to-normal vision. They were compensated £6/hr.

2.2.2 Stimulus material

The stimulus material consisted of 48 full-color 24 bit images of maximal resolution of 800×600 pixels. An example of a scene is shown in Figure 2.2. Each scene conformed to one of the 2×2 conditions: emotional versus neutral, and left versus right. In the emotional condition, a target item in the scene was emotionally evocative; in the neutral condition, an emotionally neutral target replaced the emotionally evocative target. In the left and right conditions, the target was located in the left and right part of the image respectively. This was simply generated by mirroring the entire image over a vertical axis. Half of the emotional stimuli contained positive targets and the other half contained negative ones. Examples of negative targets included people with facial tumours, a threatening animal (snake), a face showing fear and a face covered with blood. Positive targets represented people hugging or kissing, kids playing and fluffy animals. Neutral targets included bags, faces and people in neutral positions.

For each pair of dual images (i.e., pair of same background images with a different target), a common target interest area (IA) that included the neutral and emotional target for both images was defined. The IAs of the mirrored images had mirrored IAs from the original image. In the neutral condition, 9 out of the 12 scenes were artificially modified, and all 12 were modified in the emotional condition. A modification involved either the addition or alteration of the target item. Scenes were found on the Internet (except one which was a photograph taken by a member of the research group), while targets were taken from the Internet, the IAPS (Lang et al., 2008), the NimStim face database (Tottenham et al., 2009) and Hemera Photo-Objects 2.07. Images were manipulated using GIMP 2.4.0. Targets were adapted for luminance, saturation, colour and contrast in order to make the addition or replacement as natural as possible. In many cases, manual modification of the lighting of the target was necessary, and shadows and reflections were modified or added for more realism. To ensure

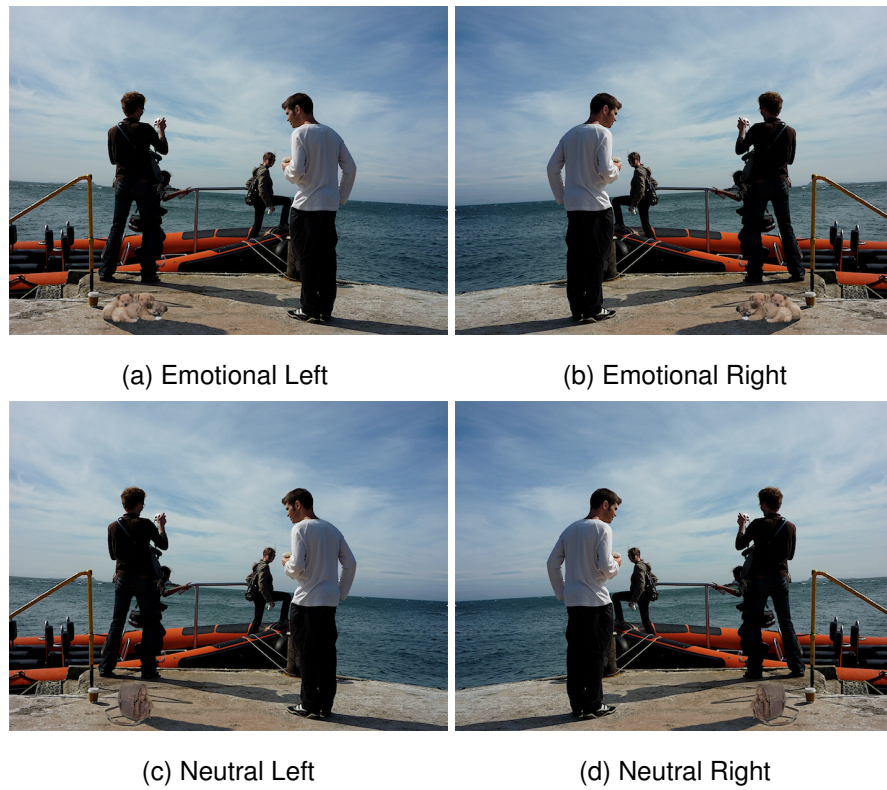


Figure 2.2: Example of scene used in the experiment, for each of the four conditions: emotional-left, emotional-right, neutral-left, and neutral-right. Between the Emotional (a, b) and Neutral (c, d) conditions, the scene differ only by one item (puppies, bag). To conform with the Left and Right conditions, the image is flipped horizontally so that the item is situated on the left (a, c), or right part of the image (b, d).

that the modifications did not lead to a difference of saliency between the neutral and emotional conditions, the Matlab implementation of a saliency model (Itti and Koch, 2000) was ran on the images. The saliency map was computed and normalised for the images. The average saliency was then computed within the target IA. A Wilcoxon signed rank test was used to compare the average saliency within the 12 IAs containing a neutral target ($Median = 0.0247$) with the 12 containing an emotional target ($Median = 0.0289$). Differences were not significant: $T = 31, p > 0.8, r = 0.04$. The target items were situated extrafoveally from the central initial fixation location (the closest target from the centre was located at 7.3° of visual angle).

Emotional valence and arousal were controlled for by asking a population of 16 participants (10 female) who did not take part in the main experiment to rate the target items. Participants were asked to rate the target present in each presented image. Its location was indicated by a superimposed red dotted circle around the target. Block content was similar as in the main experiment and stimulus presentation order was randomised for each participant. An instruction sheet explaining the meaning of emotional valence and arousal was given. The head of the participant was fixed, in order to ensure similar conditions such as viewing distance as in the main experiment. Before stimulus onset, a fixation point was displayed for a random duration between 2 and 5 seconds. The image was then displayed full screen for 10 seconds, before a dialogue box appeared in front of the image, enabling the participant to give his rating. The image was still displayed during the rating, and the participant had no time constrain. Once the rating was over, participants were given their compensation (£3) and signed a receipt. State-Trait Anxiety Inventory (STAI, Spielberger et al., 1983) score differences between participants from the main study (*State*: $M = 35.58, SE = 2.12$; *Trait*: $M = 38.63, SE = 2.27$) and from the validation study (*State*: $M = 32.88, SE = 2.01$; *Trait*: $M = 36.81, SE = 2.35$) were non-significant: $t_{30}^{state} = 0.96$ ($p > 0.3$) and $t_{30}^{trait} = 0.55$ ($p > 0.5$). On average, mean valence ratings per participant were higher for positive ($M = 2.58, SE = 0.12$) than neutral ($M = 1.09, SE = 0.11$) targets: $t_{29.77}^{Pos-Neu} = 9.82$ ($p < 10^{-10}$). Mean valence ratings per participant were lower for negative ($M = -2.06, SE = 0.28$) than for neutral targets: $t_{19.63}^{Neu-Neg} = 10.63$ ($p < 10^{-8}$). Mean arousal ratings per participant were higher for both positive ($M = 3.31, SE = 0.25$) and negative ($M = 4.54, SE = 0.39$) than neutral ($M = 2.27, SE = 0.15$): $t_{25.14}^{Pos-Neu} = 3.59$, ($p < 0.01$) and $t_{19.66}^{Neu-Neg} = 5.48$, ($p < 10^{-4}$). To sum up, emotional targets were rated significantly higher in terms of arousal than neutral stimuli, and positive (negative) targets were

rated significantly higher (lower) in terms of valence than their neutral counterpart.

2.2.3 Apparatus

Images were presented on a 21" CRT monitor at a viewing distance of 90 cm with a refresh rate of 140 Hz. Their maximum resolution was 800×600 pixels, subtending a maximum visual angle of $25.7^\circ \times 19.4^\circ$. Eye movements were monitored by an SR Research Eyelink 1000 eye-tracker. The head of the participant was fixed on a chin-rest (see Fig. 2.1). Fixation position was sampled at 1,000 Hz and saccades prior to critical fixations were detected using a 17-sample saccade detection model with a velocity threshold of $30^\circ s^{-1}$, an acceleration threshold of $8,000^\circ s^{-2}$, and a minimum amplitude of 0.5° . The right eye only was tracked while viewing was binocular. The experiment was controlled with SR Research Experiment Builder software.

2.2.4 Procedure

Each participant was presented a consent form to be signed, informing about the experiment and the emotionally evocative nature of some of the stimuli. Before the viewing task, the participants were given the STAI questionnaire to fill in.

Each participant was presented 1 of 4 blocks, each containing all 12 scenes. Each block contained 3 scenes in each of the 4 conditions: neutral-left (NL), neutral-right (NR), emotional-left (EL), emotional-right (ER). No participant was presented the same scene in more than one condition. The order of image presentation was randomised within the assigned block for each participant.

Participants were told that they would be shown 12 images for 15 seconds each, and that they would have to memorise them for a subsequent memory task. The memory task was never given. This task was chosen to ensure a thorough exploration of the scene by the participant and to facilitate comparison with past literature on scene viewing, which largely uses this task while recording eye movements (e.g. Loftus and Mackworth, 1978, Becker et al., 2007, Underwood and Foulsham, 2006, Castelhano et al., 2009, Võ and Henderson, 2009). Calibration of the eye tracker, using 9 points on the screen, was performed, followed by a validation. At the beginning of each trial, a point in the middle of the screen had to be fixated by the participant, for a fixation

check. The trial was then initiated manually by the experimenter. If inaccuracy of the eye-tracker was detected, a new calibration was performed.

2.2.5 Data processing

Raw data were first filtered and pre-processed with SR Data Viewer. Most data manipulation was carried out using Matlab 7.0 (Mathworks Inc.). Graphs and statistical tests were done with Matlab and SPSS (SPSS, Inc.). Analyses of variance (ANOVA) included valence (Neutral, Emotional) and side (Left, Right) as within-participant factors. When possible, t-tests were performed to compare two independent samples. Otherwise a Wilcoxon rank-sum test was conducted. When t-tests were applied, mean values are reported, while when Wilcoxon rank-sum tests were applied, median values are reported. No fixation within the IA occurred during the scene presentation for 16 trials (4 NL, 2 NR, 4 EL, 6 ER; 8.33% of all trials). Those trials were not included in the following analyses.

2.3 Results

2.3.1 Capture of attention

One of the main questions addressed here is whether emotional targets attract attention more than neutral ones when embedded in a natural scene. Table 2.1 and Figure 2.3 summarise the statistics reported in this section.

2.3.1.1 Number of fixations and latency to IA

The difference in attentional capture by targets across conditions was assessed by examining how early in scene exploration the targets were fixated. To do so, the difference in the index of the first fixation within the IA, and the amount of time spent exploring the scene prior to the first fixation within the IA were measured. For the number of fixations to IA, no effect of valence $F_{1,15} < 1$ ($\omega^2 = 0.032$) or side $F_{1,15} < 1$ ($\omega^2 = 0.025$) was found.

Latency to IA showed the same pattern: no effect of valence $F_{1,15} < 1$ ($\omega^2 = 0.027$), side $F_{1,15} < 1$ ($\omega^2 = 0.022$) and a non-significant interaction $F_{1,15} = 3.87$, $p > 0.05$ ($\omega^2 = 0.453$).

2.3.1.2 Incoming saccade amplitude to IA

The amplitude of the first saccade ending within the IA provides information about extrafoveal processing of emotional targets. Given the hypothesis that emotional targets capture attention extrafoveally, a larger saccade amplitude should be observed for the emotional condition than for the neutral one. The analyses showed a non-significant trend with longer saccade amplitude to emotional targets $F_{1,15} = 2.83$, $p > 0.05$ ($\omega^2 = 0.399$), no effect of side $F_{1,15} = 1.45$, $p > 0.05$ ($\omega^2 = 0.297$), and no interaction, $F_{1,15} < 1$ ($\omega^2 = 0.052$).

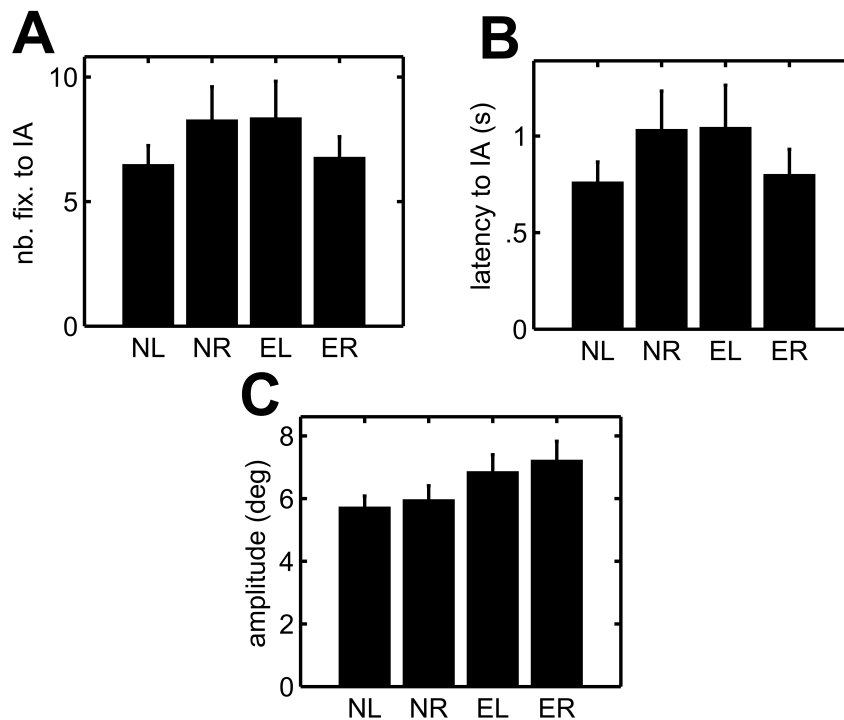


Figure 2.3: Capture of attention. Mean value and standard error of the number of fixations (A), latency (B) to IA, and amplitude of the first fixation to IA (C) across the four conditions. NL and NR indicate neutral left and neutral right, respectively, and EL and ER indicate emotional left and emotional right. See numeric values in Table 2.1.

	Conditions				$F_{1,15}$ values		
	NL	NR	EL	ER	Em	S	Em \times S
Num. fix. to IA	6.49 [0.76]	8.28 [1.33]	8.36 [1.47]	6.78 [0.82]	< 1	< 1	3.74
Latency to IA (ms)	1525 [206.4]	2069 [396.2]	2090 [435.8]	1603 [259.7]	< 1	< 1	3.87
Sacc. amp to IA (deg)	5.7 [0.35]	6.0 [0.44]	6.9 [0.54]	7.2 [0.60]	2.83	< 1	< 1

Table 2.1: Mean and [Standard Error] of the “capture of attention” variables for each of the 4 conditions: neutral-left (NL), neutral-right (NR), emotional-left (EL) and emotional-right (ER). F-ratio obtained from the repeated measures, with the factors Emotion (Em) and Side (S). None of the F values obtained were statistically significant.

2.3.2 Hold of attention

In this subsection, events occurring once the target was overtly attended were analysed, and the hold of attention by the emotional targets were compared against the neutral ones. After the target was fixated, its location within the image was not a relevant variable in these analyses. The left and right conditions were consequently collapsed for this part of the analysis. The remaining conditions were simply emotional and neutral. Table 2.2 and Figure 2.4 sum up the statistics reported in this section.

2.3.2.1 First fixation duration within IA

The durations of the first fixation on the target item can be indicative of the encoding of the fixated object (see e.g., Henderson and Hollingworth, 1999) although recent evidence suggest that fixation durations are only partially driven by visual input (Henderson and Smith, 2009; Nuthmann et al., 2010). The durations of the first fixation within the IA for neutral (*Median* = 255.3 ms) and emotional (*Median* = 249.4 ms) targets showed no significant difference with Wilcoxon rank-sum test: $T = 282, p > 0.5, r = 0.16$.

2.3.2.2 First pass number of fixations and time

We measured the number of fixations and time spent between the very first fixation within the target IA and the first subsequent fixation outside the IA. First pass number of fixations showed a significant difference between the neutral ($M = 2.40, SE = 0.21$) and emotional ($M = 3.92, SE = 0.37$) conditions: $t_{23.3} = 3.56, p < 0.02$. More fixations were placed on the emotional than neutral target. Similarly, the time spent during the first pass of the IA was longer for the emotional targets ($M = 1253.7$ ms, $SE = 93.9$) than for the neutral targets ($M = 666.1$ ms, $SE = 71.4$): $t_{30} = 4.98, p < 10^{-4}$.

2.3.2.3 Total number of fixations and dwell time

Finally, the total number of fixations and the total fixation time spent within the IAs were measured. The average total number of fixations within the IA for emotional targets ($M = 11.40, SE = 1.52$) was not significantly higher than for neutral targets ($M = 8.22, SE = 0.83$): $t_{23.14} = 1.84, p > .07$. However, the average total time spent within the IA was significantly longer for the emotional targets ($M = 3748.4$ ms, $SE = 444.8$) than for the neutral targets ($M = 2464.2$ ms, $SE = 241.4$): $t_{23.1} = 2.54, p < .02$.

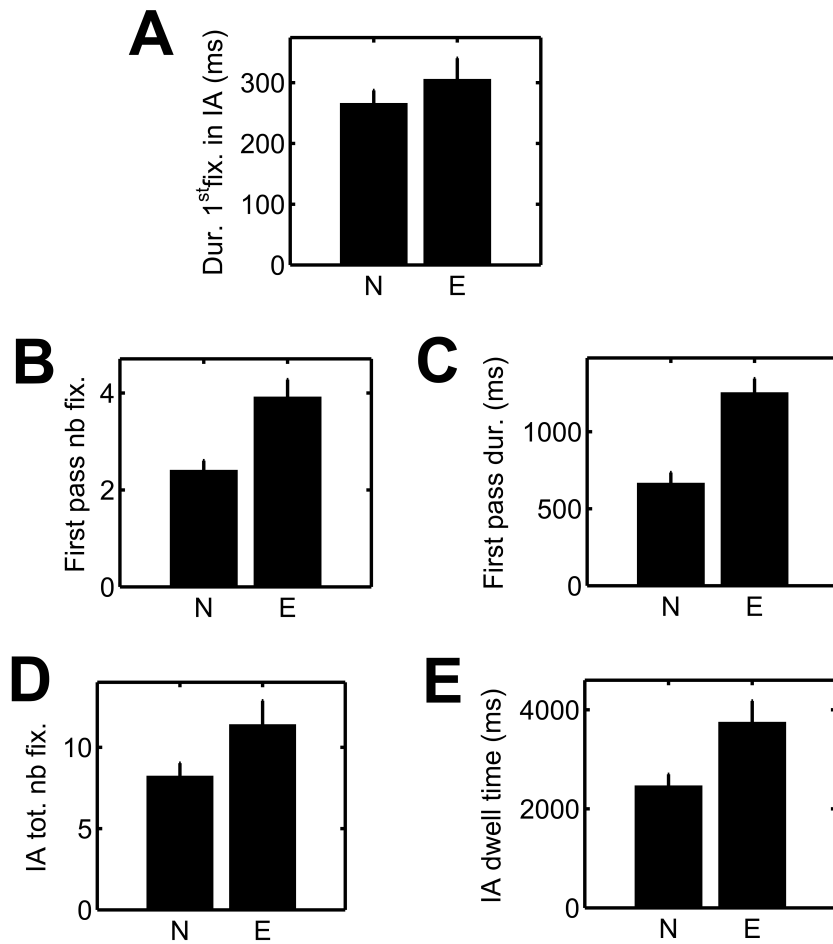


Figure 2.4: Hold of attention. Mean value and standard error of the first IA fixation duration (A), the first-pass number of fixations (B) and duration (C), the total IA number of fixations (D), and dwell time (E). N and E indicate neutral and emotional conditions, respectively. See numeric values in Table 2.2.

	Conditions		Comparison	
	Neutral	Emotional	Stat.	Value
1 st fix. duration (ms)	Mdn: 255.3	Mdn: 249.4	T	282
1 st pass nb. of fixations	2.40 [0.21]	3.92 [0.37]	$t_{23.3}$	3.56*
1 st pass duration (ms)	666.1 [71.4]	1253.7 [93.9]	t_{30}	4.98**
Tot. nb. of fix. in IA	8.22 [0.83]	11.40 [1.52]	$t_{23.14}$	1.84
Tot. IA dwell time (ms)	2464.2 [241.4]	3748.4 [444.8]	$t_{21.3}$	2.54*

* $p < .05$, two-tailed.

** $p < .01$, two-tailed.

Table 2.2: Median (Mdn), or Mean and [Standard Error] of the "hold of attention" variables for the 2 conditions: Neutral and Emotional. Ranksum (T) or t-score (t) values from the two independent sample comparison are given.

2.4 Discussion

One of the main goals of this study was to test for earlier detection of emotional target items when embedded within an entire natural image. Previous research suggests the existence of an exogenous drive of eye movements by peripherally attended emotional stimuli (see Calvo and Lang, 2004; Nummenmaa et al., 2006; Alpers, 2008; Becker and Detweiler-Bedell, 2009). However, the presented experiment suggests that when embedded in a scene, this exogenous drive disappears. At the same time, it was found that, once fixated, emotional items hold attention longer than neutral ones. This is in line with previous research reporting delayed attention disengagement or hold of attention by emotional stimuli (Calvo and Lang, 2004; Nummenmaa et al., 2006; Fox et al., 2001, 2002) and also concurs with part of the scene perception research reporting hold of attention to semantically incongruous items (de Graef et al., 1990; Henderson et al., 2004; Gareze and Findlay, 2007; Castelhamo et al., 2009; Võ and Henderson, 2009; Rayner et al., 2009).

We also found no effect of the position of the target stimulus, while previous research has suggested a right-hemisphere advantage for emotional stimuli processing (e.g., Keil et al., 2004; Calvo and Nummenmaa, 2007; Calvo and Avero, 2008). In particular, Alpers (2008) used a paradigm similar to Calvo and Lang (2004) and found that emotional stimuli were fixated earlier only when positioned on the left visual hemifield. It should be noted however that tighter controls in Alpers (2008) would have made the claim stronger (e.g., comparison of saliency between stimulus groups, an additional condition to assess a potential eye-movement bias toward the left side).

The lack of attentional capture by emotional stimuli cannot be attributed to a lack of differential emotional impact on the participants, since significant differences in valence and arousal were found from the values given by independent raters. Low-level saliency was also controlled for, using a computational saliency model (Itti and Koch, 2000): no difference between the two target groups was found.

For generalisability purposes, we tried to cover a wide range of emotional stimuli (e.g., fearful face, couple kissing, animal...). This heterogeneity in the nature of the target might be seen as a weakness, since different emotions are not processed the same way and will not generate the same reaction: a cute cat will probably not attract the eye the same way as a face covered with blood. Furthermore, given the small number of stimuli, the differential effects of positively and negatively valenced targets were not

looked at separately. This said, previous studies on emotion have also used heterogeneous emotional stimuli, in particular when using the IAPS database, and the effects of negatively and positively valenced stimuli on eye movements reported so far are qualitatively similar, with perhaps faster attentional capture by negative stimuli and longer hold of attention by positive stimuli (Calvo and Lang, 2004; Nummenmaa et al., 2006; Alpers, 2008). Importantly, significantly higher IA first-pass number of fixations and dwell time for emotional stimuli were found, which supports the idea that the manipulation was strong enough to elicit a modulation in the scene exploration process.

While the results are inconsistent with previous eye-movement studies looking at emotional stimuli in isolation, they are highly consistent with the body of data looking at eye-movements and scene perception (de Graef et al., 1990; Henderson et al., 2004; Gareze and Findlay, 2007; Castelhana et al., 2009; Võ and Henderson, 2009). The majority of experimental results indicate that gist-inconsistent targets do not elicit earlier fixations than gist-consistent ones. However, they do hold attention longer once fixated. It can be argued that both gist-inconsistent and emotional items are behaviourally relevant. Gist-inconsistent items are more informative about the environment than gist-consistent ones, while emotional items are behaviourally relevant because of their intrinsic motivational value. This is illustrated by the fact that both gist-inconsistent and emotional items are fixated more than gist-consistent and neutral ones respectively. It should be noted though that earlier fixations to inconsistent objects have been reported in some studies (Loftus and Mackworth, 1978; Becker et al., 2007; Underwood and Foulsham, 2006; Gareze and Findlay, 2007; Underwood et al., 2008). Interestingly, this discrepancy between studies has been partly attributed to a difference in sparsity of the scenes (Võ and Henderson, 2009). Less cluttered scenes enable participants to detect semantic inconsistencies more easily.

Similarly, differences in experimental design and stimuli are likely to account for the differences between the present results and previous eye-movement studies using emotional stimuli. First, each stimulus used in the present study consisted of an individual scene presented on a full screen, while the paradigms of Calvo and Lang (2004), Nummenmaa et al. (2006), Nummenmaa et al. (2009) and Becker and Detweiler-Bedell (2009) used two or four peripherally presented images with a fixation point in the centre of the screen. In the present case, foveal load was high from stimulus onset, which wasn't the case in the other paradigms. The results are in line with Calvo and Nummenmaa (2007) who reported that foveal load impairs the processing of peripherally

presented emotional stimuli.

Second, the target items were embedded in a whole image. Target search and previous eye-tracking paradigms have focused on the effects of images presented simultaneously to the participant. In those studies, the images are probably seen by the participant as independent, unrelated entities, which are localized and separated in the visual field and can contain unrelated objects. Each of them can thus be processed as a whole, independently from each other, and an emotional and semantic gist can be extracted from each entity. In the present case, objects cannot be seen independently, since they are all linked within the image. Additionally, some of the emotional target items were significantly smaller than the images used in previous research (and in particular Calvo and Lang, 2004; Nummenmaa et al., 2006, 2009). In Calvo et al. (2008), it is suggested that the processing of the emotional gist of images may come from a ‘fast’ subcortical route (see LeDoux, 1998), which would project to the amygdala via the superior colliculus. Neurons of the superior colliculus respond to stimuli situated peripherally and containing low spatial frequencies (Miller et al., 1980; Rodman et al., 1989), therefore some of the small-sized targets might not have been able to activate this pathway. However, the involvement of this subcortical pathway in visual emotional processing is debated (see Pessoa and Ungerleider, 2004; Storbeck et al., 2006). In any case, it can be hypothesised that the effects observed in previous studies are due to the ‘emotional gist’ of individual images. If this is the case, the present results make sense since the target items were not seen as independent from the rest of the scene. Semantic and emotional information for each element of the image was thus more difficult to process.

Third, the explicit task given to the participant was to memorise the scenes for a subsequent memory test. This task is unrelated to emotional appraisal of the stimuli presented, as opposed to Nummenmaa et al. (2006), and is arguably more complex than free viewing (which is the task given in Calvo and Lang, 2004; Nummenmaa et al., 2006; Becker and Detweiler-Bedell, 2009) or than asking a participant to saccade to a given location (Nummenmaa et al., 2009). Additionally, in the present experiment, 15 seconds were given to the participants to explore and memorize each scene. This is a longer display time than what has been typically used in previous eye movement research (3 seconds in Calvo and Avero, 2008; Nummenmaa et al., 2006; 8 seconds in Alpers, 2008; 4 seconds in Becker and Detweiler-Bedell, 2009). It is possible that with a shorter display time, allocation of attention has to be rushed in order to extract

the most relevant information from the scenes. This may increase the role of early attentional processes. The measures of attentional capture by emotional stimuli might therefore be less sensitive in the present design for this reason.

Finally, in previous paradigms, all stimuli presented in an experiment or block had many structural and semantic similarities, facilitating anticipation and expectation from participants. In the search paradigms cited earlier, 2×2 or 3×3 matrices of images were used. No more than four semantic categories of objects were used in a single block, with direct link between semantic category and affect. For example, in Öhman et al. (2001), all inanimate objects (mushrooms and flowers) were fear-irrelevant while all animals (spiders and snakes) were fear-relevant. In Calvo and Lang (2004); Nummenmaa et al. (2006, 2009); Calvo and Avero (2008), on every trial, one image was presented in each hemifield. In Calvo and Lang (2004) and Nummenmaa et al. (2006), all images representing inanimate objects were neutral controls, while up to two thirds of the images representing people were emotional, enabling participants to expect an emotional content in images representing people. In Becker and Detweiler-Bedell (2009), four faces were presented peripherally. The emotional expressions were limited to neutral, fearful and happy. In the present paradigm, scenes had different layouts and contents, while target locations and nature varied for each stimulus. It is likely that these differences considerably reduced expectation and anticipation effects from participants.

Considering the points discussed above, the present results make sense when put in the context of competition for limited resources. It has been observed with fMRI that enhanced activation of the amygdala and visual areas by emotional faces (vs. neutral faces) was only present when the faces were attended (Pessoa et al., 2002b). Pessoa and Ungerleider (2004) interpreted these results in terms of limited attentional resources: task-irrelevant emotional faces are processed only if sufficient resources are available. The authors went further, hypothesising that attention is a *sine qua non* for processing emotional faces. ERP recordings have led to similar observations, using facial stimuli (Holmes et al., 2003) and IAPS pictures (Schupp et al., 2007).

Recently, Humphrey et al. (2012) used a paradigm very similar to ours to test whether emotional stimuli can override the influence of saliency on eye movements when exploring a scene. Consistent with the present results, they report a higher number of fixations in IAs containing an emotional item. However, they also found that emotional items were fixated earlier than neutral ones, which contrasts with the results

of the present experiment. Scene content, structure and complexity may explain the contrasting results. More research should be carried out to understand under which conditions emotional information embedded in a visual scene can attract the eye.

Our results, seemingly contradicting previous research on attention and emotional stimuli, are in line with scene perception data, in which the attraction of attention by semantically discrepant objects may depend on the availability of attentional processing resources which itself may directly depend on stimulus complexity. In the present case, the task was demanding, stimuli were highly complex and cluttered, reducing expectation and anticipation effects from the participants. In light of the capacity-limited attentional resources view, those conditions may be sufficient to prevent an earlier attentional shift toward emotional items in realistic scenes.

2.5 Conclusion

We conducted a study assessing the capture of overt attention by emotional stimuli embedded within a complex scene. In contrast with previous research on eye movement using emotional stimuli and sparser displays, it was found that emotional targets did not attract attention more than neutral targets in natural scenes. However, once fixated, emotional targets held attention for a longer time. By making participants rate the targets for valence and arousal, the hypothesis that the targets had a null emotional impact was eliminated. Low-level ‘pop-out’ artefacts were also controlled for by comparing targets’ visual saliencies outputted by a computational model (Itti and Koch, 2000). The absence of an emotional ‘pop-out’ effect is explained by arguing that parafoveal emotional information was prevented from being processed because of the attentional demand of the task due to stimulus complexity. Further research on eye movement and emotion should focus on the manipulation of target nature and size, stimulus complexity, task difficulty, initial foveal load, participants’ anticipation by manipulating stimulus variability, and also investigate the effects of individual differences such as trait or state of anxiety.

Chapter 3

The Dot-Probe Task: Testing Attentional Bias towards Fearful Faces in Subclinical Anxiety

3.1 Introduction

This chapter describes an experiment that was conducted following several attempts to replicate the reported multiplicative effect of emotional stimuli and spatial attention on contrast sensitivity described in Phelps et al. (2006). Several pilot and unsuccessful experiments were carried out. It was then decided to move on to a simpler paradigm that also had the potential to answer many research questions. The choice was taken to attempt to replicate attentional bias towards threatening stimuli by anxious participants using the dot-probe task. This is the subject of the current chapter.

3.1.1 Anxiety

Anxiety is closely related to fear, and contains the same cognitive (such as negative thoughts, expectation of danger), somatic (increased heart rate, muscle tension, pupil dilation), emotional (feeling of terror and panic) and behavioural elements (aggression, escape). It is characterised by a constant state of fear in which the nature of the expected danger is more diffuse and abstract. Anxiety can be sub-clinical, in which case it does not constitute a disorder, but simply a higher than average state or trait of

anxiety. In acute cases, it can be considered a disorder, known as *generalised anxiety disorder*. It is characterised by a chronic state in which the feeling of anxiety causes significant distress and impairment, and is associated with symptoms such as restlessness, irritability, sleep disturbance, etc. (DSM-IV, 1994, 4th Ed., section 300.2).

A distinction is made between *state* and *trait* of anxiety, to separate cases when individuals exhibit sparse attacks of anxiety (e.g., panic attacks) between which they are calm, and individuals who feel anxious constantly. These can be measured with self-report questionnaires, such as the State-Trait Anxiety Inventory (Spielberger et al., 1983) which asks individuals about the four elements of anxiety described above. Questionnaires probing the *trait* of anxiety ask how the individual feels in general, whereas questionnaires probing the *state* ask how the individual is feeling at this particular moment in time.

See e.g. Rosenhan and Seligman (1995, chap. 8) for more details on anxiety and the generalised anxiety disorder.

3.1.2 Anxiety and the dot-probe task

Research on attentional bias towards emotional stimuli overlaps with research on emotional disorders, and more particularly anxiety and depression. It has now been experimentally established, using tasks such as the dot-probe and emotional Stroop tasks, that anxious and depressive populations exhibit a higher attentional bias towards negative stimuli than non-anxious and non-depressive populations. More specifically, anxious individuals exhibit a bias towards threatening stimuli, while depressive individuals exhibit a bias towards negative stimuli (see Bar-Haim et al., 2007; Cisler and Koster, 2010; Peckham et al., 2010, for reviews). These attentional biases are part of more general cognitive biases that also include memory and interpretation biases. These can be characterised by favouring negative memories, ruminating negative thoughts and interpreting ambiguous stimuli in a negative manner. In anxiety, current models consider that this *negative attentional bias* constitutes a cause of vulnerability to anxiety (Mathews and MacLeod, 2005), and contributes to the maintenance of anxiety states (Mogg and Bradley, 1998). Indeed, it was found that inducing a negative attentional bias by asking or training participants to attend to negative stimuli can lead to symptoms of anxiety in non-clinical participants (see Mathews and MacLeod, 2002). Behavioural treatments intended to reduce anxiety by training patients to attend away from negative

stimuli are therefore being developed and tested.

According to the cognitive-motivational model of anxiety (Mogg and Bradley, 1998), the cause for this attentional bias stems from a bias in the appraisal of stimulus valence. While attentional bias towards negative stimuli is present among everyone for sufficiently threatening stimuli, high anxiety individuals will exhibit a bias to relatively innocuous stimuli, as mild stimuli are evaluated as having a higher threat value.

While understanding attentional bias towards emotional stimuli can help to understand and reduce anxiety, understanding the attentional dysfunctions associated with anxiety may help us understand how attention towards emotional stimuli works in general. Because this biased appraisal causes a stronger attentional bias in anxiety, the attention towards emotional stimuli may be easier to study using anxious populations.

The dot-probe paradigm (MacLeod et al., 1986) has been used extensively to highlight attentional bias towards threatening stimuli in anxious populations. It consists of presenting concurrently two stimuli, one neutral and one emotional, to the participant, on each side of a fixation point. This pair of stimuli constitutes the *cue*. Then, a single *probe* stimulus is presented at the location where the neutral or emotional cue stimulus was placed. Participants have to respond to the probe as quickly as possible. Their task can be to detect the probe (as used in MacLeod et al. 1986 or Mogg et al. 1990) or to perform a discrimination task between two possible probe stimuli (as used in Mogg et al. 1994 or Fox et al. 2001). Faster responses to probe stimuli congruent to the location of the emotional stimuli is interpreted as an attentional bias towards emotional stimuli.

The cue stimuli can take different forms. Earlier studies typically used words (e.g., MacLeod et al., 1986; Mogg et al., 1994), including words such as *failure* or *death* for the threatening cue. Pictorial stimuli were widely used, most particularly facial stimuli, whose facial expression can be manipulated so that they appear threatening. Typical facial expressions used were angry faces (e.g., Fox et al., 2001; Mogg and Bradley, 2002) and fearful faces (e.g., Fox, 2002; Pourtois et al., 2004).

The dot-probe experiment can be a useful tool to investigate attentional bias, as its parameters can easily be changed to answer various questions. The nature of the cues can be manipulated (e.g., words, faces and pictures have been used in the past). The presentation duration of the cue, and the stimulus onset asynchrony between the cue and the probe, can also be changed, which allows study of the time course of attentional

deployment and disengagement.

3.1.3 The experiment

The main goal in conducting a dot-probe experiment was to provide a benchmark tool that could be used to ask and answer various research questions. The first goal of the experiment was to replicate the previous findings that anxious populations exhibit an attentional bias towards emotional stimuli (MacLeod et al., 1986; Mogg et al., 1994; Mogg and Bradley, 1999; Mogg et al., 2001; Yiend and Mathews, 2001; Bradley et al., 1997; Fox, 2002; Mogg and Bradley, 2002), i.e. a shorter reaction time to probes congruent to emotional versus neutral faces.

A second goal was to study baseline conditions, in which only neutral or only emotional stimuli are presented to the participant. Previous research has mainly studied attentional biases measuring the *difference* in reaction times between probes congruent to the location of the emotional and the neutral stimulus, when two stimuli of different emotional content were presented concurrently. Using only this bias as a measure, it is not possible to know how the presence of a negative stimulus globally influences reaction times. In particular, a baseline condition could provide information on whether the reported bias is due to fast orienting towards the emotional cue, or to a delayed disengagement away from it. A shorter reaction time for probes congruent to the negative face compared with the neutral-neutral baseline would suggest that the attentional bias is due to fast orienting towards negative stimuli, while a longer reaction time for probes congruent to the neutral face compared with a neutral-neutral baseline would be compatible with a difficulty to disengage from negative stimuli.

There is conflicting evidence concerning the mechanisms of attentional bias towards negative stimuli in anxious individuals. There is experimental evidence that, in anxious individuals, covert attentional bias is due to a difficulty to disengage from negative stimuli (see e.g., Fox et al., 2001, 2002; Koster et al., 2007) (Similarly, it was found in Chapter 2 that unselected participants showed delayed disengagement from emotional stimuli.) However, in Mogg and Bradley (1999), in which the dot-probe task was performed by an anxious population sample, neutral-happy pairs of faces were used as well as threatening-neutral pairs. The authors found that anxious participants were faster at responding to the probe when a threatening face was present. More particularly, they found, in experiment 3, that left probes congruent to the location of

threatening faces were responded to faster than left probes congruent to the location of happy faces. Similarly, in the studies carried out by Carlson and colleagues (Carlson and Reinke, 2008, 2010), that used a baseline condition as described above, but without using anxiety groups, it was found that the reaction time to congruent emotional faces was faster than the neutral-neutral baseline, suggesting that the emotional bias effect is due to orienting. However, in Carlson and Reinke (2010), it was also found that the probes incongruent to the emotional face were responded to slower than the baseline. It is therefore possible that attention towards emotional stimuli in anxiety is characterised by a preferential orienting towards the threat stimulus *and* a difficulty in disengagement from it. An additional experiment, using real neutral-neutral and threat-threat baseline conditions, and groups of participants with different average level of anxiety, could help clarify the mechanisms of emotional attentional bias in anxiety.

Finally, a third goal of the study was to conduct an experiment in which the low-level features of the stimuli (such as contrast, contours, etc.) are well controlled for. Indeed, most past research in this area little controlled for physical characteristics of the stimuli, which can induce attentional biases independently from emotional content. To our knowledge, only one study looking at attentional bias in anxiety attempted to control for low level features: in Fox (2002), a control experiment was carried out, in which the facial cue stimuli were presented upside-down. However, the control group contained a much smaller number of participants than the experimental group (6 control vs 16 experimental participants).

For the current experiment, it was decided to use facial stimuli, as they were used successfully in several past experiments (Bradley et al., 1997; Fox, 2002; Mogg and Bradley, 2002). As in Fox (2002), fearful stimuli were chosen as threatening stimuli. Fearful faces constitute a threatening stimulus as they indicate the presence of a danger. It has been found that the amygdala responds selectively to fearful expressions, with its activity increasing as the intensity of the fearful expression increases (Morris et al., 1996). Short and masked cue presentations were also chosen, as these conditions were found to generate larger effect sizes than longer stimulus presentations (Mogg and Bradley, 1999; Fox, 2002; Mogg and Bradley, 2002). The rationale for using very short stimulus presentation is that early and automatic emotional processing is thought to be particularly sensitive in anxious individuals, as opposed to late and conscious processes (Mogg et al., 1994; Bar-Haim et al., 2007). The response of the amygdala to fearful faces was found to be also present for subliminal faces (Whalen et al., 1998).

The experiment presented in this chapter, however, failed to measure an emotional bias in anxious participants. Potential explanations are considered in the Discussion (Section 3.4).

3.2 Methods

3.2.1 Participants

Subjects participating in the experiment, approved by the Psychology Department Ethical Committee at the University of Edinburgh, provided written informed consent and reported normal or corrected-to-normal vision. Participants were compensated £6/hour for their participation. Ninety-two participants were selected after having filled in an online trait of anxiety (TA) questionnaire (Spielberger et al., 1983). Age range was 18–60 (mean: 23). The group included 66 females. Participants scoring above and below 40 were assigned to the high and low anxiety group respectively. Data were collected from 47 low-anxiety (LA) and 45 high-anxiety (HA) subjects. By construction, TA differed significantly between the LA ($M = 34.6$, $SE = 0.64$) and HA ($M = 49.2$, $SE = 1.40$) groups (Mann-Whitney $U = 0$, $p < .001$). Participants were also divided into two cue Orientation groups: Upright, Inverted. The Upright group (51 participants: 18 LA + 33 HA) was presented upright facial stimuli, while the Inverted group (41 participants: 29 LA + 12 HA) was presented upside-down facial stimuli. Orientation was varied as a between-participant factor in order to limit the number of within-participant factors and for consistency with past experiments (e.g. Bradley et al., 1997; Fox, 2002; Mogg and Bradley, 2002). Group sizes were unequal as HA participants were assigned in priority to the Upright condition as this is the condition in which effects were expected. After a sufficiently large Upright-HA group and failure to find significant attentional biases in this group, it was judged unnecessary to keep on collecting data for the other groups.

3.2.2 Stimuli

Stimuli were displayed on a 40.5×30 cm ViewSonic P227f CRT monitor at a resolution of 1280×1024 pixels with a refresh rate of 100 Hz, and placed at a viewing

distance of 60 cm from the chin-rested participant. Stimuli were displayed using Psychtoolbox 3 (Brainard, 1997) under Matlab (MathWorks, Inc., Natick, MA, USA). Stimuli were presented on a grey background of intensity 13 cd.m^{-2} .

The NimStim face database (Tottenham et al., 2009) was used for the facial stimuli, from which the calm and fearful expressions of 6 male and 6 female models were taken. All non-facial parts of the images were removed, including the shoulders, neck and hair. Images were converted to grey scale, and resized to $7.4 \times 5.3 \text{ cm}$. The mirror image of each face was presented an equal number of times to its original for each experimental condition.

The faces were followed by a mask, generated by randomising the phase of the frequency content of one of the facial stimuli. The scrambled face image was cut in the shape of a face to better fit the face of the preceding stimulus.

Probe stimuli consisted of the letters E and F. They were constructed with 4 and 3 black segments respectively (one vertical and 3 or 4 horizontal). Their length was of 1 cm, and their width consisted of 1 pixel.

The fixation point consisted of a black disc (diameter: 3 mm) displayed at the centre of the screen. Stimuli were presented on the left or right side of the fixation point, on the horizontal midline of the screen. The centre of the faces, masks and probe letters were placed 7.3 cm away from the centre of the screen.

3.2.3 Procedure

The procedure is illustrated in Figure 3.1. The experiment consisted of 320 trials divided into 4 blocks. Each participant was given one of two experimental conditions: upright faces, or inverted faces. In the Inverted condition, the facial stimuli and the masks were presented upside-down. Participants were instructed to discriminate between the letter E and F as fast and accurately as possible, by pressing the key **E** or **F** on the keyboard. Participants were presented with a pair of randomly selected facial stimuli for 20 ms, which were then immediately replaced by a pair of masks for 20 ms. The letter immediately followed the masks and was displayed on the left or right side, until the participant gave their answer. The inter-trial interval displaying only the fixation point lasted 1,000 ms. The possible facial cues were: a pair of neutral faces (Neutral-Neutral: NN), a pair of fearful faces (Fearful-Fearful: FF), a neutral and

a fearful face (Neutral on the left and Fearful on the right: NF; or Fearful on the left and Neutral on the right: FN). The number of trials was equally divided between the FN, NF, NN and FF cue conditions (80 trials each), and the probe appeared on each side (Left, Right) for half of the trials (40 trials). Feedback was given at the end of every trial by playing a sound if the participant answered correctly.

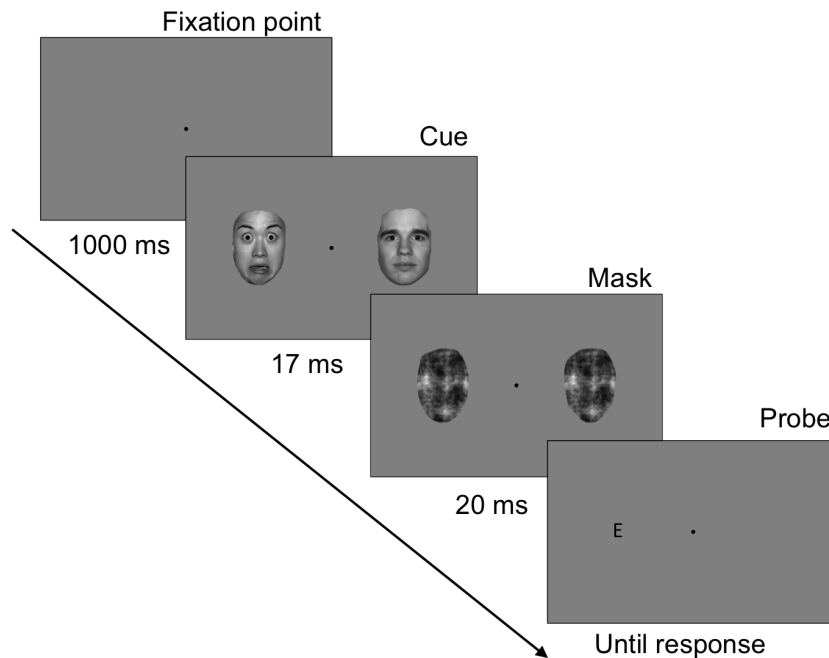


Figure 3.1: Dot-probe experiment procedure. Participants were asked to keep looking at the central fixation point. For each trial, a pair of facial stimuli was briefly presented on the screen (17 ms), immediately followed by a mask (20 ms). The pairs of faces could have the following emotional combinations: neutral-neutral, fearful-fearful, and neutral-fearful. After the mask, the probe stimulus (the letter E or F) was presented on the left side or the right side, until the participant pressed the key **E** or **F** on the keyboard.

3.2.4 Data Analysis

3.2.4.1 Accuracy and reaction time data

Both accuracy and reaction time data were looked at, although no effect on accuracy was expected (see Section 3.3.1).

The reaction time data were studied in two different ways. The average reaction time of the trimmed reaction time distributions was first looked at. Trimmed distributions are used to reduce the effect of slow outliers. The cut-off chosen to trim the distribution was, for each participant, 2.5 standard deviations above the mean (as in Fox,

2002). Using this procedure, 2.0 % of the correct trials were removed. To verify the robustness of the results, the median reaction time from the overall distributions were also studied. Because of the skewness of reaction time data and the presence of outliers (most particularly very slow reaction times), the median value is a more robust central tendency estimate than the mean. However, it has been reported that it often results in a lower statistical power than using cut-offs (Whelan, 2008).

3.2.4.2 Statistical analyses

For clarity, Figure 3.2 summarises the different analyses described below. Due to the non-normality of the accuracy data, non-parametric Kruskal-Wallis tests were performed to compare the accuracy between each Cue condition (NN, FF, Fearful-Valid: FV and Fearful-Invalid: FI), for each of the four participant groups (Upright/Inverted faces - LA/HA participants). FV corresponds to the FN and NF cues followed by a probe on the Left and on the Right respectively (i.e. at the same location as the Fearful face). FI corresponds to the FN and NF cues followed by a probe on the Right and on the Left respectively (i.e. at the same location as the Neutral face).

Median and mean reaction times were first fed into an omnibus ANOVA including within-participant factors Cue (NN, FF, FV, FI) and Side of the probe (Left, Right) as well as between-participant factors: TA group (LA, HA) and face Orientation (Upright, Inverted). The data was then broken down into subgroups and paired *t*-tests were performed to understand the nature of significant interactions.

Further analyses were then carried out within each group, in particular to test the hypothesis of a Cue effect in the HA-Upright group. For this purpose, a two-way ANOVA with Cue and probe Side was run on each group, and paired *t*-tests were run between Cue conditions.

Multiple comparisons were taken into account when using the paired *t*-tests. Bonferroni correction was applied on the significance threshold of the multiple *t*-tests run on a same data subset. As six comparisons were performed each time (NN-FF, NN-FV, NN-FI, FF-FV, FF-FI, FV-FI), the significance threshold was divided by a factor of six, leading to a threshold $p_{\text{thr}} = 0.05/6 = 8.3 \times 10^{-3}$.

To allow direct comparison with previous research, the reaction time biases were also looked at. β_{left} and β_{right} are defined as the differences in reaction time indicating the

bias towards fearful faces when the Fearful face appears on the *left* and *right* location respectively:

$$\begin{aligned}
 \beta_{left} &= FN_R - FN_L \\
 \beta_{right} &= NF_L - NF_R \\
 \beta &= \frac{\beta_{left} + \beta_{right}}{2}
 \end{aligned}
 \tag{3.1}$$

FN and NF, as defined in Section 3.2.3, indicate the pairs of Fearful and Neutral faces where the Fearful face is on the left and right position respectively. The indices L and R indicate the location of the probe (Left and Right). These biases were calculated from the mean reaction times (Section 3.3.2.1) and the median (Section 3.3.2.2). A positive bias indicates faster reaction times in the FV than in the FI condition.

The bias data β_{left} and β_{right} were first fed into an ANOVA with Fearful face side (Left, Right) as a within-participant factor, and TA and face Orientation as between-participant factors. Then, for each participant group, one-sample *t*-tests were performed on β_{left} , β_{right} and β in order to test the existence of a bias towards or away from the fearful faces.

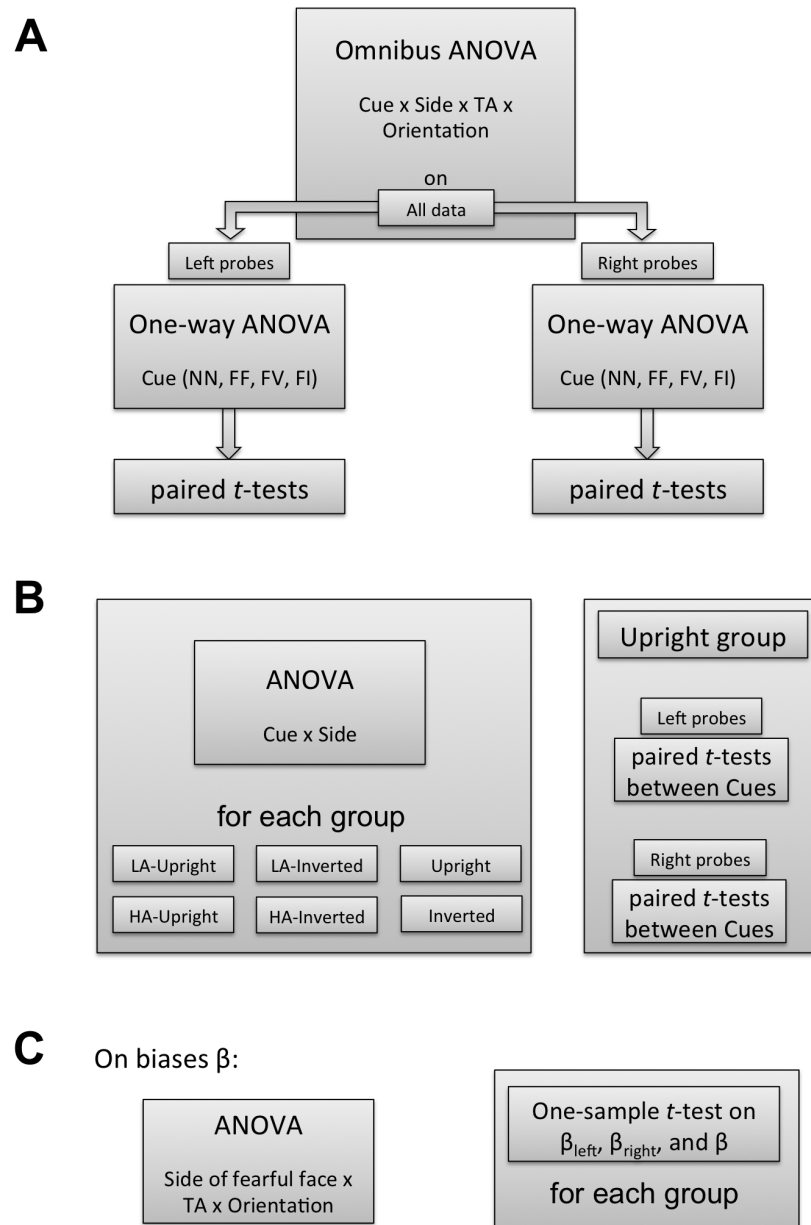


Figure 3.2: Summary of the statistical tests performed on the reaction time data. The same tests were performed on the mean and median of the reaction time distributions. **(A)**, **(B)**, and **(C)** correspond respectively to the tests performed in the first, second, and third paragraph of sections 3.3.2.1 and 3.3.2.2.

3.2.4.3 Hypotheses

The main hypothesis was that a reaction time effect of Cue for the Upright-HA group would be found, but none for the Upright-LA, Inverted-LA and Inverted-HA groups. Ideally, this would be reflected by a significant Cue \times TA \times Orientation interaction. More particularly, a positive bias towards fearful faces (i.e. shorter reaction time in the FV compared with the FI condition: β significantly positive) for the Upright-HA group, but not for the others, was expected. Shorter reaction times in the FV than in the NN condition would be compatible with a fast capture of attention by threat, while longer reaction times in the FI than in the NN conditions would be compatible with a delayed disengagement from threat. Faster reaction times in the FF than the FI and NN conditions may reflect preparation for faster action in response to potential threats (Flykt, 2006).

3.3 Results

3.3.1 Accuracy

The task was performed properly, as shown by the high correct detection rate (mean: 0.95, st. dev: 0.04). A Kruskal-Wallis test was performed on each group, with Cue condition as a four-level factor. No effect was found for the Upright-LA group ($H = 1.4$, 3 d.f., $p = 0.71$), the Inverted-LA group ($H = 2.3$, 3 d.f., $p = 0.51$), the Upright-HA ($H = 0.6$, 3 d.f., $p = 0.90$), or the Inverted-HA group ($H = 0.4$, 3 d.f., $p = 0.92$).

These null results are not surprising as the task was easy and ceiling effects were expected.

3.3.2 Reaction time data

Only trials responded to correctly were included in the following analyses. The exact same analyses were performed on the mean and median reaction time data (see Section 3.2.4.2 and Fig. 3.2 for a summary of the analyses done). A summary of the significant results is shown in Table 3.1.

3.3.2.1 Mean reaction time analysis

Sample mean reaction times are indicated on Figure 3.3. The omnibus ANOVA on the mean, with Cue and Side as within-participant factors, and TA Group (LA, HA) and Orientation (Upright, Inverted) as between participant factors led to a significant Cue \times Side interaction ($F_{3,264} = 3.08$, $p = 0.03$, partial $\eta^2 = 0.03$). No other significant effect was present. To understand the Cue \times Side interaction, two one-way ANOVAs were performed, with the four-level factor Cue (NN, FF, FV, FI), one for each side of the probe. It was found that the nature of the cue had an effect for probes located on the left-hand side ($F_{3,273} = 3.02$, $p = 0.03$, partial $\eta^2 = 0.03$), but not for probes located on the right-hand side ($F_{3,273} = 1.13$, $p = 0.30$, partial $\eta^2 = 0.01$). Fig. 3.4A graphically represents the pairwise differences for the overall sample of participants. For probes presented on the Left, paired t -tests showed a significantly shorter reaction time for the NN ($M = 522.0$ ms, $SE = 5.63$ ms) than the FF condition ($M = 527.7$ ms, $SE = 5.96$ ms): $t_{91} = 2.90$, $p = 5 \times 10^{-3} < p_{\text{thr}}$, $r = 0.30$. No significant effect was found from pairwise comparisons for conditions in which the probe was presented on the right-hand side of the screen.

To test the main hypothesis (i.e. a Cue effect for the Upright-HA group but not the others), an ANOVA on each group was performed. For the Upright-HA group, no significant effect of Cue ($F_{3,96} = 0.31$, $p = 0.82$, partial $\eta^2 = 0.01$), Side ($F_{1,32} = 1.15$, $p = 0.29$, partial $\eta^2 = 0.04$), and no Cue \times Side ($F_{3,96} = 2.63$, $p = 0.06$, partial $\eta^2 = 0.08$) interaction were present. The same analysis performed on the Upright-LA, Inverted-HA, Inverted-LA, also led to non-significant results. As exploratory analyses, the ANOVA was run on the Upright and Inverted groups (LA+HA). While the Inverted group showed no significant effect, there was a significant Cue \times Side interaction ($F_{3,150} = 3.11$, $p = 0.03$, partial $\eta^2 = 0.06$) in the Upright group. Paired t -tests were performed to look at the effect of Cue, when the probe was presented on the left-, and right-hand side. No significant effect was found for the Upright group. The Cue \times Side interaction in this group may therefore be due to non-significant pairwise differences, such as shorter reaction times for NN cues ($M = 521.8$ ms, $SE = 7.86$ ms) than FF cues ($M = 528.6$ ms, $SE = 8.40$ ms) when probes were presented on the left ($t_{50} = 2.42$, $p = 0.02$, $r = 0.32$), and shorter reaction times for probes presented on the right-hand side in the FF ($M = 526.3$ ms, $SE = 8.23$ ms) than in the FI ($M = 533.0$ ms, $SE = 9.09$ ms) cue condition ($t_{50} = 2.20$, $p = 0.03$, $r = 0.30$). See Fig. 3.4B and C for a representation of the pairwise differences.

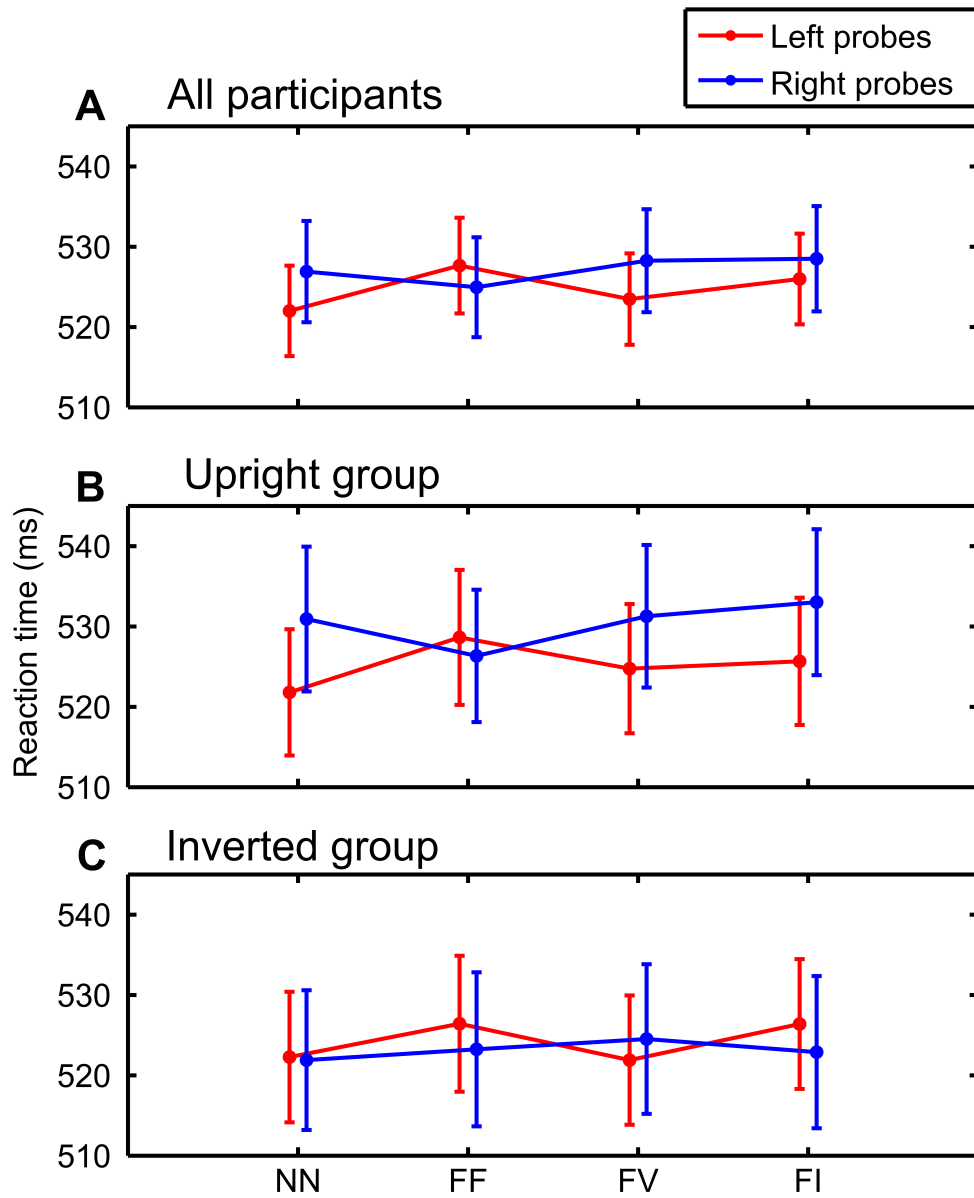


Figure 3.3: Population mean and standard error of the mean reaction times, for all participants (A), and the Upright (B) and Inverted groups (C), and for the different Cue conditions (NN, FF, FV, and FI).

Finally, the biases, calculated from the mean reaction times (Eq. 3.1), were studied. See Figure 3.5 for a graphical representation of the means and standard errors of the biases. An ANOVA with Side of the fearful face as within-participant factor, and TA and face Orientation as between-participant factors did not lead to any significant effect. Using one-sample *t*-tests, it was found that for the HA-Upright group, the mean biases were not significantly different from zero (β_{left} : $t_{32} = 1.14$, $p = 0.26$, $r = 1.20$; β_{right} : $t_{32} = -0.43$, $p = 0.67$, $r = 0.08$; β : $t_{32} = 0.83$, $p = 0.42$, $r = 0.15$). Similarly, no effect was found for biases in the LA-Upright, HA-Inverted, and LA-Inverted, as well as for the Upright and Inverted (LA+HA) groups.

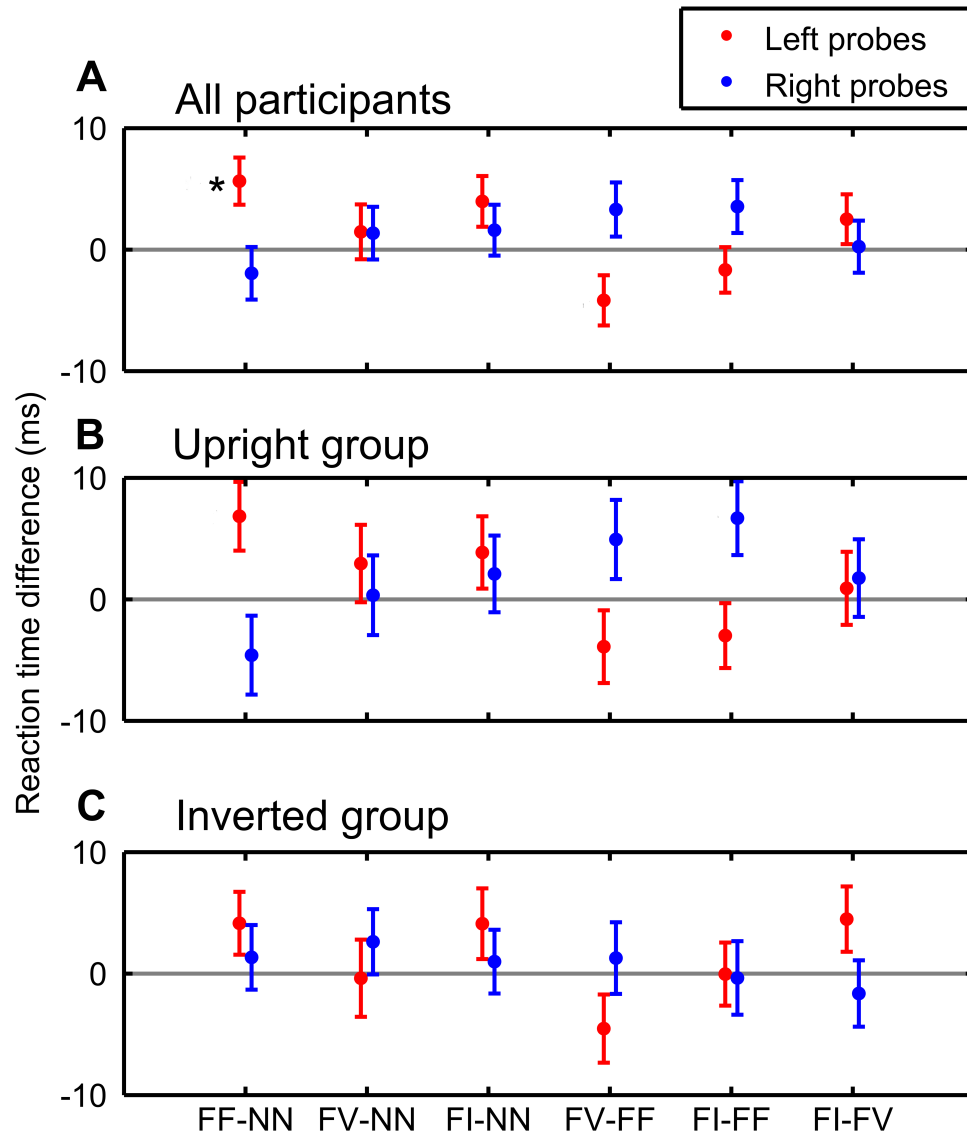


Figure 3.4: Mean and standard error of the difference in mean reaction time between Cue conditions used for t -tests, for probes presented on the left- and right-hand side. Data is shown for all participants (**A**), the Upright (**B**) and Inverted groups (**C**). Significant differences between conditions ($p < p_{\text{thr}} = 8.3 \times 10^{-3}$) are indicated by an asterisk.

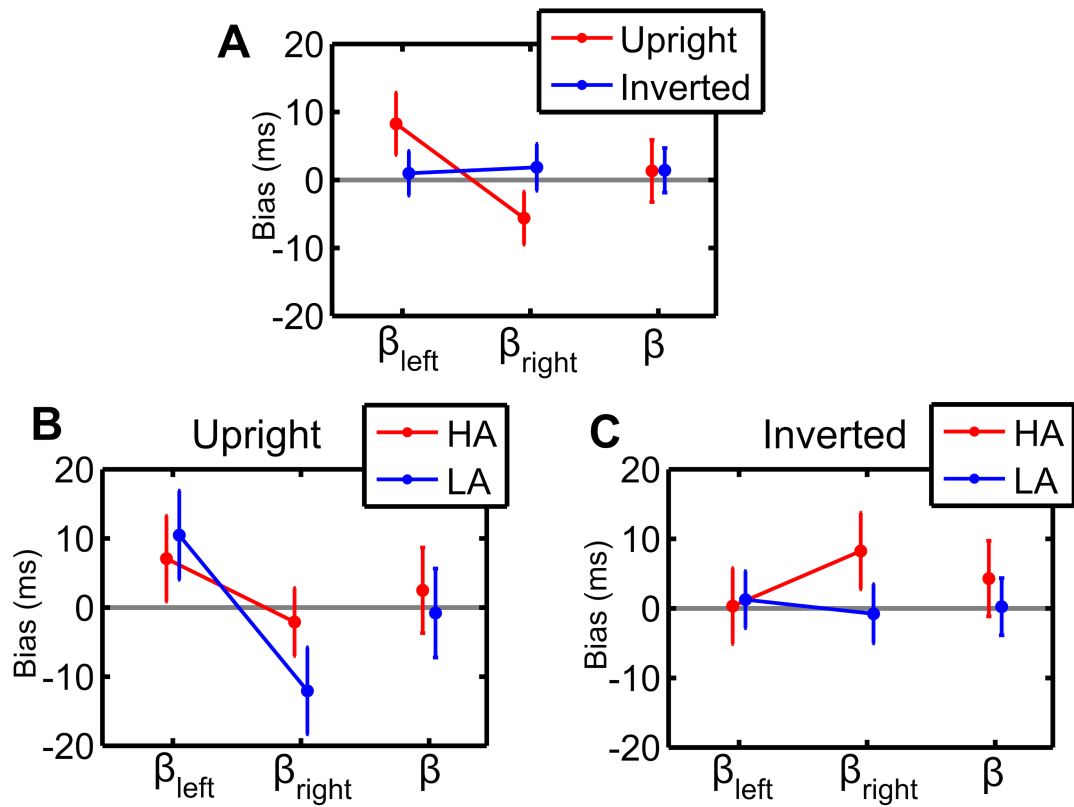


Figure 3.5: Mean and standard error of the bias scores from the means for all participants (**A**), and for the Upright (**B**) and Inverted groups (**C**). β_{left} and β_{right} are the biases corresponding to the FN and NF cues respectively, and β is their mean (see Eq. 3.1), calculated using the mean reaction time. There was no effect of fearful face Side, TA, and face Orientation. Additionally, all mean biases were non-significantly different from zero.

3.3.2.2 Median reaction time analysis

To confirm the results found using the mean from the trimmed distributions, the same statistical analyses were performed on the median of the non-trimmed distributions. The omnibus ANOVA led to significant Cue \times Side \times TA \times Orientation ($F_{3,264} = 2.732$, $p = .04$, partial $\eta^2 = .03$). All other effects were non-significant, including the Cue \times Side interaction ($F_{3,264} = 2.60$, $p = 0.053$, partial $\eta^2 = 0.03$), which was significant using the mean on the trimmed distributions. Two one-way ANOVAs with Cue (NN, FF, FV and FI) as factor, for each side of the probe, were run. A significant effect of Cue when the probe was presented on the left-hand side was found ($F_{3,273} = 3.20$, $p = 0.02$, partial $\eta^2 = 0.03$). There was no significant effect when the probe was situated on the right-hand side ($F_{3,273} < 1$). These results are consistent with those found with the mean. Paired t -tests revealed, for probes presented on the left, significantly shorter reaction times for the NN ($M = 523.8$ ms, $SE = 5.62$ ms) than for the FF ($M = 529.6$ ms, $SE = 6.02$ ms) condition: $t_{91} = 2.98$, $p = 2 \times 10^{-3} < p_{\text{thr}}$, $r = 0.30$. No significant effect when the probe was presented on the right-hand side was found. These results are largely consistent with what was found using the mean from the trimmed distributions.

As with the mean, to test the main hypothesis (effect of Cue in the HA-Upright group), and to try and better understand the significant Cue \times Side \times TA \times Orientation interaction found above, an ANOVA on each group of participants (Upright, Inverted, Upright-LA, Upright-HA, Inverted-LA, and Inverted-HA) was performed with Cue and Side as within-participant factors. Like with the mean, there was a significant Cue \times Side interaction ($F_{3,150} = 2.67$, $p = 0.05$, partial $\eta^2 = 0.05$) in the Upright (LA+HA) group, and no significant effects for the other groups (Inverted, Upright-HA, Upright-LA, Inverted-HA, Inverted-LA). As with the mean, paired t -tests between Cue conditions for Left probes, then for Right probes, were performed for the Upright group. No significant effect was found.

The bias data, calculated from Equation 3.1, but this time using the median reaction times, were fed into an ANOVA with the Side of the fearful face (Left, Right) as a within-participant factor, and TA and face Orientation as between-participant factors. No significant effect was found. Using one-sample t -tests, the biases for the Upright-HA group were found to not significantly differ from zero (β_{left} : $t_{32} = 1.23$, $p = 0.23$, $r = 0.21$; β_{right} : $t_{32} = -0.29$, $p = 0.77$, $r = 0.05$; β : $t_{32} = 1.03$, $p = 0.31$,

$r = 0.18$). Biases were non-significantly different from zero for the three other groups as well.

3.3.2.3 Summary and interpretation of the reaction time results

Overall, the results using the mean and the median are largely consistent. Table 3.1 summarises the significant effects found using the two measures.

The most consistent effect appears to be the difference in reaction time between the NN and FF conditions on the overall cohort, when the probe is presented on the left-hand side (Table 3.1, fourth line, and Fig. 3.4A). This effect is unlikely to be a false positive, as its p -value lies below the corrected threshold p_{thr} , and seems to be responsible for the significant effects involving the factors Cue and Side on the overall data. The effect is non-significant when faces are presented Upright (Table 3.1, second-last line) and Inverted (see Fig. 3.4B *vs* C). While the effect size is larger for Upright faces ($r = 0.32$, using the mean) than for Inverted faces ($r = 0.23$), the difference is not very large. Importantly, the Cue (NN, FF) \times face Orientation interaction on this dataset is not significant, using a two-way mixed factors ANOVA ($F_{1,90} < 1$ for both the mean and the median). It should be noted that the Orientation comparison is performed between participants with groups of unequal sizes. However, overall, these results indicate that the NN *versus* FF effect is likely due to low-level features of the stimuli rather than to emotion.

Importantly, no significant bias towards fearful faces was found using the bias scores (Eq. 3.1, Fig. 3.5).

Overall, it cannot be stated that a reliable and genuine emotional bias is present in the data.

Participants	Data	Stat. test	Factors	Effect ^a	<i>p</i> -value ^c	
					mean	median
All	All	ANOVA	Omnibus ^b	Cue × Side	*	<i>n.s.</i>
				Cue × Side × TA × Orientation	<i>n.s.</i>	*
				Left probes	ANOVA	Cue
		<i>t</i> -test	NN vs FF	NN < FF	**	**
Upright	All	ANOVA	Cue × Side	Cue × Side	*	*

^a For *t*-tests, the direction of the effect is indicated. e.g., NN < FF means that the reaction time in condition NN was found to be shorter than in condition FF.

^b Omnibus: Cue × Side × TA × Orientation

^c The *p*-value can be non-significant (*n.s.*), $p \leq 0.05$ (*), or, for *t*-tests, $p < p_{\text{thr}} = 8.3 \times 10^{-3}$ (**).

Table 3.1: Summary of the effects found to be significant in the reaction time data. The statistical significance of the tests performed on the median and mean reaction times are indicated (sixth and seventh columns). Tests (ANOVA or paired *t*-tests) were performed on the group of participants indicated by the first column, and on subsets of the data indicated by the second column. Factors fed into ANOVAs, or contrasts looked at with *t*-tests, are indicated in the fourth column.

3.4 Discussion

The methods used in the present experiment are similar to past dot-probe experiments. Facial stimuli were used, as in Bradley et al. (1997); Fox (2002); Mogg and Bradley (2002). Cue presentation times were very short, and followed by a mask. This procedure has also been used successfully (Mogg and Bradley, 1999, 2002), including using fearful faces (Fox, 2002). The choice of facial stimuli is also supported by neuropsychological, psychological and neurobiological evidence suggesting that emotional faces can be processed and trigger attentional resources without awareness (e.g., Vuilleumier and Schwartz, 2001; Vuilleumier et al., 2002; Pegna et al., 2005). The experiment contained control conditions, more particularly a group of participants for whom facial cues were presented upside down (Inverted group). The size of the experiment, in terms of trial number and number of participants, should have been sufficient to generate a significant bias effect, considering past effect sizes. Despite all these precautions, no attentional bias in the HA group as reported previously was found.

However the experiment conducted does present some weaknesses. Firstly, the between-participant design was imbalanced (i.e. different group sizes), which may have impaired the finding of a significant effect in the omnibus ANOVA. However, the size of the Upright-HA group was comparable to other studies, therefore a within-group effect was expected, including a significantly positive bias β .

Second, the absence of an awareness check in the paradigm prevented us from ensuring that stimuli were indeed processed subliminally, minimising the influence of strategic and conscious processes (Holender, 1986). Awareness checks consist of an additional task given to the participant. The cue stimuli are presented under the same presentation conditions as during the dot-probe task, and the participants have to perform a discrimination task on the stimuli. For instance, in Mogg and Bradley (2002), participants were given two awareness checks: one asking the gender of the facial stimuli, the other asking whether the stimuli were normal or ‘jumbled’ faces. One study did not use such checks and also failed to find an effect for short stimulus presentations (Egloff and Hock, 2003). The authors emphasise the fact that with the stimulus presentation times used in their experiment (17 ms), which is comparable to the one used in the present experiment and to past research (MacLeod and Rutherford, 1992; Mathews et al., 1996), no evidence of awareness has been found in past studies. While a weakness of the study, the absence of awareness check should not have prevented the

measurement of an effect.

Thirdly, the task given to the participants may have been too complex. Most studies used either a detection task, or a discrimination task involving simple abstract shapes (e.g., discriminating the orientation of a bar or the alignment of two dots: $\cdot\cdot$ vs $\cdot:$). The experiment presented in this chapter involved letters (E and F), that may have higher cognitive representations than dots. These higher processes might have prevented the trigger of emotional attention processes. However, it should be noted that Staugaard (2009) used the same letter discrimination task, using facial stimuli (presented for 100 and 500 ms), and found significant biases. It is however possible that the combination of short cue presentation *and* letter discrimination task prevent attentional biases from appearing.

Fourthly, the short stimulus onset asynchrony between the presentation of the cue and the probe (40 ms) may not have been sufficient for attentional processes to be triggered. Indeed transient attention peaks at around 100–120 ms after cue onset, while sustained attention is deployed in approximately 300 ms (Carrasco, 2011). Several past studies used such short stimulus onset asynchronies and obtained significant attentional biases (Mogg et al., 1994, 1995; Mogg and Bradley, 1999; Fox et al., 2002). This indicates that the presence of the probe stimulus immediately after the mask does not prevent the deployment of attention triggered by the cue stimulus, and that an emotional-attentional bias effect is measurable under these parameters.

An alternative explanation is that the reported effects with short stimulus presentation may not be as robust as they may appear at first sight in the literature. Bar-Haim et al. (2007) conducted a meta-analysis on experiments looking at attentional bias towards emotional stimuli in anxiety, including dot-probe studies. One of their procedural moderators was exposure time: very short stimulus presentations (subliminal) *versus* longer presentations of 500 ms or more (supraliminal). They found that, in anxious participants, subliminal exposure times yielded a significantly larger effect ($d = 0.61$) than supraliminal exposure times ($d = 0.31$), while non-anxious participants showed a significant bias away from subliminal threat stimuli ($d = -0.28$) but none for supraliminal presentations. Interestingly, only 6 studies were found to use subliminal presentation (with a cumulated number of 126 and 123 anxious and non-anxious control participants respectively) against 36 supraliminal presentation reports (using a total of 679 and 661 anxious and control participants respectively). Among these 6 studies (Mogg et al., 1994, 1995; Mogg and Bradley, 1999, 2002; Fox, 2002; Egloff and Hock, 2003),

3 used facial stimuli (Mogg and Bradley, 1999, 2002; Fox, 2002), while the others used words. Only three independent research teams conducted these 6 experiments (2 teams for the faces), and one study failed to find an effect with short stimulus presentations (Egloff and Hock, 2003). Together, this analysis suggests that the effect reported for short stimulus presentation, despite an effect of a medium size (according to the nomenclature defined in Orwin 1983), may not be as robust as initially thought before performing the experiment.

In contrast, Carlson and colleagues conducted a series of dot-probe experiments using artificial faces on a non-selected sample, and found fairly consistent results (Carlson and Reinke, 2008; Carlson et al., 2009; Carlson and Reinke, 2010; Carlson et al., 2011). Like in the experiment described in the present chapter, they used NN and FF baseline conditions, in order to assess the contribution of orienting and disengagement. In Carlson and Reinke (2008), besides the classical fear-congruency effect, it was found that reaction times for FV trials were faster than for any other trial type. In Carlson et al. (2009) only a bias for FV *versus* FI was reported, but only for trials where the fearful face appeared on the left visual field. In Carlson and Reinke (2010), shorter reaction times in the FV and larger in the FI, compared with the baseline, were reported, along with the classical FV *versus* FI difference in reaction times, but no hemispheric differences. These results suggest that attentional biases towards fearful faces can be observed in unselected populations, and using relatively small groups ($N = 12$ in Carlson et al. 2009 and Carlson and Reinke 2010). However, the three experiments (Carlson et al. 2009 and Carlson et al. 2011 analyse data from the same experiment) were not independent, as the same set of only four facial identities was used. This could have potentially generated biases, as the same stimuli were repeated many times during, and in this case across, experiments. A small difference between stimuli from different conditions can have a large effect, as the difference will be repeated many times when the number of stimuli is small. While the frequency content of the facial stimuli was controlled for in Carlson and Reinke (2008), local contrast or other physical features, that can only be controlled for by using inverted faces, were not.

More studies using short stimulus presentation should therefore be conducted in order to understand what prevented the effect from occurring. A first step would be to perform a follow-up experiment, using the exact same procedure, but with longer cue presentation times, such as 500 ms. If attentional biases are still absent with an anxious population, it may be that the stimulus set contains problems, or that the task somehow

inhibits the effect. An experiment using the same short and masked cues could also be conducted to ensure that the stimuli are processed subliminally, and that automatic processes are not disrupted by conscious and strategic processes (Mogg and Bradley, 2002).

3.5 Conclusion

A dot-probe experiment with high and low anxiety participants, using briefly presented facial stimuli, was conducted. The experiment was paired with a control experiment, using facial stimuli presented upside-down, to ensure that physical features could not explain any attentional bias. The hypothesis was that, in the condition in which a neutral-fearful pair was presented, high anxiety participants would be faster at discriminating the probe stimulus when presented at the location of the fearful face. No evidence of attentional bias towards fearful faces in anxiety was found.

It is difficult to draw any conclusions from null results. While some weak trends were found in the data, no robust and meaningful effect was found, and the initial hypotheses were not validated. The reasons for the failure to find an effect are likely to be methodological, and systematic tests on the parameters of the experiment would be necessary to understand what are the key parameters that prevented the attentional bias to be elicited in the anxiety group. One can nevertheless hypothesise that short stimulus presentation do not elicit attentional biases as easily as initially thought. A close analysis of the literature indicates that the effect may be less robust for short than for longer presentations, as a much smaller number of (independent) experiments were performed using these parameters. Furthermore, the experiments mentioned above with unselected participants may lack some control on the physical characteristics of the stimuli. It is therefore a hypothesis that is worth being considered and tested experimentally.

The dot-probe task, despite a low test-retest reliability (Schmukle, 2005; Staugaard, 2009), is a tool that can be used to answer many questions. More research should be performed to understand what physical characteristics of the cue stimuli trigger attentional processes, and what are the temporal characteristics of attentional bias towards emotional stimuli (Cisler et al., 2009).

Chapter 4

Early ERP Modulation by Emotional Stimuli and Attention

4.1 Abstract

Very early modulations of brain activity (i.e. before 100 ms) by emotional stimuli have been reported in the literature, particularly through the observation of the early visual event-related potential (ERP) component C1. However, the exact conditions which make C1 modulation occur are still unclear. This chapter describes experiments focusing on studying the C1 evoked by facial stimuli, under various attentional conditions. In Experiment 1, neutral and fearful faces were presented peripherally while the participant was focusing on a fixation point. No C1 modulation by attention was found. In Experiment 2 and 3, a cueing paradigm was used, asking participants to direct their attention to the left or right part of their visual field. In Experiment 2, two classes of objects (kettles and jugs) were presented in addition to neutral and fearful faces. Participants were asked to press a button only when they detected a kettle (or jug) at the cued location. The faces and their expressions were therefore irrelevant to the task. Facial expression modulated the global field potential (GFP) only in the cued locations. Furthermore, a GFP modulation independent of Cueing was found between target and non-target objects. In Experiment 3, only faces were presented, with neutral, fearful or happy expressions. Participants had to press a button when happy faces appeared at the cued location. In this case, the facial expression was task-relevant. No effect between neutral and fearful faces was found, but a stronger GFP for happy than

neutral faces was present. This effect was not dependent on cueing. Consistent with past research on the P1 component, a larger P1 amplitude was found in Experiment 2 and 3 for stimuli presented in the cued location.

The results did not confirm past research reporting a C1 component of larger amplitude for emotional stimuli, and were found using the GFP as a dependent variable rather than the average potential at a set electrodes. They do, however, suggest an early effect of fearful faces when faces are task-irrelevant, but placed at attended locations. Additionally, the results suggest that objects recognised as the target modulate the C1, independently of spatial attention. This is consistent with feature-based attention, which has been found to modulate the ERP in the C1 time range, and which is considered to operate in the whole visual field independently of spatial attention. The interpretation of the results are discussed in light of the limitations of the experiments.

4.2 Introduction

This section will first introduce the event-related potential principles and technique. This will be followed by a short review of ERP studies of emotional faces and attention, before focusing on studies looking at very early latencies (i.e. before 100 ms). The purpose and design of the experiments are then introduced.

4.2.1 Scalp EEG and ERPs

The electro-encephalographic (EEG) signal reflects some of the brain electrical activity, and is recorded through electrodes placed on the scalp of an individual. The signal is measured in Volts over time, and is defined as the difference of potential at the set of electrodes and a reference electrode or group of electrodes. The scalp EEG is extensively used in cognitive neuroscience, as well as clinical research. It also constitutes an efficient diagnostic tool, most notably to determine the nature and characteristics of seizures.

The discovery of the human EEG signal is attributed to Hans Berger (1873–1941), who first reported his recordings in 1929, using two electrodes, placed on a fronto-occipital axis. By the thirties, the potential clinical applications of the EEG arose with the first recordings of epileptic spikes by Fischer and Löwenbach (Sanei and Chambers, 2007).

Evoked potentials, or event-related potentials (ERP), generated by averaging the EEG signal locked to a particular event (often a sensory stimulation), were first recorded by Dawson in 1947 (Walsh et al., 2005). The methods applied nowadays in ERP research use the same principles as the ones used by pioneers such as Berger and Dawson.

4.2.1.1 Origins of the EEG signal

The EEG signal, like the magneto-encephalographic (MEG) signal, is a direct measurement of neural activity. Neurons generate electric signals known as action potentials or spikes, which travel through the axon of the neurons towards synapses. Spikes are generated when the potential of the neuron, maintained at approximately -70 mV at rest by keeping an excess of anions in the cell, reaches the threshold potential (typically ≈ -60 mV). The potential of the cell is altered when excitatory or inhibitory signals flow from pre-synaptic neurons. Receiving synaptic inputs will generate currents of ions flowing in and out the cell. In the case of excitatory synaptic activity, cation channels will open at the level of the dendrites, generating a flow of cations inside the cell (depolarising the cell towards its threshold potential). Because of this, the extra-cellular fluid at the level of the dendrites will be slightly negatively charged (with respect to the surroundings). Cations inside the cell travel along the dendrites towards the body of the cell. The cations are then released, generating a slightly positively charged area in the extra-cellular fluid around the dendrites closer to the soma. In the case of pyramidal cells, whose body and dendrites are aligned along an axis, the negatively charged area at the level of the dendrites, paired with this positively charged area near the body of the cell, can be modelled as a dipole (two point electric charges of opposite polarity located close together). It is the electric field generated by this dipole that is thought to be the main contributor to the local field potential (LFP) and EEG signals (see e.g. Coles and Rugg, 1995; Luck, 2005; Lindén et al., 2010; but see Riera et al., 2012). The movement of free charges (in this case electrons and ions) is affected by the electric field generated by the dipoles. It is this movement of charges at the location of the scalp electrodes (affected by brain activity) that is measured by the EEG.

However, the currents generated by a single neuron are too small to be detected by scalp electrodes. It is the superposition of thousands or millions of synchronised neuronal activity that can be measured. Thus only neurons aligned so that signals sum

each other up (instead of cancelling each other out) can be measured. This is mostly the case in the neo-cortex, where pyramidal cells are aligned perpendicularly to the cortical surface, with most dendrites pointing towards the surface.

4.2.1.2 Measuring and generating the ERP

The EEG is measured by a set of electrodes, which are placed at standardised locations on the scalp. In the present case, to facilitate electrode placement, caps with orifices in which the electrodes are placed were used. The electrodes followed an extended version of the 10–20 system (Jasper, 1958). To enhance contact between the electrodes and the scalp, a conductive gel is used.

The system used in the present experiments is the Biosemi Active-Two system (Biosemi B.V.), which does not use the typical reference and ground electrodes. Instead, a feed-back loop of electrodes is used: an active electrode named Common Mode Sense (CMS) and a passive electrode called Driven Right Leg (DRL). This feed-back loop drives the average potential of the subject as close as possible to the potential of the amplifier. The signal is recorded with reference to the DRL electrode, but the signal is re-referenced offline by the user. The signal is recorded and stored digitally after amplification and digitation.

The choice of the reference affects the shape of the signal and has to be chosen carefully. To be consistent with most of the literature studying the C1 component, the average potential of the mastoid electrodes was used as a reference (see Section 4.3). For topographical analyses, the average reference was used (see Appendix 4.A), as the piece of software used for map clustering requires the use of such reference. The rationale behind this choice is that topographical and micro-state analyses are often a first step before source reconstruction, whose algorithms recalculate the data to a common reference in order to prevent violation of the quasi-stationarity assumption (the assumption that the net source activity at each instant in the brain sums to zero; see Murray et al., 2008). It is to be noted that the reference does not alter the topography itself, but only its scale and offset.

From the EEG signal, the event-related potentials (ERP) are calculated through simply averaging portions of the EEG signal time-locked to the event (in the present case the onset of a visual stimulus) across multiple trials. This averaging procedure is done to increase the signal to noise ratio. The noise can come from individual electrodes, or

variability in the neural signal.

Before actually averaging the signal, the raw EEG data are filtered in order to remove frequencies that contain more noise and less useful neural signals. Only the signal between 0.1 Hz and 40 Hz is typically kept. Filtering parameters have to be considered carefully, as they can easily distort the signal and generate misinterpretations of the data (see Chapter 5 for details). The EEG signal has to be inspected (either manually or with the help of an algorithm) to remove the numerous artifacts it contains, such as muscle contraction signals, eye movements, blinks, jumps in potential, etc. Then, the offset of the portions of the signal to be averaged together (the epochs) is removed by subtracting a baseline potential, typically chosen as the average potential during a time-window directly preceding the event (typically between 50 and 200 ms, in the present case 100 ms). Finally, the epochs are averaged together to generate the ERP.

4.2.1.3 Interpreting the ERP

The resulting ERP signal reflects the average neural activity time-locked to an event (most often a sensory event), recorded at each of the scalp electrodes. It offers a resolution of the order of the millisecond, which makes EEG an excellent tool for studying the time course of cognitive and neural processes. As the ERP signal is directly dependent on neural activity, any significant change in the ERP signal is interpreted as a change in neural activity. A difference in strength of activity, but with identical topographies between two conditions, is typically interpreted as a change in the strength of the same underlying sources. A change in topography will be interpreted as either a change in the location of the sources or a change in the relative strengths between the sources.

Traditionally, however, the ERP signal is often reduced to a unidimensional signal, by taking one electrode or averaging the potential of a set of electrodes. The time signal is then reduced to a scalar value by averaging the potential over a predefined time window. It is this potential that is compared between experimental conditions.

The choice of electrodes and time windows is done to isolate *components*, which are defined by a latency, a location on the scalp, and a functional sensitivity. For instance, the N170 component is a negative peak that can be observed at approximately 170 ms post visual stimulation at parieto-occipital sites, and is thought to be sensitive to facial stimuli. The choice of component to study is informed by past research, and its goal is

to simplify the huge amount of information contained within the ERP signal.

The research presented in this chapter focuses on the C1 component, characterised by a broad negativity centred on the centro-parietal part of the scalp, and typically occurring between 40 and 90 ms (see 4.2.3 for details).

4.2.2 Fear-laden face processing, ERPs and attention

Emotional facial processing, and its timing in particular, have attracted a lot of interest for the past 15 years. The ERP literature on which components are sensitive to facial expressions provides a complex picture, with a wide variation in reported results, possibly due to variations of methods (different stimuli, tasks, experimental methods, analysis methods). Typically, ERP modulations by facial emotions are reported after the N170 component, up to after 1 s after stimulus onset. Only recently, earlier components such as the N170, the P1 and the C1 are considered to be potentially modulated by facial expression (see Section 4.2.3 below for a review of studies reporting the very early modulations). Some components, such as the mid-latency late positive potential or the P300, are typically associated with post-perceptual processes, and are sometimes considered to reflect an ‘increased’ processing of emotional stimuli. Similarly, the N2pc, found to be modulated by facial expression, is also associated with attentional orienting. For a detailed review of works on the effects of facial expression on the ERP and their implications for our understanding of emotional facial processing, see Vuilleumier and Pourtois (2007),

Many behavioural studies have found that emotional faces can trigger attentional processes (in particular through the dot-probe task, see Chapter 3). This has been confirmed by ERP investigations using this same paradigm, with a larger P1 component for probes presented at a cued location being found (Pourtois et al., 2004; Fox et al., 2008; Santesso et al., 2008). Additionally, fearful faces presented in bilateral stimulations were also found to generate an N2pc component, consistent with a capture of attention by fearful faces (Eimer and Kiss, 2006; Fox et al., 2008). These results are consistent with a fairly ‘automatic’ (i.e. independent from attentional resources) processing of facial expressions. The degree of this automaticity has been debated, in particular for processes occurring in the amygdala (see Vuilleumier et al., 2001; Dolan and Vuilleumier, 2003, but see Pessoa et al., 2002a,b). However, some processes linked to facial expression processing do appear to be strongly affected by attention. In particular,

orienting attention away from faces reduces (or, in some cases, extinguishes) effects of emotional faces processing. This has been found using functional neuroimaging (Vuilleumier et al., 2001; Pessoa et al., 2002a,b) and ERPs (Holmes et al., 2003; Eimer et al., 2003).

The present chapter mainly focuses on two aspects of emotional facial processing using ERP. First, whether facial expression can generate very early modulations, i.e. before 100 ms post-stimulus onset. Second, whether such a modulation is dependent on endogenous attention. A body of the literature considers very early processes to be reflexive, and these are often associated to the so-called subcortical route that would bypass the visual cortex to reach the amygdala free of attentional modulation (Morris et al., 1999). While the existence or significance of such a pathway is debated (Pessoa and Adolphs, 2010) and ERP does not enable testing of whether such a subcortical route is implicated in the processing, we propose to test the sensitivity of very early ERPs to facial expression and sustained attention by focusing on the early visual component C1.

4.2.3 Very early processing of facial expression

The C1 is considered as the first evoked potential component occurring after visual stimulation. Its properties in terms of timing, topography and sources were extensively studied and described in Jeffreys and Axford (1972a,b) and Clark et al. (1995). The C1 occurs between 40 and 100 ms post-stimulus onset with a highly subject-dependent topography and its topography is strongly dependent on the location of the stimulus (Jeffreys and Axford, 1972a,b; Clark et al., 1995; Proverbio et al., 2007; Kelly et al., 2008). These topographical characteristics were found to be in agreement with the structure of the striate cortex. The primary visual cortex lies within and around the calcarine sulcus, or fissure, on each hemisphere. The left (resp. right) visual hemifield projects to the right (resp. left) hemisphere, and the upper (resp. lower) visual hemifield projects to the ventral (resp. dorsal) side of the calcarine fissure (Holmes, 1945). Jeffreys and Axford (1972a) noted that horizontal octant stimuli in the upper and lower hemifield project to the ‘floor’ and ‘ceiling’ of the fissure respectively, generating roughly vertical dipoles of opposite orientation, and generating opposite potential polarity on the scalp. The authors found a strong agreement between this model, known as the ‘cruciform model’, and the C1 scalp distribution, indicating that the generators of the C1

lie in V1. These observations were then confirmed with further topographical analyses and source localisation techniques (Gomez Gonzalez et al., 1994; Clark et al., 1995).

Until recently, the C1 was considered to be sensitive to stimulus characteristics only and unaffected by attention, unlike the subsequent P1 and N1 components (Gomez Gonzalez et al., 1994; Clark et al., 1995; Hillyard and Anllo-Vento, 1998). However, C1 modulations by spatial attention (Proverbio et al., 2007; Kelly et al., 2008; Fu et al., 2009, 2010b) and attentional load (Fu et al., 2009; Rauss et al., 2009; Fu et al., 2010b but see Fu et al., 2010a) have recently been reported (see Rauss et al., 2011b for a detailed review).

A whole body of the literature has however focused on early processing of facial stimuli, most probably because of the idea that emotional stimuli, and in particular fear-laden stimuli, are processed early to allow for fast reaction. To our knowledge, the first paper reporting an early effect between faces was Pizzagalli et al. (1999), who reported a change of scalp topography at 80 ms between liked and disliked faces, using faces presented unilaterally. This study was followed by Eger et al. (2003) that also found early topographic differences, using dichoptic bilateral positive, negative and neutral facial stimuli. Neither study was specifically designed to generate a large C1 component, as the stimuli were presented along the horizontal midline, and the effect was found through topographical analysis. Pourtois et al. (2004) presented pairs of faces bilaterally in the upper-hemifield as cueing stimuli in a dot-probe task, and reported an increased C1 amplitude for fearful-neutral compared with happy-neutral stimuli. The C1 amplitude in the fearful-neutral condition was correlated with the P1 amplitude generated by the subsequent valid target, and could therefore be an indication of the capture of attention by the emotional face. Two attempts of replication, however, did not succeed: Eldar et al. (2010) found a larger C1 for anxious participants presented with the angry-neutral pair, compared with the non-anxious population, but found no effect between happy-neutral and angry-neutral condition, and no P1 validity effect. Similarly, Santesso et al. (2008) failed to find an early C1 effect as well. Finally, West et al. (2011) reported a modulation of C1 consistent with an increase of activity in V1 neurons retinotopically corresponding to the location of the fearful faces, following the cruciform model of V1.

These ERP studies are complemented by event-related field (ERF) studies. The early MEG response has been linked to facial processing (Itier et al., 2006; Linkenkaer-Hansen et al., 1998; Liu et al., 2002; Tanskanen et al., 2005). Halgren et al. (2000)

reported an effect of facial expression at around 100 ms post-stimulus onset. Liu and Ioannides (2010) found modulations by facial expression in the superior temporal sulcus and the right amygdala before 70 ms. Morel et al. (2009) reported an emotional effect depending on the repetition of stimuli between a first and second presentation. Few studies explored the effects of endogenous attention and facial emotional processing on very early components. Bayle and Taylor (2010) presented faces with neutral, fearful and happy facial expressions under different attentional conditions: attend-to-emotion or attend-to-identity. Interestingly, they found that early frontal activity (≈ 90 ms) was increased for fearful faces only in the attend-to-identity condition. In both attentional conditions however, fearful faces generated stronger early occipital activity. The authors suggested that these results are compatible with the existence of two early processes involved in emotional face processing: one process in the posterior regions, not modulated by attention, and the other one evident in frontal regions, that would constitute an alerting system and could be inhibited by attention. This alerting process, the authors argue, could use the hypothetical subcortical visual pathway (Morris et al., 1999), which would explain the very early onset of frontal activity.

It is to be noted, however, that a large portion of the studies reviewed here used high-pass filters with a high cut-off. Their results should therefore be considered with caution (see Chapter 5 and Appendix A).

4.2.4 The experiments

Here, three experiments aimed at better understanding the factors that modulate very early visual processing, and emotional processing in particular, are presented. Considering the conflicting findings on modulation by facial expression as well as the fact that C1 appears to be sensitive to visual attention, the hypothesis that attention is of principal importance for the observation of robust C1 modulation by facial expression was made. Additionally, the influence of C1 by non-emotional objects under different attentional conditions was investigated.

In Experiment 1, the sensitivity of the C1 component to fearful facial expression was tested by presenting a face unilaterally in the upper visual field, while the participant fixated on the fixation point and were asked to report trials in which the fixation point changes colour. To control for low-level features of the stimuli, to which the C1 is known to be sensitive, faces were also presented upside-down. The design of this

experiment was inspired by Eimer and Kiss (2006), which found an N2pc modulation by fearful faces while the task of the participants was to detect changes in luminance of the fixation cross. It was hypothesised that upright fearful faces would generate a larger C1 component, but no effect of emotion was found.

In Experiment 2, participants were asked to orient their attention to different locations of the visual field whilst still performing a task unrelated to the faces. Participants were cued to the left or right side of their upper visual field by a central arrow, after which four possible classes of stimuli could be presented: neutral faces, fearful faces, jugs and kettles. Participants had to respond to jugs (or kettles), while ignoring faces. In addition to studying the effects of spatial attention and emotional stimuli, this enabled us, in parallel, to test whether target objects could elicit C1 modulations, as has been reported only once, to our knowledge (Proverbio et al., 2007). The following hypotheses were made: (i) a larger C1 component for cued fearful faces than cued neutral faces, and possibly (ii) a larger C1 component for cued target objects than non-target objects. We did not find any result using the methods defined *a priori*. During exploratory analyses of the C1 time window, however, a stronger global field potential (GFP) was found for cued neutral faces than cued fearful faces, as well as a stronger GFP for non-target objects, independent of cueing.

Experiment 3 focused on the facial stimuli, and asked whether the neutral *versus* fearful effect would be present when the task was relevant to the faces. For this purpose, happy faces were introduced, and participants had to respond to happy faces cued to the cue only. It was hypothesised that the C1 would be larger for cued fearful faces than neutral fearful faces. Again, this hypothesis was not validated. It was however found that a significantly stronger GFP was generated for happy faces, unrelated to cueing.

4.3 Methods

4.3.1 Participants

The experiments were approved by the Psychology Department Ethical Committee at the University of Edinburgh. Participants provided written informed consent and reported right-handedness and normal or corrected-to-normal vision; they were compensated at a rate of £6/hour. Data were collected from 21 subjects for Experiment 1,

27 for Experiment 2, and 26 for Experiment 3. In both Experiments 1 and 2, one participant's data were removed because of excessive ERP artefacts. In Experiment 3, two participant's data were removed, one due to poor behavioural results, and the other due to a technical issue. The thesis is therefore reporting data from 20 participants in Experiment 1 (age range: 19–30, mean: 23, 10 female), 26 in Experiment 2 (age range: 18–50, mean: 23, 16 female), and 24 in Experiment 3 (age range: 18–33, mean: 22, 16 female). There was no significant age difference between the three groups [$F_{2,67} = 0.036$, $p = 0.96$]. Prior to the experiment, participants were asked to complete a State-Trait Anxiety Inventory (STAI) questionnaire (Spielberger et al., 1983). There was no significant difference between the state [$F_{2,67} = 1.376$, $p = 0.26$] and trait [$F_{2,67} = 2.360$, $p = 0.10$] of anxiety across the three experiments.

4.3.2 Stimuli

In Experiment 1, stimuli were displayed on a 40.5 × 30 cm ViewSonic P227f CRT monitor at a resolution of 1,280 × 1,024 pixels, with a refresh rate of 75 Hz. In Experiments 2 and 3, stimuli were displayed on a 47.5 × 29.5 cm Samsung SyncMaster LCD monitor at a resolution of 1,680 × 1,050 pixels, with a refresh rate of 100 Hz. In all experiments, the screen was placed at a viewing distance of 70 cm from the chin-rested participant. Stimuli were presented using Psychtoolbox 3 (Brainard, 1997) under Matlab (MathWorks, Inc., Natick, MA, USA).

Example stimuli are shown in Figure 4.1D. The same neutral and fearful facial stimuli used in the dot-probe experiment (Chap. 3) were used for the three experiments. The happy facial expression was taken from the same 6 male and 6 female models of the NimStim face database (Tottenham et al., 2009). All non-facial parts of the images were removed, including the shoulders, neck and hair. Non-facial stimuli consisted of 12 metal kettles and 12 glass jugs, selected from the Internet. These objects were chosen because kettles and jugs have a height to width ratio comparable to faces, can easily be discriminated from faces and from each other, and are presumably emotionally neutral. Familiar object categories, whose different instances vary between each other were preferred, but in a manner that would keep within-category perceptual variance relatively low. All stimuli were converted to grey scale, resized to the bounding box size (height: 15.3 cm; width: 11.5 cm), normalised for mean pixel value and RMS contrast, and presented on a black background. The mirror image of each stimulus was

presented an equal number of times to its original for each experimental condition.

See Figures 4.1A and 4.1B for a representation of the screens presented to the participants. Stimuli were presented in the upper visual hemifield, to elicit a reliable C1 component characterised by a widespread centro-parietal negativity (Jeffreys and Axford, 1972a,b). For this purpose, the light grey fixation point (diameter: 0.5 cm) was placed at the bottom of the screen on its vertical median. The horizontal distance of the centre of the fixation point to the inner vertical side of the stimulus bounding box was 13.75 cm, while its vertical distance to the lower horizontal edge of the stimulus bounding box was 4.3 cm. Cue arrows consisted of two perpendicular 0.5 cm long light-grey segments, placed at a distance of 0.5 cm from the fixation point, and pointed towards the upper left or upper right.

4.3.3 Procedure

Figure 4.1A summarises the procedure of Experiment 1 and Figure 4.1D provides examples of stimuli used. Experiment 1 consisted of 960 trials, divided into 5 blocks of 192 trials. Neutral and fearful faces were presented upright or upside-down (inverted condition). Faces were presented for 300 ms, and the inter-stimulus interval was randomised between 1,200 and 2,100 ms. One sixth of the trials (160) were GO trials, to which the participant had to respond by pressing the space bar of the keyboard with the index of their right-hand. In these trials, the fixation point turned red for the 300 ms during which the face was displayed. Because the detection of the target could attenuate modulations by facial expression (Eimer and Kiss, 2006), the target trials were not included in the analysis of this experiment.

Figure 4.1B summarises the procedure of Experiment 1 and Figure 4.1D provides examples of stimuli used. Experiment 2 consisted of 1,152 trials divided into 3 blocks. The stimuli consisted of facial (neutral and fearful faces) and non-facial (jugs and kettles) stimuli. Cues were presented for 200 ms and stimuli for 300 ms, separated by an interval of 750 ms. Participants were given 1,300 ms post-stimulus onset to press the button. Time between stimulus offset and cue onset of the next trial was randomised and ranged from 1,400 to 2,300 ms. Half of the stimuli were presented on the left-hand side, and half of them were cued. Cueing (cued, uncued) and stimulus presentation side (left, right) were counter-balanced for each stimulus type within each block. One eighth of the trials were therefore GO trials: half of the participants were instructed

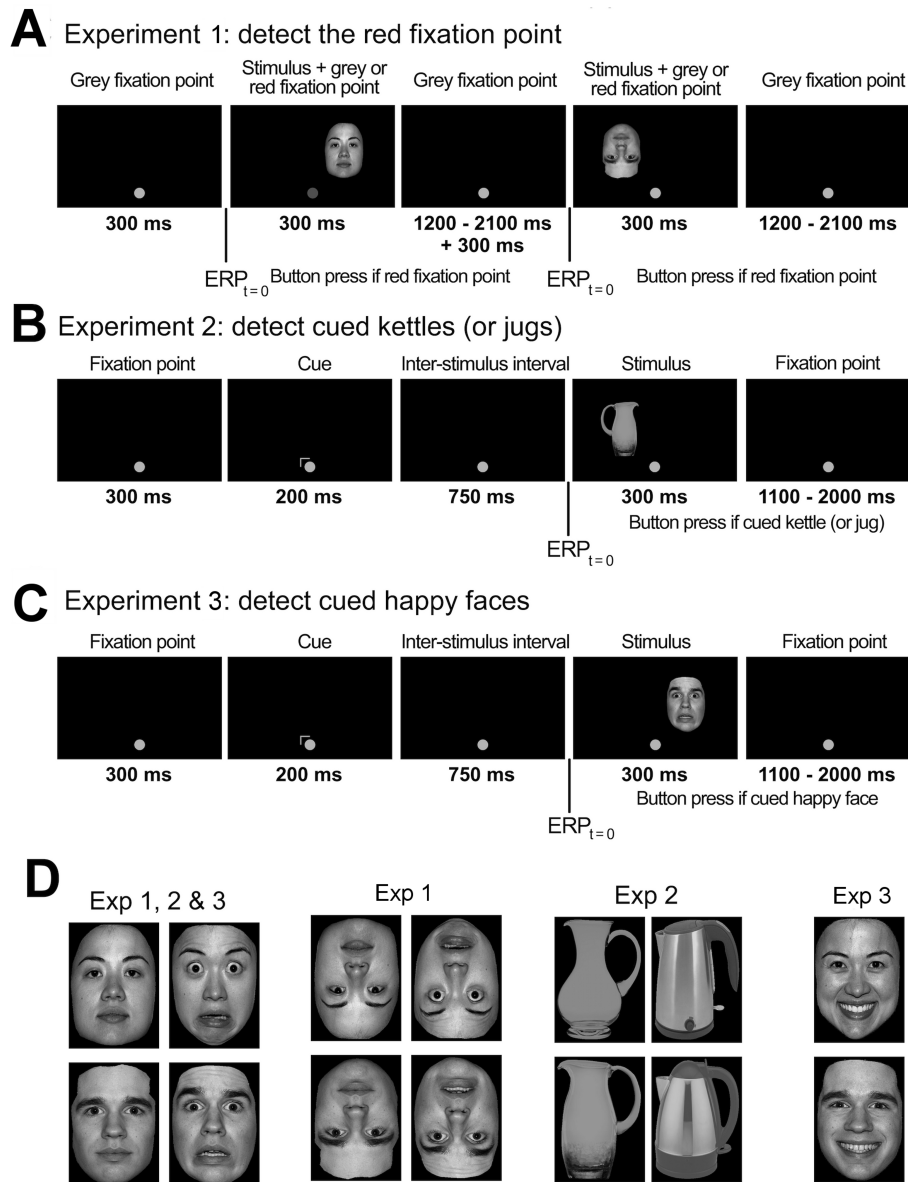


Figure 4.1: Stimuli and procedure used in the three experiments. **(A)** Two example trials of Experiment 1: a target neutral right upright trial followed by a non-target neutral left inverted trial. Neutral and fearful faces were presented upright or upside down in the left or right upper hemifield. In target trials, the grey fixation point turned red (dark grey on the figure) during facial stimulus display; participants were instructed to press a button when detecting the red fixation point. **(B)** Example trial (cued left jug trial) of Experiment 2. A cue pointing left or right appeared near the fixation point, followed by a stimulus in the upper left or right hemifield. Half of the participants were instructed to press a button when detecting a jug at the cued location, the other half was instructed to detect cued kettles. **(C)** Example trial (uncued fearful right) of Experiment 3. The task was to press a button when detecting a happy face at the cued location, while maintaining fixation on the dot. **(D)** Two examples of stimuli for each condition used in the three experiments. Experiment 1 used neutral and fearful faces, upright and inverted; Experiment 2 used neutral and fearful faces, as well as jugs and kettles; Experiment 3 used neutral, fearful and happy faces.

to press a button (space bar of the keyboard with the index of their right-hand) when detecting a jug at the cued location, and the other half when detecting a kettle at the cued location. Prior to the experiment, participants were told that the stimuli would consist of faces and objects, and that the objects consisted of kettles and jugs. The kettles and the jugs were shown to the participant prior to the experiment.

Figure 4.1C summarises the procedure of Experiment 1 and Figure 4.1D provides examples of stimuli used. Experiment 3 consisted of 1,120 trials divided into 4 blocks. Following a cue pointing left or right, neutral, fearful and happy faces were presented on the upper left or right visual field. Half of the stimuli were presented on the left-hand side, and half of them were cued. Happy faces were presented on 352 trials, while the 768 remaining trials were equally divided between neutral and fearful facial expressions. Participants were instructed to press a button (space bar of the keyboard with the index of their right-hand) when they detected a happy face at the cued location (176 trials = 11/70 of trials), while maintaining fixation on the central dot. The happy faces were shown to the participants before the experiment. The timing of each event on the screen was the same as in Experiment 2.

For Experiments 2 and 3, the cue indicated the location of the task-relevant stimulus. While participants were instructed to keep their eyes on the fixation point, the stimulus onset asynchrony between the cue and the stimulus (950 ms) provided sufficient time for participants to saccade to the cued location. To prevent such saccades, eye movements were monitored online. The eye tracker was calibrated before starting the experiment.

Participants were given a number of practice trials before any data were recorded. The experiments were paused approximately every 6 minutes to give the participant an opportunity to rest. Correct detection rate and average reaction time (RT) were given as feedback to the participant at the end of each block.

4.3.4 Data Acquisition

EEG was recorded using a BioSemi Active-Two system (BioSemi B.V., Amsterdam, Netherlands). The activity at 64 Ag-AgCl scalp electrodes following the location and label of the extended 10–20 system (Jasper, 1958), along with 4 electro-oculography (EOG) electrodes (above and below the right eye, and on the outer canthi) and 2 mas-

toid electrodes, was digitised on 24 bits with a sample rate of 1024 Hz.

Eye movements of the best calibrated eye were recorded with an Eyelink 1000 (SR Research, Ltd., Kanata, Ontario, Canada) during Experiments 2 and 3 to ensure that participants were fixating on the dot throughout the experiment. Calibration and validation were performed in the beginning of each block. Eye movements were monitored online. In a small number of trials, some participants did not keep their eyes on the fixation dot. In these cases, participants were reminded to follow the instructions and to fixate the dot. Corresponding trials were rejected offline.

4.3.5 EEG Data Pre-processing

Pre-processing was performed using the EEGLAB toolbox (Delorme and Makeig, 2004) under Matlab and custom scripts. The EEG signal was low-pass filtered using a basic finite impulse response filter with a cut-off frequency of 40 Hz. No high-pass filter was used (see Chap. 5). Data were down-sampled to 512 Hz, epoched using stimulus onset time as time origin, and referenced to the average mastoids. Artifactual epochs were removed using a semi-automatic procedure labelling epochs containing EOG data beyond 100 μV in absolute value. The data were visually inspected and epochs containing artefacts were removed. On average, 723 trials per participant remained for Experiment 1, 918 for Experiment 2, and 962 trials for Experiment 3. Finally, the data were baseline-corrected by subtracting from each electrode its average value in the 100 ms time window preceding stimulus onset. In Experiment 1, only correct NO-GO trials were analysed. In Experiments 2 and 3, only correct GO trials and correct NO-GO trials were analysed.

As some channels were sometimes noisy, channel interpolation was performed. This step was necessary for the Global Field Power (GFP) and topographical analyses (see below). Some electrodes were systematically defective for a significant duration of Experiment 3: electrodes P10 and TP8 needed fixing and were ultimately sent to BioSemi for repair. Interpolation was performed on the epoched data. Noisy electrodes were identified by visually inspecting the continuous data and the grand average for each participant, using the average reference. The interpolation algorithm used was the spherical interpolation built in EEGLAB. On average, 0.85 electrodes per participant were interpolated for Experiment 1, 2.30 for Experiment 2, and 0.75 for Experiment 3.

4.3.6 Data Analysis and Reduction

Consistent with previous reports using large stimuli located in the upper hemifield (e.g. Pourtois et al. 2004, Pourtois et al. 2008, Rauss et al. 2009), a negative deflection of the C1 was found for all three experiments, peaking at around 90 ms, and largest at centroparietal electrodes (see Fig. 4.2 left). The waveforms of Experiments 2 and 3 were morphologically different from Experiment 1 (Fig. 4.3, 4.5 and 4.7). This can be due to potentials evoked by the onset and offset of the cue, absent in Experiment 1, occurring respectively at 950 and 750 ms prior stimulus onset. This difference can also be due to the difference in attention condition between the two kinds of experiments: attention was oriented to the fixation point in Experiment 1 and to the cued visual hemifield in Experiments 2 and 3. This does not affect the results, as while the morphology of the waveforms and the topography differ, the potential evoked by the facial stimuli is still present. The C1 was immediately followed by a positive potential observed at parietal-occipital electrodes, at approximately 110 ms post-stimulus onset, consistent with the P1 component (see Fig. 4.2 right, 4.4, 4.6 and 4.8).

For statistical analysis of the C1, voltage was averaged over two electrodes on each hemisphere (CP1, P1, CP2, P2). Repeated-measures analyses of variance (ANOVAs) were performed on the amplitude of the two regions, averaged over the 50–100 ms time interval. The factors of the repeated-measures ANOVA for Experiment 1 were Emotion (Neutral, Fearful) and Orientation (Upright, Inverted). For Experiment 2, two separate ANOVAs were performed: one for the facial stimuli, with factors Emotion (Neutral, Fearful) and Cueing (Cued, Uncued), and one for the Object stimuli with factors Target Status (Target, Non-Target) and Cueing. Finally, for Experiment 3, a repeated-measures ANOVA with Emotion (Neutral, Fearful, Happy) and Cueing was performed. Significant effects were investigated by breaking down the ANOVA and by running post-hoc *t*-tests.

The P1 component was also studied, over electrodes PO7 and PO8, in the 100–130 ms time window (see the scalp distribution in Fig. 4.2). The same repeated-measures ANOVAs as for the C1 component were carried out.

Exploratory analyses were performed including the data from all electrodes, using the Global Field Power (GFP, Lehmann and Skrandies, 1980). The GFP is defined as the spatial standard deviation of the potentials from all scalp electrodes:

$$\text{GFP}_x(t) = \text{std}(x_1(t), \dots, x_n(t)) \quad (4.1)$$

with n the number of electrodes and $x_i(t)$ the potential at electrode i at time t . The GFP offers the advantage of not depending on the choice of reference. It measure the overall response strength of the ERP waveform, without providing or using information on the spatial distribution of the potential (Murray et al., 2008). For each participant, the GFP at each time point was calculated from the ERP of each condition, and then averaged, providing one value per participant per condition. The GFP values were then compared across conditions using the same statistical tools as for the electrode potentials. The GFP was studied in the C1 and P1 time windows. Only analyses of the C1 time window are reported here as the GFP in the P1 time window mirrored the results of electrodes PO7 and PO8.

Further analyses involving topographical information were also carried out. As these analyses did not alter the understanding of the data, and for clarity considerations, they are described in Appendix 4.A.

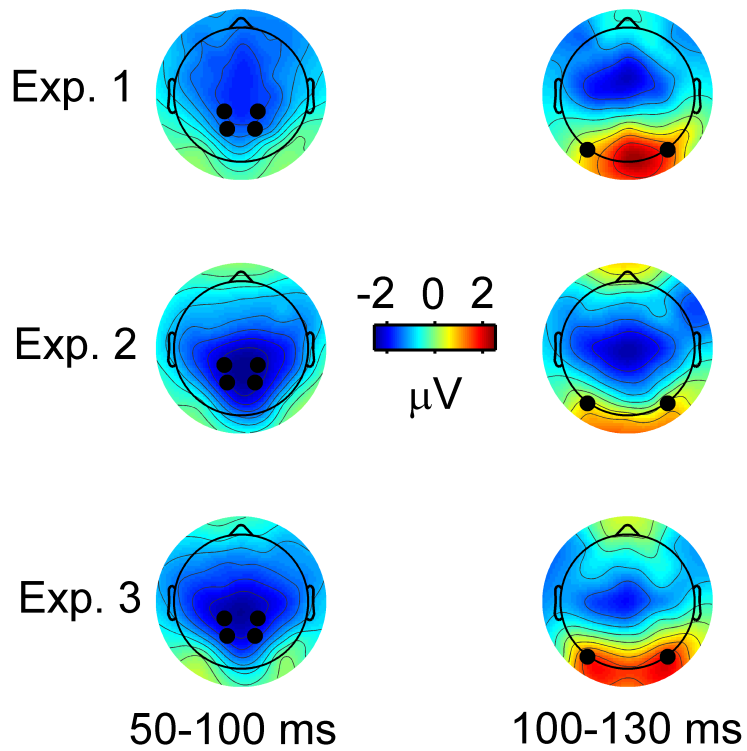


Figure 4.2: Average potential across all conditions for Experiments 1, 2 and 3, for the time intervals 50–100 ms (C1) and 100–130 ms (P1). Consistent with the literature, the C1 time window is characterised by a widespread negativity over the centro-parietal region, and the P1 time window by positive potentials in the parieto-occipital region. The location of the electrodes used for statistical analyses are indicated by the black dots (CP1, CP2, P1, P2 for the C1 time window, and PO7, PO8 for the P1).

4.4 Results

4.4.1 Experiment 1

Experiment 1 was aimed at finding C1 modulation by facial expression by presenting upright and inverted neutral and fearful faces while the participants were asked to detect a change of colour of the fixation point. A larger C1 amplitude was expected for upright fearful, compared to neutral faces.

Average correct detection rate of target trials in Experiment 1 was 99.69%, and the false alarm rate 0.06%. The average RT for correct trials was 419.0 ms. The mean RT reported exclude the correct trials with a RT beyond two standard deviations above the participant's mean.

The analysis of the mean potential at electrodes CP1, CP2, P1 and P2 in the 50–100 ms time interval did not find any significant effect. Importantly, the Emotion \times Orientation interaction was not significant ($F < 1$), and there was no main Emotion ($F < 1$) or Orientation effect ($F_{1,19} = 2.57$, $p = 0.14$, partial $\eta^2 = 0.12$).

The omnibus ANOVA on the GFP between 50 and 100 ms only led to a significant Orientation effect ($F_{1,19} = 5.54$, $p = 0.03$, partial $\eta^2 = 0.2$), reflecting a stronger GFP for Inverted, compared to Upright, faces. There was no effect of Emotion ($F_{1,19} = 3.14$, $p = 0.09$, partial $\eta^2 = 0.23$) and no significant interaction for Emotion \times Orientation ($F_{1,19} = 1.42$, $p = 0.25$, partial $\eta^2 = 0.07$).

No significant effect on the P1 amplitude (electrodes PO7 and PO8 between 100 and 130 ms) was found. In particular, the main effect of Emotion, and the interaction Emotion \times Orientation were non-significant (F s < 1).

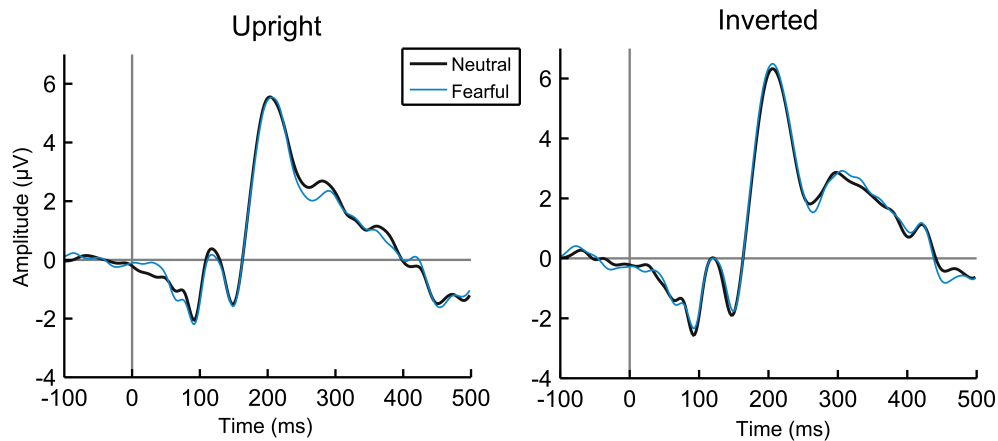


Figure 4.3: Average ERP for Experiment 1 at electrodes CP1, P1, CP2, P2, for Neutral and Fearful facial expressions presented upright (left) and upside-down (right). No significant differences in C1 were found at these electrodes.

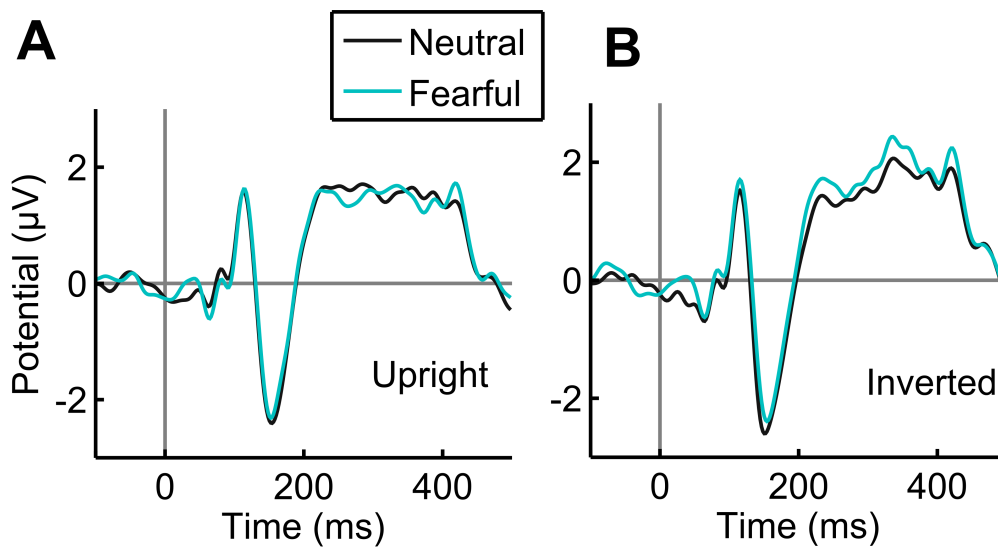


Figure 4.4: Average ERP for Experiment 1 at electrodes PO7 and PO8, for Neutral and Fearful facial expressions presented upright (A) and upside-down (B). No significant differences in P1 were found at these electrodes.

4.4.2 Experiment 2

In Experiment 2, both facial (neutral and fearful) and object stimuli were presented to the participants in a cueing paradigm. Participants were asked to press a button when the target object (kettle or jug, depending on which participant) appeared at the cued location, while ignoring the faces and fixating the fixation point. Spatial attention was thus oriented towards or away from the appearing stimuli, and the task was irrelevant to the faces. Potentials evoked by the faces were analysed separately from the ones evoked by the object stimuli.

The correct detection rate was 94.1%, and the false alarm rate was 0.5%. Mean RT of correct trials was 583.5 ms.

4.4.2.1 Faces

A larger C1 was expected for cued-fearful faces compared to cued-neutral faces. Additionally, a larger C1 and P1 for cued, compared to uncued trials, were expected.

C1 amplitude generated by the faces did not show any effect of Emotion ($F < 1$) or Cueing ($F_{1,25} = 3.08$, $p = 0.09$, partial $\eta^2 = 0.1$). Importantly, the Emotion \times Cueing interaction was non-significant ($F < 1$).

The analysis of the GFP led to a significant Emotion \times Cueing interaction: $F_{1,25} = 7.16$, $p = 0.01$, partial $\eta^2 = 0.22$. Post-hoc tests found a significantly stronger GFP for Neutral-Cued compared to Fearful-Cued faces ($t_{25} = 2.62$, $p < 8 \cdot 10^{-3}$) as well as Neutral-Cued compared to Neutral-Uncued faces ($t_{25} = 2.63$, $p < 8 \cdot 10^{-3}$). The interaction is shown on Fig. 4.9A. The direction of the effect for Cued facial stimuli was thus opposite to the one expected.

This change in GFP in the Cued condition was accompanied by a topography change (see Section 4.A.2.1), suggesting that the neural generators are, in addition to changing their strength globally, are also changing locations or relative strengths between the Neutral-Cued and Fearful-Cued conditions.

Analysis of the P1 amplitude confirmed the hypothesis on Cueing: a Cueing main effect ($F_{1,25} = 6.776$, $p = 0.02$, partial $\eta^2 = 0.21$) was found, reflecting a larger P1 for Cued, compared to Uncued trials. The Emotion effect and the Emotion \times Cueing interaction were non-significant ($F_s < 1$).

4.4.2.2 Objects

The C1 amplitude generated by the objects did not present any main effect of Target Status ($F_{1,25} = 1.93$, $p = 0.18$, partial $\eta^2 = 0.07$) or significant interaction with Target Status ($F_{1,25} < 1$).

The GFP analysis led to a significant effect of Target Status: $F_{1,25} = 8.23$, $p = 8 \cdot 10^{-3}$, partial $\eta^2 = 0.25$, reflecting a stronger GFP for Non-Target stimuli than for Target stimuli (see Fig. 4.9B). The direction of the effect was thus opposite to the one expected. There was no other significant effect. In particular, the Target Status \times Cueing interaction was non-significant ($F_{1,25} < 1$).

Again, the Cueing hypothesis on the P1 component was confirmed: a significant effect of Cueing ($F_{1,25} = 14.23$, $p = 0.001$, partial $\eta^2 = 0.36$) was found, reflecting a larger P1 amplitude for Cued trials. The effect of Target Status and the Target Status \times Cueing interaction were non-significant ($F_s < 1$).

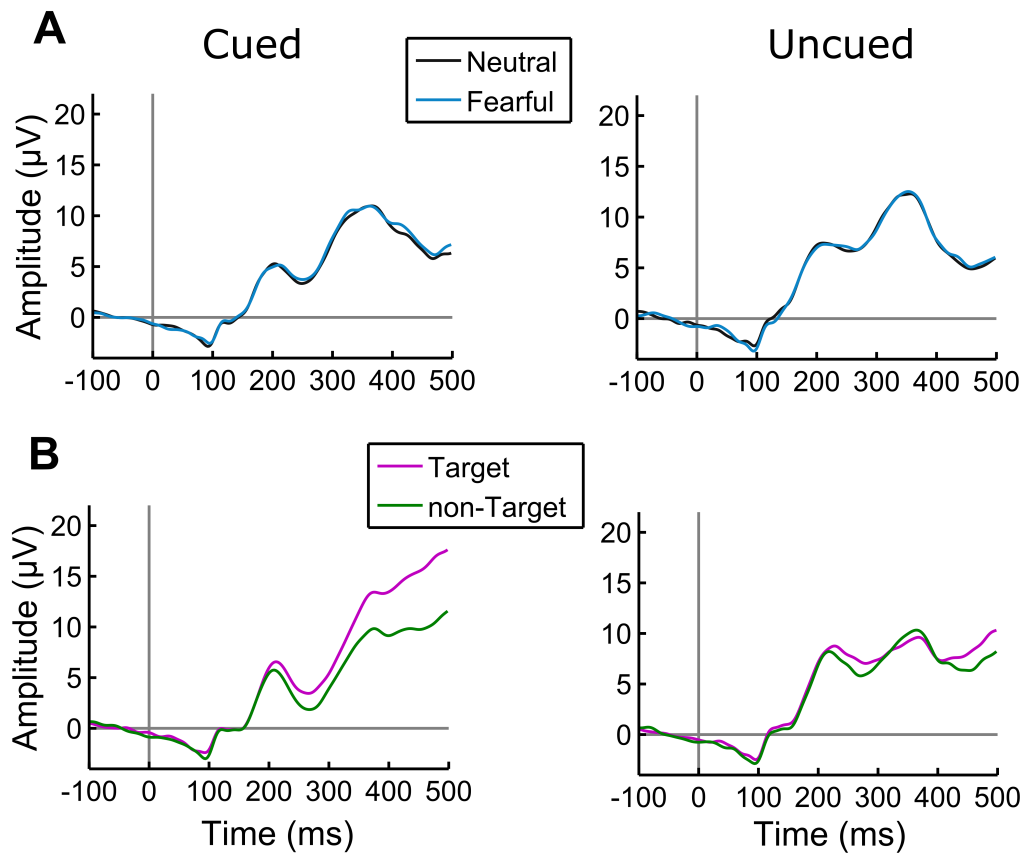


Figure 4.5: Average ERP for Experiment 2 at electrodes CP1, P1, CP2, P2, for Neutral and Fearful faces **(A)** and Target and Non-Target objects **(B)** in the Cued and Uncued conditions. No significant differences in C1 were found at these electrodes.

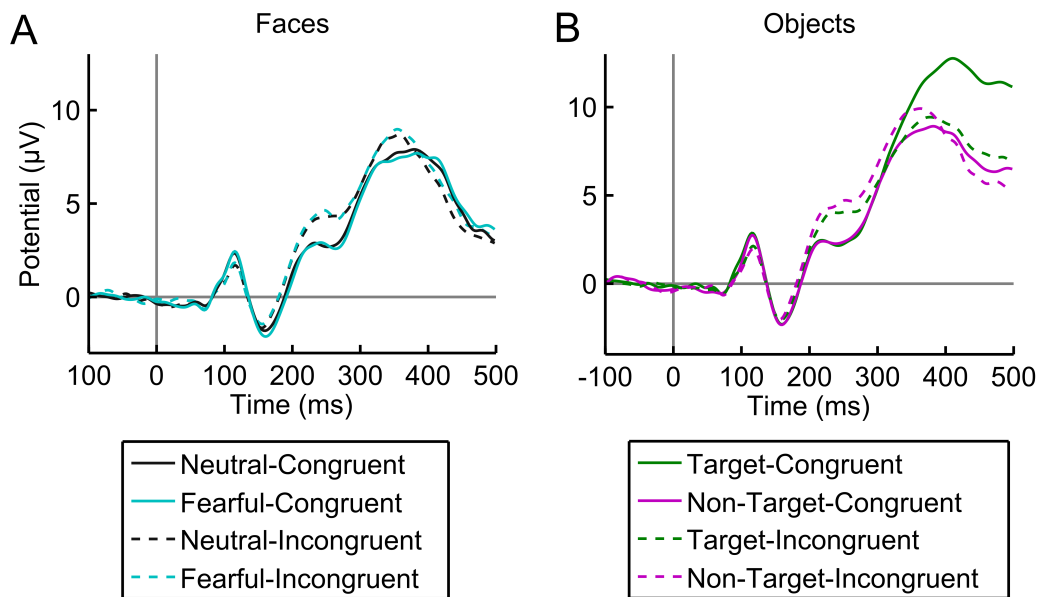


Figure 4.6: Average ERP for Experiment 2 at electrodes PO7 and PO8, for Neutral and Fearful faces (**A**) and Target and Non-Target objects (**B**) in the Cued and Uncued conditions. A significantly larger P1 was measured at these electrodes for cued trials, compared to uncued trials.

4.4.3 Experiment 3

Experiment 3 was intended to test the influence of intentional attention to facial expression on the C1 component. Neutral, Fearful and Happy faces were presented to the participants in a cueing paradigm. Participants had to press a button when detecting a Happy face at the cued location while maintaining fixation on the fixation point.

The correct detection rate was 95.4%, and the false alarm rate was 1.1%. Mean RT of correct trials was 622.5 ms.

Again, according to past literature, a larger C1 was expected for cued-fearful faces, compared to cued-neutral faces.

The C1 measured at CP1, CP2, P1 and P2 between 50 and 100 ms did not show any main effect of Emotion ($F_{2,46} = 1.19$, $p = 0.32$, partial $\eta^2 = 0.05$) or Cueing ($F < 1$). The Emotion \times Cueing interaction was non-significant ($F_{2,46} = 1.78$, $p = 0.19$, partial $\eta^2 = 0.07$).

The GFP analysis, however, led to a significant Emotion effect: $F_{2,46} = 3.57$, $p = 0.04$, partial $\eta^2 = 0.13$. This effect is characterised by a significantly stronger GFP for Happy than Neutral ($t_{23} = 2.32$, $p = 0.01$) and Fearful ($t_{23} = 1.87$, $p = 0.04$) condi-

tions. See Figure 4.9C.

The Cueing ($F_{1,23} = 1.98$, $p = 0.17$, partial $\eta^2 = 0.08$) and the Emotion \times Cueing interaction ($F_{2,46} = 2.67$, $p = 0.08$, partial $\eta^2 = 0.10$) were both non-significant.

The P1 analysis led to a significant Cueing effect ($F_{1,23} = 33.83$, $p < 0.001$, partial $\eta^2 = 0.60$). The Emotion ($F_{4,6} = 2.04$, $p = 0.14$, partial $\eta^2 = 0.08$) and the Emotion \times Cueing interaction ($F_{2,46} = 1.11$, $p = 0.34$, partial $\eta^2 = 0.05$) were non-significant.

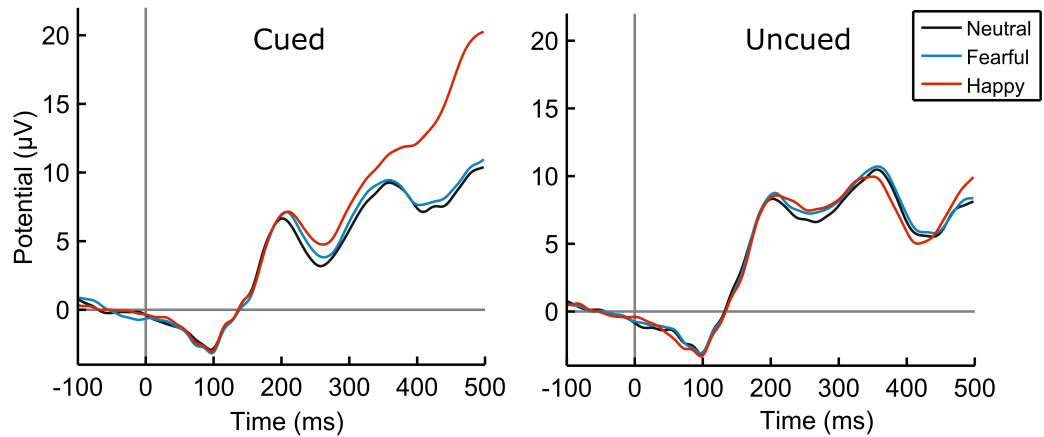


Figure 4.7: Average ERP for Experiment 3 at electrodes CP1, P1, CP2, P2, for Neutral, Fearful and Happy faces in the Cued (left) and Uncued (right) conditions. No significant differences in C1 were found at these electrodes.

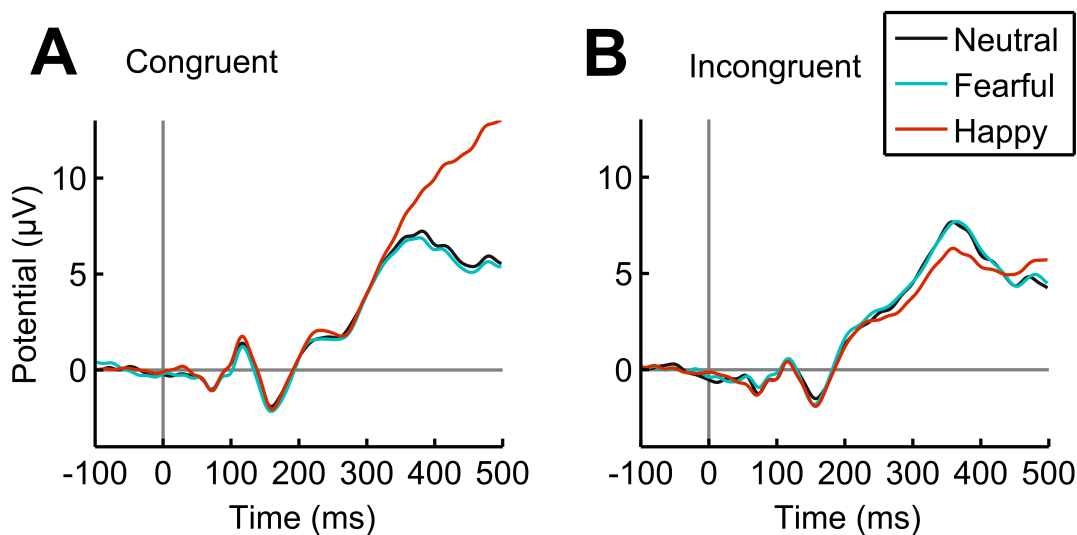


Figure 4.8: Average ERP for Experiment 3 at electrodes PO7 and PO8, for Neutral, Fearful and Happy faces in the Cued (A) and Uncued (B) conditions. A significantly larger P1 was measured at these electrodes for cued trials, compared to uncued trials.

4.4.4 Experiment 2 & 3

To investigate how reliable were the differences of pattern between Experiments 2 and 3 for Neutral and Fearful expression trials, a mixed ANOVA including the between-participant factor Experiment (Exp. 2, Exp. 3) was performed on the amplitude of the electrode subset and of GFP.

As no significant effect involving Cueing or Emotion was found on the electrode amplitude in the C1 time window, no significant interaction was expected between the two experiments. Indeed, the ANOVA did not lead to any effect or interaction involving Emotion.

As the Emotion \times Cueing patterns are different between Experiments 2 and 3 using the GFP in the C1 time window (a significant Neutral-Cued *vs* Fearful-Cued difference in Exp. 2, and no Neutral-Fearful difference in Exp. 3), one would expect a significant Experiment \times Emotion \times Cueing interaction. The ANOVA with factors Emotion, Cueing and Experiment indeed led to a significant Emotion \times Cueing \times Experiment interaction ($F_{1,48} = 9.49$, $p = 3 \cdot 10^{-3}$, partial $\eta^2 = 0.17$), indicating that the different Emotion \times Cueing patterns between Experiments 2 and 3 are reliable.

The P1 analysis only led to the Cueing effect ($F_{1,48} = 19.11$, $p < 0.001$, partial $\eta^2 = 0.29$) that was found both Experiments 2 and 3.

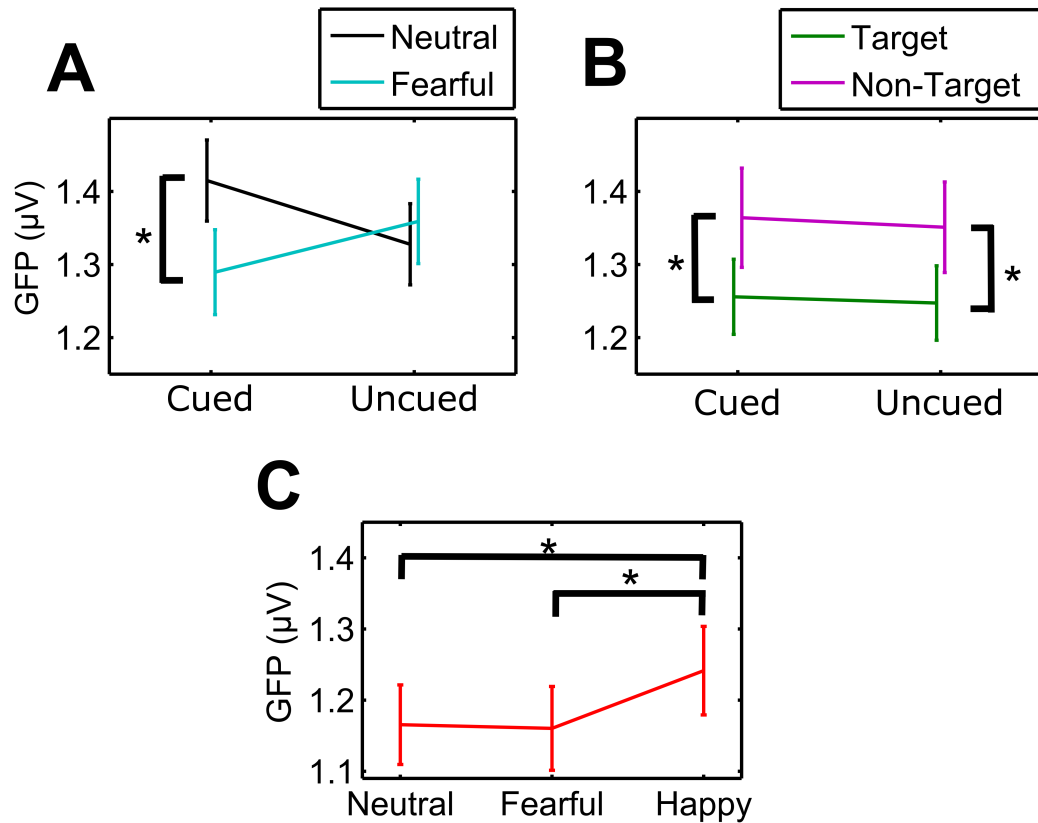


Figure 4.9: Mean \pm standard error of the GFP in the C1 time window for various conditions of Experiments 2 and 3. **(A)**: Experiment 2, facial stimuli. The Emotion \times Cueing interaction is significant. In particular, the difference between the Neutral-Cued and Fearful-Cued condition is significant. **(B)**: Experiment 2, object stimuli. Non-Target were found to have a significantly larger GFP than Target objects. **(C)**: Experiment 3. The GFP in the Happy condition was significantly stronger than for Neutral and Fearful conditions.

4.5 Discussion

After summarising the results of the three ERP experiments, the present section discusses different features of these results. First, the facial expression effect found in Experiment 2 is discussed (Section 4.5.2), followed by a discussion of its dependence on attentional conditions (Section 4.5.3). The data also suggests effects of feature recognition, discussed in Section 4.5.4.

Further discussion on the underlying neural activity responsible for the effects is performed in Section 4.5.5. The use of the GFP as an adequate measure of the C1 is considered in Section 4.5.6. Finally, the limitations of the three studies are considered in Section 4.5.7.

4.5.1 Results summary

C1 analysis of the electrode potential from the 4 electrodes did not show any significant effect. Analysis of the GFP, however, led to:

- A significant Emotion \times Cueing interaction for facial stimuli in Experiment 2, characterised by a significantly stronger GFP for the Neutral than the Fearful condition when spatially attended;
- A significantly stronger GFP for Non-Target object stimuli compared to Target ones. This effect was independent from Cueing;
- A significant Emotion effect in Experiment 3, characterised by a significantly stronger GFP for Happy compared to Neutral and Fearful faces. This effect was independent from Cueing.

No Emotion or Target Status effect was found on the P1 component. However, a very reliable Cueing effect was found in Experiments 2 and 3, with a larger P1 amplitude for Cued trials.

4.5.2 Early modulation by facial expression

The results of the experiments suggest that fearful faces can indeed elicit a C1 modulation, but that the attentional conditions are crucial to observe it. An effect was found

only when the task given to the participants was *not* related to the expression of the faces and when spatial attention was directed at the location of the faces.

As reviewed in Section 4.2.3, early modulations were reported in the literature. The results of Experiment 2 are therefore to be added to the list of studies finding very early effects of facial expression.

The direction of the effect, was, however, surprising. A stronger GFP was found for Neutral compared to Fearful faces. Previous reports typically found larger C1 amplitudes for emotional stimuli (Pourtois et al., 2004; Eldar et al., 2010; Stolarova et al., 2006). The results from West et al. (2011) are consistent with a larger C1 for fearful faces presented in the upper-hemifield. However, none of these studies used the GFP as a dependent variable. Indeed, an increase of GFP is not equivalent to an increase of electrode amplitude when a topographic change occurs.

4.5.3 Interactions with attention

The emotional effect described above appears to depend both on cueing and the nature of the task.

4.5.3.1 Effects of cueing on facial stimulus processing

Experiments 2 and 3 found a very reliable main Cueing effect in the P1, but not in the C1, time range. This result is highly consistent with a large portion of the literature, reporting an absence of modulation by spatial attention in the C1 time range, and a larger P1 for spatially attended stimuli (see e.g. Hillyard et al., 1998 for a review). Only recently, effects of spatial attention have been reported in the C1 range (Kelly et al., 2008; Proverbio et al., 2007; Poghosyan and Ioannides, 2008). The newly found C1 sensitivity may be explained by differences in methodology. Between-participant variability in C1 topography was taken into account in Kelly et al. (2008) and Proverbio et al. (2007). Poghosyan and Ioannides (2008) used a source estimation procedure, fixing the location of the dipoles and avoiding the averaging of the signal over a long time window.

While no simple cueing effect was found in the C1 time window, Experiment 2 found a Cueing \times Emotion interaction, showing an emotion effect only for cued stimuli. This

is in line with previous research, finding that ERP modulations by facial expression, typically occurring after 100 ms, are abolished if stimuli are outside the spatial focus of spatial attention (Eimer et al., 2003; Holmes et al., 2003). Similarly, modulation of activity by emotional stimuli in visual cortices, including V1, was also found to be reduced by the absence of attention (Vuilleumier et al., 2001; Pessoa et al., 2002b). The present data extend these results, suggesting that the effects of attention on emotional processing can occur already on the C1 timescale, i.e. within 100 ms.

From the previous lack of evidence for C1 modulation by attention and the assumption that C1 indexes early V1 activity, it has been suggested that attention modulation in V1 is caused by slow, delayed re-entrant feedback from higher areas (Martínez et al., 1999; Noesselt et al., 2002; Di Russo et al., 2003; Hillyard and Anllo-Vento, 1998). Also, in some monkey studies, attentional modulation in lower visual cortices appears to occur late (Buffalo et al., 2010). However, recent results, including the ones presented here, suggest that under some circumstances attention acts much faster and modulates C1 (Khoe et al., 2005; Wu et al., 2005; Kelly et al., 2008; Fuller et al., 2009; Rauss et al., 2009; Fu et al., 2010a). This very early modulation by attention is in line with monkey research in which attentional modulation was observed as early as 19 ms post-stimulus onset in the thalamic reticular nucleus and after 26 ms in the lateral geniculate nucleus (McAlonan et al., 2008), suggesting that visual information can be modulated subcortically even before reaching the visual cortex. In V1 simple cells, activity was observed to be modulated 30 ms after visual input (McAdams and Clay Reid, 2005), while in V4 attentional modulation was observed in monkeys from 60 ms (Luck et al., 1997), i.e. within 50–100 ms C1 time window defined. Finally, reports of pre-stimulus baseline activity modulation in monkey and humans (Luck et al., 1997; Kastner et al., 1999) suggest that modulation by attention may occur even before stimulus presentation. This is possible because, as in most endogenous attention experiments, the cue provides attentional information long before the stimulus arrives.

4.5.3.2 Effect of the task on facial stimulus processing

Additionally to this spatial cueing effect, no Neutral-Fearful difference was found in Experiment 3, where the task involved the discrimination of emotions. The task given to the participants in Experiment 2 did not involve the facial expressions, as only the kettles and jugs had to be detected.

The large majority of studies looking at very early facial expression effects involved tasks in which the facial expression was irrelevant ('implicit' emotion processing). For instance, in Pourtois et al. (2004), participants focused on the orientation of bars presented subsequently. In West et al. (2011), participants were given a colour-matching task, and in Morel et al. (2009), participants had to detect direct stimulus repetitions.

Bayle and Taylor (2010) noted that studies using a task involving implicit emotion processing reported modulation by facial expression before 130 ms (citing Eger et al., 2003; Eimer et al., 2003; Halgren et al., 2000; Holmes et al., 2003; Kawasaki et al., 2001; Pizzagalli et al., 1999; Streit et al., 2003), while those using an explicit emotion processing reported modulation after 250 ms (citing Krolak-Salmon et al., 2001, 2003). However, in Eimer et al. (2003), where an emotion discrimination task was used, modulations by emotion were observed before 250 ms but after 150 ms (the first modulation reported lay in the 160–215 ms time window).

In contrast to the studies cited above, Bayle and Taylor (2010) tested the influence of the task on very early facial expression effects. In one condition, participants had to attend to the identity of the faces, and in the other, to their facial expression. Using a source localisation method, the authors report that in both attentional conditions, fearful expressions generated stronger occipital activity than the neutral faces. Additionally, they report stronger frontal activity for fearful faces in the attend-to-identity condition only. The authors argue that two early pathways may involve emotional face processing, one posterior and independent of attention, and one anterior pathway, active only for incidental processing for alerting purposes. An alternative interpretation, mentioned by the authors but little developed, is that this frontal activity reflects higher processes that inhibit facilitated responses to fear in order to perform the attend-to-identity task. The exact active region reported by Bayle and Taylor (2010) is Brodmann Area 46, part of the middle frontal gyrus of the dorsolateral prefrontal cortex (DLPC, Rajkowska and Goldman-Rakic, 1995). The DLPC projects to the amygdala (although weakly) and the superior colliculus (Selemon and Goldman-Rakic, 1988), two structures involved in the putative 'low road' for fast emotional stimulus processing (Morris et al., 1999). Functionally, it has been found to be linked to emotion regulation (Banks et al., 2007), as well as self-control in decision making using appetitive stimuli (Hare et al., 2009). These results are compatible with the hypothesis of an inhibitory role of the DLPC on reflexive fear processing.

Fairly consistent with the results reported in Bayle and Taylor (2010), a difference in

topography between neutral and fearful faces was present in the cued faces of Experiment 2 (see Appendix 4.A). However, no Neutral-Fearful GFP effect was found in Experiment 3, as would be expected by increased occipital activity reported in Bayle and Taylor (2010). As very little data on very early effects of facial expression and attention has been reported, more research is necessary to validate the conclusions of the present experiments.

It should be noted that subsequent modulations by facial expression are not inhibited by a task explicitly related to emotion processing. Eimer et al. (2003) found modulations from 180 ms using an emotion discrimination task. When spatial attention was oriented away from the faces, all the emotion effects disappeared. It is thus possible that very early processes behave in a different manner, in particular that they may trigger attentional processes, as was suggested in Pourtois et al. (2004). Further investigation of the data, looking concurrently at early and later modulations, should be carried out (see Section 4.6.1).

4.5.4 Target detection effect

In addition to the Neutral-Fearful effect, a Target effect was also found in Experiment 2. Also, Happy facial expressions generated a stronger GFP than Neutral and Fearful faces in Experiment 3. Previous research does not provide any evidence for happy facial expression effects on the C1 (Pourtois et al., 2004; Santesso et al., 2008; Eldar et al., 2010). As the Happy face and the Target are confounded in Experiment 3, it is reasonable to think that the effect is either due to physical features of the Happy faces, or to the fact that they constitute the target category. Experiment 2, however, provides stronger evidence that the Target Status may be at play in Experiment 3, as a difference in GFP was found between Target and Non-Target objects, while the physical features of the objects were controlled for by counter-balancing the nature of the target across participants (but see potential limitations in Section 4.5.7).

A target effect would mean that stimulus categorisation, or categorisation of their features, occurs within the C1 time window. Object categorisation is typically thought to occur from 150 ms post-stimulus onset (VanRullen and Thorpe, 2001). It should be noted however that the natural stimuli used in these experiments were much more complex and variable.

Given the low perceptual variance of the stimuli, object recognition may here be assimilated to feature recognition (as objects of the same category share similar features), which is presumably faster. Thus, the change in task between Experiments 2 and 3 may be understood as a change in feature-based attention. From this perspective, the present results appear compatible with Zhang and Luck (2008), where feature-based attention was associated with ERP modulations in the C1 time window. Furthermore, modulations of activity in V1 by feature-based attention were also reported (Saenz et al., 2002). Together, these results suggest that visual features are processed and selected in the very early stages of visual processing.

An interesting feature of the Target effects of Experiment 2 and the Happy effect of Experiment 3 is that it does not appear to depend on Cueing. This is in agreement with the characteristics of feature-based attention which was found, from single-cell recordings in monkey (most particularly in areas V4 and MT), to modulate the activity of neurons across the whole visual field, even for the neurons whose receptive field lay in spatially irrelevant locations (McAdams and Maunsell, 2000; Saenz et al., 2002; Hayden and Gallant, 2009). Feature-based and spatial attention are thus considered two processes of independent origins, according to the ‘feature similarity gain model’ of attention (Treue and Martinez Trujillo, 1999). Interestingly, the P1 time window was only sensitive to Cueing, and not to Target Status, which is in agreement with this view of independent processes. However, Hayden and Gallant (2009) reported a small interaction term between feature-based and spatial attention, which was not detected in the present data.

4.5.5 Underlying neural activity

Early research on C1 has suggested that this component indexes striate cortex activity (Jeffreys and Axford, 1972a; Clark et al., 1995). This view is often echoed in contemporary research, sometimes with the idea that C1 reflects the initial volley of sensory afferents in V1 (see e.g. Stolarova et al., 2006; Kelly et al., 2008; Pourtois et al., 2008; Rauss et al., 2009; Jacoby et al., 2011; West et al., 2011). However, it should be noted that Jeffreys and Axford (1972a) distinguished two components before the P1: C1 (latency 65–80 ms) and C2 (latency 90–110 ms). It was noted in Jeffreys and Axford (1972a) and Jeffreys and Axford (1972b) that the features of the C2 distribution, unlike the C1, are not compatible with a striate source. Many reports, including ours,

although only mentioning the C1 component, also include the later C2 component, and therefore extrastriate activity in the time window.

Additionally, using highly constrained source modelling and EEG/MEG, Hagler et al. (2009) and Ales et al. (2010a) found that the onset latencies of areas V1, V2 and V3 differ only slightly. Poghosyan and Ioannides (2007) reported areas V4, V5 and MT+ activity to onset before 80 ms. Monkey electrophysiology found that the earliest response of many extrastriate areas occurs before 65 ms in the macaque, including MT (≤ 40 ms), V3, MST/FST, SMA, FEF (≤ 50 ms), TE3, V2, V4, 7ip, TEm/TEa, TAa/TPO, 8a, PreFR, SEF, PreM (≤ 65 ms) (Lamme and Roelfsema, 2000). Even considering the shorter activation latencies for monkeys (approximately 3:5 ratio compared to humans, see Kelly et al. 2012), the activation profile in the monkey before 65 ms provides a good indication that the ERP between 50 and 100 ms does not solely reflect activity in V1.

There is, for now, little experimental evidence for high-order processes such as object recognition occurring within the first 100 ms after stimulus onset. The activation profile of the visual cortex is however not incompatible with such high-order processes taking place in this time window, as areas such as V4, involved in object recognition, are activated before 100 ms.

4.5.6 Electrode amplitude versus GFP

The C1 measured at a subset of four electrodes (CP1, P1, CP2, P2) failed to find any significant effect. Therefore none of the *a priori* hypotheses were validated. These electrode sites were chosen in a semi data-driven manner, taking into account both the literature and the spatial distribution of the C1 in the grand-average. As reported before, the C1 component shows large topographical between-participant variability (Jeffreys and Axford, 1972a; Clark et al., 1995; Kelly et al., 2008), which may reduce the effectiveness of choosing electrodes at fixed scalp locations across participants and may explain why no effect could be found using the electrode subset.

Kelly et al. (2008) developed a method to take into account between-participant topographical changes. A preliminary mapping experiment is carried out in order to find the stimulus locations and the electrode site generating the largest C1. Once the mapping is performed, the actual experiment is run with the determined stimulus locations

and the data analysed using the electrodes determined *a priori*. Despite its advantages, this method leaves a lot of room to the experimenter (8 possible stimulus locations and 164 electrode locations in that case), and therefore for arbitrariness. This may reduce the replicability of the results.

The GFP may be a more suitable way to study the C1. The GFP, a measure independent from the reference, uses the information from all electrodes, and measures how “strong” in amplitude a map is, regardless of its topography. This may explain why the GFP found effects as opposed to the subset of electrodes. A method using a stimulus location mapping method, but using the GFP as a dependent variable, may be as effective as the one used in (Kelly et al., 2008), while reducing potential arbitrariness or subjectivity from the experimenter.

4.5.7 Limitations

To inspect the time course of the GFP effects reported, the paired differences in the GFP, and their statistical significance using a paired *t*-test, were plotted as a function of time (see Fig. 4.10). The emotion effect of Experiment 2 (Fig. 4.10A, left) and the Happy effect of Experiment 3 (Fig. 4.10B) appear to be statistically significant at fairly well-defined intervals after 50 ms and with little significant fluctuations before and directly after stimulus presentations. The Target effect of Experiment 2 (Fig. 4.10A, right), while still showing significance at a well-defined interval between 70 and 100 ms post-stimulus onset, shows significant fluctuations for prolonged periods of time before stimulus presentation. The Target effect found in Experiment 2, though statistically robust, may be due to fluctuations, as there is no clear departure from baseline in Figure 4.10A right. Furthermore, the Happy effect found in Experiment 3 may be due to a pure low-level effect independent of the task, as Experiment 1 did not test the sensitivity of the C1 for happy faces. Although in agreement with Bayle and Taylor (2010), the possible confound in Experiment 3 paired to a possible false positive in Target effect in Experiment 2 makes it necessary to consider the Target effect very cautiously. More data would be necessary to conclude more definitely on this particular issue.

As is common in ERP studies, stimuli with low within-category variance were used and presented repeatedly to reduce EEG inter-trial variability and increase statistical power. It cannot be ruled out that this could have caused adaptation to the task and stimuli, and

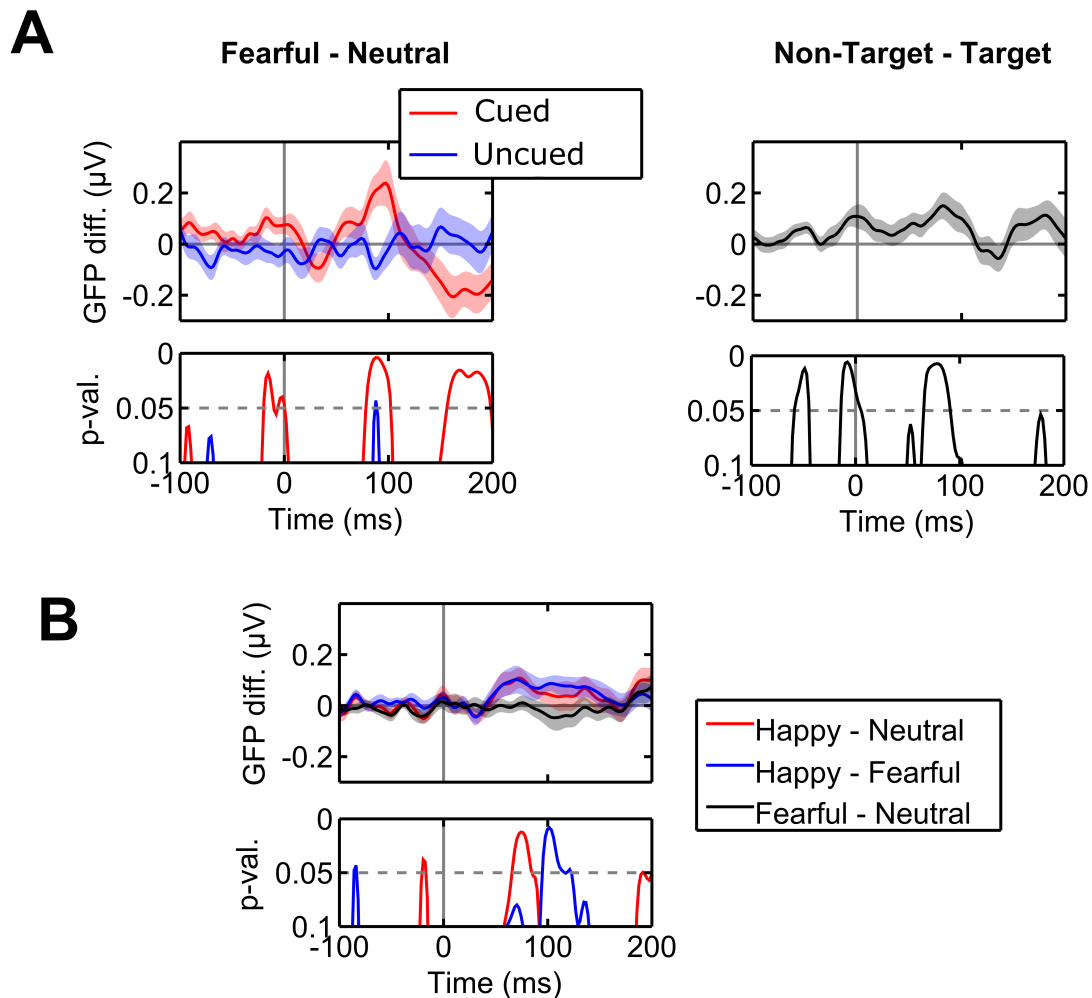


Figure 4.10: Mean \pm standard error of pairwise GFP differences from -100 to 200 ms, and associated p -values. **(A)**: Experiment 2: differences between the Fearful and Neutral conditions (left), and Non-Target and Target conditions (right). **(B)**: Differences between the emotional and neutral faces.

potentially learning. Stimulus categorisation could have been speeded up, by “tuning” lower areas to respond to target stimuli in a specific manner measurable in the C1 time window through spatial attention and perceptual learning. Such an interpretation is supported by reports of C1 modulation by perceptual learning (Pourtois et al., 2008), very early effect of implicit learning (Chaumon et al., 2008) and very early interaction between facial stimulus repetition and facial stimulus expression (Morel et al., 2009). However, it was also found that extensive training on a set of photographs to categorise did not decrease the processing time of the stimuli (Fabre-Thorpe et al., 2001).

Additionally, while tasks differed between Experiments 2 and 3, the context of the stimuli was also a difference between these two experiments. Experiment 2 contained

both faces and objects in equal proportions, while Experiment 3 only contained faces. Additionally, 1/8 trials were Target-cued trials (i.e. GO trials) in Experiment 2, while 1/6 were Happy-cued in Experiment 3. Morel et al. (2009) reported very early contextual effect with facial stimuli of different expressions, showing that this may be an important factor. The effect of the frequency of GO trials in odd-ball paradigms is well known, though typically appearing at later latencies (see e.g. Gonsalvez and Polich, 2002).

Finally, no effect was found using standard electrode potentials, and the present results largely rely on the GFP, which is not a standard measure. While the finding that the GFP may be a more sensitive measure than the individual electrodes to study the C1 is potentially important (see Section 4.5.6), it also constitutes a limitation as comparison with past research is indirect.

4.6 Conclusion

This set of experiments did not manage to replicate past C1 effects reported in the literature. In particular, using the average amplitude on a subset of electrodes, no larger C1 component was found for emotional stimuli, as reported in Pourtois et al. (2004), Stolarova et al. (2006) and West et al. (2011).

Consistent with earlier research on endogenous attention (Hillyard and Anllo-Vento, 1998), no cueing effect was found in the C1 time window, but a very reliable P1 cueing effect was measured.

After exploratory data analysis, it was found that the GFP may be a more sensitive measure to find C1 modulations than choosing electrodes at fixed locations, as the C1 topography exhibits between-subject variability that may reduce the sensitivity of classical approaches (Kelly et al., 2008; Proverbio et al., 2007).

Using this measure, a statistically reliable Neutral-Fearful effect was found, but was only present when the facial expression was task-irrelevant and the faces were spatially attended. This may be an indication that early reflexive processes detecting fear are triggered only when the facial expression is processed incidentally or that processes are triggered to inhibit reflexive fear processing to perform the emotion-irrelevant task (see also Bayle and Taylor, 2010). The present results suggest that the fearful-neutral modulation is absent when the facial stimuli are not attended spatially, which is in line

with past research on emotional stimuli looking at later processes (Eimer and Holmes, 2007; Pessoa et al., 2002b).

Finally, the experiments provide some evidence for a Target recognition effect. In Experiment 3, the (target) Happy face was associated with a stronger GFP than the Neutral and Fearful faces. In Experiment 2, Target objects had a weaker GFP than Non-Target objects. These two effects were both independent from Cueing, which is compatible with the fact that feature-based attentional modulation affects neurones across the whole visual field (Hayden and Gallant, 2009). Therefore, these results may be an indication of very early feature or object recognition.

It should be stressed that the use of the GFP as an independent variable was *post-hoc*, i.e. performed after failure to find an effect using the subset of electrodes. Furthermore, the studies show some limitations that make the interpretation of parts of the results provisional. In particular, the Happy effect of Experiment 3 could be due to physical features of the happy stimuli, while the time course of the Target-Non-Target GFP difference shows significant fluctuations before stimulus onset. The results should therefore be considered as exploratory, and further work would be necessary to validate them.

4.6.1 Extension of the studies

Further work on these data should focus on exploring the subsequent components, and look for correlations between them and the C1.

Given the limitations of this set of experiments, further tests should be conducted to replicate the effects on the one hand, and to remove the ambiguity of interpretation of the results on the other hand.

First, an extension of Experiment 2 could be conducted, with Neutral and Fearful faces as targets (counter-balanced between participants). According to the results of Experiment 3, the Neutral-Fearful effect should vanish, as the facial expression will be task-relevant. However, a Target effect should be expected. Additionally, a control experiment similar to Experiment 1 should be conducted, using the stimuli used in Experiment 3 (i.e. including Happy faces) to ensure that the Happy facial effect is not perceptual.

Appendix 4.A Topographical analyses

Topographical analyses were also carried out to explore the data. As the results little alter the interpretations arising from the GFP analysis, they are provided in the current Appendix.

Topographical analyses were performed using some of the methods described in Murray et al. (2008). Map clustering, micro-state segmentation of the ERPs and map fitting were performed in order to assess topographical changes in the 50–100 ms time interval across conditions. Clustering and segmentation were performed on the 0–400ms segment of the ERPs. For Experiments 1 and 3, all conditions were subjected to the clustering together (outputting a common set of maps between conditions). For Experiment 2, clustering for the facial and object conditions were performed separately. This was chosen to limit the computational complexity of the calculations, and to provide more easily interpretable results. The clustering and segmentation were performed using the “Topographic Atomise & Agglomerate Hierarchical Clustering” algorithm, implemented in CarTool 3.51 *. The algorithm takes as an input the maps for each participant, condition and time point. It groups the maps that look similar into clusters and outputs a limited amount of map templates. The optimal number of clusters was determined using the Cross Validation (CV) measure, a modified version of the predictive residual variance, which should be minimal. In practice, a compromise had to be found between the CV value and the number of clusters. The number of clusters with minimal CV were taken for Experiments 1 and 3. For Experiment 2, because the minimum CV was reached for too high a number of templates, a local minimum and a minimum of the derivative of CV as a function of number of clusters were chosen. The temporal information is then taken into account for the segmentation step. When portions of the ERP at distinct time windows are labeled to a same map template, it is split into distinct segments. Very short segments (less than 3 time points) are also removed. After this procedure, the 400 ms long time window contained 11 distinct labels for Experiment 1, 9 for the faces and 11 for the objects in Experiment 2, and 12 for Experiment 3. Finally, to assess the topography between different conditions in the 50–100 ms interval, the templates of the segments intersecting with this interval (three maps for each group of conditions in the present case, shown on Fig. 4.11) were

*The Cartool software (brainmapping.unige.ch/cartool) has been programmed by Denis Brunet, from the Functional Brain Mapping Laboratory, Geneva, Switzerland, and is supported by the Center for Biomedical Imaging (CIBM) of Geneva and Lausanne.

“fitted” to the maps of the segment for each condition and participant, using the Global Explained Variance (GEV). The GEV can be understood as the mean of spatial correlations across time, weighted by the GFP at every time frame (see Eq. 4.2). As stronger maps have a more reliable topography, a stronger weight is given to time frames with a stronger GFP in the GEV. For a constant GFP across time, the GEV is equivalent to the mean spatial correlation. The GEV is defined as:

$$\text{GEV}_{\mathbf{U},\mathbf{T}} = \frac{\sum_{t=t_1}^{t_n} (\text{GFP}_{\mathbf{U}}(t) \cdot C_{\mathbf{U}(t),\mathbf{T}})^2}{\sum_{t=t_1}^{t_n} \text{GFP}_{\mathbf{U}}^2(t)} \quad (4.2)$$

$$C_{\mathbf{U}(t),\mathbf{T}} = \frac{\sum_{k=1}^{n_{\text{chan}}} U_k(t) \cdot T_k}{\sqrt{\sum_{k=1}^{n_{\text{chan}}} U_k^2(t)} \cdot \sqrt{\sum_{k=1}^{n_{\text{chan}}} T_k^2}}$$

with $t_1 = 50$ ms, $t_n = 100$ ms, $\Delta t = 3.9$ ms, $\mathbf{U}(t) = (U_k(t))_{k=1..n_{\text{chan}}}$ the array of potentials measured at the n_{chan} locations at time frame t for the condition and participant considered, and $\mathbf{T}(t) = (T_k(t))_{k=1..n_{\text{chan}}}$ the map template considered. $\text{GFP}_{\mathbf{U}}(t)$ is the GFP of $\mathbf{U}(t)$ and $C_{\mathbf{U}(t),\mathbf{T}}$ is the spatial correlation (equivalent to the Pearson cross-correlation coefficient) between $\mathbf{U}(t)$ and \mathbf{T} . This “fitting” step was implemented in Matlab.

ANOVAs were then carried out, adding Map as a factor to test how well each map explains the data in the interval. Because of strong violations of the normality assumptions by the ANOVA, a permutation method was also used to calculate the p -value associated with the F value (see e.g. Anderson and Ter Braak, 2003). This procedure involved generating 2,000 iterations of the ANOVA, randomising the condition label of the GEV values within each participant. The p -value calculated from the randomisation is indicated by p_r , while the p value calculated directly from the F distribution is indicated by p . Significant interactions including the factor Map are interpreted as an indication that the topography differs across conditions, as the global variance explained by templates significantly differs across conditions.

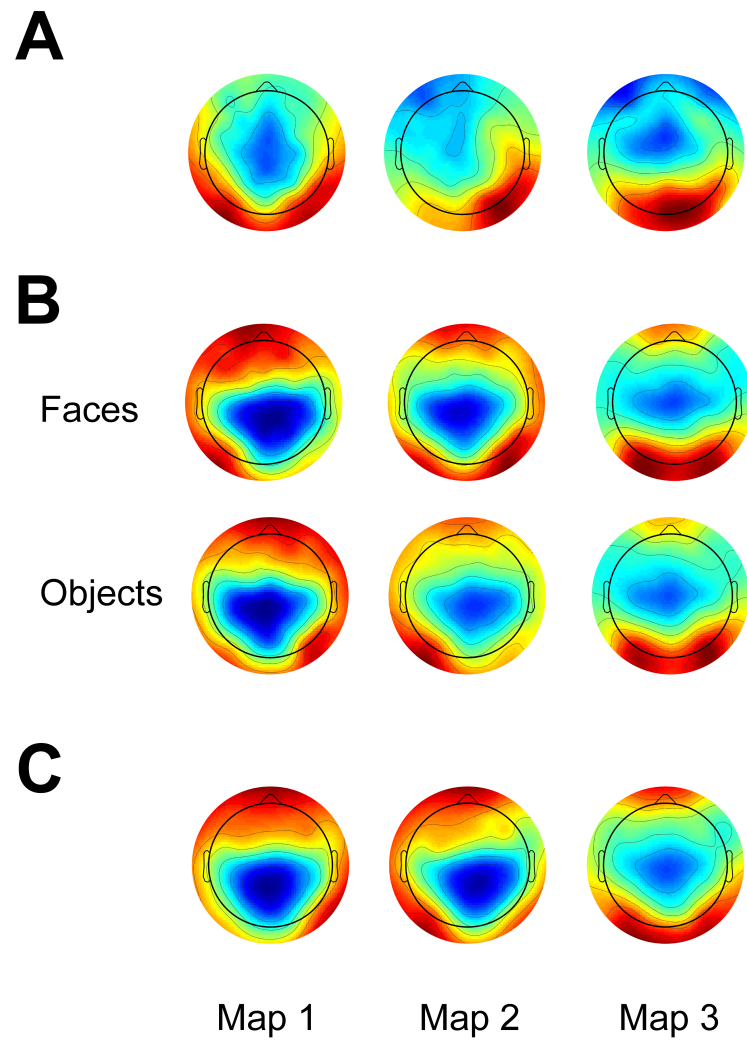


Figure 4.11: Templates of the three segments intersecting with the C1 interval 50–100 ms for Experiment 1 (**A**), Experiment 2 (**B**) and Experiment 3 (**C**). The average reference is used, and the GFP of each map is normalised. The label (Map 1, 2, 3) corresponds to the levels used in the “fitting” and the ANOVA.

4.A.1 Experiment 1

An ANOVA was performed on the GEV explained by each of the maps shown on Figure 4.11A. The factors were Emotion, Orientation, Side, Map (Map 1, Map 2, Map 3). For clarity purposes, only significant interactions involving Map and Emotion are reported.

There was a significant Emotion \times Side \times Map interaction ($F_{2,36} = 3.37$, $p = 0.046$, partial $\eta^2 = 0.16$, $p_r = 0.05$), shown on Figure 4.12. Further tests using only two maps found that the interaction was only present with Maps 1 and 3 ($F_{1,18} = 5.22$, $p = 0.035$, partial $\eta^2 = 0.23$, $p_r = 0.035$). Running two ANOVAs with Emotion and Side as factors, with Map fixed (at the values Map 1 and Map 3), it was found that while Maps 1 and 3 were both better at explaining Left than Right stimulus presentations ($F_{1,18} = 9.872$, $p = 6 \cdot 10^{-3}$, partial $\eta^2 = 0.35$, $p_r = 6 \cdot 10^{-3}$ for Map 1, and $F_{1,18} = 7.204$, $p = 0.016$, partial $\eta^2 = 0.29$, $p_r = 0.016$ for Map 3), only Map 3 generated a Side \times Emotion interaction ($F_{1,18} = 5.31$, $p = 0.03$, partial $\eta^2 = 0.23$, $p_r = 0.04$). The GEV by Map 3 was significantly larger for Fearful-Right than Neutral-Right participants ($F_{1,18} = 8.1$, $p = 0.01$, partial $\eta^2 = 0.31$, $p_r = 0.01$).

This Emotion \times Side \times Map interaction was not dependent on the orientation of the facial stimuli, as the Emotion \times Orientation \times Side \times Map was nonsignificant ($F_{2,36} = 0.59$, $p = 0.56$, partial $\eta^2 = 0.03$, $p_r = 0.57$). The effect is therefore likely to be perceptual, rather than generated by the emotional content of the faces.

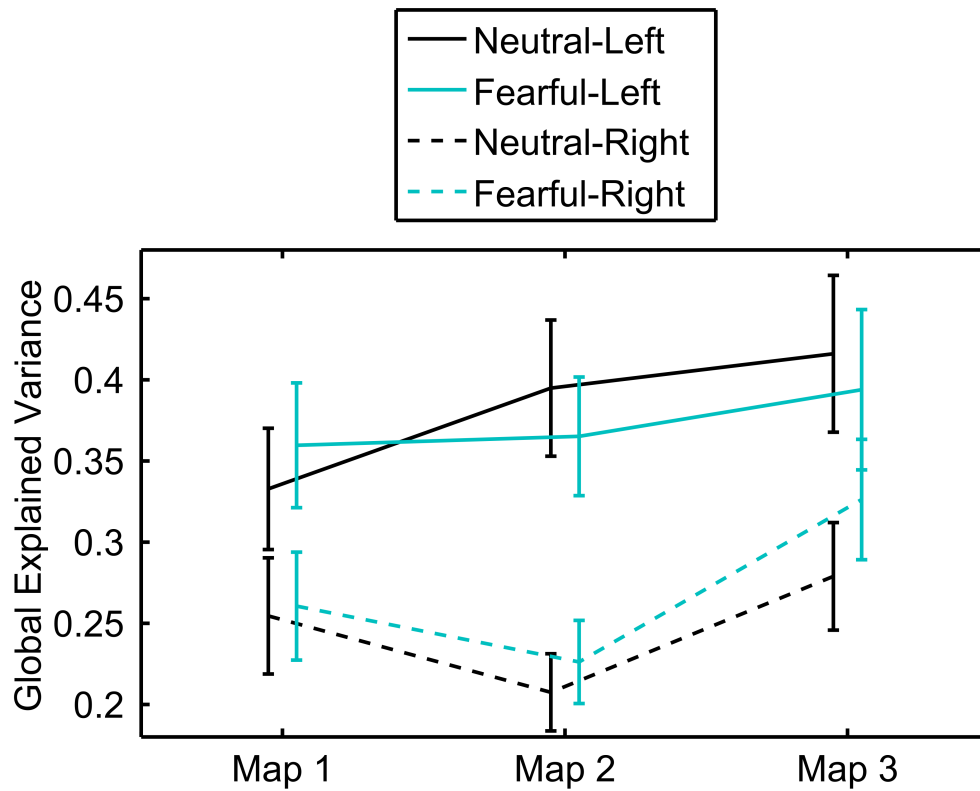


Figure 4.12: Average Global Explained Variance (\pm population standard error) by each map, for the Neutral/Fearful-Left/Right conditions. This Emotion \times Side \times Map interaction is significant. In particular the GEV explained by Map 3 in the Fearful-Right condition is significantly larger than for the Neutral-Right condition.

4.A.2 Experiment 2

4.A.2.1 Faces

The three map templates used for the ANOVA are shown on Figure 4.11B, top. The Emotion \times Cueing \times Side \times Map ANOVA led to a significant 4-way interaction ($F_{2,50} = 4.05$, $p = 0.02$, partial $\eta^2 = 0.14$, $p_r = 0.027$). This interaction is characterised by a significant Emotion \times Side \times Map interaction in the Cued ($F_{2,50} = 5.24$, $p = 9 \cdot 10^{-3}$, partial $\eta^2 = 0.17$, $p_r = 9 \cdot 10^{-3}$), but not in the Uncued condition ($F < 1$, $p_r = 0.45$). For the Neutral-Left-Cued condition, there is no significant difference in GEV between all three maps ($F < 1$, $p_r > 0.5$), while for the Fearful-Left-Cued condition, Map 2 explains significantly better than Map 1 ($F_{1,25} = 5.91$, $p = 0.02$, partial $\eta^2 = 0.19$, $p_r = 0.03$). Furthermore, Map 3 explains significantly better the Neutral-Right-Cued than the Fearful-Right-Cued condition ($F_{1,25} = 6.45$, $p = 0.02$, $p_r = 0.02$). The full interaction is shown on Figure 4.13.

These results suggest that, along with the change of GFP between Neutral-Cued and Fearful-Cued faces (see Section 4.4.2.1), there is also a topographical change between these two conditions. The neural generators are thus not only changing their ‘summed’ strength, but also either their relative strengths or their positions.

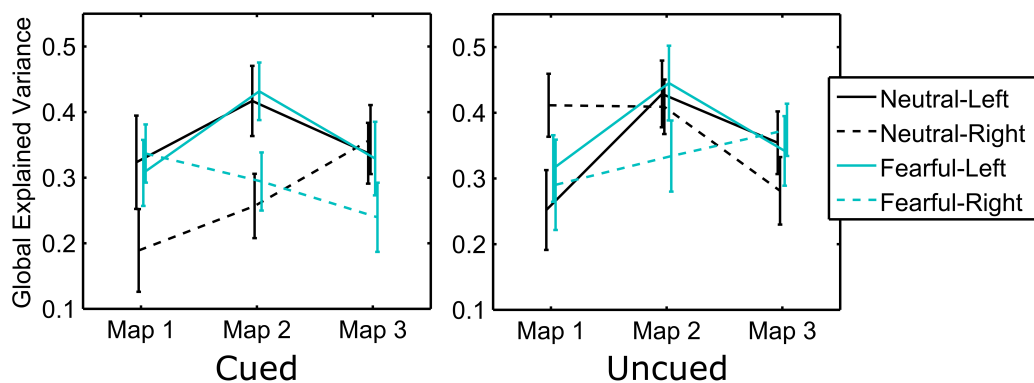


Figure 4.13: Experiment 2, facial stimuli: Global variance explained by the three maps for each condition. The 4-way Emotion \times Cueing \times Side \times Map interaction shown is significant. In particular, the Emotion \times Side \times Map interaction is significant in the Cued condition.

4.A.2.2 Objects

The GEV analysis using Target Status (Target, Non-Target) \times Cueing \times Side \times Map (Map 1, Map 2, Map 3, shown in Fig. 4.11B, bottom) as factors in the repeated-measures ANOVA did not lead to any significant effect involving Map and Target Status.

4.A.3 Experiment 3

The Emotion (Neutral, Fearful, Happy) \times Cueing \times Side \times Map (Map 1, Map 2, Map 3, shown in Fig. 4.11C) ANOVA on the GEV did not find any significant effect involving Map and Emotion.

Chapter 5

The Effects of Filtering on Early ERP and ERF Components*

5.1 Introduction

Event-related potentials and event-related fields (ERP/ERF), generated by averaging electro- and magneto-encephalographic (EEG/MEG) signals respectively, provide unique insights into human brain processes with unrivalled time resolution. Because the signal is weak and noisy, raw data typically require several pre-processing steps, including filtering and removal or attenuation of artifacts, before epoching and averaging over trials and participants. Filtering is an efficient way to increase the signal-to-noise ratio by removing frequency bands that mainly contain non-neural or irrelevant information. In EEG, both high frequencies (typically above 30 or 40 Hz), as well as low frequencies (typically below 1 Hz or less) are often filtered out. There has been a recent interest in the effects of filtering on ERP signals and their interpretation. In VanRullen (2011), the dangers of low-pass filtering and its effect on estimating onset times were examined. In a related commentary (Rousselet, 2012), it was shown that the effects of low-pass filtering might be limited, but that high-pass filtering can lead to problematic onset time distortions, which can be largely circumvented by using causal filtering. The present paper focuses on the early C1 component and the removal of low frequencies.

Low frequency signals can be of non-neural origin, such as electrodermal activity, drying, or chemical stabilization of the electrolyte due to thermal changes and contact

*This chapter is an adaptation of Acunzo et al. (2012), provided in Appendix B.

with the skin (see e.g., Hennighausen et al., 1993; Tallgren et al., 2005; Vanhatalo et al., 2005). In addition, the neural signal itself contains drifts and low frequencies, that can have cognitive significance (Grey Walter et al., 1964; Fitzgerald et al., 2001; Monto et al., 2008; Palva and Palva, 2012; Vanhatalo et al., 2005; Carmen Pastor et al., 2008)) but might not be relevant for the study.

Low frequency signals are removed with a high-pass filter. High-pass filtering can be understood as a way to force the average signal to be zero within a time window of a certain duration, thus eliminating slowly varying components. The higher the cut-off frequency (the frequency at which a 3 dB attenuation is attained), the shorter the time window, and the shorter the time during which the signal is allowed to depart from zero. As it shall be demonstrated, this can lead to significant distortions of the data.

The layout of this chapter is as follows. After discussing some principles behind commonly used filters, different filters are applied to real EEG data. It is demonstrated that high-pass filtering with an excessively high cut-off frequency can introduce systematic distortions to the signal and can lead to false results and interpretations. Although a well-known textbook warns of the dangers of filters and recommends a maximum cut-off value of 0.1 Hz in high-pass filters (Luck, 2005), a review of published papers reveals that many studies do not conform to this recommendation, which may have led to false conclusions, in particular concerning early modulations.

5.2 Filtering alters the shape of the signal

Although filtering can improve the signal-to-noise ratio, it can also distort the signal in an unwanted manner. A commonly known distortion introduced by filtering, often described in EEG/MEG data processing software manuals, is phase delay. Phase delay shifts the frequency components in time, which is undesirable given the core importance of the event timing in ERP/ERFs. Phase delay is particularly an issue for causal filters, for which the output at a given time only depends on past and present, but not future, input. Linear frequency-dependent phase delay, meaning that all frequencies will be delayed by the same amount, can be implemented with causal Finite Impulse Response (FIR) filters. This minimises distortion of the overall shape of the signal, but may generate large delays up to hundreds of milliseconds. Infinite Impulse Response (IIR) high-pass filters, such as Butterworth or Ellipsoid filters, commonly implemented

in EEG/MEG software packages, can achieve comparable filtering performance to FIR filters with fewer computational resources and with less delay (see e.g., Lynn, 1989). However, their non-linear phase response can generate strong distortions of the signal.

Because of the drawbacks of causal filtering and with the advent of computerised data processing and storage, acausal filtering has gained popularity. As the output of an acausal filter depends both on past and future input, acausal filters are applied offline on stored data. The advantage of acausal filters is that they can be constructed to have no phase delay at all, in which case they are called zero phase-shift filters. Commonly, these acausal filters are implemented with a causal filter run twice over the data: once forwards and once backwards. Apart from doubling the order of the filter, the backwards pass counterbalances any delays that the forward run introduces. Because of the absence of delay and the reduced distortions induced by forward-backward filters, guidelines and software manuals more or less explicitly advise their use (see e.g. Picton et al., 2000). In the following, the term acausal is used to indicate zero phase-shift acausal filters, as these are the most relevant for EEG/MEG processing.

Figure 5.1A shows the effect of a causal Butterworth filter applied forwards, and applied both forwards and backwards for two artificial example signals: a boxcar signal (left) and an artificial waveform (right). The artificial waveform was constructed with a sum of three Gaussian functions: $\sum_{i=1}^3 a_i e^{-\frac{(t-m_i)^2}{2s_i^2}}$ with parameters $a_1 = 1 \mu\text{V}$, $m_1 = 0.1 \text{ s}$, $s_1 = 0.02 \text{ s}$; $a_2 = -0.5 \mu\text{V}$, $m_2 = 0.2 \text{ s}$, $s_2 = 0.04 \text{ s}$; $a_3 = 3 \mu\text{V}$, $m_3 = 0.4 \text{ s}$, $s_3 = 0.07 \text{ s}$. Due to the non-linearity of the phase response of the Butterworth filter, the shape of the signals is significantly distorted in the causal case (top row). Note however that all the distortions happen after signal onset. In the forward-backward case, distortions are remarkably reduced compared to the causal case, but the signal is distorted more than one second prior to signal onset (bottom row).

These distortions can lead to misinterpretation, in particular in the typical situations where one studies the onset of a particular component, or of a divergence between two waveforms. Figure 5.1B illustrates this point, showing two signals that are initially the same, but differ after one second (top). When a causal filter is applied, the timing of the divergence of the two signals is preserved (middle). However, after applying an acausal filter, differences between the two signals are observable where they were identical before filtering, even before the onset of the two signals (bottom). The difference in the later part contaminates the early part of the waveform.

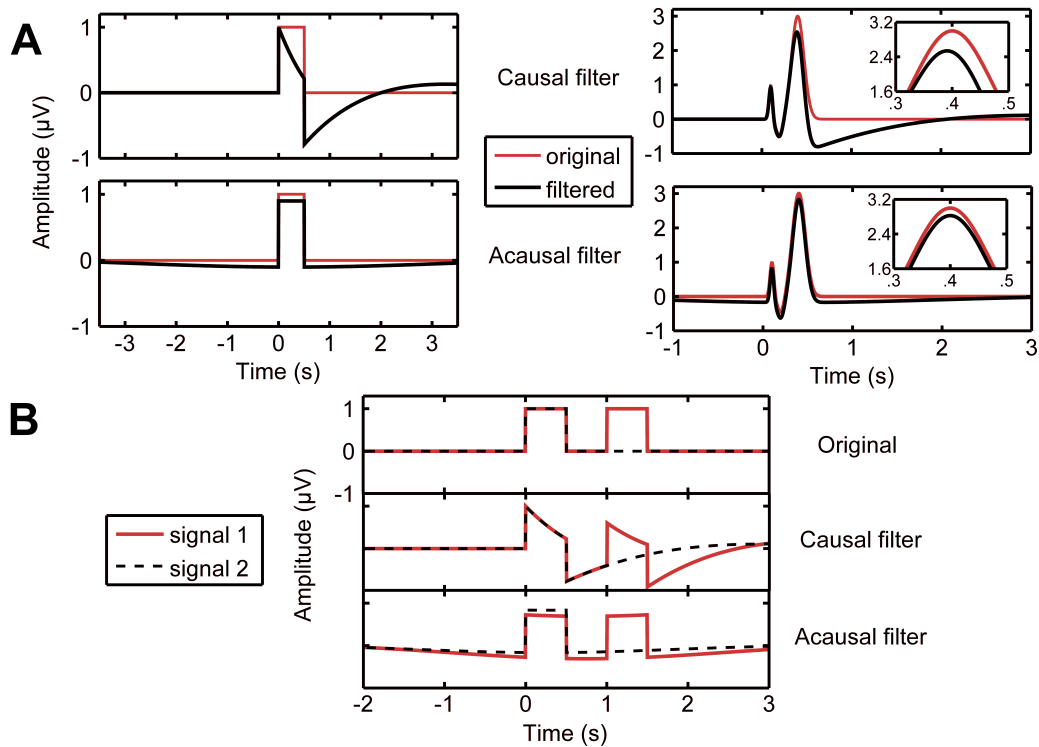


Figure 5.1: The effect of causal and acausal high-pass filtering on artificial signals. **(A)**: A boxcar signal (left) and an artificial waveform (right) were filtered with one forward pass of the filter (top), and with a forward and backward pass (bottom). The acausal filter preserves the shape of the signal much better than the causal filter, and, as opposed to the causal filter, preserves the latency of the third peak of the artificial waveform (see detail). However, it induces distortion before the onset of the signal. **(B)**: Two artificial signals differing only between 1 and 1.5 s (top). When filtered with the causal filter (middle), the two signals differ from $t = 1$ s, like the original signals. The acausal filter (bottom), however, introduces differences even before the onset of both signals at $t = 0$. The filter was a 3rd order Butterworth filter with 0.5 Hz cut-off frequency.

With a causal filter, a difference in the unfiltered waveforms may lead to differences later in time, but cannot affect earlier timepoints, supporting inferences that the effect started at this time at the latest. However, with an acausal filter, distortions are spread both forward and backward in time. In this case, it is not possible to state when the effect starts: it can only be concluded that the waveforms differed at some point in time.

5.3 Effects of filtering on actual EEG data

To illustrate the problematic effects of filtering in practice, some of the data from Chapter 4 is submitted to various high-pass filters. The original purpose of the experiment was to investigate the effects of spatial attention and facial expression on the C1 component of the visual ERP. The C1 component is characterized by a widespread centroparietal negativity (or positivity) peaking before 100 ms, evoked by presenting stimuli in the upper (or lower) hemifield and using an average mastoid reference (Clark et al., 1995). The results of this experiment are described in Chapter 4. Using these data, it is shown how high-pass filters can affect the shape of a real waveform, and how subsequent components can add systematic biases to earlier components and lead to erroneous interpretations. In addition, it is shown that filter parameters are critical for the proper interpretation of early components, and more particularly the C1 component.

5.3.1 Methods

5.3.1.1 Stimuli and Procedure

Stimuli and procedure are the same as Experiment 3 of Chapter 4 and are described in detail in section 4.3. Twenty-four right-handed participants were first presented with an arrow near the fixation point, pointing left or right, for 200 ms. After an interstimulus interval of 750 ms, a facial stimulus was presented for 300 ms on the side congruent or incongruent to the cue arrow, and presented on the upper visual hemifield to elicit a negative C1 (Jeffreys and Axford, 1972a; Clark et al., 1995). Facial stimuli showed three expressions: neutral, fearful, and happy. The experiment consisted of 1,120 trials per participant, with 352 trials for the Happy facial expression condition, and 768

trials equally divided between the Neutral and Fearful conditions. Participants were instructed to press a button when detecting a happy face at the congruent location only (176 trials), while fixating on the fixation point.

5.3.1.2 Data Acquisition

EEG was recorded using a BioSemi Active-Two system (BioSemi B.V., Amsterdam, Netherlands), which has a DC coupled amplifier. The activity at 64 Ag-AgCl scalp electrodes following the location and label of the extended 10–20 system (Jasper, 1958), along with 4 electro-oculography (EOG) electrodes (above and below the right eye, and on the outer canthi) and 2 mastoid electrodes, was digitised on 24 bits with a sample rate of 1,024 Hz.

5.3.2 Data processing

Pre-processing was performed using the EEGLAB toolbox (Delorme and Makeig, 2004) under Matlab (Mathworks, Inc., Natick, MA, USA), and custom scripts. The EEG signal was first re-referenced to the average mastoids, and low-pass filtered with a cut-off value of $f_c = 40$ Hz, using the default FIR filter implemented in EEGLAB: a least square linear-phase filter of order 75 with a transition bandwidth (the range of frequencies between the bandcut and the bandpass) of 6 Hz, run forward and backward. Though it should be kept in mind that low-pass filters may also induce artifacts (VanRullen, 2011), the low amplitude of the higher frequencies in the EEG signal reduces the risk of serious alteration of the waveform. Rousselet (2012) found little artifactual effect of low-pass filtering on real EEG data. Furthermore, as this preliminary filtering step is done for all subsequent high-pass filtering conditions, it does not alter the conclusions on high-pass filtering. The continuous data were then resampled to 256 Hz. High-pass filters with cut-offs f_c of 0.05, 0.1, 0.5, and 1 Hz were then applied to study the effects of filtering. Testing lower cut-off values was found to be unnecessary as little effect was observable up to 0.1 Hz. The default EEGLAB parameters were used for this filtering step as well: the filters used were least square linear phase FIR high-pass filters run forward and backward. Their transition bandwidth was $0.15 \times f_c$ and their order $3 \times \text{fix}(f_s/f_c)$, with f_s the sampling frequency (256 Hz), and fix the function that rounds downwards to nearest integer. For each of the filtered sets of raw data, epoching was performed using facial stimulus onset time as time origin, and each channel was

baselined using the 100 ms interval preceding stimulus onset. To remove artifactual epochs, a semi-automatic procedure was run on the non high-pass filtered data, labelling epochs containing EOG data beyond 70 μV in absolute value. The data were visually inspected and epochs containing artifacts were removed. The same trials were used for all filtering conditions. On average, 936 correctly answered and artifact-free trials per participant contributed to the grand-average ERP.

5.3.2.1 Data analysis

Voltage from electrodes P1, P2, CP1 and CP2 was averaged to generate the ERPs. For the C1 component, mean amplitude of the 50–100 ms interval was calculated. For the purpose of this paper, only results from the Congruent attentional condition are presented here. A one-way ANOVA with Emotion (Neutral, Fearful, Happy) was performed for each filter cut-off value. Normality was tested using a Kolmogorov-Smirnov test, and sphericity using a Mauchly test. Normality hypotheses were confirmed. When indicated, a Greenhouse-Geisser (GG) correction was applied to compensate for sphericity violations.

5.3.3 Results

Figure 5.2 shows grand-average ERPs for each emotional condition (Neutral, Fearful, Happy) averaged over all participants and the electrodes CP1, CP2, P1 and P2. Figure 5.2A shows the waveforms without high-pass filtering. Figure 5.2C zooms in on the waveform between -100 and 500 ms, containing the C1. After reaching a negative peak at 100 ms (as expected with stimuli presented in the upper visual hemifield, see Clark et al., 1995), the waveforms exhibit a globally positive-going excursion, peaking at around 500 ms. The amplitude of this deflection is largest in the Happy condition, which corresponds to target trials during which participants had to press a button.

High-pass filtering strongly affected the shape of the waveforms. As the cut-off frequency of the filter is increased, the late positive component disappears (Fig. 5.2B, E, and F). But simultaneously, the early part of the waveform is pushed downwards. This effect is similar to the distortion observed in Figure 5.1A (bottom row). Only when a low cut-off frequency of 0.1 Hz was used, was the waveform not drastically affected (Fig. 5.2D).

In parallel with its impact on the shape of the ERP, scalp topographies (averaged across the latency period from 50–100 ms) are affected by filtering (Fig. 5.2C-F, insets). The indicated dissimilarity measures how each map is different from the non-filtered map. The dissimilarity (Lehmann and Skrandies, 1980) is defined by:

$$\begin{aligned} \text{DISS}_{u,v} &= \sqrt{\frac{\sum_{i=1}^n (u'_i - v'_i)^2}{n}} \\ u'_i &= \frac{u_i}{\text{GFP}_u} \\ v'_i &= \frac{v_i}{\text{GFP}_v} \end{aligned} \quad (5.1)$$

with u_i the i^{th} of the n electrodes of map u . The GFP is defined by Equation 4.1. A dissimilarity of 0 means that the two maps are identical, and a dissimilarity of 2 means that the two maps are inverted. As a consequence, high-pass filtering may alter results for studies using topography information, such as microstate analysis, independent component analysis, or source reconstruction.

Next, the apparent modulation of the C1 amplitude with experimental condition was examined. Figure 5.3A shows that the modulation strongly changes as a function of the cut-off value. Significance tests (Fig. 5.3B) show that, in the present experiment, apparently reliable effects arise as the filter cut-off frequency increases, at 0.5 Hz ($F_{2,46} = 9.38$, $p < 10^{-3}$) and 1 Hz ($F_{2,46} = 9.53$, $p < 10^{-3}$), while there is no significant effect for lower cut-off values.

To better understand the mechanisms behind these effects, a direct test of whether the C1 effect observed at high cut-offs was due to a subsequent late component that contaminates C1 through the acausality of the filter was performed. Late components are known to be affected by facial expression and target recognition (Eimer and Holmes, 2002; Picton, 1992; Rozenkrants and Polich, 2008). To quantify these effects, the Late Positive Complex (LPC) was measured as the averaged waveform between 400 and 500 ms. Consistent with the literature, the LPC showed a larger positive excursion for the Happy faces target than for the other conditions ($F_{1,17,27.01} = 34.05$, $p < 10^{-5}$, GG corrected). $\Delta\text{LPC}_{\text{HN}}$ (and $\Delta\text{LPC}_{\text{FN}}$) was defined as the change in LPC amplitude in the Happy versus Neutral conditions (resp. Fearful versus Neutral), in the unfiltered condition. Similarly, $\Delta\text{C1}_{\text{HN}}$ (and $\Delta\text{C1}_{\text{FN}}$) is the difference of C1 amplitude between the Happy and Neutral conditions (resp. Fearful and Neutral) in the unfiltered condition,

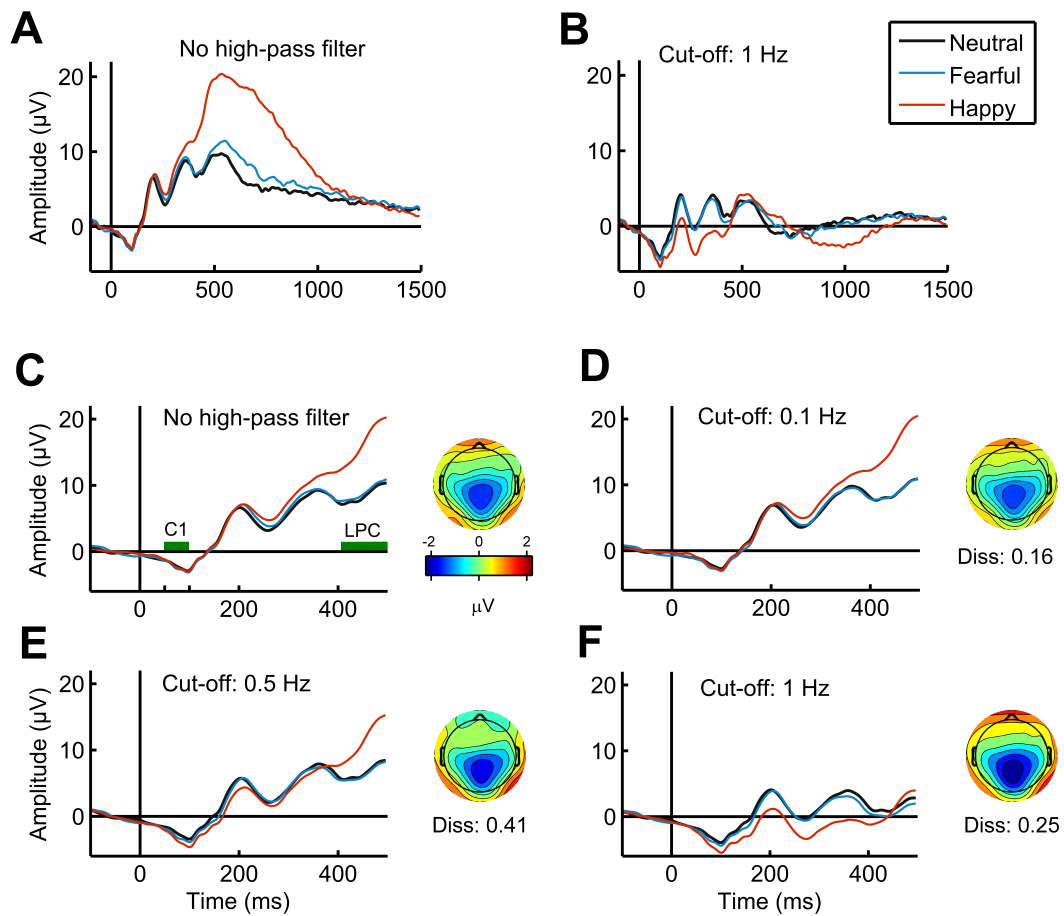


Figure 5.2: The effect of filtering on ERP data from Experiment 3 (Chapter 4). ERPs are averaged over all 24 participants, and over electrodes CP1, CP2, P1 and P2, for various high-pass cut-off frequencies, and for each experimental condition (Neutral, Fearful, and Happy). **(A, B)**: ERPs from -100 to 1500 ms, without a high-pass filter **(A)**, and with an acausal high-pass filter, a filter of cut-off of 1 Hz applied forward and backward **(B)**. The shape of the waveform is drastically affected. The slow and later component disappears with filtering, and the earlier components are pushed downwards. **(C-F)**: Zoom of the ERPs up to 500 ms post-stimulus onset. Raw data was high-pass filtered with an acausal filter, with different cut-off frequencies. The time windows used to quantify the C1 (50–100 ms) and the LPC (400–500 ms) are indicated in **(C)**. Scalp topography calculated from the C1 time window is shown for each filter condition. The potential was re-referenced to the average. Dissimilarity indicates how each map is different from the non-filtered map. Due to eye-blink artifacts occurring after 500 ms, the ERPs shown in **(A)** and **(B)** were calculated using a subset of the epochs used in **(C-F)**.

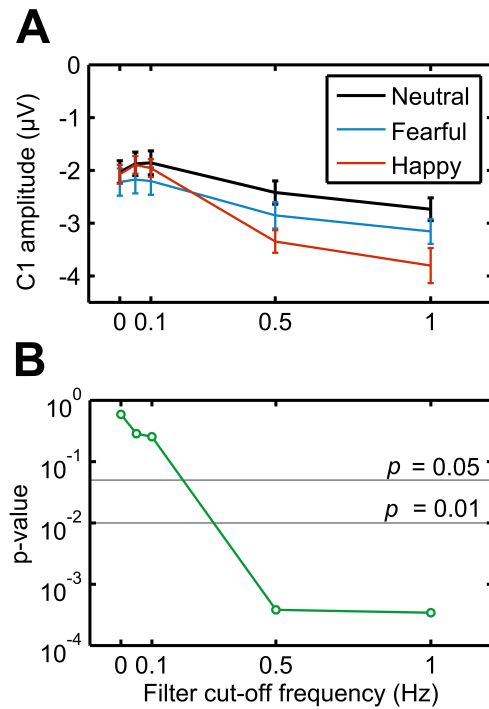


Figure 5.3: Effects of high-pass cut-off frequency on the C1 component across experimental conditions. **(A)**: Average amplitude at electrodes CP1, CP2, P1 and P2, between 50 and 100 ms, for each experimental condition (Neutral, Fearful, Happy), and for different cut-off values of the acausal FIR filter. **(B)**: P-values from one-way ANOVAs. High cut-offs lead to highly significant, but erroneous, results. A cut-off of 0 Hz indicates that no high-pass filter was applied.

and $\Delta C1_{HN}^{f_c=1}$ and $\Delta C1_{FN}^{f_c=1}$ in the filtered condition with a 1 Hz cut-off. These values were calculated for each participant.

To evaluate the link between the LPC and the C1 amplitude, ΔLPC was correlated with $\delta C1$, defined as the change in $\Delta C1$ caused by the filtering ($\delta C1 = \Delta C1^{f_c=1} - \Delta C1$). $\delta C1$ is positive for most participants, as the C1 effect is larger with the high-pass filter than without (see e.g. Fig. 5.2C versus F). Figure 5.4 shows the correlation between the Neutral/Happy modulation ΔLPC_{HN} and the change in C1 effect $\delta C1_{HN}$, and similarly for the Neutral/Fearful modulation (ΔLPC_{FN} and $\delta C1_{FN}$). A strong correlation was found in both cases ($\rho_{HN} = 0.95$, $p < 10^{-8}$, and $\rho_{FN} = 0.71$, $p = 10^{-4}$). The first correlation reflects the contamination by the large late positive amplitude in the Happy condition that can be observed in Figure 5.2. The second correlation (Neutral/Fearful) is noteworthy and shows subtler effects. Although there is no statistically significant LPC effect ($t_{23} = 1.01$, $p = 0.32$), a clear correlation exists on the individual level, contributing to the significant C1 Neutral/Fearful effect in the filtered waveform ($t_{23} = 2.06$, $p = 0.05$). This shows that even portions of the grand-average waveform that do not show a significant effect can contribute to the bias.

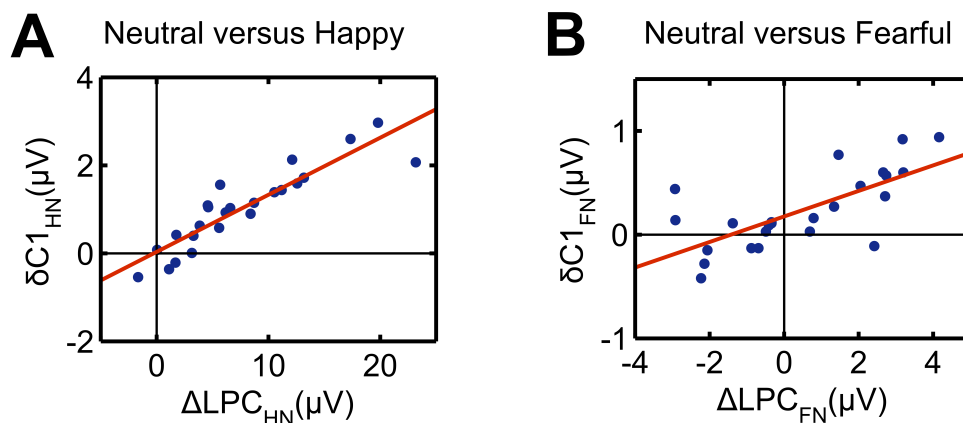


Figure 5.4: Correlation between the LPC effect in the unfiltered condition and the change in the C1 effect between the unfiltered and filtered conditions, in the Neutral and Happy conditions (**A**) and the Neutral and Fearful conditions (**B**). Each point corresponds to a participant. The significant correlations show that the subsequent LPC effect, observable in the unfiltered waveforms (see Fig. 5.2A and 5.2C), contributes substantially to the systematic bias of the C1 component.

To ensure that the C1 effect observed in the filtered waveform was indeed due to a subsequent component, a causal filter (4th order high-pass Butterworth filter with 1 Hz cut-off) was used. While the waveform also appears distorted when compared with the waveform without high-pass filtering (see Fig. 5.5), no significant C1 effect was found

($F_{2,46} < 1$). Together, these results confirm that the C1 effect in the present data is due to subsequent components, in particular the LPC, and is completely artifactual.

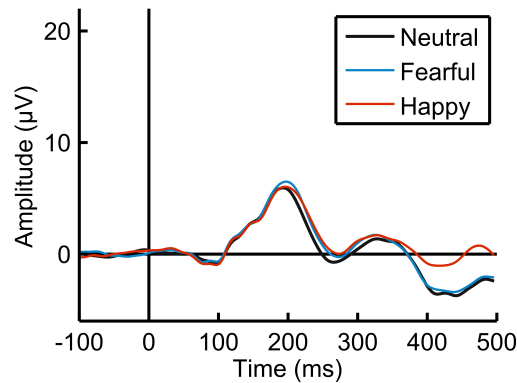


Figure 5.5: ERP waveforms filtered with a causal high-pass filter. The filter used was a 4th order Butterworth filter of cut-off 1 Hz. The shape of the waveform is strongly altered, but no early artifactual C1 effect is present in comparison to the ERP generated after applying an acausal high-pass filter (cf. Fig. 5.2F). This is consistent with the hypothesis that the C1 effect observed with an acausal filter at the same cut-off value was due to signal differences occurring subsequently.

5.4 Discussion

In summary, it was shown that high-pass filtering of the raw EEG data can distort the resulting ERP waveforms, and induce systematic biases between conditions. For this reason, high-pass filtering should be used parsimoniously in EEG/MEG data, and the cut-off frequency should be kept as low as possible under normal circumstances. The present analysis on real EEG data shows how a late slow component can induce a systematic bias in an earlier component when using commonly used acausal filters, which can lead to erroneous interpretations. A highly statistically significant modulation of C1 by stimulus condition was found. It was then shown to be completely artifactual.

The recent years have been characterised by an increasing interest in the very early visual components, happening before 100 ms after stimulus onset, and thought to be associated with activity in the striate (Jeffreys and Axford, 1972a; Clark et al., 1995), and perhaps extrastriate visual cortices (Foxe and Simpson, 2002; Ales et al., 2010b, but see Kelly et al., 2012). When peaking, these components are often labeled C1 and M90 for the event-related potential (ERP) and event-related field (ERF) waveforms respectively. These early processes, and in particular, the C1 component, were thought

to be only modulated by the physical characteristics of the triggering stimulus, but immune to endogenous modulations, and more specifically attention (Martínez et al., 1999; Noesselt et al., 2002; Di Russo et al., 2003; Hillyard et al., 1998). More recently, however, C1 modulations by attention and attentional load (Khoe et al., 2005; Wu et al., 2005; Kelly et al., 2008; Fu et al., 2009; Rauss et al., 2009; Fu et al., 2010b; Rauss et al., 2011a), perceptual learning (Pourtois et al., 2008), anxiety (Eldar et al., 2010), and emotional stimuli or faces (Pourtois et al., 2004; Stolarova et al., 2006; West et al., 2011) were reported. Similarly, very early ERF modulations by attention (e.g., Poghosyan and Ioannides, 2008; Ioannides and Poghosyan, 2012) and facial expression (e.g., Morel et al., 2009; Bayle and Taylor, 2010) have been reported. While these results are extremely exciting, as they suggest that our brain processes and modulates visual information more quickly than is generally thought, difficulties of replication (e.g., Santesso et al., 2008; Fu et al., 2010a) make it hard to draw conclusions on what mechanisms are at play. One possible reason for such inconsistencies is that experimental paradigms and methods vary widely.

In light of the present findings, the high-pass filter cut-off value used in these studies was examined. It was found that out of the 13 ERP/ERF attention studies finding a very early effect, 5 used a cut-off higher than 0.5 Hz. Similarly, 6 out of 10 studies reporting early effects of facial expression used a cut-off higher than 0.5 Hz. Only one study reporting no early effect while using a high cut-off was found (Streit et al., 2003). See Appendix A for a list of the studies surveyed.

The inconsistency of results may therefore be a combination of filtering artifacts, publication bias, and the presence of genuine early effects. Future research in this area should seek to elucidate the conditions under which very early components are modulated by taking care to minimise possible biases induced by high-pass filtering (see Section 5.5).

Additionally, papers were examined from the *Journal of Neuroscience*, *Cerebral Cortex*, *NeuroImage*, *Human Brain Mapping*, and the *Journal of Cognitive Neuroscience*, published or accepted between January 2011 and March 2012. Papers using ERP or ERF amplitudes either directly, for source estimation, or for independent component analysis were included, and studies interested in restricted frequency bands (event-related oscillations, event-related synchronisations/desynchronisations, time-frequency analyses, and power analyses) were excluded. Although the issues presently discussed are also relevant for intra-cranial EEG, only data measured from scalp recordings was

included. The results are consistent with those reported by Rousselet (2012): out of the 185 scrutinised studies satisfying the criteria set, it was found that 80 (43%) of them used a cut-off above 0.1 Hz. Half of those, i.e. 40 studies (21 %), used a cut-off of 1 Hz or higher. The proportion of studies using a cut-off higher than 0.1 Hz and using MEG was comparable to those using EEG (18/40, or 45% vs 65/155, or 42%). The vast majority of these reports do not specify whether a causal or acausal filter was used, but the few which do used a zero phase-shift filter. Additionally, most papers do not specify why such a high cut-off value was used, and those who do invoked the classical reasons of signal-to-noise ratio increase and slow trends removal.

While the potential dangers of filtering were already described in Luck (2005), and while the majority of laboratories use digital high-pass filtering knowingly and parsimoniously, it appears that it is necessary to change the practices of more than a third of the works, and to possibly reinterpret a non-negligible portion of the literature. However, we do not claim that the conclusions of all reports using a high cut-off frequency are erroneous. The nature and extent of biases induced by filtering depend on the shape of the waveform, the type of filter used, and the specific component studied. Rather, these studies should be regarded keeping the possibility of a filter-induced bias in mind.

5.5 Guidelines

The following guidelines should be considered to minimise artifacts due to high-pass filtering:

- Only use offline high-pass filtering if necessary. Visually inspect the data beforehand to judge if too much drift is present. Only if the data are indeed noisy and show a large amount of drift, consider applying a high-pass filter.
- To choose the cut-off of the high-pass filter, we reiterate the guideline stated in Luck (2005): set the high-pass filter cut-off value to 0.01 Hz by default. For less docile participants whose data may be noisier, such as children or certain kinds of patients, consider the possibility of a higher cut-off, such as 0.05 or 0.1 Hz maximum.
- If, for any reason, a filter with a higher cut-off is applied, check the results against data filtered with a lower cut-off. Try to understand any discrepancy in the results

and make sure they are not due to biases induced by filtering (e.g. with analyses as used in the present paper).

- To check the distortion induced by a filter, generate a grand average waveform with and without having applied a filter on the raw data, and ensure that the overall morphology is not affected.
- Acausal zero-phase shift filters do not delay the signal but can generate distortions backward in time. If one is interested in the earliest moment when an effect occurs, a causal filter is preferred (see also Rousselet, 2012). If one is interested in the timing of a peak, a zero phase-shift filter should be preferred.
- Finally, as stated in Picton et al. (2000), the nature of the filter used should be specified. In particular, a vast majority of the reports omit to mention the causality of the filter, which, as seen above, may be critical for the interpretation of the data.

Chapter 6

General Discussion

6.1 Summary of the results

This thesis examined interactions between the processing of visual emotional stimuli and visual attention at various levels. Emotional stimuli are known to be processed preferentially and to trigger attentional processes under certain conditions. Also, attending away from emotional stimuli can modulate, or extinguish, their processing. However, much remains to be understood concerning the characteristics of these interactions, the context in which they operate, their mechanisms and the brain structures involved. This thesis explored some aspects of these interactions.

In Chapter 2, the influence on overt attention of emotional items embedded in visual scenes was investigated. Past research suggests that emotional information has a strong influence on oculomotor control, characterised by early detection and fixation of emotional information, and by more time spent fixating on the emotional information (Calvo and Lang, 2004; Nummenmaa et al., 2006; Calvo et al., 2008; Nummenmaa et al., 2009). The experiment described in Chapter 2 indeed found that emotional items were attended for a longer period of time than neutral items, confirming this aspect of past research. However, emotional items were not found to be attended earlier than neutral items, as would have been expected from this same literature. This suggests that extra-foveal emotional information fails to trigger attentional shifts in this particular context. A possible explanation is that perceptual load prevents the emotional information from being detected, as not enough resources are available to process extra-foveal emotional information (see e.g., Yates et al., 2010, on how attentional

load may disrupt emotional processing).

In Chapter 3, covert spatial attentional shifts to emotional faces were investigated using a dot-probe task (MacLeod et al., 1986). Masked and shortly presented facial stimuli were used as cues. Unlike previous research (Mogg and Bradley, 1999, 2002; Fox, 2002), reliably faster reaction times for probes positioned at the location congruent to the fearful face were *not* found. Although the failed replication may be due to the particular parameters of the experiment (absence of awareness check, letter discrimination task, etc.), it is also possible that attentional biases found when using masked and shortly presented cues are not as reliable as when using longer cue stimulus presentations. Few experiments using subliminal cues have been carried out, and most of them were not independent replications (Bar-Haim et al., 2007).

In Chapter 4, the speed of visual emotional stimulus perception was investigated by testing the sensitivity of very early ERP components to facial expression. The joint influence of endogenous attention on these components was also looked at. It was found that fearful faces generated a different ERP before 100 ms (characterised by a weaker GFP) when spatially attended *and* task-irrelevant. This suggests that an influence of emotion on visual processing can be triggered very early in the case of incidental emotional information processing. Our experiments suggest that these fast processes can be inhibited when the stimuli are not spatially attended, as occurs for subsequent processes (Holmes et al., 2003), or when the emotional information is attended voluntarily. This dependency of very early processes on the task-irrelevance of emotion information had been reported by Bayle and Taylor (2010), and is compatible with an early alerting system (possibly using the subcortical route, Morris et al., 1999) which subsequently directs attention to the emotional information. In parallel, this experiment looked at the effect of the target stimulus on very early components. A GFP effect was found between target and non-target stimuli, which was independent from spatial attention. This independence from spatial attention is in line with data from feature-based attention (McAdams and Maunsell, 2000; Saenz et al., 2002; Hayden and Gallant, 2009). However, the results and the design of the studies make it difficult to conclude definitely on this particular issue.

Finally, in Chapter 5, a potential flaw in a large part of the ERP and ERF literature was pointed out. This appears to be particularly problematic for works studying very early processes. Using a high-pass filter with a cut-off higher than 0.1 Hz can generate systematic biases due to the smearing of subsequent effects in the ERP. It was found

that about half of works looking at very early attention and facial expression effects use high-pass filters that may lead to such biases.

6.2 Methodological contributions

An important part of the work carried out may contribute to improve some aspects of methodology in ERP methods.

During exploratory analyses, it was found that the GFP appeared more sensitive than individual electrodes to experimental conditions in the C1 time range. A likely reason is the high individual variability of the C1, due to individual differences in the shape of the calcarine fissure (see e.g. Ales et al., 2010b). While a couple of studies pointed out the need to take individual differences into account to study the functional sensitivity of the C1 (Proverbio et al., 2007; Kelly et al., 2008), the GFP may provide a simple and straightforward solution, as this measure is independent from topography.

A potentially serious issue having implication in all ERP and ERF research was pointed out in Chapter 5. The widespread use of high cut-off zero-phase shift filters may distort the signal in a systematic manner, and induce misinterpretation of the data. While this issue has been pointed out before (Luck, 2005; Rousselet, 2012), the work carried out emphasised the issue for studies looking at particularly early latencies. The review of the literature following illustrations of the distortions in artificial and real ERP data should help researchers realise the extent of the issue and adapt their methods.

6.3 The ‘automaticity’ of emotion processing

A large part of the literature on emotional processing is intending to characterise to what degree emotional stimulus processing is ‘automated’, or independent from attention and awareness. Results are widely conflicting, possibly because researchers use different methods, paradigms and definitions of ‘automaticity’. Additionally, this automaticity is often paired with the hypothesis that visual emotional stimuli are processed via a fast subcortical route bypassing visual cortices to reach the amygdala, so that emotional information can be processed quickly.

6.3.1 Independence from attention?

A substantial amount of research investigates and discusses whether emotional information is processed automatically and independently of attention and processing resources.

This is the case for oculo-motor research. In Nummenmaa et al. (2006), participants were presented an image on each side of the fixation point. Even when instructed not to look at the emotional image, participants were more likely to direct their first fixation to the emotional image, which was interpreted as being due to the fact that emotion is attended reflexively. More convincing are the results presented in Nummenmaa et al. (2009). Participants were instructed to saccade to the left or right image, depending on a cue. Saccadic reaction times were slower when participants had to saccade away from the emotional image. In another experiment, participants were instructed to saccade vertically between the two images. Saccades were found to present a curvature away from the emotional image, which is a characteristic of saccades in the presence of a distractor. This body of data provides evidence for an automatic influence of emotion on eye movements. The images were irrelevant to the task, and the effects obtained with emotional images were similar to the ones obtained with conventional distractors (e.g. Doyle and Walker, 2001, for the saccade curvature effect). Research using the dot-probe task also provides evidence that emotional stimuli, and in particular fearful cues, exert an influence on behaviour in an unconscious manner, at least for anxious people. As we saw, this may be particularly true for longer cue presentations.

In both cases (eye-movement and dot-probe research), however, the emotional information, though task irrelevant, may be attended covertly. In Nummenmaa et al. (2006) and associated publications, images covered a large part of the visual field while perceptual load at fixation was null. In the dot-probe task, the cues appear before the probe, and it is likely that the attention of the participants is spread over a large portion of the visual field as the task-relevant probe appears subsequently at either location of the cue.

These data may thus provide evidence for *involuntary*, rather than *automatic*, emotional processing, as no pressure is exerted on the attentional system to attend away from the emotional stimuli. An automatic process will be triggered regardless of available computing resources, whereas an involuntary one means that it will happen or be facilitated if resources are available. However, an involuntary process may, in turn,

automatically influence or trigger subsequent processes such as attentional orienting or eye movements.

The eye-movement data presented in this thesis is not in conflict with this interpretation. Eye movements *were* influenced by emotional items, but only once fixated. As discussed in Section 2.4, perceptual load (due to scene clutter) and task load may not have provided enough available resources to enable semantic and emotional information extra-foveally, which in turn prevented subsequent influence on eye-movement.

If the absence of effect in the dot-probe data of Chapter 3 is indeed due to short cue stimulus presentation times, it does not provide support for automaticity either. It was however found that subliminal visual presentation of emotional information can elicit specific ERPs (Kiss and Eimer, 2008), activate subcortical structures Liddell et al. (2005) and activate the para-sympathetic system (Williams et al., 2006). It may be that, in our case, further processing is necessary to trigger subsequent reflexive shifts of attention.

The hypothesis that emotional stimuli are processed automatically has also been explored with neuroimaging and electrophysiology techniques. A typical experiment consists of presenting a pair of stimuli or two different classes, e.g. houses and faces. The house stimuli are always neutral, while the face can be neutral or emotional. Participants are asked to attend to the house or the face while their brain activity is recorded. The processing of emotional information under attended and unattended conditions can thus be compared. Using fMRI, Vuilleumier et al. (2001) found that while activity of the fusiform gyrus was dependent on both attention and emotion (in an additive manner), the activity of the amygdala was independent from attention. These data support the hypothesis that emotional information is processed 'automatically' in the amygdala, i.e. regardless of the attentional condition. However, using a comparable paradigm involving high attentional load, Pessoa et al. (2002b) found that the amygdala was dependent on the attentional condition: the differential activity of the amygdala between emotional conditions vanished when attention was directed away from the faces. While the conflicting results may be explained by subtle differences in the task (e.g. the task given in Pessoa et al. 2002b when attending away from the faces may have been more demanding than in Vuilleumier et al. 2001), Brosch and Wieser (2011) suggested that the explanation may lie in the low temporal resolution of the fMRI. They pointed to intracranial electrophysiology (Pourtois et al., 2010) and MEG data (Luo et al., 2010) finding that the early part of the amygdala response

(before 190 ms) is not dependent on attentional conditions, while the later part is.

The ERP data presented in Chapter 4 does not support this view. While very early modulations by fearful facial expression were found, these were dependent both on spatial attention (attending away prevented the effect, Experiment 2) and on the task-relevance of the facial expression (explicit attention to emotion also prevented the effect, Experiment 3). ERPs do not allow us to discriminate between brain structures without source localisation techniques. However, activity of the amygdala, despite its depth and its nucleus structure, can be detected using source modelling methods (Attal et al., 2007). Thus, changes in amygdala activity should be reflected as changes in topography and/or amplitude of the ERP. No effect of emotion was found in Experiment 2 when faces were spatially unattended, or when emotion was processed explicitly (Experiment 3), which does not support the automaticity hypothesis. This said, little research on very early EEG/MEG latencies has been carried out, in particular using different attentional conditions. Bayle and Taylor (2010) did find results compatible with the ones reported in Chapter 4, as very early emotional processing dependent on attention was found. It should be noted, however, that they did not find any activity in the amygdala, but hypothesised that the frontal activation they detected was activated through a subcortical pathway.

While further research is needed to determine to what extent emotional processing is automatic, the research presented in this thesis suggests that emotional processing is highly dependent on attention. Chapter 2 found that emotional stimuli could modulate eye-movements only after being overtly attended, while Chapter 4 found that very early neutral-fearful modulations were dependent on both spatial attention and the task-relevance of the facial expression. These results are however not against the hypothesis that subsequent processes to emotional processing are triggered reflexively.

6.3.2 The subcortical route

Linked to the question of automaticity is the question of the neural pathway used to process emotional information. The involvement of a subcortical visual pathway involving the superior colliculus, the pulvinar and the amygdala has been put forward by extrapolating to humans the existence of an auditory subcortical route responsible for auditory emotional conditioning in mice (LeDoux, 1998, chap. 6). The existence of such a pathway is supported by a varied corpus of data. Morris et al. (1999) and Liddell

et al. (2005) reported an activation of the structures putatively involved in this subcortical route during 'unseen' (subliminal) fear. Neuropsychological data from blindsight patients, whose primary visual cortex (or part of it) is lesioned, also provides evidence for the existence of such a pathway. Morris et al. (2001) reported amygdala activation in such a patient when fear-conditioned faces were presented in the blind portion of the visual field. Interestingly, the patient in Pegna et al. (2005), whose right amygdala was also activated when presented with fearful faces, was able to guess the type of emotional face being presented without being able to 'see' it consciously. These data are compatible with the standard hypothesis that the subcortical route is involved in pre-attentive, automatic, emotional processing. Additional indirect evidence comes from the sensitivity of the structures involved in this pathway to low-pass filtered images of fearful faces (Vuilleumier et al., 2003b), which is in line with the fact that neurones in the superior colliculus respond to low spatial frequencies (Miller et al., 1980; Rodman et al., 1989). This is in line with a route that would process coarse (i.e. low spatial frequency) information.

The existence, or significance of this pathway, is however disputed. In Pessoa and Adolphs (2010), the idea of a prominent role of the subcortical visual route in emotion processing is argued against. First, the authors argue that emotional information is not processed faster than non-emotional information, and that the latencies in processing emotional information can also be explained by cortical (and not only subcortical) pathways. Second, they argue against the idea that the amygdala processes only coarse information. Finally, they point out that there is no strong evidence for a superior colliculus-pulvinar-amygdala pathway in primates when considering anatomical data. While the existence of a collicular-pulvinar pathway is established, there is no strong evidence for a connection from the pulvinar to the amygdala. Furthermore, the activity of the inferior pulvinar, which receives input from the superior colliculus, does not reflect collicular activity being more linked to visual attention and awareness. Pessoa and Adolphs (2010) argues for a model of different waves of activity, involving cortical and subcortical structures for emotional processing.

As seen above, the work presented in this thesis does not provide evidence for automatic processes, even in the earliest stages of processing (Chapter 4), and therefore does not support the current model of the subcortical route. If, assuming that the amygdala is sensitive to low spatial frequency information (but see Pessoa and Adolphs, 2010), the absence of capture of overt attention by emotional items in the eye-tracking

study (Chapter 2) may be due to the fact that some items were fairly small, and thus containing too high spatial frequencies to activate the subcortical route. The change in topography between neutral and fearful faces found in ERP Experiment 2 (Appendix 4.A) is compatible with Bayle and Taylor (2010), who found activation in frontal areas in response to fearful faces only when the facial expression was unattended. Bayle and Taylor (2010) argue that this frontal activation may come from the subcortical route, which would however somewhat contradict the standard hypothesis that the subcortical route supports automated, pre-attentive processes. Furthermore, it was found, in Chapter 4, Experiment 2, that this early modulation vanished when spatial attention was oriented away from the faces. Perceptual load cannot explain this interaction with spatial attention as only one stimulus was presented at a time. This suggests that if this modulation by emotion indeed reflects an alerting system, supported or not by the subcortical route, it is still dependent on visual attention.

The existence of the subcortical route, putatively processing coarse visual information that would enable a fast detection of danger by the amygdala independently of attention, is still debated and evidence for its significance in humans is, for the moment, only indirect. However, many behavioural, eye-tracking and neuroimaging studies do attempt to interpret their data in light of this hypothesis. In our case, early modulations by emotion were found. This supports the idea of a very fast pathway for emotional processing, however these modulations were also modulated by attention, which goes against the view of a subcortical pathway that would operate independently of attentional resources.

6.4 Future work

In this section, ideas of future work, built upon the experiments presented in this thesis, are described.

6.4.1 Emotional stimulus processing in complex environment

The eye-tracking experiment presented in Chapter 2 enabled us to study the influence of emotional information on behaviour in conditions relatively closer to reality than most experiments on emotion and attention. Indeed, participants were presented

with complex scenes, and were free to fixate anywhere on the scene for 15 s. This contrasts with simple monochromatic stimuli or pairs of stimuli flashed for a few hundred milliseconds while maintaining fixation and performing an unrelated task. It was found that emotional items did not influence eye-movement before having been fixated directly, unlike experiments using less ecologically valid paradigms (e.g. Calvo and Lang, 2004). It would be interesting to investigate why this absence of effect occurred in our case.

Visual scenes are a complex (i.e. cluttered) ensemble of physically coherent and linked items. The effects of clutter and ‘link’ could be investigated separately.

Scene clutter can be manipulated (Rosenholtz et al., 2007; Henderson et al., 2009) to test its influence on how early emotional items will be fixated. A 2×2 design can be imagined, in which scenes have high or low clutter, and a particular item has a neutral or emotional valence. The expected result is that high clutter will reduce the difference in time before first fixation between neutral and emotional items. It was indeed found that perceptual load influences emotional stimulus processing (Yates et al., 2010).

Additionally, in the paradigm used in Calvo and Lang (2004), pairs of unrelated scenes were used, enabling participants to extract a gist for each scene. In a visual scene, however, all elements are linked with the background, and only one gist is extracted by the viewer. An experiment testing the influence of the ‘link’ between the items can be imagined. Images could be designed so that they contain two ‘subscenes’. In one condition, the two sub-scenes are neutral, while in the other, one is emotional. The other manipulation consists of linking (or not) the two sub-scenes. In the ‘Unlinked’ condition, the sub-scenes would be cropped so that they appear as two independent images, while in the ‘Linked’ condition, the whole scene would be presented (and the two sub-scenes integrated in the whole image). As in the Linked condition clutter will be higher, patterns would be added in the empty space to ensure equal perceptual load in both conditions. The expected result is that emotional items would be fixated earlier in the Unlinked condition, as an emotional gist can be extracted from the emotional sub-scene, which would be more difficult in the Linked condition.

6.4.2 The psychometric properties of the dot-probe task

Despite the many experiments carried out using the dot-probe task, still little is known concerning its psychometric properties (Cisler et al., 2009). The failure to find an effect in the experiment presented in Chapter 3 may be revelatory of how little is known about the precise set of parameters that help or prevent an attentional bias to be measured. This is particularly important given the fact that this paradigm has potential clinical applications (see Section 3.1.2).

A natural follow-up of the experiment carried out would be to use the same design, but using 500 ms presentation duration for the cue stimuli. If an effect were successfully measured, it would indicate that longer cue presentations are necessary to observe an effect.

The minimum display time necessary to observe an effect would be a useful parameter to know, both for basic research and subsequent clinical applications. Reaction times biases in the dot-probe task were found to exhibit very poor test-retest reliability (Schmukle, 2005; Staugaard, 2009). EEG methods may therefore prove useful in this case. The amplitude of the P1 component elicited by the probe onset was found to be enhanced in emotion-congruent trials (Pourtois et al., 2004; Santesso et al., 2008; Fox et al., 2008, but see Eldar et al., 2010), and may arguably be a more reliable measure than reaction time. To assess the influence of cue stimulus duration, masked stimuli may be used in order to interrupt further perceptual processing (see e.g. Lamme and Roelfsema, 2000). In such an experiment, the cue will be displayed for a duration ranging between e.g., 10 and 500 ms. The influence of cue duration on P1 amplitude enhancement (an indication of covert attentional orienting to the location of the probe) could then be evaluated using single-trial analysis methods (see e.g., Gaspar et al., 2011).

Additional parameters could also be tested using the same method, including cue-probe onset asynchrony, cue size, type, distance from fixation, etc.

These experiments would help to pin down the parameters that provide the strongest and most reliable attentional effects. This is a *sine qua non* to carry out research on attentional bias efficiently using this paradigm.

6.4.3 Early ERP modulations

6.4.3.1 Eliciting a reliable C1

As reviewed in Chapter 4, EEG/MEG research into very early modulations by attention and facial expression is burgeoning. Along with improving filtering methods to avoid false results, methodological improvements taking into account individual differences are, if not necessary, highly desirable, in order to make C1 measurements more sensitive to experimental manipulations.

Kelly et al. (2008) used an individual mapping method to determine optimal location of pairs of stimulus and pairs of electrodes to measure C1 modulations by spatial attention. It was proposed in Section 4.5.6 that the GFP could be a useful tool to study the C1, as it does not rely on any topographical information, and is not subject to experimenters' judgement. The GFP could be paired to more exhaustive mapping methods, such as the multi-focal visual-evoked potential method described in Hood et al. (2003), allowing simultaneous measure of ERPs from many regions of the visual field (Kelly, personal communication, 13 June 2012). The development of methods enabling reliable measurement of the C1 will be extremely helpful for research looking at very early ERP modulations

6.4.3.2 Facial expression and feature-based attention

The results presented in Chapter 4 indicate that facial expression modulates very early components of the evoked potential, and that these modulations are dependent on both spatial attention and the task. Further experiments should be carried out to confirm this effect.

A replication of Experiments 2 and 3, using an improved design, should be carried out in order to confirm the results. A possible design would be the following. All conditions would follow a repeated-measure design, which was not the case for the experiments presented in Chapter 4 (the task was different *between* experiments). The stimulus content would be identical between conditions to avoid contextual or stimulus repetition effects (see e.g., Morel et al., 2009). Three sub-categories could be used for faces and objects: neutral, fearful and happy faces, and e.g., kettles, jugs, and bottles. The experiment would be composed of two blocks, one for each task. In one block,

participants would be asked to detect kettles (or jugs, or bottles), and in the other fearful faces (or neutral faces, or happy faces). A different, larger set of objects and facial stimuli should preferably be used. Additionally, a control experiment using inverted stimuli should be run to control for the effects of low-level features.

This design should enable testing of whether the emotion C1 effect, modulated by spatial attention and task, can be replicated. It would also enable testing of the hypothesis that target stimuli generate a different C1 strength than non-target objects, indicating very early feature detection processes. If this effect is confirmed, this could change our understanding of the time course of object processing, which is currently thought to occur after 100 ms (see e.g., Kirchner and Thorpe, 2006).

6.5 Conclusion

Various methods were used in the present thesis to approach the interaction between emotional visual stimulus processing and visual attention.

An eye-tracking experiment (Chapter 2) investigated whether past eye-movement research on overt attention and emotional stimuli was extensible to scene perception. In particular, we tested whether emotional items embedded in complex scenes attracted and held the eye. Like previous studies using independent images, it was found that emotional items held overt attention. However, no evidence for emotional items to attract attention was found. Further research is needed to understand the reasons of this discrepancy.

A dot-probe experiment (Chapter 3) did not replicate past results, but an analysis of the literature found that short and masked cue presentations may not generate as robust effects as longer cue presentations. Further research should attempt to investigate the psychometrics of the dot-probe task.

ERP experiments (Chapter 4) confirmed past observations of very early ERP modulations by facial expression, and found that they depend on the attentional conditions. However, the direction of the effect contradicts past research, and further work is needed to conclude more definitely. An effect apparently linked to feature-based attention and object identification was also observed. Further work to confirm this observation is also needed to conclude more definitely.

The work on the ERP experiments was fruitful from a methodological point of view. The use of the GFP as an alternative to individual electrode potential was proposed to study the C1. Additionally, a potential flaw due to offline high-pass filters applied on the raw data was found to be a source of concern for an important part of the ERP/ERF literature, and in particular in the literature interested in very early components (Chapter 5).

Finally, this work was put in the wider context of the hypothesised ‘automaticity’ of emotional processing and the putative subcortical route. It was concluded that the results of the presented experiments do not support or reject the existence of the subcortical route, but are not consistent with the hypothesis that emotional stimuli are processed automatically.

Appendix A

Early ERP/ERF modulations: survey of filter cut-offs

This appendix lists the studies looking at very early effects, surveyed in Chapter 5. Table A.1 lists studies looking at facial expression effects, and Table A.2 the ones looking at attention. It is to be noted that many more studies of attention and facial expression were carried out and did *not* report very early effects. The list of studies *failing* to report an effect should therefore not be considered exhaustive, but indicative. The list of studies reporting an early effect should be considered more exhaustive.

Report	Method	Online filter ^a	Offline filter ^a	Effect ^b	At risk ^c
Pizzagalli et al. (1999)	EEG	0.3 – 100	1.5 – 30	Y	Y
Streit et al. (1999)	MEG	unspecified	DC – 45	N	N
Halgren et al. (2000)	MEG	0.03 – 90	None	Y	N
	EEG	0.01 – 100	None	N	N
Eger et al. (2003)	EEG	unspecified	1.6 – 70 *	Y	Y
Streit et al. (2003)	MEG	unspecified	1 – 45	N	Y
Susac et al. (2004)	MEG	0.1 – 200	DC – 30	N	N
	MEG	0.1 – 200	DC – 40	N	N
Pourtois et al. (2004)	EEG	0.01 – 100	DC – 30	Y	N
Morel et al. (2009)	MEG	DC – 100	None	Y	N
	EEG	0.16 – 100	None	Y	N
Santesso et al. (2008)	EEG	0.1 – 200	DC – 30	N	N
Bayle et al. (2009)	MEG	DC – 300	None	Y	N
Bayle and Taylor (2010)	MEG	DC – 200	1 – 30	Y	Y
Hung et al. (2010)	MEG	DC – 100	1 – 50	Y	Y
Eldar et al. (2010)	EEG	0.1 – 100	DC – 30	N	N
Susac et al. (2010)	MEG	0.1 – 200	DC – 40	N	N
Liu and Ioannides (2010)	MEG	DC – 200	3 – 200	Y	Y
West et al. (2011)	EEG	unspecified	1 – 30	Y	Y

^a Low cut-off (Hz) – High cut-off (Hz). ‘DC’ indicates that there was no low cut-off (low-pass filter), and ‘Inf’ indicates that there was no high cut-off (high-pass filter).

^b Presence of an early effect: we report ‘Y’ if a modulation was reported before 100 ms.

^c At risk of bias: we report ‘Y’ if the offline high-pass filter cut-off is higher than 0.5 Hz.

* The report does not specify whether the filter was applied online or offline.

Table A.1: Filter cut-offs for ERP/ERF studies looking at early facial expression effects

Report	Method	Online filter ^a	Offline filter ^a	Effect ^b	At risk ^c
Gomez Gonzalez et al. (1994)	EEG	0.01 – 100	causal 1.2 – Inf ADJAR	N	N
Clark et al. (1995)	EEG	0.01 – 100	ERP low-passed	N	N
Martínez et al. (1999)	EEG	0.01 – 80	None	N	N
Martínez et al. (2001)	EEG	0.01 – 80	ADJAR	N	N
Noesselt et al. (2002)	E/MEG	DC – 50	None	N	N
Di Russo et al. (2003)	EEG	0.1 – 80 Notch 60	ERP low-passed	N	N
Khoe et al. (2005)	EEG	0.1 – 80	ERP low-passed	Y	N
Wu et al. (2005)	EEG	0.1 – 75	None	Y	N
Fu et al. (2005)	EEG	0.1 – 40	None	N	N
Proverbio et al. (2007)	EEG	0.01 – 70	None	Y	N
Fu et al. (2008)	EEG	0.1 – 40	ADJAR	N	N
Kelly et al. (2008)	EEG	0.05 – 100	DC – 45	Y	N

^a Low cut-off (Hz) – High cut-off (Hz). ‘DC’ indicates that there was no low cut-off (low-pass filter), and ‘Inf’ indicates that there was no high cut-off (high-pass filter). ADJAR (Woldorff, 1993) is a digital manipulation aimed at removing the adjacent and earlier ERP, e.g. the ERP generated by an earlier cue.

^b Presence of an early effect: we report ‘Y’ if a modulation was reported before 100 ms.

^c At risk of bias: we report ‘Y’ if the offline high-pass filter cut-off is higher than 0.5 Hz.

* The report does not specify whether the filter was applied online or offline.

Table A.2: Filter cut-offs for ERP/ERF studies looking at early attention effects

Report	Method	Online filter ^a	Offline filter ^a	Effect ^b	At risk ^c
Poghosyan and Ioannides (2008)	MEG	DC – 800	1 – Inf	Y	Y
Fu et al. (2009)	EEG	0.1 – 40*	None	Y	N
Rauss et al. (2009)	EEG	0.01 – 100	0.5 – 30	Y	Y
Zani and Proverbio (2009)	EEG	0.16 – 50	None	Y	N
Karns and Knight (2009)	MEG	unspecified	1 – 50	Y	Y
Proverbio et al. (2010)	EEG	0.016-100	ERP low-passed	Y	N
Fu et al. (2010b)	EEG	0.1 – 40	ADJAR	Y	N
Fu et al. (2010a)	EEG	0.1 – 40	None	N	N
Rauss et al. (2011b)	EEG	0.01 – 100 Notch 50	0.5 – Inf	Y	Y
Ioannides and Poghosyan (2012)	MEG	DC – 800	1 – Inf	Y	Y

Table A.2: Filter cut-offs for ERP/ERF studies looking at early attention effects (continued)

Appendix B

Published Papers

No Emotional “Pop-Out” Effect in Natural Scene Viewing

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It has been shown that attention is drawn toward emotional stimuli. In particular, eye movement research suggests that gaze is attracted toward emotional stimuli in an unconscious, automated manner. We addressed whether this effect remains when emotional targets are embedded within complex real-world scenes. Eye movements were recorded while participants memorized natural images. Each image contained an item that was either neutral, such as a bag, or emotional, such as a snake or a couple hugging. We found no latency difference for the first target fixation between the emotional and neutral conditions, suggesting no extrafoveal “pop-out” effect of emotional targets. However, once detected, emotional targets held attention for a longer time than neutral targets. The failure of emotional items to attract attention seems to contradict previous eye-movement research using emotional stimuli. However, our results are consistent with studies examining semantic drive of overt attention in natural scenes. Interpretations of the results in terms of perceptual and attentional load are provided.

Keywords: visual attention, eye movement, emotional processing, scene perception

Visual attention is a key mechanism of human cognition, enabling us to select relevant visual stimuli by prioritizing the processing of certain features or aspects of the incoming information. Characterizing attentional processes is, therefore, a *sine qua non* for the understanding of cognition. A crucial issue is the extent to which high-level information, such as semantic or emotional information, plays a role in the exogenous drive of covert and overt attention.

Emotional stimuli, by definition, are stimuli with high motivational value, important for survival of the individual or the species. From an evolutionary point of view, individuals who can detect and react to these stimuli fast will be advantaged. The capture of attention by emotional stimuli has, therefore, received a great deal of interest. It is now known that these stimuli can capture and hold attention more easily than neutral stimuli, but the neural mechanisms of these interactions are yet to be understood (Vuilleumier, 2005).

Visual search paradigms have been used to assess whether emotional and, in particular, fear-relevant targets are detected

faster than fear-irrelevant targets. Many of these studies have found a search advantage for emotional items, such as snakes, in comparison to neutral items, such as mushrooms (e.g., Öhman, Flykt, & Esteves, 2001; Flykt, 2005; Blanchette, 2006; Fox, Griggs, & Mouchlianitis, 2007). However, further studies have shown that the situation is more complex (see, e.g., Tipples, Young, Quinlan, Broks, & Ellis, 2002; Lipp, Derakshan, Waters, & Logies, 2004; Soares, Esteves, & Flykt, 2009; Flykt, 2006). Cave and Batty (2006) interpreted these contrasting results as follows: “[T]hreat itself, as opposed to [visual] features associated with threat, seems to be less of a factor in visual search than was first suggested” (p. 636). In line with this hypothesis, Coelho, Cloete, and Wallis (2010) used schematic face and face-like stimuli and suggested that the search advantage for particular facial expression is driven by low-level features. As noted by Soares et al. (2009), discrepancies between experimental results are probably caused by variations in the search tasks, making it difficult to draw definite conclusions about the search mechanisms.

Eye-movement research has also shown that emotional stimuli attract overt attention (Calvo & Lang, 2004; Nummenmaa, Hyönä, & Calvo, 2006, 2009; Alpers, 2008). In these studies, participants were peripherally presented two images while their eye movements were recorded. When an emotional image was presented concurrently with a neutral image, the probability of the first fixation landing on the emotional picture was higher. It was also shown that participants fixated the emotional image for a longer time. In Nummenmaa et al. (2006), even when explicitly instructed to attend to the neutral image, participants first fixated on the emotional image. Finally, a more recent study (Nummenmaa et al., 2009) examined saccade latency when participants were instructed to look either left or right when a distractor image was presented on each side. It was found that saccade latency was delayed when the image opposite to the instructed direction was emotional. Saccade trajectories were also modulated by surrounding emo-

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tional content: When participants were instructed to saccade vertically while presented distractor images on the sides, the saccade curved away from emotional images. In Becker and Detweiler-Bedell (2009), participants were instructed to passively look at an array of four faces while their eye movements were recorded. Interestingly, the researchers found that participants avoided looking at the threatening face as early as the first saccade, suggesting an early evaluation of the face valence, biasing subsequent eye movements.

These results suggest that eye movements are modulated by emotional content within the visual field in an unconscious, automated manner. This is consistent with paradigms looking at covert attention, which suggest that emotional stimuli can modulate attention even when they are task-irrelevant (Bar-Haim, Lamy, Pergamin, Backermans-Kranenburg, & van Ijzendoorn, 2007).

However, the research discussed above used particular viewing conditions. First, the stimuli used usually contained a small number of independent images or items. Because the items were independent (i.e., content and location were unrelated), an independent “emotional gist” could have been extracted for each item. Additionally, the items were often presented extrafoveally while the participant was fixating on a dot in the center of the screen. This low initial foveal load might have facilitated the emotional processing of the images. Finally, the high frequency of emotional stimuli, together with the low variance of semantic content, and the few possible locations where items could be displayed may have eased the task of the participants by increasing the expectation of the participant for emotional stimuli. If previous research shows that attention and eye movements are modulated by extrafoveal emotional content under these particular conditions, it is unclear whether these effects would remain under more natural conditions where perceptual and foveal load is high and where objects are part of a whole scene.

To answer this question, we adapted a paradigm initially developed to assess the effects of semantic gist violation on eye movements (Loftus & Mackworth, 1978). Participants’ eye movements were recorded while viewing scenes in which one target object did not fit with the rest of the image (e.g., an octopus in a farm). Interestingly, items violating the gist do not seem to generate any semantic “pop-out” effect, but do hold attention longer than non-violating items (De Graef, Christiaens, & d’Ydewalle, 1990; Henderson, Weeks, & Hollingworth, 1999; Gareze & Findlay, 2007; Castelhana, Mack, & Henderson, 2009; Vö & Henderson, 2009; Rayner, Castelhana, & Yang, 2009; but see Loftus & Mackworth, 1978; Becker, Pashler, & Lubin, 2007; Underwood & Foulsham, 2006; Gareze & Findlay, 2007; Underwood, Templeman, Lamming, & Foulsham, 2008).

We developed a set of stimuli consisting of pairs of realistic scenes. Each pair consisted of two photographs, which solely differed by a target item: In one condition, this item had a neutral valence, and in the other, it had an emotional (i.e., positive or negative) valence. Participants were asked to try to remember those images for a subsequent memory test while their eye movements were recorded. Additionally, scenes were horizontally flipped, so that the target item was presented on the left or right side of the initial fixation point. Target item position (left or right) and valence (neutral or emotional) were then the conditions of our 2 × 2 within-participant design.

According to previous research on eye movements and emotional stimuli, we hypothesized that emotional items would pop-out and be fixated earlier than neutral targets. However, research on eye-movement and scene perception suggests that no such pop-out should occur. Further, we tested the hypothesis that emotional targets would be fixated earlier if located on the left-hand side of the initial fixation point. Previous research suggests laterality effects, with a right hemisphere advantage to process emotional stimuli (see, e.g., Keil, Morati, Sabatinelli, Bradley, & Lang, 2005; Calvo & Nummenmaa, 2007; Calvo & Avero, 2008). In particular, in the context of eye-movement research, Alpers (2008) used the same paradigm as Calvo and Lang (2004) and reported that the effects of the emotional content on the first fixation observed in previous experiments were present only when the emotional picture was presented in the left hemifield. Finally, we hypothesized that participants would fixate on the emotional targets for a longer time than the neutral ones, as both the literature on emotional stimuli (Calvo & Lang, 2004, and replications) and scene perception (De Graef et al., 1990; Henderson et al., 1999; Gareze & Findlay, 2007; Castelhana et al., 2009; Vö & Henderson, 2009; Rayner et al., 2009) would suggest.

Method

The procedure and stimuli were approved by the University of Edinburgh Department of Psychology Ethics Committee.

Participants

Sixteen participants (10 female) participated in the experiment, most of whom were students in the University of Edinburgh recruited through an internal university website. All participants reported normal or corrected-to-normal vision. They were compensated £6/hr.

Stimulus Material

Stimulus design. The stimulus material consisted in 48 full-color 24 bit images of maximal resolution of 800 × 600 pixels. Each scene conformed to one of the 2 × 2 conditions: emotional versus neutral and left versus right. In the emotional condition, a target item in the scene was emotionally evocative; in the neutral condition, an emotionally neutral target replaced the emotionally evocative target. In the left and right conditions, the target was located in the left and right part of the image, respectively, generated by simply mirroring the entire image over a vertical axis. Half of the emotional stimuli contained positive targets and the other half contained negative ones. Examples of negative targets included people with facial tumors, a threatening animal (e.g., snake), a face showing fear, and a face covered with blood. Positive targets represented people hugging or kissing, children playing, or fluffy animals. Neutral targets included bags, faces, or whole characters. An example of a scene is shown in Figure 1.

Emotional valence and arousal were controlled by asking a population of 16 participants (10 female) who did not take part in the main experiment to rate the target items. Emotional targets were rated significantly higher in terms of arousal than neutral stimuli. Positive (negative) targets were rated significantly higher

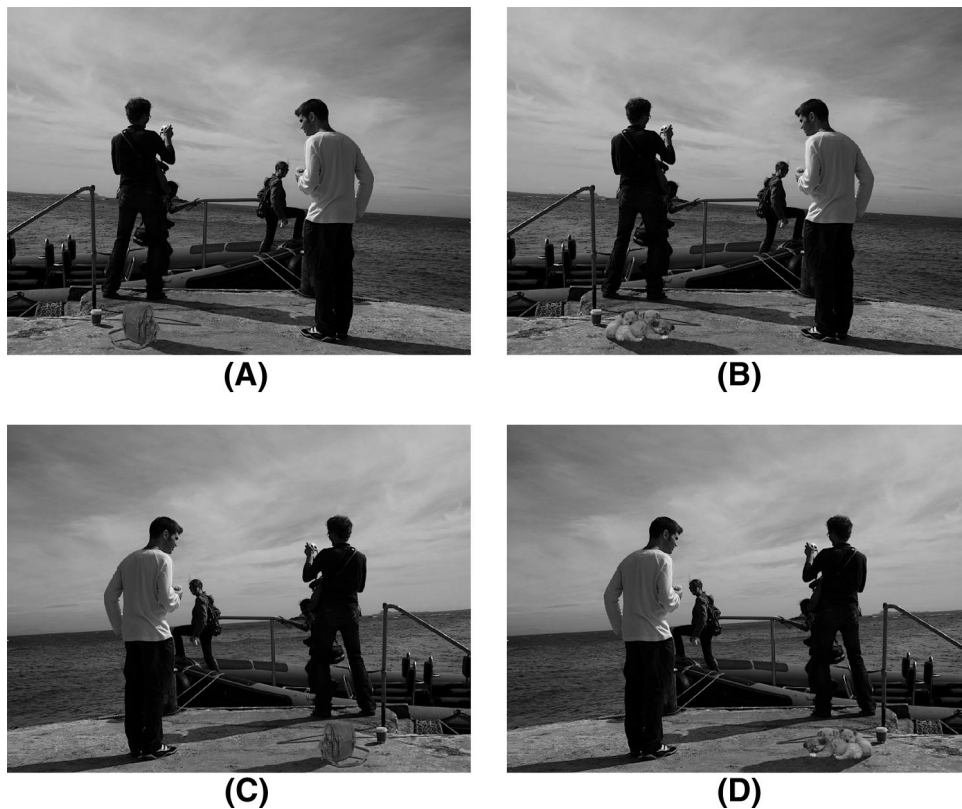


Figure 1. Example of scene presented to the participants. The four conditions of an example scene: neutral-left (A), emotional-left (B), neutral-right (C), and emotional-right (D). The neutral and emotional conditions differ by one item (bag/dogs), whereas the left and right conditions are the horizontally flipped versions of one another. Each participant was presented only one of the four conditions of every scene. Scenes were presented in full color.

(lower, respectively) in terms of valence than their neutral counterpart. More details on the procedure and results of the stimulus validation study are given in the Appendix.

For each pair of dual images (i.e., pair of same background images with a different target), we defined a common target interest area (IA) that included the neutral and emotional target for both images. The IAs of the mirrored images had mirrored IAs from the original image.

In the neutral condition, 9 of the 12 scenes were artificially modified, and all 12 were modified in the emotional condition. A modification involved either the addition or alteration of the target item. Scenes were found on the Internet (except one, which was a photograph taken by a member of the research group), whereas targets were taken from the Internet, the International Affective Picture System (IAPS; Lang, Bradley, & Curthbert, 2008), the NimStim face database (Tottenham et al., 2009), and Hemera Photo-Objects 2.07 (Hemera Technologies, Seattle, WA). Images were manipulated using GIMP 2.4.0 (available at: <http://www.gimp.org>; accessed January 24, 2011). Targets were adapted for luminance, saturation, color, and contrast in order to make the addition or replacement as natural as possible. In many cases, manual modification of the lighting of the target was necessary, and shadows and reflections were modified or added for more realism. To ensure that the modifications did not lead to a differ-

ence of saliency between the neutral and emotional conditions, we ran the Matlab implementation of a saliency model (Itti & Koch, 2000) on our images. The saliency map was computed and normalized for the images. The average saliency was then computed within the target IA. A Wilcoxon signed-rank test was used to compare the average saliency within the 12 IAs containing a neutral target ($Mdn = 0.0247$), with the 12 containing an emotional target ($Mdn = 0.0289$). Differences were not significant: $T = 31, p > .8, r = .04$.

Apparatus

Images were presented on a 21" CRT monitor at a viewing distance of 90 cm with a refresh rate of 140 Hz. Their maximum resolution was 800×600 pixels, subtending a maximum visual angle of 25.7×19.4 degrees. Eye movements were monitored by an SR Research EyeLink 1000 eye-tracker (SR Research, Ltd., Kanata, Ontario, Canada). The head of the participant was fixed on a chin-rest. Fixation position was sampled at 1,000 Hz, and saccades prior to critical fixations were detected using a 17-sample saccade detection model with a velocity threshold of 30 deg/s, an acceleration threshold of 8,000 deg/s², and a minimum amplitude of 0.5 degrees. The right eye only was tracked, whereas viewing

was binocular. The experiment was controlled with SR Research Experiment Builder software.

Procedure

Each participant was presented a consent form to be signed, informing about the experiment and the emotionally evocative nature of some of the stimuli. Before the viewing task, the participants were given the State Trait Anxiety Inventory (STAI; Spielberger, Gorsuch, & Lushene, 1970) questionnaire to fill in.

Each participant was presented one of four blocks, each containing all 12 scenes. Each block contained three scenes in each of the four conditions: neutral-left (NL), neutral-right (NR), emotional-left (EL), and emotional-right (ER). No participant was presented the same scene in more than one condition. The order of image presentation was randomized within the assigned block for each participant.

Participants were told that they would be shown 12 images for 15 s each, and that they would have to memorize them for a subsequent memory task. The memory task was never given. Calibration of the eye tracker, using nine points on the screen, was performed, followed by a validation. At the beginning of each trial, a point in the middle of the screen had to be fixated by the participant, for a fixation check. The trial was then initiated manually by the experimenter. If inaccuracy of the eye-tracker was detected, a new calibration was performed.

Eye-Movement Data Manipulation

Raw data were first filtered and preprocessed with SR Data Viewer. Most data manipulation was carried out using Matlab 7.0 (MathWorks, Inc., Natick, MA). Graphs and statistical tests were done with Matlab and SPSS (SPSS, Inc., Chicago, IL). Analyses of variance (ANOVAs) included valence (neutral, emotional) and side (left, right) as within-participant factors. When possible, *t* tests were performed to compare two independent samples. Otherwise, a Wilcoxon's rank-sum test was conducted.

No fixation within the IA occurred during the scene presentation for 16 trials (4 NL, 2 NR, 4 EL, and 6 ER; 8.33% of all trials). Those trials were not included in the following analyses.

Results

Capture of Attention

One of the main questions that we address here is whether emotional targets attract attention more than neutral ones when

embedded in a natural scene. Table 1 and Figure 2 summarize the statistics reported in this section.

Number of fixations and latency to IA. To assess the difference in attentional capture by targets across conditions, we examined how early in scene exploration the targets were fixated. To do so, we looked at the difference in the number of fixations prior to the first fixation within the IA, and at the amount of time spent exploring the scene prior to the first fixation within the IA. For the number of fixations to IA, no effect of valence $F(1, 15) < 1$ ($\omega^2 = .032$) or side $F(1, 15) < 1$, ($\omega^2 = .025$) was found. A nonsignificant valence-side interaction $F(1, 15) = 3.74$, $p > .05$ ($\omega^2 = .447$) was found, with fewer fixations to IA for the neutral-left and emotional-right conditions, compared with neutral-right and emotional-left, whereas we would have expected fewer fixations for the emotional-left versus emotional-right.

Latency to IA showed the same pattern: no effect of valence $F(1, 15) < 1$ ($\omega^2 = .027$), side $F(1, 15) < 1$, ($\omega^2 = .022$) and a nonsignificant interaction $F(1, 15) = 3.87$, $p > .05$ ($\omega^2 = .453$).

Incoming saccade amplitude to IA. The amplitude of the first saccade ending within the IA provides information about extrafoveal processing of emotional targets. Given the hypothesis that emotional targets capture attention extrafoveally, we should observe a larger saccade amplitude for the emotional condition than for the neutral one. The analyses showed a nonsignificant trend, with longer saccade amplitude to emotional targets $F(1, 15) = 2.83$, $p > .05$ ($\omega^2 = .399$), no effect of side $F(1, 15) = 1.45$, $p > .05$ ($\omega^2 = .297$), and no interaction, $F(1, 15) < 1$ ($\omega^2 = .052$).

Hold of Attention

In this subsection, we analyzed events occurring once the target was overtly attended and compared the hold of attention by the emotional targets against the neutral ones. After the target was fixated, its location within the image was not a relevant variable in these analyses. We consequently collapsed the left and right conditions for this part of the analysis. The remaining conditions were simply emotional and neutral. Table 2 and Figure 3 summarize the statistics reported in this section.

First fixation duration within IA. The durations of the first fixation on the target item can be indicative of the encoding of the fixated object (see, e.g., Henderson & Hollingworth, 1999), although recent evidence suggest that fixation durations are only partially driven by visual input (Henderson & Smith, 2009; Nuthmann, Smith, Engbert, & Henderson, 2010). The durations of the first fixation within the IA for neutral ($Mdn = 255.3$ ms) and emotional ($Mdn = 249.4$ ms) targets showed no significant difference with Wilcoxon's rank-sum test: $T = 282$, $p > .5$, $r = .16$.

Table 1

Capture of Attention: Summary

	Conditions				F values		
	NL	NR	EL	ER	Em	S	Em × S
Number of fixations to IA	6.49 (.76)	8.28 (1.33)	8.36 (1.47)	6.78 (.82)	<1	<1	3.74
Latency to IA (ms)	1,525 (206.4)	2,069 (396.2)	2,090 (435.8)	1,603 (259.7)	<1	<1	3.87
Saccade amp to IA (deg)	5.7 (.35)	6.0 (.44)	6.9 (0.54)	7.2 (.60)	2.83	<1	<1

Note. Mean and (standard error) of the "capture of attention" variables for each of the four conditions: neutral-left (NL), neutral-right (NR), emotional-left (EL), and emotional-right (ER). *F*-ratio obtained from the repeated measures, with the factors emotion (Em) and side (S). None of the *F* values obtained were statistically significant.

NO EMOTIONAL POP-OUT IN NATURAL SCENE VIEWING

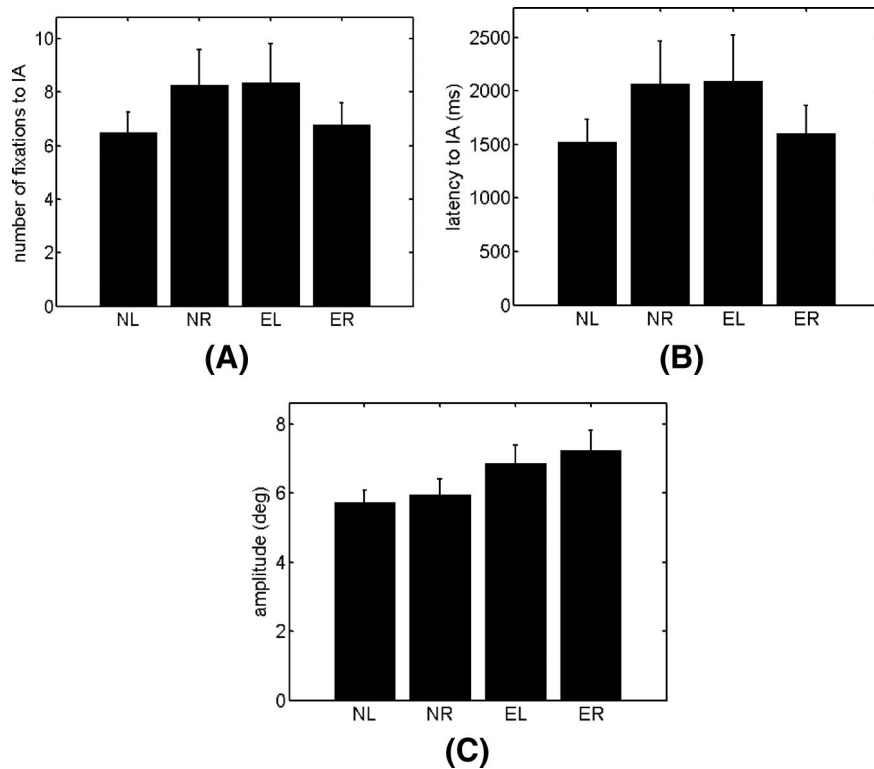


Figure 2. Capture of attention. Mean value and standard error of the number of fixations (A), latency (B) to IA, and amplitude of the first fixation to IA (C) across the four conditions. NL and NR indicate neutral left and neutral right, respectively, and EL and ER indicate emotional left and emotional right. See numeric values in Table 1.

First-pass number of fixations and time. We measured the number of fixations and time spent between the very first fixation within the target IA and the first subsequent fixation outside the IA.

First-pass number of fixations showed a significant difference between the neutral ($M = 2.40$, $SE = 0.21$) and emotional ($M = 3.92$, $SE = 0.37$) conditions: $t(23.3) = 3.56$, $p < .02$. More fixations were placed on the emotional than neutral target.

Similarly, the time spent during the first pass of the IA was longer for the emotional targets ($M = 1253.7$ ms, $SE = 93.9$) than

for the neutral targets ($M = 666.1$ ms, $SE = 71.4$): $t(30) = 4.98$, $p < 10^{-4}$.

Total number of fixations and dwell time. Finally, we measured the total number of fixations and the total fixation time spent within the IAs.

The average total number of fixations within the IA for emotional targets ($M = 11.40$, $SE = 1.52$) was not significantly higher than for neutral targets ($M = 8.22$, $SE = 0.83$): $t(23.14) = 1.84$, $p > .07$. However, the average total time spent within the IA was significantly longer for the emotional targets ($M = 3748.4$ ms,

Table 2
Hold of Attention: Summary

	Conditions		Comparison	
	Neutral	Emotional	Stat.	Value
First fixation duration (ms)	<i>Mdn</i> 255.3	<i>Mdn</i> 249.4	<i>T</i>	282
First-pass number of fixations	2.40 (.21)	3.92 (.37)	<i>t</i>	3.56*
First-pass duration (ms)	666.1 (71.4)	1,253.7 (93.9)	<i>t</i>	4.98**
Total number of fixations in IA	8.22 (.83)	11.40 (1.52)	<i>t</i>	1.84
Total IA dwell time (ms)	2,464.2 (241.4)	3,748.4 (444.8)	<i>t</i>	2.54*

Note. Median or mean and (standard error) of the “hold of attention” variables for the two conditions: neutral and emotional. Rank-sum (*T*) or *t*-score (*t*) values from the two independent sample comparison are given.

* $p < .05$, two-tailed. ** $p < .01$, two-tailed.

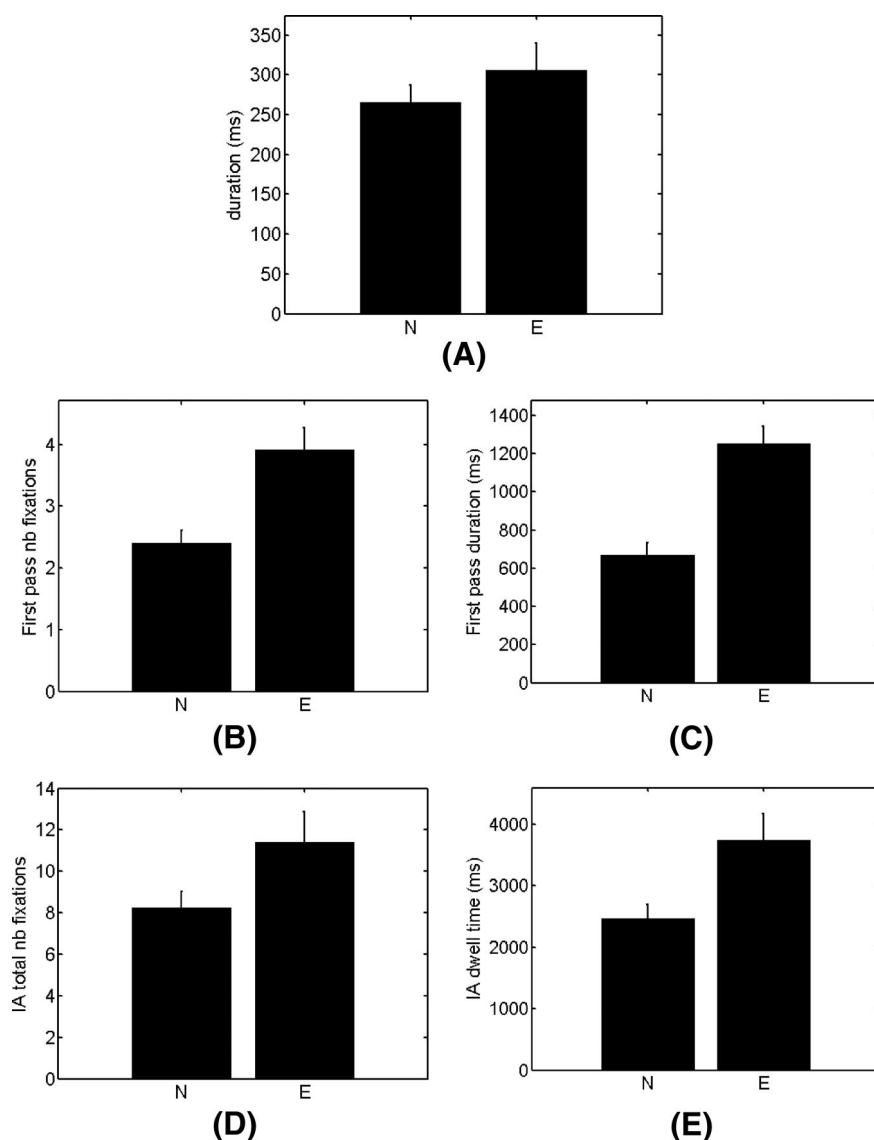


Figure 3. Hold of attention. Mean value and standard error of the first IA fixation duration (A), the first-pass number of fixations (B) and duration (C), the total IA number of fixations (D), and dwell time (E). N and E indicate neutral and emotional conditions, respectively. See numeric values in Table 2.

$SE = 444.8$) than for the neutral targets ($M = 2464.2$ ms, $SE = 241.4$): $t(23.1) = 2.54$, $p < .02$.

Discussion

One of the main aims of this study was to test for earlier detection of emotional target items when embedded within an entire natural image. Previous research suggests the existence of an exogenous drive of eye movements by peripherally attended emotional stimuli (see Calvo & Lang, 2004; Nummenmaa et al., 2006, 2009; Alpers, 2008; Becker & Detweiler-Bedell, 2009). However, our experiment suggests that when embedded in a scene, this exogenous drive disappears. At the same time, we found that once fixated, emotional items hold attention longer than neutral ones, which is in line with previous

research reporting delayed attention disengagement or hold of attention to emotional stimuli (Calvo & Lang, 2004; Nummenmaa et al., 2006; Fox, Russo, Bowles, & Dutton, 2001; Fox, Russo, & Dutton, 2002) and part of the scene perception research reporting hold of attention to semantically incongruous items (De Graef et al., 1990; Henderson et al., 1999; Gareze & Findlay, 2007; Castelhana et al., 2009; Vö & Henderson, 2009; Rayner et al., 2009).

We also found no effect of the position of the target stimulus, whereas previous research has suggested a right-hemisphere advantage for emotional stimuli processing (e.g., Keil et al., 2005; Calvo & Nummenmaa, 2007; Calvo & Avero, 2008). In particular, Alpers (2008) used a paradigm similar to Calvo and Lang (2004) and found that emotional stimuli were fixated

earlier only when positioned on the left visual hemifield. It should be noted, however, that tighter controls in Alpers (2008) would have made the claim stronger (e.g., comparison of saliency between stimulus groups; an additional condition to assess a potential eye-movement bias toward the left side).

The lack of attentional capture by emotional stimuli cannot be attributed to a lack of differential emotional impact on the participants, because significant differences in valence and arousal were found from the values given by independent raters (see Appendix). We also controlled for low-level saliency, using a computational saliency model (Itti & Koch, 2001): No difference between the two target groups was found.

We tried to cover a wide range of stimuli (e.g., fearful face, couple kissing, animal, etc.). This heterogeneity in the nature of the target might be seen as a weakness, because different emotions are not processed the same way and will not generate the same reaction: A cute cat will probably not attract the eye the same way as a face covered with blood. Further, given the small number of stimuli, we did not look separately at the differential effects of positively and negatively valenced targets. This said, previous studies on emotion have also used heterogeneous emotional stimuli, in particular when using the IAPS database, and the effects of negatively and positively valenced stimuli on eye movements reported, so far, are qualitatively similar, with perhaps faster attentional capture by negative stimuli and longer hold of attention by positive stimuli (Calvo & Lang, 2004; Nummenmaa et al., 2006; Alpers, 2008). Importantly, we found significantly higher IA first-pass number of fixations and dwell time for emotional stimuli, which supports the idea that our manipulation was strong enough to elicit a modulation in the scene-exploration process.

Although our results are inconsistent with previous eye-movement studies looking at emotional stimuli in isolation, they are highly consistent with the body of data looking at eye movements and scene perception (De Graef et al., 1990; Henderson et al., 1999; Gareze & Findlay, 2007; Castelhana et al., 2009; Vö & Henderson, 2009). The majority of experimental results indicate that gist-inconsistent targets do not elicit earlier fixations than gist-consistent ones. However, they do hold attention longer once fixated. We can argue that both gist-inconsistent and emotional items are behaviorally relevant. Gist-inconsistent items are more informative about the environment than gist-consistent ones, whereas emotional items are behaviorally relevant because of their intrinsic motivational value. This is illustrated by the fact that both gist-inconsistent and emotional items are fixated more than gist-consistent and neutral ones, respectively. It should be noted, though, that earlier fixations to inconsistent objects have been reported in some studies (Loftus & Mackworth, 1978; Becker et al., 2007; Underwood & Foulsham, 2006; Gareze & Findlay, 2007; Underwood et al., 2008). Interestingly, this discrepancy between studies has been partly attributed to a difference in sparsity of the scenes (Vö & Henderson, 2009). Less-cluttered scenes enable participants to detect semantic inconsistencies more easily.

Similarly, differences in experimental design and stimuli are likely to account for the differences between our results and previous eye-movement studies using emotional stimuli. First, each stimulus used in our study consisted of an individual scene presented on a full screen. This is in contrast with the paradigms

used in Calvo and Lang (2004), Nummenmaa et al. (2006, 2009), and Becker and Detweiler-Bedell (2009), which consisted of two or four peripherally presented images with a fixation point in the center of the screen. In our case, foveal load was high from stimulus onset, which was not the case in the other paradigms. Our results are in line with Calvo and Nummenmaa (2007), who reported that foveal load impairs the processing of peripherally presented emotional stimuli.

Second, our target items were embedded in a whole image. Target search and previous eye-tracking paradigms have focused on the effects of images presented simultaneously to the participant. In those studies, the images are probably seen by the participant as independent, unrelated entities, which are localized and separated in the visual field and can contain unrelated objects. Each of them can thus be processed as a whole, independently from each other, and an emotional and semantic gist can be extracted from each entity. In our case, objects cannot be seen independently, because they are all linked within the image. Additionally, some of our emotional target items were significantly smaller than the images used in previous research (and, in particular, Calvo & Lang, 2004; Nummenmaa et al., 2006, 2009). In Calvo, Nummenmaa, and Hyönä (2008), it is suggested that the processing of the emotional gist of images may come from a “fast” subcortical route (see Le Doux, 1995), which would project to the amygdala, via the superior colliculus. Neurons of the superior colliculus respond to stimuli situated peripherally and containing low spatial frequencies (Miller, Pasik, & Pasik, 1980; Rodman, Gross, & Albright, 1989); therefore, some of our small-sized targets might not have been able to activate this pathway. However, the involvement of this subcortical pathway in visual emotional processing is still debated (see Pessoa & Ungerleider, 2004; Storbeck, Robinson, & McCourt, 2006). In any case, we can hypothesize that the effects observed in previous studies are due to the “emotional gist” of individual images. If this is the case, our results make sense, because the target items were not seen as independent from the rest of the scene. Semantic and emotional information for each element of the image was thus more difficult to process.

Third, the explicit task given to the participant was to memorize the scenes for a subsequent memory test. This task was unrelated to emotional appraisal of the stimuli presented, as opposed to Nummenmaa et al. (2006), and is arguably more complex than free viewing (which was the task given in Calvo & Lang, 2004; Nummenmaa et al., 2006; and Becker & Detweiler-Bedell, 2009) or than asking a participant to saccade to a given location (Nummenmaa et al., 2009). Additionally, in our experiment, 15 s were given to the participants to explore and memorize each scene. This is a longer display time than what has been typically used in previous eye movement research (3 s in Calvo & Lang, 2004; Nummenmaa et al., 2006; 8 s in Alpers, 2008; and 4 s in Becker & Detweiler-Bedell, 2009). It is possible that with a shorter display time, allocation of attention has to be rushed in order to extract the most relevant information from the scenes. This may increase the role of early attentional processes. The measures of attentional capture by emotional stimuli might, therefore, be less sensitive in our design for this reason.

Finally, in previous paradigms, all stimuli presented in an experiment or block had many structural and semantic similarities, facilitating anticipation and expectation from participants. In the

search paradigms cited earlier, 2×2 or 3×3 matrices of images were used. No more than four semantic categories of objects were used in a single block, with a direct link between semantic category and affect. For example, in Öhman et al. (2001), all inanimate objects (i.e., mushrooms and flowers) were fear-irrelevant, whereas all animals (i.e., spiders and snakes) were fear-relevant. In Calvo and Lang (2004), Nummenmaa et al. (2006, 2009), and Calvo et al. (2008), on every trial, one image was presented in each hemifield. In Calvo and Lang (2004) and Nummenmaa et al. (2006), all images representing inanimate objects were neutral controls, whereas up to two thirds of the images representing people were emotional, enabling participants to expect an emotional content in images representing people. In Becker and Detweiler-Bedell (2009), four faces were presented peripherally. The emotional expressions were limited to neutral, fearful, and happy. In our paradigm, scenes had different layouts and contents, whereas target locations and nature varied for each stimulus. We think that these differences considerably reduced expectation and anticipation effects from participants.

Considering the points discussed above, our results make sense when put in the context of competition for limited resources. It has been observed with fMRI that enhanced activation of the amygdala and visual areas by emotional faces (vs. neutral faces) was only present when the faces were attended (Pessoa, McKenna, Gutierrez, & Ungerleider, 2002). Pessoa and Ungerleider (2004) interpreted these results in terms of limited attentional resources: Task-irrelevant emotional faces are processed only if sufficient resources are available. The researchers went further, hypothesizing that attention is a *sine qua non* for processing emotional faces. Event-related potential (ERP) recordings have led to similar observations, using facial stimuli (Holmes, Vuilleumier, & Eimer, 2003) and IAPS pictures (Schupp et al., 2007).

Our results, seemingly contradicting previous research on attention and emotional stimuli, are in line with scene-perception data, in which the attraction of attention by semantically discrepant objects may depend on the availability of attentional processing resources, which in turn may directly depend on stimulus complexity. In our case, the task was demanding and stimuli were highly complex and cluttered, reducing expectation and anticipation effects from the participants. In light of the capacity-limited attentional resources view, these conditions may be sufficient to prevent an earlier attentional shift toward emotional items in realistic scenes.

Conclusion

We conducted a study assessing the capture of overt attention by emotional stimuli embedded within a complex scene. In contrast with previous research on eye movement using emotional stimuli and sparser displays, we found that emotional targets did not attract attention more than neutral targets in natural scenes. However, once fixated, emotional targets held attention for a longer time. By making participants rate the targets for valence and arousal, we eliminated the hypothesis that our targets had a null emotional impact. We also controlled for low-level pop-out artifacts by comparing targets' visual saliencies outputted by a computational model (Itti & Koch, 2000). We explained the absence of an emotional pop-out effect by arguing that because of stimulus complexity, the task is attentionally demanding, preventing para-

focal emotional information from being processed given the limited attentional resources available. Further research on eye movement and emotion should focus on the manipulation of target nature and size, stimulus complexity, task difficulty, initial foveal load, participants' anticipation by manipulating stimulus variability, and also investigate the effects of individual differences, such as trait or state of anxiety.

References

- Alpers, G. (2008). Eye-catching: Right hemisphere attentional bias for emotional pictures. *Laterality: Asymmetries of Body, Brain & Cognition*, *13*(2), 158–178.
- Bar-Haim, Y., Lamy, D., Pergamin, L., Backermans-Kranenburg, M. J., & van Ijzendoorn, M. H. (2007). Threat-related attentional bias in anxious and nonanxious individuals: A meta-analytic study. *Psychological Bulletin*, *133*(1), 1–24.
- Becker, M. W., & Detweiler-Bedell, B. (2009). Early detection and avoidance of threatening faces during passive viewing. *The Quarterly Journal of Experimental Psychology*, *62*(7), 1257–1264.
- Becker, M. W., Pashler, H., & Lubin, J. (2007). Object-intrinsic oddities draw early saccades. *Journal of Experimental Psychology: Human Perception and Performance*, *33*(1), 20–30.
- Blanchette, I. (2006). Snakes, spiders, guns, and syringes: How specific are evolutionary constraints on the detection of threatening stimuli? *The Quarterly Journal of Experimental Psychology*, *59*(8), 1484–1504.
- Calvo, M. G., & Avero, P. (2008). Affective priming of emotional pictures in parafoveal vision: Left visual field advantage. *Cognitive, Affective, & Behavioral Neuroscience*, *8*(1), 41–53.
- Calvo, M. G., & Lang, P. J. (2004). Gaze patterns when looking at emotional pictures: Motivationally biased attention. *Motivation and Emotion*, *28*(3), 221–243.
- Calvo, M. G., & Nummenmaa, L. (2007). Processing of unattended emotional visual scenes. *Journal of Experimental Psychology: General*, *136*(3), 347–369.
- Calvo, M. G., Nummenmaa, L., & Hyönä, J. (2008). Emotional scenes in peripheral vision: Selective orienting and gist processing, but not content identification. *Emotion*, *8*(1), 68–80.
- Castelhano, M. S., Mack, M. L., & Henderson, J. M. (2009). Viewing task influences eye movement control during active scene perception. *Journal of Vision*, *9*(3), 15.
- Cave, K., & Batty, M. (2006). From searching for features to searching for threat: Drawing the boundary between preattentive and attentive vision. *Visual Cognition*, *14*(4), 629–646.
- Coelho, C., Cloete, S., & Wallis, G. (2010). The face-in-the-crowd effect: When angry faces are just cross(es). *Journal of Vision*, *10*(7), 14.
- De Graef, P., Christiaens, D., & d'Ydewalle, G. (1990). Perceptual effects of scene context on object identification. *Psychological Research*, *52*(4), 317–329.
- Flykt, A. (2005). Visual search with biological threat stimuli: Accuracy, reaction times, and heart rate changes. *Emotion*, *5*(3), 349–353.
- Flykt, A. (2006). Preparedness for action: Responding to the snake in the grass. *The American Journal of Psychology*, *119*(1), 29–43.
- Fox, E., Griggs, L., & Mouchlianitis, E. (2007). The detection of fear-relevant stimuli: Are guns noticed as quickly as snakes? *Emotion*, *7*(4), 691–696.
- Fox, E., Russo, R., Bowles, R., & Dutton, K. (2001). Do threatening stimuli draw or hold visual attention in subclinical anxiety? *Journal of Experimental Psychology: General*, *130*(4), 681–700.
- Fox, E., Russo, R., & Dutton, K. (2002). Attentional bias for threat: Evidence for delayed disengagement from emotional faces. *Cognition & Emotion*, *16*(3), 355–379.
- Gareze, L., & Findlay, J. M. (2007). Absence of scene context effects in object detection and eye gaze capture. In R. van Gompel, M. Fischer, W.

- Murray, & R. Hill (Eds.), *Eye movements: A window on mind and brain*. Oxford: Elsevier.
- Henderson, J. M., & Hollingworth, A. (1999). High-level scene perception. *Annual Review of Psychology, 50*, 243–271.
- Henderson, J. M., & Smith, T. J. (2009). How are eye fixation durations controlled during scene viewing? Further evidence from a scene onset delay paradigm. *Visual Cognition, 17*(6), 1055–1082.
- Henderson, J. M., Weeks, P. A., & Hollingworth, A. (1999). The effects of semantic consistency on eye movements during complex scene viewing. *Journal of Experimental Psychology: Human Perception and Performance, 25*(1), 210–228.
- Holmes, A., Vuilleumier, P., & Eimer, M. (2003). The processing of emotional facial expression is gated by spatial attention: Evidence from event-related brain potentials. *Cognitive Brain Research, 16*(2), 174–184.
- Itti, L., & Koch, C. (2000). A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Research, 40*, 1489–1506.
- Keil, A., Moratti, S., Sabatinelli, D., Bradley, M. M., & Lang, P. J. (2005). Additive effects of emotional content and spatial selective attention on electrocortical facilitation. *Cerebral Cortex, 15*(8), 1187–1197.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2008). International affective picture system (IAPS): Affective ratings of pictures and instruction manual. Tech. Rep. No. A-8, University of Florida, Gainesville, FL.
- Le Doux, J. E. (1995). In search of an emotional system in the brain: Leaping from fear to emotion and consciousness. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 1049–1061). Cambridge, MA: MIT Press.
- Lipp, O. V., Derakshan, N., Waters, A. M., & Logies, S. (2004). Snakes and cats in the flower bed: Fast detection is not specific to pictures of fear-relevant animals. *Emotion, 4*(3), 233–250.
- Loftus, G. R., & Mackworth, N. H. (1978). Cognitive determinants of fixation location during picture viewing. *Journal of Experimental Psychology: Human Perception and Performance, 4*(4), 565–572.
- Miller, M., Pasik, P., & Pasik, T. (1980). Extrageniculostriate vision in the monkey. VII. Contrast sensitivity functions. *Journal of Neurophysiology, 43*(6), 1510–1526.
- Nummenmaa, L., Hyönä, J., & Calvo, M. G. (2006). Eye movement assessment of selective attentional capture by emotional pictures. *Emotion, 6*(2), 257–268.
- Nummenmaa, L., Hyönä, J., & Calvo, M. G. (2009). Emotional scene content drives the saccade generation system reflexively. *Journal of Experimental Psychology: Human Perception and Performance, 35*(2), 305–323.
- Nuthmann, A., Smith, T. J., Engbert, R., & Henderson, J. M. (2010). CRISP: A computational model of fixation durations in scene viewing. *Psychological Review, 117*(2), 382–405.
- Öhman, A., Flykt, A., & Esteves, F. (2001). Emotion drives attention: Detecting the snake in the grass. *Journal of Experimental Psychology: General, 130*(3), 446–478.
- Pessoa, L., McKenna, M., Gutierrez, E., & Ungerleider, L. G. (2002). Neural processing of emotional faces requires attention. *Proceedings of the National Academy of Sciences, of the USA, 99*(17), 11458–11463.
- Pessoa, L., & Ungerleider, L. G. (2004). Neuroimaging studies of attention and the processing of emotion-laden stimuli. *Progress in Brain Research, 144*, 171–182.
- Rayner, K., Castelano, M. S., & Yang, J. (2009). Eye movements when looking at unusual/weird scenes: Are there cultural differences? *Journal of Experimental Psychology: Learning, Memory, and Cognition, 35*(1), 254–259.
- Rodman, H. R., Gross, C. G., & Albright, T. D. (1989). Afferent basis of visual response properties in area mt of the macaque. I. Effects of striate cortex removal. *Journal of Neuroscience, 9*(6), 2033–2050.
- Schupp, H. T., Stockburger, J., Bublitzky, F., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2007). Explicit attention interferes with selective emotion processing in human extrastriate cortex. *BMC Neuroscience, 8*, 16.
- Soares, S., Esteves, F., & Flykt, A. (2009). Fear, but not fear-relevance, modulates reaction times in visual search with animal distractors. *Journal of Anxiety Disorders, 23*(1), 136–144.
- Spielberger, C. D., Gorsuch, R., & Lushene, R. (1970). *The State-Trait Inventory (STAI) test manual*. Palo Alto, CA: Consulting Psychology Press.
- Storbeck, J., Robinson, M. D., & McCourt, M. E. (2006). Semantic processing precedes affect retrieval: The neurological case for cognitive primacy in visual processing. *Review of General Psychology, 10*(1), 41–55.
- Tipples, J., Young, A. W., Quinlan, P., Broks, P., & Ellis, A. W. (2002). Searching for threat. *The Quarterly Journal of Experimental Psychology: Section A, 55*(3), 1007–1026.
- Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., . . . Nelson, C. A. (2009). The NimStim set of facial expressions: Judgments from untrained research participants. *Psychiatry Research, 168*(3), 242–249.
- Underwood, G., & Foulsham, T. (2006). Visual saliency and semantic incongruency influence eye movements when inspecting pictures. *The Quarterly Journal of Experimental Psychology, 59*(11), 1931–1949.
- Underwood, G., Templeman, E., Lamming, L., & Foulsham, T. (2008). Is attention necessary for object identification? Evidence from eye movements during the inspection of real-world scenes. *Consciousness and Cognition, 17*(1), 159–170.
- Võ, M. L.-H., & Henderson, J. M. (2009). Does gravity matter? Effects of semantic and syntactic inconsistencies on the allocation of attention during scene perception. *Journal of Vision, 9*(3), 15.
- Vuilleumier, P. (2005). How brains beware: Neural mechanisms of emotional attention. *Trends in Cognitive Sciences, 9*(12), 585–594.

(Appendix follows)

Appendix

Stimulus Validation Study

Sixteen participants (10 female) who did not take part in the main experiment were asked to rate the emotional valence and arousal of each target. Participants were asked to rate the target present in each of the images shown. Its location was indicated by a superimposed red dotted circle around the target. Block content was similar as in the main experiment, and stimulus presentation order was randomized for each participant. An instruction sheet explaining the meaning of emotional valence and arousal was given. The head of the participant was fixed in order to ensure similar conditions, such as viewing distance as in the main experiment. Before stimulus onset, a fixation point was displayed for a random duration between 2 and 5 s. The image was then displayed full screen for 10 s, before a dialog box appeared in front of the image, enabling the participant to give their rating. The image was still displayed during the rating, and the participant had no time constraint. Once the rating was over, participants were given their compensation (£3) and signed a receipt.

STAI score differences between participants from the main study (State: $M = 35.58$, $SE = 2.12$; Trait: $M = 38.63$, $SE = 2.27$) and from the validation study (State: $M = 32.88$, $SE = 2.01$; Trait: $M = 36.81$, $SE = 2.35$) were nonsignificant: $t_{\text{state}}(30) = .96$ ($p > .3$) and $t_{\text{trait}}(30) = .55$ ($p > .5$). On average, mean valence ratings per participant were higher for positive ($M = 2.58$, $SE = .12$) than neutral ($M = 1.09$, $SE = .11$) targets: $t_{\text{P-Nu}}(29.77) = 9.82$ ($p < 10^{-10}$). Mean valence ratings per participant were lower for negative ($M = -2.06$, $SE = .28$) than for neutral targets: $t_{\text{Nu-Ng}}(19.63) = 10.63$ ($p < 10^{-8}$). Mean arousal ratings per participant were higher for both positive ($M = 3.31$, $SE = .25$) and negative ($M = 4.54$, $SE = .39$) than neutral ($M = 2.27$, $SE = .15$): $t_{\text{P-Nu}}(25.14) = 3.59$ ($p < .01$) and $t_{\text{Nu-Ng}}(19.66) = 5.48$ ($p < 10^{-4}$).

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Basic Neuroscience

Systematic biases in early ERP and ERF components as a result of high-pass filtering

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H I G H L I G H T S

- ▶ We evaluate artifacts due to high-pass filtering used to preprocess ERP/ERF data.
- ▶ High-pass filtering can lead to systematic biases between conditions.
- ▶ About 40% of surveyed papers used methods that can lead to such biases.
- ▶ Guidelines to minimize high-pass filtering artifacts are provided.

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The event-related potential (ERP) and event-related field (ERF) techniques provide valuable insights into the time course of processes in the brain. Because neural signals are typically weak, researchers commonly filter the data to increase the signal-to-noise ratio. However, filtering may distort the data, leading to false results. Using our own EEG data, we show that acausal high-pass filtering can generate a systematic bias easily leading to misinterpretations of neural activity. In particular, we show that the early ERP component C1 is very sensitive to such effects. Moreover, we found that about half of the papers reporting modulations in the C1 range used a high-pass digital filter cut-off above the recommended maximum of 0.1 Hz. More generally, among 185 relevant ERP/ERF publications, 80 used cutoffs above 0.1 Hz. As a consequence, part of the ERP/ERF literature may need to be re-analyzed. We provide guidelines on how to minimize filtering artifacts.

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1. Introduction

Event-related potentials and event-related fields (ERP/ERF), generated by averaging electro- and magneto-encephalographic (EEG/MEG) signals respectively, provide unique insights into human brain processes with unrivalled time resolution. Because the signal is weak and noisy, raw data typically require several pre-processing steps, including filtering and removal or attenuation of artifacts, before epoching and averaging over trials and participants. Filtering is an efficient way to increase the signal-to-noise ratio by removing frequency bands that mainly contain non-neural or irrelevant information. In EEG, both high frequencies (typically above 30 or 40 Hz), as well as low frequencies (typically below 1 Hz or less) are often filtered out. There has been a recent interest in the effects of filtering on ERP signals and their interpretation. In

VanRullen (2011), the dangers of low-pass filtering and its effect on estimating onset times were examined. In a related commentary (Rousselle, 2012), it was shown that the effects of low-pass filtering might be limited, but that high-pass filtering can lead to problematic onset time distortions, which can be largely circumvented by using causal filtering. The present paper focuses on the early C1 component and the removal of low frequencies.

Low frequency signals can be of non-neural origin, such as electrodermal activity, drying, or chemical stabilization of the electrolyte due to thermal changes and contact with the skin (see e.g., Hennighausen et al., 1993; Tallgren et al., 2005; Vanhatalo et al., 2005). In addition, the neural signal itself contains drifts and low frequencies, that can have cognitive significance (Grey Walter et al., 1964; Fitzgerald et al., 2001; Monto et al., 2008; Palva and Palva, 2012; Vanhatalo et al., 2005; Pastor et al., 2008) but might not be relevant for the study.

Low frequency signals are removed with a high-pass filter. High-pass filtering can be understood as a way to force the average signal to be zero within a time window of a certain duration, thus eliminating slowly varying components. The higher the cut-off

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frequency (the frequency at which a 3 dB attenuation is attained), the shorter the time window, and the shorter the time during which the signal is allowed to depart from zero. As we shall demonstrate, this can lead to significant distortions of the data.

The layout of this paper is as follows. After discussing some principles behind commonly used filters, we apply different filters to our own EEG data. We demonstrate that high-pass filtering with an excessively high cut-off frequency can introduce systematic distortions to the signal and can lead to false results and interpretations. Although a well-known textbook warns of the dangers of filters and recommends a maximum cut-off value of 0.1 Hz in high-pass filters (Luck, 2005), a review of published papers reveals that many studies do not conform to this recommendation, which may have led to false conclusions, in particular concerning early modulations.

2. Filtering alters the shape of the signal

Although filtering can improve the signal-to-noise ratio, it can also distort the signal in an unwanted manner. A commonly known distortion introduced by filtering, often described in EEG/MEG data processing software manuals, is phase delay. Phase delay shifts the frequency components in time, which is undesirable given the core importance of the event timing in ERP/ERFs. Phase delay is particularly an issue for causal filters, for which the output at a given time only depends on past and present, but not future, input. Linear frequency-dependent phase delay, meaning that all frequencies will be delayed by the same amount, can be implemented with causal Finite Impulse Response (FIR) filters. This minimizes distortion of the overall shape of the signal, but may generate large delays up to hundreds of milliseconds. Infinite Impulse Response (IIR) high-pass filters, such as Butterworth or Ellipsoid filters, commonly implemented in EEG/MEG software packages, can achieve comparable filtering performance to FIR filters with fewer computational resources and with less delay (see e.g., Lynn, 1989). However, their

non-linear phase response can generate strong distortions of the signal.

Because of the drawbacks of causal filtering and with the advent of computerized data processing and storage, acausal filtering has gained popularity. As the output of an acausal filter depends both on past and future input, acausal filters are applied offline on stored data. The advantage of acausal filters is that they can be constructed to have no phase delay at all, in which case they are called zero phase-shift filters. Commonly, these acausal filters are implemented with a causal filter run twice over the data: once forwards and once backwards. Apart from doubling the order of the filter, the backwards pass counterbalances any delays that the forward run introduces. Because of the absence of delay and the reduced distortions induced by forward-backward filters, guidelines and software manuals more or less explicitly advise their use (see e.g., Picton et al., 2000). In the following, we use the term acausal to indicate zero phase-shift acausal filters, as these are the most relevant for EEG/MEG processing.

Fig. 1A shows the effect of a causal Butterworth filter applied forwards, and applied both forwards and backwards for two artificial example signals: a boxcar signal (left) and an artificial waveform (right). The artificial waveform was constructed with a sum of three Gaussian functions: $f(t) = \sum_{i=1}^3 a_i e^{-(t-m_i)^2/2s_i^2}$ with parameters $a_1 = 1 \mu\text{V}$, $m_1 = 0.1 \text{ s}$, $s_1 = 0.02 \text{ s}$; $a_2 = -0.5 \mu\text{V}$, $m_2 = 0.2 \text{ s}$, $s_2 = 0.04 \text{ s}$; $a_3 = 3 \mu\text{V}$, $m_3 = 0.4 \text{ s}$, $s_3 = 0.07 \text{ s}$. Due to the non-linearity of the phase response of the Butterworth filter, the shape of the signals is significantly distorted in the causal case (top row). Note however that all the distortions happen after signal onset. In the forward-backward case, distortions are remarkably reduced compared to the causal case, but the signal is distorted more than one second prior to signal onset (bottom row).

These distortions can lead to misinterpretation, in particular in the typical situations where one studies the onset of a particular component, or of a divergence between two waveforms. Fig. 1B

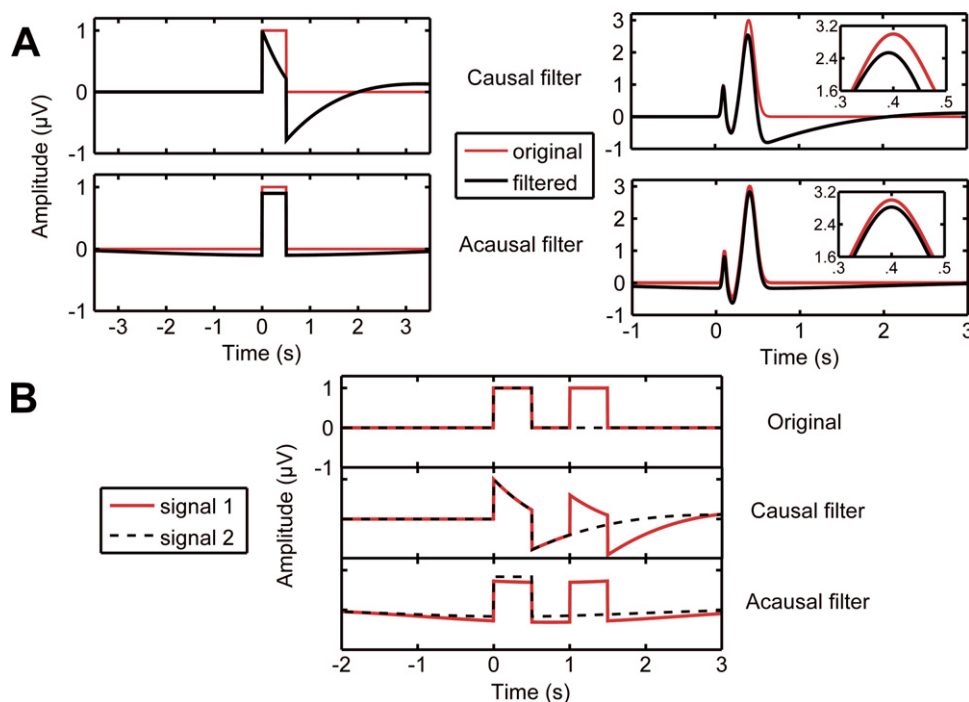


Fig. 1. The effect of causal and acausal high-pass filtering on artificial signals. (A): A boxcar signal (left) and an artificial waveform (right) were filtered with one forward pass of the filter (top), and with a forward and backward pass (bottom). The acausal filter preserves the shape of the signal much better than the causal filter, and, as opposed to the causal filter, preserves the latency of the third peak of the artificial waveform (see detail). However, it induces distortion before the onset of the signal. (B): Two artificial signals differing only between 1 and 1.5 s (top). When filtered with the causal filter (middle), the two signals differ from $t = 1 \text{ s}$, like the original signals. The acausal filter (bottom), however, introduces differences even before the onset of both signals at $t = 0$. The filter was a 3rd order Butterworth filter with 0.5 Hz cut-off frequency.

illustrates this point, showing two signals that are initially the same, but differ after one second (top). When a causal filter is applied, the timing of the divergence of the two signals is preserved (middle). However, after applying an acausal filter, differences between the two signals are observable where they were identical before filtering, even before the onset of the two signals (bottom). The difference in the later part contaminates the early part of the waveform.

With a causal filter, a difference in the unfiltered waveforms may lead to differences later in time, but cannot affect earlier timepoints, supporting inferences that the effect started at this time *at the latest*. However, with an acausal filter, distortions are spread both forward and backward in time. In this case, it is not possible to state when the effect starts: it can only be concluded that the waveforms differed at some point in time.

3. Effects of filtering on actual EEG data

To illustrate the problematic effects of filtering in practice, we submitted some of our own data to various high-pass filters. The original purpose of the experiment was to investigate the effects of spatial attention and facial expression on the C1 component of the visual ERP. The C1 component is characterized by a widespread centro-parietal negativity (or positivity) peaking before 100 ms, evoked by presenting stimuli in the upper (or lower) hemifield and using an average mastoid reference (Clark et al., 1995). The results of this experiment and its detailed interpretation will be presented elsewhere. Using these data, we show how high-pass filters can affect the shape of a real waveform, and how subsequent components can add systematic biases to earlier components and lead to erroneous interpretations. In addition, we show that filter parameters are critical for the proper interpretation of early components, and more particularly the C1 component.

3.1. Methods

3.1.1. Stimuli and procedure

Stimuli and procedure will be described in more detail elsewhere. All procedures were approved by the Psychology Department Ethical Committee at the University of Edinburgh. Twenty-four right-handed participants were first presented with an arrow near the fixation point, pointing left or right, for 200 ms. After an interstimulus interval of 750 ms, a facial stimulus was presented for 300 ms on the side congruent or incongruent to the cue arrow, and presented on the upper visual hemifield to elicit a negative C1 (Jeffreys and Axford, 1972; Clark et al., 1995). Facial stimuli showed three expressions: neutral, fearful, and happy. The experiment consisted of 1120 trials per participant, with 352 trials for the Happy facial expression condition, and 768 trials equally divided between the Neutral and Fearful conditions. Participants were instructed to press a button when detecting a happy face at the congruent location only (176 trials), while fixating on the fixation point.

3.1.2. Data acquisition

EEG was recorded using a BioSemi Active-Two system (BioSemi B.V., Amsterdam, Netherlands), which has a DC coupled amplifier. The activity at 64 Ag-AgCl scalp electrodes following the location and label of the extended 10–20 system (Jasper, 1958), along with 4 electrooculographic (EOG) electrodes (above and below the right eye, and on the outer canthi) and 2 mastoid electrodes, was digitized on 24 bits with a sample rate of 1024 Hz.

3.1.3. Data processing

Pre-processing was performed using the EEGLAB toolbox (Delorme and Makeig, 2004) under Matlab (Mathworks, Inc.,

Natick, MA, USA), and custom scripts. The EEG signal was first re-referenced to the average mastoids, and low-pass filtered with a cut-off value of $f_c = 40$ Hz, using the default FIR filter implemented in EEGLAB: a least square linear-phase filter of order 75 with a transition bandwidth (the range of frequencies between the bandcut and the bandpass) of 6 Hz, run forward and backward. Though it should be kept in mind that low-pass filters may also induce artifacts (VanRullen, 2011), the low amplitude of the higher frequencies in the EEG signal reduces the risk of serious alteration of the waveform. Rousselet (2012) found little artifactual effect of low-pass filtering on real EEG data. Furthermore, as this preliminary filtering step is done for all subsequent high-pass filtering conditions, it does not alter our conclusions on high-pass filtering. The continuous data were then resampled to 256 Hz. High-pass filters with cut-offs f_c of 0.05, 0.1, 0.5, and 1 Hz were then applied to study the effects of filtering. Testing lower cut-off values was found to be unnecessary as little effect was observable up to 0.1 Hz. We used the default EEGLAB parameters for this filtering step as well: the filters used were least square linear phase FIR high-pass filters run forward and backward. Their transition bandwidth was $0.15 \times f_c$ and their order $3 \times \text{fix}(f_s/f_c)$, with f_s the sampling frequency (256 Hz), and fix the function that rounds downwards to nearest integer. For each of the filtered sets of raw data, epoching was performed using facial stimulus onset time as time origin, and each channel was baselined using the 100 ms interval preceding stimulus onset. To remove artifactual epochs, a semi-automatic procedure was run on the non high-pass filtered data, labeling epochs containing EOG data beyond $70 \mu\text{V}$ in absolute value. The data were visually inspected and epochs containing artifacts were removed. The same trials were used for all filtering conditions. On average, 936 correctly answered and artifact-free trials per participant contributed to the grand-average ERP.

3.2. Data analysis

Voltage from electrodes P1, P2, CP1 and CP2 was averaged to generate the ERPs. For the C1 component, mean amplitude of the 50–100 ms interval was calculated. For the purpose of this paper, only results from the Congruent attentional condition are presented here. A one-way ANOVA with Emotion (Neutral, Fearful, Happy) was performed for each filter cut-off value. We tested for normality using a Kolmogorov–Smirnov test, and for sphericity using a Mauchly test. Normality hypotheses were confirmed. When indicated, a Greenhouse–Geisser (GG) correction was applied to compensate for sphericity violations.

4. Results

Fig. 2 shows grand-average ERPs for each emotional condition (Neutral, Fearful, Happy) averaged over all participants and the electrodes CP1, CP2, P1 and P2. Fig. 2A shows the waveforms without high-pass filtering. Fig. 2C zooms in on the waveform between –100 and 500 ms, containing the C1. After reaching a negative peak at 100 ms (as expected with stimuli presented in the upper visual hemifield, see Clark et al., 1995), the waveforms exhibit a globally positive-going excursion, peaking at around 500 ms. The amplitude of this deflection is largest in the Happy condition, which corresponds to target trials during which participants had to press a button.

High-pass filtering strongly affected the shape of the waveforms. As the cut-off frequency of the filter is increased, the late positive component disappears (Fig. 2B, E and F). But simultaneously, the early part of the waveform is pushed downwards. This effect is similar to the distortion observed in Fig. 1A (bottom row). Only

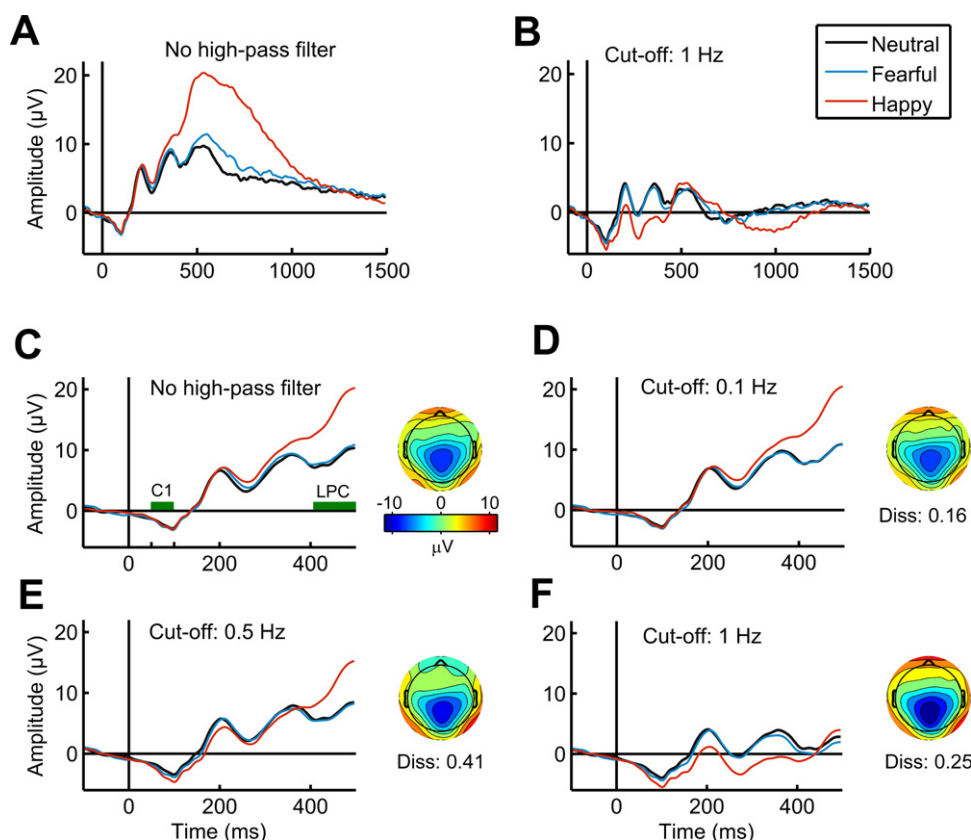


Fig. 2. The effect of filtering on ERP data from an experiment on emotional face processing. ERPs are averaged over all 24 participants, and over electrodes CP1, CP2, P1 and P2, for various high-pass cut-off frequencies, and for each experimental condition (Neutral, Fearful, and Happy). (A, B): ERPs from -100 to 1500 ms, without a high-pass filter (A), and with an acausal high-pass filter, a filter of cut-off of 1 Hz applied forward and backward (B). The shape of the waveform is drastically affected. The slow and later component disappears with filtering, and the earlier components are pushed downwards. (C–F): Zoom of the ERPs up to 500 ms post-stimulus onset. Raw data was high-pass filtered with an acausal filter, with different cut-off frequencies. The time windows used to quantify the C1 (50 – 100 ms) and the LPC (400 – 500 ms) are indicated in (C). Scalp topography calculated from the C1 time window is shown for each filter condition. The potential was re-referenced to the average. Dissimilarity indicates how each map is different from the non-filtered map. Due to eye-blink artifacts occurring after 500 ms, the ERPs shown in (A) and (B) were calculated using a subset of the epochs used in (C–F).

when a low cut-off frequency of 0.1 Hz was used, was the waveform not drastically affected (Fig. 2D).

In parallel with its impact on the shape of the ERP, scalp topographies (averaged across the latency period from 50 to 100 ms) are affected by filtering (Fig. 2C–F, insets). The indicated dissimilarity measures how each map is different from the non-filtered map. A dissimilarity of 0 means that the two maps are identical, and a dissimilarity of 2 means the two maps are inverted (see Lehmann and Skrandies, 1980). As a consequence, high-pass filtering may alter results for studies using topography information, such as microstate analysis, independent component analysis, or source reconstruction.

Next, we examined the apparent modulation of the C1 amplitude with experimental condition. Fig. 3A shows that the modulation strongly changes as a function of the cut-off value. Significance tests (Fig. 3B) show that, in our experiment, apparently reliable effects arise as the filter cut-off frequency increases, at 0.5 Hz ($F_{2,46} = 9.38$, $p < 10^{-3}$) and 1 Hz ($F_{2,46} = 9.53$, $p < 10^{-3}$), while there is no significant effect for lower cut-off values.

To better understand the mechanisms behind these effects, we tested directly whether the C1 effect observed at high cut-offs was due to a subsequent late component that contaminates C1 through the acausality of the filter. Late components are known to be affected by facial expression and target recognition (Eimer and Holmes, 2002; Picton, 1992; Rozenkrants and Polich, 2008). To quantify these effects, we measured the Late Positive Complex

(LPC) as the averaged waveform between 400 and 500 ms. Consistent with the literature, the LPC showed a larger positive excursion for the Happy faces target than for the other conditions ($F_{1,17,27,01} = 34.05$, $p < 10^{-5}$, GG corrected). We defined ΔLPC_{HN} (and ΔLPC_{FN}) as the change in LPC amplitude in the Happy versus Neutral conditions (resp. Fearful versus Neutral), in the *unfiltered* condition. Similarly, $\Delta C1_{HN}$ (and $\Delta C1_{FN}$) is the difference of C1 amplitude between the Happy and Neutral conditions (resp. Fearful and Neutral) in the *unfiltered* condition, and $\Delta C1_{HN}^{f_c=1}$ and $\Delta C1_{FN}^{f_c=1}$ in the *filtered* condition with a 1 Hz cut-off. We calculated these values for each participant.

To evaluate the link between the LPC and the C1 amplitude, we correlated ΔLPC with $\delta C1$, defined as the change in $\Delta C1$ caused by the filtering $\delta C1 = \Delta C1^{f_c=1} - \Delta C1$. $\delta C1$ is positive for most participants, as the C1 effect is larger with the high-pass filter than without (see e.g., Fig. 2C versus F). Fig. 4 shows the correlation between the Neutral/Happy modulation ΔLPC_{HN} and the change in C1 effect $\delta C1_{HN}$, and similarly for the Neutral/Fearful modulation (ΔLPC_{FN} and $\delta C1_{FN}$). We found a strong correlation in both cases ($\rho_{HN} = 0.95$, $p < 10^{-8}$, and $\rho_{FN} = 0.71$, $p = 10^{-4}$). The first correlation reflects the contamination by the large late positive amplitude in the Happy condition that can be observed in Fig. 2. The second correlation (Neutral/Fearful) is noteworthy and shows subtler effects. Although there is no statistically significant LPC effect ($t_{23} = 1.01$, $p = 0.32$), a clear correlation exists on the individual level, contributing to the significant C1 Neutral/Fearful effect in the filtered

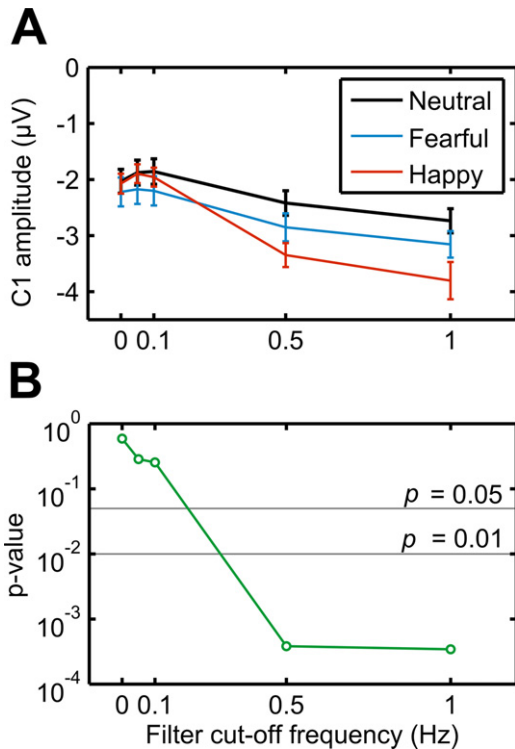


Fig. 3. Effects of high-pass cut-off frequency on the C1 component across experimental conditions. (A): Average amplitude at electrodes CP1, CP2, P1 and P2, between 50 and 100 ms, for each experimental condition (Neutral, Fearful, Happy), and for different cut-off values of the acausal FIR filter. (B): P-values from one-way ANOVAs. High cut-offs lead to highly significant, but erroneous, results. A cut-off of 0 Hz indicates that no high-pass filter was applied.

waveform ($t_{23} = 2.06, p = 0.05$). This shows that even portions of the grand-average waveform that do not show a significant effect can contribute to the bias.

To ensure that the C1 effect observed in the filtered waveform was indeed due to a subsequent component, we used a causal filter (4th order high-pass Butterworth filter with 1 Hz cut-off). While the waveform also appears distorted when compared with the waveform without high-pass filtering (see Fig. 5), we failed to find a significant C1 effect ($F_{2,46} < 1$). Together, these results confirm that the C1 effect in our data is due to subsequent components, in particular the LPC, and is completely artifactual.

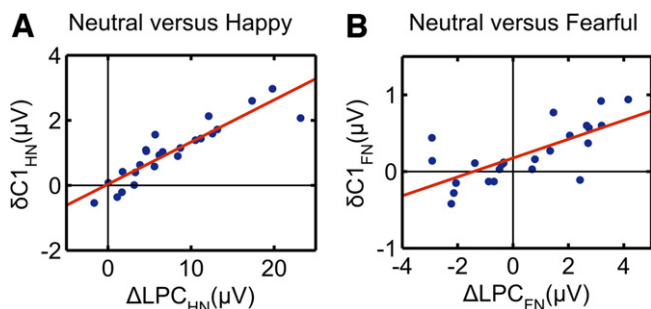


Fig. 4. Correlation between the LPC effect in the unfiltered condition and the change in the C1 effect between the unfiltered and filtered conditions, in the Neutral and Happy conditions (A) and the Neutral and Fearful conditions (B). Each point corresponds to a participant. The significant correlations show that the subsequent LPC effect, observable in the unfiltered waveforms (see Fig. 2A and C), contributes substantially to the systematic bias of the C1 component.

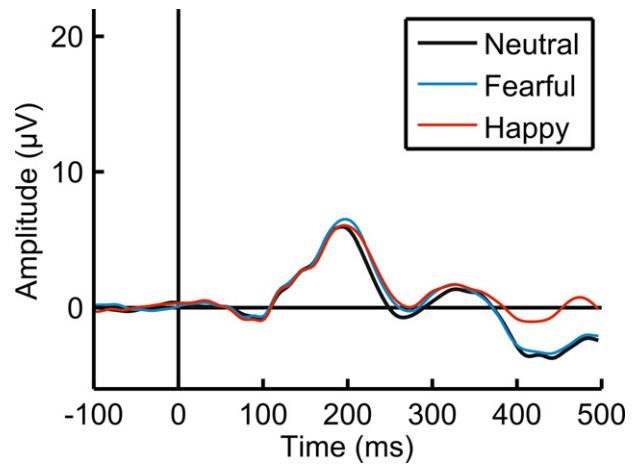


Fig. 5. ERP waveforms filtered with a causal high-pass filter. The filter used was a 4th order Butterworth filter of cut-off 1 Hz. The shape of the waveform is strongly altered, but no early artifactual C1 effect is present in comparison to the ERP generated after applying an acausal high-pass filter (cf. Fig. 2F). This is consistent with the hypothesis that the C1 effect observed with an acausal filter at the same cut-off value was due to signal differences occurring subsequently.

5. Discussion

In summary, we showed that high-pass filtering of the raw EEG data can distort the resulting ERP waveforms, and induce systematic biases between conditions. For this reason, high-pass filtering should be used parsimoniously in EEG/MEG data, and the cut-off frequency should be kept as low as possible under normal circumstances. Our analysis on real EEG data shows how a late slow component can induce a systematic bias in an earlier component when using commonly used acausal filters, which can lead to erroneous interpretations. We found a highly statistically significant modulation of C1 by stimulus condition, but showed that it was completely artifactual.

The recent years have been characterized by an increasing interest in the very early visual components, happening before 100 ms after stimulus onset, and thought to be associated with activity in the striate (Jeffreys and Axford, 1972; Clark et al., 1995), and perhaps extrastriate visual cortices (Foxe and Simpson, 2002; Ales et al., 2010, but see Kelly et al., 2012). When peaking, these components are often labeled C1 and M90 for the event-related potential (ERP) and event-related field (ERF) waveforms respectively. These early processes, and in particular, the C1 component, were thought to be only modulated by the physical characteristics of the triggering stimulus, but immune to endogenous modulations, and more specifically attention (Martínez et al., 1999; Noesselt et al., 2002; Di Russo et al., 2003; Hillyard et al., 1998). More recently, however, C1 modulations by attention and attentional load (Khoe et al., 2005; Wu et al., 2005; Kelly et al., 2008; Fu et al., 2009; Rauss et al., 2009; Fu et al., 2010a; Rauss et al., 2011), perceptual learning (Pourtois et al., 2008), anxiety (Eldar et al., 2010), and emotional stimuli or faces (Pourtois et al., 2004; Stolarova et al., 2006; West et al., 2011) were reported. Similarly, very early ERF modulations by attention (e.g., Poghosyan and Ioannides, 2008; Ioannides and Poghosyan, 2012) and facial expression (e.g., Morel et al., 2009; Bayle and Taylor, 2009) have been reported. While these results are extremely exciting, as they suggest that our brain processes and modulates visual information more quickly than is generally thought, difficulties of replication (e.g., Santesso et al., 2008; Fu et al., 2010b) make it hard to draw conclusions on what mechanisms are at play. One possible reason for such inconsistencies is that experimental paradigms and methods vary widely.

In light of our findings, we examined the high-pass filter cut-off value used in these studies. We found that out of the 13 ERP/ERF attention studies finding a very early effect, 5 used a cut-off higher than 0.5 Hz. Similarly, 6 out of 10 studies reporting early effects of facial expression used a cut-off higher than 0.5 Hz. We found only one study reporting no early effect while using a high cut-off.

The inconsistency of results may therefore be a combination of filtering artifacts, publication bias, and the presence of genuine early effects. Future research in this area should seek to elucidate the conditions under which very early components are modulated by taking care to minimize possible biases induced by high-pass filtering (see Section 6).

Additionally, we inspected papers from the Journal of Neuroscience, Cerebral Cortex, NeuroImage, Human Brain Mapping, and the Journal of Cognitive Neuroscience, published or accepted between January 2011 and March 2012. We included papers using ERP or ERF amplitudes either directly, for source estimation, or for independent component analysis, but excluded studies interested in restricted frequency bands (event-related oscillations, event-related synchronizations/desynchronizations, time-frequency analyses, and power analyses). Although the issues presently discussed are also relevant for intra-cranial EEG, we only focused on data measured from scalp recordings. Our results are consistent with those reported by Rousseelet (2012): out of the 185 scrutinized studies satisfying our criteria, we found that 80 (43%) of them used a cut-off above 0.1 Hz. Half of those, i.e. 40 studies (21%), used a cut-off of 1 Hz or higher. The proportion of studies using a cut-off higher than 0.1 Hz and using MEG was comparable to those using EEG (18/40, or 45% versus 65/155, or 42%). The vast majority of these reports do not specify whether a causal or acausal filter was used, but the few which do used a zero phase-shift filter. Additionally, most papers do not specify why such a high cut-off value was used, and those who do invoked the classical reasons of signal-to-noise ratio increase and slow trends removal.

While the potential dangers of filtering were already described in Luck (2005), and while the majority of laboratories use digital high-pass filtering knowingly and parsimoniously, it appears that it is necessary to change the practices of more than a third of the works, and to possibly reinterpret a non-negligible portion of the literature. However, we do not claim that the conclusions of all reports using a high cut-off frequency are erroneous. The nature and extent of biases induced by filtering depend on the shape of the waveform, the type of filter used, and the specific component studied. Rather, these studies should be regarded keeping the possibility of a filter-induced bias in mind.

6. Summary and guidelines

The following guidelines should be considered to minimize artifacts due to high-pass filtering:

- Only use offline high-pass filtering if necessary. Visually inspect the data beforehand to judge if too much drift is present. Only if the data are indeed noisy and show a large amount of drift, consider applying a high-pass filter.
- To choose the cut-off of the high-pass filter, we reiterate the guideline stated in Luck (2005): set the high-pass filter cut-off value to 0.01 Hz by default. For less docile participants whose data may be noisier, such as children or certain kinds of patients, consider the possibility of a higher cut-off, such as 0.05 or 0.1 Hz maximum.
- If, for any reason, a filter with a higher cut-off is applied, check the results against data filtered with a lower cut-off. Try to understand any discrepancy in the results and make sure they are not

due to biases induced by filtering (e.g., with analyses as used in the present paper).

- To check the distortion induced by a filter, generate a grand average waveform with and without having applied a filter on the raw data, and ensure that the overall morphology is not affected.
- Acausal zero-phase shift filters do not delay the signal but can generate distortions backward in time. If one is interested in the earliest moment when an effect occurs, a causal filter is preferred (see also Rousseelet, 2012). If one is interested in the timing of a peak, a zero phase-shift filter should be preferred.
- Finally, as stated in Picton et al. (2000), the nature of the filter used should be specified. In particular, a vast majority of the reports omit to mention the causality of the filter, which, as we saw, may be critical for the interpretation of the data.

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References

- Ales JM, Yates JL, Norcia AM. V1 is not uniquely identified by polarity reversals of responses to upper and lower visual field stimuli. *Neuroimage* 2010;52:1401–9.
- Bayle DJ, Taylor MJ. Attention inhibition of early cortical activation to fearful faces. *Brain Res* 2009;1313:113–23.
- Clark VP, Fan S, Hillyard SA. Identification of early visual evoked potential generators by retinotopic and topographic analyses. *Hum Brain Mapp* 1995;2:170–87.
- Delorme A, Makeig S. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J Neurosci Methods* 2004;134:9–21.
- Di Russo F, Martínez A, Hillyard SA. Source analysis of event-related cortical activity during visuo-spatial attention. *Cereb Cortex* 2003;13:486–99.
- Eimer M, Holmes A. An ERP study on the time course of emotional face processing. *Neuroreport* 2002;13:427–31.
- Eldar S, Yankelevitch R, Lamy D, Bar-Haim Y. Enhanced neural reactivity and selective attention to threat in anxiety. *Biol Psychol* 2010;85:252–7.
- Fitzgerald RD, Lamm C, Oczenski W, Stimpfl T, Vycudilik W, Bauer H. Direct current auditory evoked potentials during wakefulness, anesthesia, and emergence from anesthesia. *Anesth Analg* 2001;92:154–60.
- Foxe JJ, Simpson G. Flow of activation from V1 to frontal cortex in humans. *Exp Brain Res* 2002;142:139–50, 2001.
- Fu S, Huang Y, Luo Y-J, Wang Y, Fedota JR, Greenwood PM, et al. Perceptual load interacts with involuntary attention at early processing stages: event-related potential studies. *Neuroimage* 2009;48:191–9.
- Fu S, Fedota JR, Greenwood PM, Parasuraman R. Early interaction between perceptual load and involuntary attention: an event-related potential study. *Neurosci Lett* 2010a;468:68–71.
- Fu S, Fedota JR, Greenwood PM, Parasuraman R. Dissociation of visual C1 and P1 components as a function of attentional load: an event-related potential study. *Biol Psychol* 2010b;85:171–8.
- Grey Walter W, Cooper R, Aldridge VJ, McCallum WC, Winter AL. Contingent negative variation: an electric sign of sensorimotor association and expectancy in the human brain. *Nature* 1964;203:380–4.
- Hennighausen E, Heil M, Rosler F. A correction method for DC drift artifacts. *Electroencephalogr Clin Neurophysiol* 1993;86:199–204.
- Hillyard SA, Vogel EK, Luck SJ. Sensory gain control (amplification) as a mechanism of selective attention: electro-physiological and neuroimaging evidence. *Philos Trans R Soc Lond B: Biol Sci* 1998;353:1257–70.
- Ioannides AA, Poghosyan V. Spatiotemporal dynamics of early spatial and category-specific attentional modulations. *Neuroimage* 2012;60:1638–51.
- Jasper HA. The ten-twenty system of the international federation. *Electroencephalogr Clin Neurophysiol* 1958;10:371–5.
- Jeffreys DA, Axford J. Source locations of pattern-specific components of human visual evoked potentials. I. Component of striate cortical origin. *Exp Brain Res* 1972;16:1–21.
- Kelly SP, Gomez-Ramirez M, Foxe JJ. Spatial attention modulates initial afferent activity in human primary visual cortex. *Cereb Cortex* 2008;18:2629–36.
- Kelly SP, Schroeder CE, Lalor EC. What does polarity inversion of extrastriate activity tell us about striate contributions to the early VEP? A comment on Ales et al. (2010). *NeuroImage*, 2012.

- Khoe W, Mitchell JF, Reynolds JH, Hillyard SA. Exogenous attentional selection of transparent superimposed surfaces modulates early event-related potentials. *Vision Res* 2005;45:3004–14.
- Lehmann D, Skrandies W. Reference-free identification of components of checkerboard-evoked multichannel potential fields. *Electroencephalogr Clin Neurophysiol* 1980;48:609–21.
- Luck SJ. An introduction to the event-related potential technique. Cambridge, Massachusetts: The MIT Press; 2005.
- Lynn PA. An introduction to the analysis and processing of signals. third ed. New York: Hemisphere Publishing Corporation; 1989.
- Martínez A, Anillo-Vento L, Sereno MI, Frank LR, Buxton RB, Dubowitz DJ, et al. Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nat Neurosci* 1999;2:364–9.
- Monto S, Palva S, Voipio J, Palva JM. Very slow EEG fluctuations predict the dynamics of stimulus detection and oscillation amplitudes in humans. *J Neurosci* 2008;28:8268–72.
- Morel S, Ponz A, Mercier M, Vuilleumier P, George N. EEG-MEG evidence for early differential repetition effects for fearful, happy and neutral faces. *Brain Res* 2009;1254:84–98.
- Noesselt T, et al. Delayed striate cortical activation during spatial attention. *Neuron* 2002;35:575–87.
- Palva JM, Palva S. Infra-slow fluctuations in electrophysiological recordings, blood-oxygenation-level-dependent signals, and psychophysical time series. *NeuroImage*, 2012.
- Pastor MC, Bradley MM, Löw A, Versace F, Moltó J, Lang PJ. Affective picture perception: emotion, context, and the late positive potential. *Brain Res* 2008;1189:145–51.
- Picton TW. The P300 wave of the human event-related potential. *J Clin Neurophysiol* 1992;9:456–79.
- Picton TW, Bentin S, Berg P, Donchin E, Hillyard SA, Johnson R, et al. Guidelines for using human event-related potentials to study cognition: recording standards and publication criteria. *Psychophysiology* 2000;37:127–52.
- Poghosyan V, Ioannides AA. Attention modulates earliest responses in the primary auditory and visual cortices. *Neuron* 2008;58:802–13.
- Pourtois G, Grandjean D, Sander D, Vuilleumier P. Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cereb Cortex* 2004;14:619–33.
- Pourtois G, Rauss KS, Vuilleumier P, Schwartz S. Effects of perceptual learning on primary visual cortex activity in humans. *Vision Res* 2008;48:55–62.
- Rauss KS, Pourtois G, Vuilleumier P, Schwartz S. Attentional load modifies early activity in human primary visual cortex. *Hum Brain Mapp* 2009;30:1723–33.
- Rauss KS, Schwartz S, Pourtois G. Top-down effects on early visual processing in humans: a predictive coding framework. *Neurosci Biobehav Rev* 2011;35:1237–53.
- Rousselle GA. Does filtering preclude us from studying ERP time-courses? *Front Psychol* 2012;3:131.
- Rozenkrants B, Polich J. Affective ERP processing in a visual oddball task: arousal, valence, and gender. *Clin Neurophysiol* 2008;119:2260–5.
- Santesso DL, Meuret AE, Hofmann SG, Mueller EM, Ratner KG, Roesch EB, et al. Electrophysiological correlates of spatial orienting towards angry faces: a source localization study. *Neuropsychologia* 2008;46:1338–48.
- Stolarova M, Keil A, Moratti S. Modulation of the C1 visual event-related component by conditioned stimuli: evidence for sensory plasticity in early affective perception. *Cereb Cortex* 2006;16:876–87.
- Tallgren P, Vanhatalo S, Kaila K, Voipio J. Evaluation of commercially available electrodes and gels for recording of slow EEG potentials. *Clin Neurophysiol* 2005;116:799–806.
- Vanhatalo S, Voipio J, Kaila K. Full-band EEG. (FbEEG): an emerging standard in electroencephalography. *Clin Neurophysiol* 2005;116:1–8.
- VanRullen R. Four common conceptual fallacies in mapping the time course of recognition. *Front Psychol* 2011;2:365.
- West GL, Anderson AK, Ferber S, Pratt J. Electrophysiological evidence for biased competition in V1 for fear expressions. *J Cogn Neurosci* 2011;23:3410–8.
- Wu Y, Chen J, Han S. Neural mechanisms of attentional modulation of perceptual grouping by collinearity. *Neuroreport* 2005;16:567–70.

Bibliography

- Acunzo, D. J. (2008). Capture of Overt Attention by Emotional Targets in Natural Scenes. Master's thesis, The University of Edinburgh.
- Acunzo, D. J. and Henderson, J. M. (2011). No emotional “pop-out” effect in natural scene viewing. *Emotion*, 11(5):1134–1143.
- Acunzo, D. J., MacKenzie, G., and van Rossum, M. C. W. (2012). Systematic biases in early ERP and ERF components as a result of high-pass filtering. *Journal of Neuroscience Methods*, 209(1):212–218.
- Ales, J. M., Carney, T., and Klein, S. A. (2010a). The folding fingerprint of visual cortex reveals the timing of human V1 and V2. *NeuroImage*, 49(3):2494–2502.
- Ales, J. M., Yates, J. L., and Norcia, A. M. (2010b). V1 is not uniquely identified by polarity reversals of responses to upper and lower visual field stimuli. *NeuroImage*, 52(4):1401–1409.
- Alpers, G. W. (2008). Eye-catching: Right hemisphere attentional bias for emotional pictures. *Laterality: Asymmetries of Body, Brain and Cognition*, 13(2):158–178.
- American Psychiatric Association (1994). *Diagnostic and Statistical Manual of Mental Disorders*. American Psychiatric Association, Washington DC, fourth edition.
- Anderson, A. K. and Phelps, E. A. (2001). Lesions of the human amygdala impair enhanced perception of emotionally salient events. *Nature*, 411:305–309.
- Anderson, M. J. and Ter Braak, C. J. F. (2003). Permutation Tests for Multi-Factorial Analysis of Variance. *Journal of Statistical Computation and Simulation*, 73(2):85–113.
- Attal, Y., Bhattacharjee, M., Yelnik, J., Cottureau, B., Lefèvre, J., Okada, Y., Bardinet, E., Chupin, M., and Baillet, S. (2007). Modeling and Detecting Deep Brain Activity

- with MEG & EEG. In *29th Annual International Conference of the IEEE EMBS*, pages 4937–4949, Lyon, France.
- Awh, E., Armstrong, K. M., and Moore, T. (2006). Visual and oculomotor selection: links, causes and implications for spatial attention. *Trends in Cognitive Sciences*, 10(3):124–130.
- Balconi, M., Brambilla, E., and Falbo, L. (2009). Appetitive vs. defensive responses to emotional cues. Autonomic measures and brain oscillation modulation. *Brain Research*, 1296:72–84.
- Banks, S. J., Eddy, K. T., Angstadt, M., Nathan, P. J., and Phan, K. L. (2007). Amygdala frontal connectivity during emotion regulation. *Social, Cognitive, and Affective Neuroscience*, 2(4):303–312.
- Bar-Haim, Y., Lamy, D., Pergamin, L., Backermans-Kranenburg, M. J., and van Ijzendoorn, M. H. (2007). Threat-Related Attentional Bias in Anxious and Nonanxious Individuals: A Meta-Analytic Study. *Psychological Bulletin*, 133(1):1–24.
- Bayle, D. J., Hénaff, M.-A., and Krolak-Salmon, P. (2009). Unconsciously Perceived Fear in Peripheral Vision Alerts the Limbic System: A MEG Study. *PLoS ONE*, 4(12):e8207.
- Bayle, D. J. and Taylor, M. J. (2010). Attention Inhibition of Early Cortical Activation to Fearful Faces. *Brain Research*, 1313:113–123.
- Becker, M. W. and Detweiler-Bedell, B. (2009). Early detection and avoidance of threatening faces during passive viewing. *Quarterly Journal of Experimental Psychology*, 62(7):1257–1264.
- Becker, M. W., Pashler, H., and Lubin, J. (2007). Object-intrinsic oddities draw early saccades. *Journal of Experimental Psychology: Human Perception and Performance*, 33(1):20–30.
- Bradley, B. P., Mogg, K., Millar, N., Conham-Carter, C., Fergusson, E., Jenkins, J., and Parr, M. (1997). Attentional Biases for Emotional Faces. *Cognition and Emotion*, 11(1):25–42.
- Brainard, D. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10:433–436.
- Broadbent, D. E. (1982). Task combination and selective intake of information. *Acta psychologica*, 50(3):253–290.

- Brosch, T. and Wieser, M. J. (2011). The (Non)Automaticity of Amygdala Responses to Threat: On the Issue of Fast Signals and Slow Measures. *Journal of Neuroscience*, 31(41):14451–14452.
- Buffalo, E. A., Fries, P., Landman, R., Liang, H., and Desimone, R. (2010). A backward progression of attentional effects in the ventral stream. *Proceedings of the National Academy of Sciences of the United States of America*, 107(1):361–365.
- Calvo, M. G. and Avero, P. (2008). Affective priming of emotional pictures in parafoveal vision: Left visual field advantage. *Cognitive, Affective, & Behavioral Neuroscience*, 8(1):41–53.
- Calvo, M. G. and Lang, P. J. (2004). Gaze Patterns When Looking at Emotional Pictures: Motivationally Biased Attention. *Motivation and Emotion*, 28(3):221–243.
- Calvo, M. G. and Nummenmaa, L. (2007). Processing of unattended emotional visual scenes. *Journal of Experimental Psychology: General*, 136(3):347–369.
- Calvo, M. G., Nummenmaa, L., and Hyona, J. (2008). Emotional scenes in peripheral vision: Selective orienting and gist processing, but not content identification. *Emotion*, 8(1):68–80.
- Carlson, J. M. and Reinke, K. S. (2008). Masked fearful faces modulate the orienting of covert spatial attention. *Emotion*, 8(4):522–529.
- Carlson, J. M. and Reinke, K. S. (2010). Spatial attention-related modulation of the N170 by backward masked fearful faces. *Brain and Cognition*, 73(1):20–27.
- Carlson, J. M., Reinke, K. S., and Habib, R. (2009). A left amygdala mediated network for rapid orienting to masked fearful faces. *Neuropsychologia*, 47(5):1386–1389.
- Carlson, J. M., Reinke, K. S., LaMontagne, P. J., and Habib, R. (2011). Backward masked fearful faces enhance contralateral occipital cortical activity for visual targets within the spotlight of attention. *Social, Cognitive, and Affective Neuroscience*, 6(5):639–645.
- Carmen Pastor, M., Bradley, M. M., Löw, A., Versace, F., Moltó, J., and Lang, P. J. (2008). Affective picture perception: Emotion, context, and the late positive potential. *Brain Research*, 1189:145–151.
- Carrasco, M. (2006). Covert attention increases contrast sensitivity: psychophysical, neurophysiological and neuroimaging studies. In Martinez-Conde, Macknik, Mar-

- tinez, Alonso, and Tse, editors, *Progress in Brain Research*, pages 33–70. Elsevier, B.V.
- Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, 51(13):1484–1525.
- Castelhano, M. S., Mack, M. L., and Henderson, J. M. (2009). Viewing task influences eye movement control during active scene perception. *Journal of Vision*, 9(3):1–15.
- Chaumon, M., Drouet, V., and Tallon-Baudry, C. (2008). Unconscious associative memory affects visual processing before 100 ms. *Journal of Vision*, 8(3):1–10.
- Cisler, J. M., Bacon, A. K., and Williams, N. L. (2009). Phenomenological Characteristics of Attentional Biases Towards Threat: A Critical Review. *Cognitive Therapy and Research*, 33:221–234.
- Cisler, J. M. and Koster, E. H. W. (2010). Mechanisms of attentional biases towards threat in anxiety disorders: An integrative review. *Clinical Psychology Review*, 30(2):203–216.
- Clark, V. P., Fan, S., and Hillyard, S. A. (1995). Identification of Early Visual Evoked Potential Generators by Retinotopic and Topographic Analyses. *Human Brain Mapping*, 2:170–187.
- Coles, M. G. H. and Rugg, M. D. (1995). Event-related potentials: an introduction. In Rugg, M. D. and Coles, M. G. H., editors, *Electrophysiology of Mind: Event-related potentials and Cognition*, pages 1–26. Oxford University Press, Oxford, England.
- Corbetta, M. and Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3(3):215–229.
- de Graef, P., Christiaens, D., and d’Ydewalle, G. (1990). Perceptual effects of scene context on object identification. *Psychological Research*, 52(4):317–329.
- Delorme, A. and Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1):9–21.
- Desimone, R. (1998). Visual attention mediated by biased competition in extrastriate visual cortex. *Philosophical Transactions of the Royal Society of London B.*, 353:1245–1255.

- Desimone, R. and Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18:193–222.
- Di Russo, F., Martínez, A., and Hillyard, S. A. (2003). Source Analysis of Event-related Cortical Activity during Visuo-spatial Attention. *Cerebral Cortex*, 13:486–499.
- Dolan, R. J. and Vuilleumier, P. (2003). Amygdala automaticity in emotional processing. *Annals of the New York Academy of Sciences*, 985:348–355.
- Doyle, M. and Walker, R. (2001). Curved saccade trajectories: Voluntary and reflexive saccades curve away from irrelevant distractors. *Experimental Brain Research*, 139(3):333–344.
- Eger, E., Jedynak, A., Iwaki, T., and Skrandies, W. (2003). Rapid extraction of emotional expression: evidence from evoked potential fields during brief presentation of face stimuli. *Neuropsychologia*, 41:808–817.
- Egloff, B. and Hock, M. (2003). Assessing attention allocation toward threat-related stimuli: a comparison of the emotional Stroop task and the attentional probe task. *Personality and Individual Differences*, 35:475–483.
- Eimer, M. and Holmes, A. (2002). An ERP study on the time course of emotional face processing. *NeuroReport*, 13(4):427–431.
- Eimer, M. and Holmes, A. (2007). Event-related brain potential correlates of emotional face processing. *Neuropsychologia*, 45(1):15–31.
- Eimer, M., Holmes, A., and McGlone, F. P. (2003). The role of spatial attention in the processing of facial expression: an ERP study of rapid brain responses to six basic emotions. *Cognitive, Affective, & Behavioral Neuroscience*, 3(2):97–110.
- Eimer, M. and Kiss, M. (2006). Attentional capture by task-irrelevant fearful faces is revealed by the N2pc component. *Biological Psychology*, 74:108–112.
- Eldar, S., Yankelevitch, R., Lamy, D., and Bar-Haim, Y. (2010). Enhanced neural reactivity and selective attention to threat in anxiety. *Biological Psychology*, 85(2):252–257.
- Fabre-Thorpe, M., Delorme, A., Marlot, C., and Thorpe, S. J. (2001). A limit to the speed of processing in ultra-rapid visual categorization of novel natural scenes. *Journal of Cognitive Neuroscience*, 13(2):171–180.

- Fitzgerald, R. D., Lamm, C., Oczenski, W., Stimpfl, T., Vycudilik, W., and Bauer, H. (2001). Direct current auditory evoked potentials during wakefulness, anesthesia, and emergence from anesthesia. *Anesthesia and analgesia*, 92(1):154–160.
- Flykt, A. (2006). Preparedness for action: Responding to the snake in the grass. *American journal of psychology*, 119(1):29–43.
- Fox, E. (2002). Processing emotional facial expressions: the role of anxiety and awareness. *Cognitive, Affective, & Behavioral Neuroscience*, 2(1):52–63.
- Fox, E. (2008). *Emotion Science*. Cognitive and Neuroscientific Approaches to Understanding Human Emotions. Palgrave Macmillan.
- Fox, E., Derakshan, N., and Shoker, L. (2008). Trait anxiety modulates the electrophysiological indices of rapid spatial orienting towards angry faces. *NeuroReport*, 19(3):259–263.
- Fox, E., Russo, R., Bowles, R., and Dutton, K. (2001). Do threatening stimuli draw or hold visual attention in subclinical anxiety? *Journal of Experimental Psychology: General*, 130(4):681–700.
- Fox, E., Russo, R., and Dutton, K. (2002). Attentional bias for threat: Evidence for delayed disengagement from emotional faces. *Cognition and Emotion*, 16(3):355–379.
- Foxe, J. J. and Simpson, G. (2002). Flow of activation from V1 to frontal cortex in humans. *Experimental Brain Research*, 142(1):139–150.
- Fu, S., Fedota, J. R., Greenwood, P. M., and Parasuraman, R. (2010a). Dissociation of visual C1 and P1 components as a function of attentional load: An event-related potential study. *Biological Psychology*, 85(1):171–178.
- Fu, S., Fedota, J. R., Greenwood, P. M., and Parasuraman, R. (2010b). Early interaction between perceptual load and involuntary attention: An event-related potential study. *Neuroscience Letters*, 468(1):68–71.
- Fu, S., Greenwood, P. M., and Parasuraman, R. (2005). Brain mechanisms of involuntary visuospatial attention: an event-related potential study. *Human Brain Mapping*, 25(4):378–390.
- Fu, S., Huang, Y., Luo, Y.-J., Wang, Y., Fedota, J. R., Greenwood, P. M., and Para-

- suraman, R. (2009). Perceptual load interacts with involuntary attention at early processing stages: Event-related potential studies. *NeuroImage*, 48(1):191–199.
- Fu, S., Zinni, M., Squire, P. N., Kumar, R., Caggiano, D. M., and Parasuraman, R. (2008). When and where perceptual load interacts with voluntary visuospatial attention: An event-related potential and dipole modeling study. *NeuroImage*, 39(3):1345–1355.
- Fuller, S., Park, Y., and Carrasco, M. (2009). Cue contrast modulates the effects of exogenous attention on appearance. *Vision Research*, page 13.
- Gareze, L. and Findlay, J. M. (2007). Absence of scene context effects in object detection and eye gaze capture. In van Gompel, R. P. G., Fischer, M. H., Murray, W. S., and Hill, R. L., editors, *Eye movements: A window on mind and brain*, pages 617–637. Elsevier, Amsterdam, Netherlands.
- Garrido, M. I., Barnes, G. R., Sahani, M., and Dolan, R. J. (2012). Functional Evidence for a Dual Route to Amygdala. *Current Biology*, 22(2):129–134.
- Gaspar, C. M., Rousselet, G. A., and Pernet, C. R. (2011). Reliability of ERP and single-trial analyses. *NeuroImage*, 58(2):620–629.
- Gomez Gonzalez, C. M., Clark, V. P., Fan, S., Luck, S. J., and Hillyard, S. A. (1994). Sources of attention-sensitive visual event-related potentials. *Brain Topography*, 7(1):41–51.
- Gonsalvez, C. L. and Polich, J. (2002). P300 amplitude is determined by target-to-target interval. *Psychophysiology*, 39(3):388–396.
- Grey Walter, W., Cooper, R., Aldridge, V. J., McCallum, W. C., and Winter, A. L. (1964). Contingent Negative Variation: An Electric Sign of Sensorimotor Association and Expectancy in the Human Brain. *Nature*, 203:380–384.
- Hagler, D. J., Halgren, E., Martínez, A., Huang, M., Hillyard, S. A., and Dale, A. M. (2009). Source Estimates for MEG/EEG Visual Evoked Responses Constrained by Multiple, Retinotopically-Mapped Stimulus Locations. *Human Brain Mapping*, 30(4):1290–1309.
- Halgren, E., Raij, T., Marinkovic, K., Jousmäki, V., and Hari, R. (2000). Cognitive response profile of the human fusiform face area as determined by MEG. *Cerebral Cortex*, 10(1):69–81.

- Hare, T. A., Camerer, C. F., and Rangel, A. (2009). Self-Control in Decision-Making Involves Modulation of the vmPFC Valuation System. *Science*, 324(5927):646–648.
- Hayden, B. Y. and Gallant, J. L. (2009). Combined effects of spatial and feature-based attention on responses of V4 neurons. *Vision Research*, 49(10):1182–1187.
- Henderson, J. M., Chanceaux, M., and Smith, T. J. (2009). The influence of clutter on real-world scene search: Evidence from search efficiency and eye movements. *Journal of Vision*, 9(1):32–32.
- Henderson, J. M. and Hollingworth, A. (1999). High-Level Scene Perception. *Annual Review of Psychology*, 50:243–271.
- Henderson, J. M. and Smith, T. J. (2009). How are eye fixation durations controlled during scene viewing? Further evidence from a scene onset delay paradigm. *Visual Cognition*, 17(6):1055–1082.
- Henderson, J. M., Weeks, P. A., and Hollingworth, A. (1999). The Effects of Semantic Consistency on Eye Movements During Complex Scene Viewing. *Journal of Experimental Psychology: Human Perception and Performance*, 21(1):210–228.
- Henderson, J. M., Weeks, P. A., and Hollingworth, A. (2004). The Effects of Semantic Consistency on Eye Movements During Complex Scene Viewing. *Journal of Experimental Psychology: Human Perception and Performance*, 25(1):210–228.
- Hennighausen, E., Heil, M., and Rosler, F. (1993). A correction method for DC drift artifacts. *Electroencephalography and clinical neurophysiology*, 86:199–204.
- Hillyard, S. A. and Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences of the United States of America*, 95:781–787.
- Hillyard, S. A., Vogel, E. K., and Luck, S. J. (1998). Sensory Gain Control (Amplification) as a Mechanism of Selective Attention: Electro-Physiological and Neuroimaging Evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 353(1373):1257–1270.
- Holender, D. (1986). Semantic activation without conscious identification in dichotic listening, parafoveal vision, and visual masking: A survey and appraisal. *Behavioral and Brain Sciences*, 9(1):1–66.
- Holmes, A., Vuilleumier, P., and Eimer, M. (2003). The processing of emotional facial

- expression is gated by spatial attention: evidence from event-related brain potentials. *Cognitive Brain Research*, 16(2):174–184.
- Holmes, G. (1945). The Organization of the Visual Cortex in Man. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 132(869):348–361.
- Hood, D. C., Odel, J. G., and Winn, B. J. (2003). The Multifocal Visual Evoked Potential. *Journal of Neuro-ophthalmology*, 23(4):279–289.
- Humphrey, K., Underwood, G., and Lambert, T. (2012). Saliency of the lambs: A test of the saliency map hypothesis with pictures of emotive objects. *Journal of Vision*, 12(1):22–22.
- Hung, Y., Lou Smith, M., Bayle, D. J., Mills, T., Cheyne, D., and Taylor, M. J. (2010). Unattended emotional faces elicit early lateralized amygdala–frontal and fusiform activations. *NeuroImage*, 50(2):727–733.
- Ioannides, A. A. and Poghosyan, V. (2012). Spatiotemporal dynamics of early spatial and category-specific attentional modulations. *NeuroImage*, 60(3):1638–1651.
- Itier, R. J., Herdman, A. T., George, N., Cheyne, D., and Taylor, M. J. (2006). Inversion and contrast-reversal effects on face processing assessed by MEG. *Brain Research*, 1115(1):108–120.
- Itti, L. and Koch, C. (2000). A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Research*, 40:1489–1506.
- Jacoby, O., Visser, T. A. W., Hart, B. C., Cunnington, R., and Mattingley, J. B. (2011). No Evidence for Early Modulation of Evoked Responses in Primary Visual Cortex to Irrelevant Probe Stimuli Presented during the Attentional Blink. *PLoS ONE*, 6(8):1–7.
- James, W. (1890). *The Principles of Psychology*, volume 1. Henry Holt and Company, New York.
- Jasper, H. A. (1958). The ten-twenty system of the international federation. *Electroencephalography and clinical neurophysiology*, 10:371–375.
- Jeffreys, D. A. and Axford, J. (1972a). Source Locations of Pattern-Specific Components of Human Visual Evoked Potentials. I. Component of Striate Cortical Origin. *Experimental Brain Research*, 16(1):1–21.

- Jeffreys, D. A. and Axford, J. (1972b). Source Locations of Pattern-Specific Components of Human Visual Evoked Potentials. II. Component of Extrastriate Cortical Origin. *Experimental Brain Research*, 16(1):22–40.
- Karns, C. M. and Knight, R. T. (2009). Intermodal auditory, visual, and tactile attention modulates early stages of neural processing. *Journal of Cognitive Neuroscience*, 21(4):669–683.
- Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., and Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, 22(4):751–761.
- Kawasaki, H., Adolphs, R., Kaufman, O., Damasio, H., Damasio, A. R., Granner, M., Bakken, H., Hori, T., and Howard III, M. A. (2001). Single-neuron responses to emotional visual stimuli recorded in human ventral prefrontal cortex. *Nature Neuroscience*, 4(1):15–16.
- Keil, A., Moratti, S., Sabatinelli, D., Bradley, M. M., and Lang, P. J. (2004). Additive Effects of Emotional Content and Spatial Selective Attention on Electrocortical Facilitation. *Cerebral Cortex*, 15(8):1187–1197.
- Kelly, S. P., Gomez-Ramirez, M., and Foxe, J. J. (2008). Spatial Attention Modulates Initial Afferent Activity in Human Primary Visual Cortex. *Cerebral Cortex*, 18(11):2629–2636.
- Kelly, S. P., Schroeder, C. E., and Lalor, E. C. (2012). What does polarity inversion of extrastriate activity tell us about striate contributions to the early VEP? A comment on Ales et al. (2010). *NeuroImage*, pages 1–4.
- Khoe, W., Mitchell, J. F., Reynolds, J. H., and Hillyard, S. A. (2005). Exogenous attentional selection of transparent superimposed surfaces modulates early event-related potentials. *Vision Research*, 45(24):3004–3014.
- Kirchner, H. and Thorpe, S. J. (2006). Ultra-rapid object detection with saccadic eye movements: visual processing speed revisited. *Vision Research*, 46(11):1762–1776.
- Kiss, M. and Eimer, M. (2008). ERPs reveal subliminal processing of fearful faces. *Psychophysiology*, 45(2):318–326.
- Koster, E. H. W., Verschuere, B., Burssens, B., Custers, R., and Crombez, G. (2007).

- Attention for emotional faces under restricted awareness revisited: do emotional faces automatically attract attention? *Emotion*, 7(2):285–295.
- Krolak-Salmon, P., Fischer, C., Vighetto, A., and Mauguière, F. (2001). Processing of facial emotional expression: spatio-temporal data as assessed by scalp event-related potentials. *European Journal of Neuroscience*, 13(5):987–994.
- Krolak-Salmon, P., Hénaff, M.-A., Isnard, J., Tallon-Baudry, C., Guénot, M., Vighetto, A., Bertrand, O., and Mauguière, F. (2003). An Attention Modulated Response to Disgust in Human Ventral Anterior Insular. *Annals of neurology*, 53(4):446–453.
- Lamme, V. A. and Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, 23(11):571–579.
- Lang, P. J., Bradley, M. M., and Cuthbert, B. N. (2008). *International Affective Picture System (IAPS): Affective ratings of pictures and instruction manual. Report A-8*. University of Florida, Gainesville, Florida.
- LeDoux, J. E. (1998). *The Emotional Brain. The Mysterious Underpinnings of Emotional Life*. Phoenix, London.
- Lehmann, D. and Skrandies, W. (1980). Reference-free identification of components of checkerboard-evoked multichannel potential fields. *Electroencephalography and clinical neurophysiology*, 48(6):609–621.
- Liddell, B. J., Brown, K. J., Kemp, A. H., Barton, M. J., Das, P., Peduto, A., Gordon, E., and Williams, L. M. (2005). A direct brainstem–amygdala–cortical ‘alarm’ system for subliminal signals of fear. *NeuroImage*, 24(1):235–243.
- Lindén, H., Pettersen, K. H., and Einevoll, G. T. (2010). Intrinsic dendritic filtering gives low-pass power spectra of local field potentials. *Journal of Computational Neuroscience*, 29(3):423–444.
- Linkenkaer-Hansen, K., Palva, J. M., Sams, M., Hietanen, J. K., Aronen, H. J., and Ilmoniemi, R. J. (1998). Face-selective processing in human extrastriate cortex around 120 ms after stimulus onset revealed by magneto- and electroencephalography. *Neuroscience Letters*, 253(3):147–150.
- Liu, J., Harris, A., and Kanwisher, N. (2002). Stages of processing in face perception: an MEG study. *Nature Neuroscience*, 5(9):910–916.

- Liu, L. and Ioannides, A. A. (2010). Emotion separation is completed early and it depends on visual field presentation. *PLoS ONE*, 5(3):e9790.
- Loftus, G. R. and Mackworth, N. H. (1978). Cognitive determinants of fixation location during picture viewing. *Journal of Experimental Psychology: Human Perception and Performance*, 4(4):565–572.
- Luck, S. J. (2005). *An Introduction to the Event-Related Potential Technique*. The MIT Press, Cambridge, Massachusetts.
- Luck, S. J., Chelazzi, L., Hillyard, S. A., and Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology*, 77(1):24–42.
- Luo, Q., Holroyd, T., Majestic, C., Cheng, X., Schechter, J., and Blair, R. J. (2010). Emotional Automaticity Is a Matter of Timing. *Journal of Neuroscience*, 30(17):5825–5829.
- Lynn, P. A. (1989). *An Introduction to the Analysis and Processing of Signals*. Hemisphere Publishing Corporation, New York, third edition edition.
- MacLeod, C., Mathews, A., and Tata, P. (1986). Attentional Bias in Emotional Disorders. *Journal of Abnormal Psychology*, 95(1):15–20.
- MacLeod, C. and Rutherford, E. M. (1992). Anxiety and the selective processing of emotional information: mediating roles of awareness, trait and state variables, and personal relevance of stimulus materials. *Behaviour Research and Therapy*, 30(5):479–491.
- Martínez, A., Anllo-Vento, L., Sereno, M. I., Frank, L. R., Buxton, R. B., Dubowitz, D. J., Wong, E. C., Hinrichs, H., Heinze, H.-J., and Hillyard, S. A. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neuroscience*, 2(4):364–369.
- Martínez, A., Di Russo, F., Anllo-Vento, L., Sereno, M. I., Buxton, R. B., and Hillyard, S. A. (2001). Putting spatial attention on the map: timing and localization of stimulus selection processes in striate and extrastriate visual areas. *Vision Research*, 41(10-11):1437–1457.
- Mathews, A. and MacLeod, C. (2002). Induced processing biases have causal effects on anxiety. *Cognition and Emotion*, 16(3):331–354.

- Mathews, A. and MacLeod, C. (2005). Cognitive Vulnerability to Emotional Disorders. *Annual Review of Clinical Psychology*, 1(1):167–195.
- Mathews, A., Ridgeway, V., and Williamson, D. A. (1996). Evidence for attention to threatening stimuli in depression. *Behaviour Research and Therapy*, 34(9):695–705.
- McAdams, C. J. and Clay Reid, R. (2005). Attention Modulates the Responses of Simple Cells in Monkey Primary Visual Cortex. *Journal of Neuroscience*, 25(47):11023–11033.
- McAdams, C. J. and Maunsell, J. H. R. (2000). Attention to Both Space and Feature Modulates Neuronal Responses in Macaque Area V4. *Journal of Neurophysiology*, 83(3):1751–1755.
- McAlonan, K., Cavanaugh, J., and Wurtz, R. H. (2008). Guarding the gateway to cortex with attention in visual thalamus. *Nature*, 456(7220):391–394.
- Miller, M., Pasik, P., and Pasik, T. (1980). Extrageniculostriate vision in the monkey. VII. Contrast sensitivity functions. *Journal of Neurophysiology*, 43(6):1510–1526.
- Mogg, K. and Bradley, B. P. (1998). A cognitive-motivational analysis of anxiety. *Behaviour Research and Therapy*, 36(9):809–848.
- Mogg, K. and Bradley, B. P. (1999). Orienting of Attention to Threatening Facial Expressions Presented under Conditions of Restricted Awareness. *Cognition and Emotion*, 13(6):713–740.
- Mogg, K. and Bradley, B. P. (2002). Selective orienting of attention to masked threat faces in social anxiety. *Behaviour Research and Therapy*, 40:1403–1414.
- Mogg, K., Bradley, B. P., and Hallowell, N. (1994). Attentional Bias to Threat: Roles of Trait Anxiety, Stressful Events, and Awareness. *Quarterly Journal of Experimental Psychology*, 47A(4):841–864.
- Mogg, K., Bradley, B. P., and Williams, R. (1995). Attentional bias in anxiety and depression: The role of awareness. *British Journal of Clinical Psychology*, 34(1):17–36.
- Mogg, K., Mathews, A., Bird, C., and Macgregor-Morris, R. (1990). Effects of stress and anxiety on the processing of threat stimuli. *Journal of Personality and Social Psychology*, 59(6):1230–1237.

- Mogg, K., McNamara, J., Powys, M., Rawlinson, H., Seiffer, A., and Bradley, B. P. (2001). Selective attention to threat: A test of two cognitive models of anxiety. *Cognition and Emotion*, 14(3):375–399.
- Monto, S., Palva, S., Voipio, J., and Palva, J. M. (2008). Very Slow EEG Fluctuations Predict the Dynamics of Stimulus Detection and Oscillation Amplitudes in Humans. *Journal of Neuroscience*, 28(33):8268–8272.
- Moore, T., Armstrong, K. M., and Fallah, M. (2003). Visuomotor origins of covert spatial attention. *Neuron*, 40(4):671–683.
- Morel, S., Ponz, A., Mercier, M., Vuilleumier, P., and George, N. (2009). EEG-MEG evidence for early differential repetition effects for fearful, happy and neutral faces. *Brain Research*, 1254(C):84–98.
- Morris, J. S., DeGelder, B., Weiskrantz, L., and Dolan, R. J. (2001). Differential extrageniculostriate and amygdala responses to presentation of emotional faces in a cortically blind field. *Brain*, 124(6):1241–1252.
- Morris, J. S., Frith, C. D., Perrett, D. I., Rowland, D., Young, A. W., Calder, A. J., and Dolan, R. J. (1996). A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature*, 383:812–815.
- Morris, J. S., Öhman, A., and Dolan, R. J. (1999). A subcortical pathway to the right amygdala mediating “unseen” fear. *Proceedings of the National Academy of Sciences of the United States of America*, 96:1680–1685.
- Murray, M. M., Brunet, D., and Michel, C. M. (2008). Topographic ERP Analyses: A Step-by-Step Tutorial Review. *Brain Topography*, 20(4):249–264.
- Nakayama, K. and Mackeben, M. (1989). Sustained and transient components of focal visual attention. *Vision Research*, 29(11):1631–1647.
- Noesselt, T., Hillyard, S. A., Woldorff, M. G., Schoenfeld, A., Hagner, T., Jäncke, L., Tempelmann, C., Hinrichs, H., and Heinze, H.-J. (2002). Delayed Striate Cortical Activation during Spatial Attention. *Neuron*, 35:575–587.
- Nummenmaa, L., Hyona, J., and Calvo, M. G. (2006). Eye Movement Assessment of Selective Attentional Capture by Emotional Pictures. *Emotion*, 6(2):257–268.
- Nummenmaa, L., Hyona, J., and Calvo, M. G. (2009). Emotional scene content drives

- the saccade generation system reflexively. *Journal of Experimental Psychology: Human Perception and Performance*, 35(2):305–323.
- Nuthmann, A. and Henderson, J. M. (2010). Object-based attentional selection in scene viewing. *Journal of Vision*, 10(8):20–20.
- Nuthmann, A., Smith, T. J., Engbert, R., and Henderson, J. M. (2010). CRISP: A Computational Model of Fixation Durations in Scene Viewing. *Psychological Review*, 117(2):382–405.
- O'Connor, D. H., Fukui, M. M., Pinsk, M. A., and Kastner, S. (2002). Attention modulates responses in the human lateral geniculate nucleus. *Nature Neuroscience*, 5(11):1203–1209.
- Öhman, A. (2005). The role of the amygdala in human fear: Automatic detection of threat. *Psychoneuroendocrinology*, 30(10):953–958.
- Öhman, A., Flykt, A., and Esteves, F. (2001). Emotion Drives Attention: Detecting the Snake in the Grass. *Journal of Experimental Psychology: General*, 130(3):446–478.
- Orwin, R. G. (1983). A fail-safe N for Effect Size in Meta-Analysis. *Journal of Educational Statistics*, 8(2):157–159.
- Palva, J. M. and Palva, S. (2012). Infra-slow fluctuations in electrophysiological recordings, blood-oxygenation-level-dependent signals, and psychophysical time series. *NeuroImage*.
- Peckham, A. D., McHugh, R. K., and Otto, M. W. (2010). A meta-analysis of the magnitude of biased attention in depression. *Depression and Anxiety*, 27(12):1135–1142.
- Pegna, A. J., Khateb, A., Lazeyras, F., and Seghier, M. L. (2005). Discriminating emotional faces without primary visual cortices involves the right amygdala. *Nature Neuroscience*, 8(1):24–25.
- Pessoa, L. and Adolphs, R. (2010). Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating biological significance. *Nature Reviews Neuroscience*, 11(11):773–783.
- Pessoa, L., Kastner, S., and Ungerleider, L. G. (2002a). Attentional control of the processing of neutral and emotional stimuli. *Cognitive Brain Research*, 15:31–45.

- Pessoa, L., McKenna, M., Gutierrez, E., and Ungerleider, L. G. (2002b). Neural processing of emotional faces requires attention. *Proceedings of the National Academy of Sciences of the United States of America*, 99(17):11458–11463.
- Pessoa, L. and Ungerleider, L. G. (2004). Neuroimaging studies of attention and the processing of emotion-laden stimuli. In Heywood, Milner, and Blakemore, editors, *Progress in Brain Research*, pages 171–182. Elsevier BV.
- Pestilli, F., Ling, S., and Carrasco, M. (2008). A population-coding model of attention's influence on contrast response: Estimating neural effects from psychophysical data. *Vision Research*, page 10.
- Petersen, S. E., Robinson, D. L., and Morris, J. D. (1987). Contributions of the pulvinar to visual spatial attention. *Neuropsychologia*, 25(1A):97–105.
- Phelps, E. A., Ling, S., and Carrasco, M. (2006). Emotion facilitates perception and potentiates the perceptual benefits of attention. *Psychological Science*, 17(4):292–299.
- Picton, T. W. (1992). The P300 wave of the human event-related potential. *Journal of Clinical Neurophysiology*, 9(4):456–479.
- Picton, T. W., Bentin, S., Berg, P., Donchin, E., Hillyard, S. A., Johnson, R., Miller, G. A., Ritter, W., Ruchkin, D. S., Rugg, M. D., and Taylor, M. J. (2000). Guidelines for using human event-related potentials to study cognition: recording standards and publication criteria. *Psychophysiology*, 37(2):127–152.
- Pizzagalli, D. A., Regard, M., and Lehmann, D. (1999). Rapid emotional face processing in the human right and left brain hemispheres: an ERP study. *NeuroReport*, 10(13):2691–2698.
- Poghosyan, V. and Ioannides, A. A. (2007). Precise mapping of early visual responses in space and time. *NeuroImage*, 35(2):759–770.
- Poghosyan, V. and Ioannides, A. A. (2008). Attention Modulates Earliest Responses in the Primary Auditory and Visual Cortices. *Neuron*, 58(5):802–813.
- Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, 32(1):3–25.
- Pourtois, G., Grandjean, D., Sander, D., and Vuilleumier, P. (2004). Electrophysiological

- ical Correlates of Rapid Spatial Orienting Towards Fearful Faces. *Cerebral Cortex*, 14(6):619–633.
- Pourtois, G., Rauss, K. S., Vuilleumier, P., and Schwartz, S. (2008). Effects of perceptual learning on primary visual cortex activity in humans. *Vision Research*, 48(1):55–62.
- Pourtois, G., Spinelli, L., Seeck, M., and Vuilleumier, P. (2010). Temporal precedence of emotion over attention modulations in the lateral amygdala: Intracranial ERP evidence from a patient with temporal lobe epilepsy. *Cognitive, Affective, & Behavioral Neuroscience*, 10(1):83–93.
- Proverbio, A. M., Del Zotto, M., and Zani, A. (2007). Inter-individual differences in the polarity of early visual responses and attention effects. *Neuroscience Letters*, 419(2):131–136.
- Proverbio, A. M., Del Zotto, M., and Zani, A. (2010). Electrical neuroimaging evidence that spatial frequency-based selective attention affects V1 activity as early as 40–60 ms in humans. *BMC Neuroscience*, 11(1):59.
- Rajkowska, G. and Goldman-Rakic, P. S. (1995). Cytoarchitectonic definition of prefrontal areas in the normal human cortex: II. Variability in locations of areas 9 and 46 and relationship to the Talairach Coordinate System. *Cerebral Cortex*, 5(4):323–337.
- Rauss, K. S., Pourtois, G., Vuilleumier, P., and Schwartz, S. (2009). Attentional load modifies early activity in human primary visual cortex. *Human Brain Mapping*, 30(5):1723–1733.
- Rauss, K. S., Pourtois, G., Vuilleumier, P., and Schwartz, S. (2011a). Effects of attentional load on early visual processing depend on stimulus timing. *Human Brain Mapping*, 33(1):63–74.
- Rauss, K. S., Schwartz, S., and Pourtois, G. (2011b). Top-down effects on early visual processing in humans: A predictive coding framework. *Neuroscience and Biobehavioral Reviews*, 35(5):1237–1253.
- Rayner, K., Castelhana, M. S., and Yang, J. (2009). Eye movements when looking at unusual/weird scenes: Are there cultural differences? *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 35(1):254–259.

- Raz, A. and Buhle, J. (2006). Typologies of attentional networks. *Nature Reviews Neuroscience*, 7(5):367–379.
- Riera, J. J., Ogawa, T., Goto, T., Sumiyoshi, A., Nonaka, H., Evans, A., Miyakawa, H., and Kawashima, R. (2012). Pitfalls in the dipolar model for the neocortical EEG sources. *Journal of Neurophysiology*, 108(4):956–975.
- Rizzolatti, G., Riggio, L., Dascola, I., and Umiltá, C. (1987). Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychologia*, 25(1A):31–40.
- Robinson, D. L. and Kertzman, C. (2002). Covert Orienting of Attention in Macaques. III. Contributions of the Superior Colliculus. *Journal of Neurophysiology*, 74(2):713–721.
- Rodman, H. R., Gross, C. G., and Albright, T. D. (1989). Afferent basis of visual response properties in area MT of the macaque. I. Effects of striate cortex removal. *Journal of Neuroscience*, 9(6):2033–2050.
- Rosenhan, D. L. and Seligman, M. E. P. (1995). *Abnormal Psychology*. W. W. Norton & Company, Inc., New York, London, third edition.
- Rosenholtz, R., Li, Y., and Nakano, L. (2007). Measuring visual clutter. *Journal of Vision*, 7(2):17–17.
- Rousselet, G. A. (2012). Does Filtering Preclude Us from Studying ERP Time-Courses? *Frontiers in Psychology*, 3.
- Rozenkrants, B. and Polich, J. (2008). Affective ERP processing in a visual oddball task: Arousal, valence, and gender. *Clinical Neurophysiology*, 119(10):2260–2265.
- Saenz, M., Buracas, G. T., and Boynton, G. M. (2002). Global effects of feature-based attention in human visual cortex. *Nature Neuroscience*, 5(7):631–632.
- Sanei, S. and Chambers, J. (2007). *EEG Signal Processing*. John Wiley & Sons, Ltd, Chichester, England.
- Santesso, D. L., Meuret, A. E., Hofmann, S. G., Mueller, E. M., Ratner, K. G., Roesch, E. B., and Pizzagalli, D. A. (2008). Electrophysiological correlates of spatial orienting towards angry faces: a source localization study. *Neuropsychologia*, 46(5):1338–1348.

- Schmukle, S. C. (2005). Unreliability of the Dot Probe Task. *European Journal of Personality*, 19:595–605.
- Scholl, B. J. (2001). Objects and attention: the state of the art. *Cognition*, 80(1-2):1–46.
- Schupp, H. T., Stockburger, J., Bublatzky, F., Junghofer, M., Weike, A. I., and Hamm, A. O. (2007). Explicit attention interferes with selective emotion processing in human extrastriate cortex. *BMC Neuroscience*, 8:16.
- Selemon, L. D. and Goldman-Rakic, P. S. (1988). Common cortical and subcortical targets of the dorsolateral prefrontal and posterior parietal cortices in the rhesus monkey: evidence for a distributed neural network subserving spatially guided behavior. *Journal of Neuroscience*, 8(11):4049–4068.
- Spielberger, C. D., Gorsuch, R. L., Lushene, R., Vagg, P. R., and Jacobs, G. A. (1983). *Manual for the State-Trait Anxiety Inventory*.
- Staugaard, S. R. (2009). Reliability of two versions of the dot-probe task using photographic faces. *Psychology Science Quarterly*, 51(3):339–350.
- Stolarova, M., Keil, A., and Moratti, S. (2006). Modulation of the C1 visual event-related component by conditioned stimuli: evidence for sensory plasticity in early affective perception. *Cerebral Cortex*, 16(6):876–887.
- Storbeck, J., Robinson, M. D., and McCourt, M. E. (2006). Semantic Processing Precedes Affect Retrieval: The Neurological Case for Cognitive Primacy in Visual Processing. *Review of General Psychology*, 10(1):41–55.
- Streit, M., Dammers, J., Simsek-Kraues, S., Brinkmeyer, J., Wolwer, W., and Ioannides, A. (2003). Time course of regional brain activations during facial emotion recognition in humans. *Neuroscience Letters*, 342:101–104.
- Streit, M., Ioannides, A. A., Liu, L., Wölwer, W., Dammers, J., Gross, J., Gaebel, W., and Müller-Gärtner, H. W. (1999). Neurophysiological correlates of the recognition of facial expressions of emotion as revealed by magnetoencephalography. *Cognitive Brain Research*, 7(4):481–491.
- Susac, A., Ilmoniemi, R. J., Pihko, E., Ranken, D., and Supek, S. (2010). Early cortical responses are sensitive to changes in face stimuli. *Brain Research*, 1346(C):155–164.

- Susac, A., Ilmoniemi, R. J., Pihko, E., and Supek, S. (2004). Neurodynamic studies on emotional and inverted faces in an oddball paradigm. *Brain Topography*, 16(4):265–268.
- Tallgren, P., Vanhatalo, S., Kaila, K., and Voipio, J. (2005). Evaluation of commercially available electrodes and gels for recording of slow EEG potentials. *Clinical Neurophysiology*, 116(4):799–806.
- Tanskanen, T., Nasanen, R., Montez, T., Päällysaho, J., and Hari, R. (2005). Face recognition and cortical responses show similar sensitivity to noise spatial frequency. *Cerebral Cortex*, 15(5):526–534.
- Torralba, A., Oliva, A., Castelhana, M. S., and Henderson, J. M. (2006). Contextual guidance of eye movements and attention in real-world scenes: The role of global features in object search. *Psychological Review*, 113(4):766–786.
- Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., Marcus, D. J., Westerlund, A., Casey, B., and Nelson, C. A. (2009). The NimStim set of facial expressions: Judgments from untrained research participants. *Psychiatry Research*, 168(3):242–249.
- Treue, S. and Martinez Trujillo, J. C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature*, 399:575–579.
- Underwood, G. and Foulsham, T. (2006). Visual saliency and semantic incongruency influence eye movements when inspecting pictures. *Quarterly Journal of Experimental Psychology*, 59(11):1931–1949.
- Underwood, G., Templeman, E., Lamming, L., and Foulsham, T. (2008). Is attention necessary for object identification? Evidence from eye movements during the inspection of real-world scenes. *Consciousness and Cognition*, 17(1):159–170.
- Vanhatalo, S., Voipio, J., and Kaila, K. (2005). Full-band EEG (FbEEG): an emerging standard in electroencephalography. *Clinical Neurophysiology*, 116(1):1–8.
- VanRullen, R. (2011). Four common conceptual fallacies in mapping the time course of recognition. *Frontiers in Psychology*, 2:365.
- VanRullen, R. and Thorpe, S. J. (2001). Is it a bird? Is it a plane? Ultra-rapid visual categorisation of natural and artificial objects. *Perception*, 30(6):655–668.
- Võ, M. L.-H. and Henderson, J. M. (2009). Does gravity matter? Effects of semantic

- and syntactic inconsistencies on the allocation of attention during scene perception. *Journal of Vision*, 9(3):24–24.
- von Helmholtz, H. (1896). *Handbuch der Physiologischen Optik, Dritter Abschnitt, Zweite Auflage*. Voss, Hamburg.
- Vossel, S., Weidner, R., Driver, J., Friston, K. J., and Fink, G. R. (2012). Deconstructing the Architecture of Dorsal and Ventral Attention Systems with Dynamic Causal Modeling. *Journal of Neuroscience*, 32(31):10637–10648.
- Vuilleumier, P., Armony, J. L., Clarke, K., Husain, M., Driver, J., and Dolan, R. J. (2002). Neural response to emotional faces with and without awareness: event-related fMRI in a parietal patient with visual extinction and spatial neglect. *Neuropsychologia*, 40(12):2156–2166.
- Vuilleumier, P., Armony, J. L., and Dolan, R. J. (2003a). Reciprocal Links Between Emotion and Attention. In Frackowiak, R. S. J., editor, *Human Brain Function*, pages 419–444. San Diego: Academic Press, San Diego.
- Vuilleumier, P., Armony, J. L., Driver, J., and Dolan, R. J. (2001). Effects of Attention and Emotion on Face Processing in the Human Brain: An Event-Related fMRI Study. *Neuron*, 30:829–841.
- Vuilleumier, P., Armony, J. L., Driver, J., and Dolan, R. J. (2003b). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nature Neuroscience*, 6(6):624–631.
- Vuilleumier, P. and Pourtois, G. (2007). Distributed and interactive brain mechanisms during emotion face perception: Evidence from functional neuroimaging. *Neuropsychologia*, 45(1):174–194.
- Vuilleumier, P. and Schwartz, S. (2001). Emotional facial expressions capture attention. *Neurology*, 56(2):153–158.
- Walsh, P., Kane, N., and Butler, S. (2005). The clinical role of evoked potentials. *Journal of Neurology, Neurosurgery & Psychiatry*, 76(suppl II):ii16–ii22.
- West, G. L., Anderson, A. K., Ferber, S., and Pratt, J. (2011). Electrophysiological evidence for biased competition in V1 for fear expressions. *Journal of Cognitive Neuroscience*, 23(11):3410–3418.
- Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M. B., and Jenike,

- M. A. (1998). Masked Presentations of Emotional Facial Expressions Modulate Amygdala Activity without Explicit Knowledge. *Journal of Neuroscience*, 18(1):411–418.
- Whelan, R. (2008). Effective Analysis of Reaction Time Data. *The Psychological Record*, 58:475–482.
- Williams, L. M., Liddell, B. J., Kemp, A. H., Bryant, R. A., Meares, R. A., Peduto, A. S., and Gordon, E. (2006). Amygdala–prefrontal dissociation of subliminal and supraliminal fear. *Human Brain Mapping*, 27(8):652–661.
- Woldorff, M. G. (1993). Distortion of ERP averages due to overlap from temporally adjacent ERPs: Analysis and correction. *Psychophysiology*, 30:98–119.
- Wu, Y., Chen, J., and Han, S. (2005). Neural mechanisms of attentional modulation of perceptual grouping by collinearity. *NeuroReport*, 16(6):567–570.
- Yarbus, A. L. (1967). *Eye movements and vision*. Plenum Press, New York.
- Yates, A., Ashwin, C., and Fox, E. (2010). Does emotion processing require attention? The effects of fear conditioning and perceptual load. *Emotion*, 10(6):822–830.
- Yiend, J. and Mathews, A. (2001). Anxiety and attention to threatening pictures. *Quarterly Journal of Experimental Psychology: Section A*, 54(3):665–681.
- Zajonc, R. B. (1980). Feeling and thinking: preferences need no inferences. *American Psychologist*, 35(2):151–175.
- Zani, A. and Proverbio, A. M. (2009). Selective attention to spatial frequency gratings affects visual processing as early as 60 msec. poststimulus. *Perceptual and motor skills*, 109(1):140–158.
- Zhang, W. and Luck, S. J. (2008). Feature-based attention modulates feedforward visual processing. *Nature Neuroscience*, 12(1):24–25.