

**An eye (region) sensitivity during early face perception:
The N170 is modulated by facial context and featural fixation**

by

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Author's Declaration

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

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

Abstract

The N170 is a face-sensitive ERP component that also demonstrates a particular sensitivity to the eyes. Specifically, the N170 responds maximally to isolated eye regions (i.e., two eyes), as well as to eye fixations within a face. Here I compared N170 modulations when facial features (left eye, right eye, nasion, nose, and mouth) were fixated in isolation or within a full face. Fixation on the desired feature was continuously enforced using a gaze-contingent eye-tracking procedure. In order to further assess this eye sensitivity, I also compared the N170 response to single isolated eyes and the classically-used eye region. The N170 was largest and most delayed when features were fixated in isolation, compared to equivalent fixations in a full face. An eye sensitivity within a face context was observed, with larger N170 amplitudes elicited when the left or right eye was fixated. Mouth fixation yielded the smallest and most delayed N170 within a face, and showed the largest amplitude difference between fixation in isolation and fixation within a face. For isolated features, single eyes did not differ from mouths, yielding significantly larger and faster N170 responses compared to isolated noses. Alternatively, isolated eye regions elicited consistently larger and shorter N170 responses compared to single isolated eyes, irrespective of eye or nasion fixation. These results highlight the importance of the eyes in early face perception, and provide compelling support for an interplay between featural and holistic neural mechanisms. These findings also provide novel evidence of an increased sensitivity to the presence of two symmetric eyes within the eye region compared to only one eye, consistent with an eye region detector rather than an eye detector *per se*.

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Table of Contents

Author's Declaration	ii
Abstract	iii
Acknowledgements	iv
List of Figures	vi
List of Tables	viii
Chapter 1: INTRODUCTION	1
Chapter 2: METHOD	8
Chapter 3: EYE SENSITIVITY WITHIN A FACE	18
Chapter 4: FEATURAL FIXATION – ISOLATION VS. FULL FACE	23
Chapter 5: SINGLE EYE VS. EYE REGION	31
Chapter 6: GENERAL DISCUSSION	39
References	44
Appendix 1	48

List of Figures

Figure 1. *Panel A:* Examples of the 14 study conditions. Participants always fixated on the same location of the computer screen, and each stimulus was presented offset to ensure the participant’s gaze landed on one of the five featural fixations (nasion, left eye, right eye, nose, or mouth). Note that eye positions are referenced from the observer’s perspective (i.e., left eye indicates the left eye of the image). Coloured boxes represent conditions included in each of the analyses: i) impact of low-level features on eye sensitivity in a full face context (research question #1; red box), ii) modulation of N170 responding to features in isolation and in a full face context (research question #2; blue box), iii) single eye vs. eye region with eye fixations (research question #3a; purple box), and iv) single eye vs. eye region with nasion fixation (research question #3b; yellow box). *Panel B:* Stimulus exemplars (one full face and one isolated eye region) with image size and angular distances between featural fixations. The purple circles represent the non-overlapping 1.92° ROIs centered on each feature, which were used to reject eye movements for each condition, and were identical in pixel intensity and RMS contrast.11

Figure 2. Trial example with left eye fixation on a face. First, the fixation cross was displayed on the screen as a fixation trigger for a minimum of 306 ms and a maximum of ten seconds ($M = 555 \text{ ms} \pm 122$). If the trigger was not activated within this time period, the trial was aborted and a drift correct was initiated. Once the fixation trigger was activated, the stimulus was presented for 259 ms, followed by a response screen (with a fixation cross) for a maximum of 706 ms. Responses were only required for oddball trials (i.e., infrequent inverted stimuli).14

Figure 3. Peak N170 amplitudes and latencies for full face fixations. *Panel A:* Group ERP waveforms for each featural fixation within a full face (averaged across the electrodes at which the N170 was maximal for each participant). *Panel B:* Mean N170 peak amplitudes for each fixation location within a full face. Note the larger amplitudes in the right hemisphere. Left and right eye fixations yielded the largest N170 amplitudes, followed by nose and nasion fixations, with mouth fixation eliciting the smallest N170 amplitude. *Panel C:* Mean N170 peak latencies for each fixation location within a full face. Note the faster latencies for nasion and nose fixations, followed by ipsilateral eye fixations, with contralateral eye and mouth fixations producing the slowest latencies.20

Figure 4: Peak N170 amplitudes and latencies for facial features fixated in isolation or within a full face context. *Panel A:* Group N170 ERP waveforms for each fixated feature presented in isolation (purple) or in a full face context (green), for each hemisphere (averaged across the electrodes at which N170 was maximal for each participant). *Panel B:* Mean N170 peak amplitudes for each fixated feature comparing isolated and full face conditions (averaged across hemispheres) *Panel C:* Mean N170 amplitude difference scores (isolated feature – full face) for each fixated feature, averaged across hemispheres. Note the larger amplitude difference for mouth fixation relative to all other featural fixations. *Panel D:* Mean N170 latency difference scores (isolated – full face) for each featural fixation, across each hemisphere. Note the significantly larger latency difference for nose fixation relative to all other featural fixations, as well as larger latency reductions for eye fixations in the hemisphere contralateral to visual field presentation.26

Figure 5. Peak N170 amplitudes and latencies for isolated eye conditions with left and right eye fixations. *Panel A:* Group ERP waveforms for isolated eye conditions with left eye fixation. *Panel B:* Group ERP waveforms for isolated eye conditions with right eye fixation. *Panel C:* Mean N170 amplitudes for isolated eye conditions with left and right eye fixations in each hemisphere. Note the larger N170 amplitudes for isolated eye regions compared to single isolated eyes. *Panel D:* Mean N170 latencies for isolated eye conditions with left and right eye fixations in each hemisphere. Note the significantly shorter N170 latencies to eye regions compared to single isolated eyes, an effect enhanced in the hemisphere contralateral to parafoveal eye information. 34

Figure 6. Peak N170 amplitudes and latencies for isolated eye conditions with nasion fixation. *Panel A:* Group ERP waveforms for isolated eye conditions with nasion fixation. The FF-Na condition (from Chapter 3) was added for visual comparison. *Panel B:* Mean N170 amplitudes for isolated eye conditions with nasion fixation in the left and right hemispheres. Note the enhanced N170 amplitudes for the eye region relative to single eyes, and the right-hemispheric lateralization for the eye region and single left eye. *Panel C:* Mean N170 latencies for isolated eye conditions with nasion fixation in the left and right hemispheres. Note the prolonged N170 latencies for single eyes compared to the eye region, particularly in the hemisphere ipsilateral to parafoveal eye information.36

List of Tables

Table 1. Mean pixel intensity and RMS contrast for each featural fixation based on a pre-defined 1.92° ROI. Standard deviations are in parentheses. 12

Table 2. Number of participants who showed a maximal N170 peak at the left (PO7, P9, and CB1) and right (PO8, P8, P10, and CB2) hemisphere electrode locations. 16

Chapter 1: INTRODUCTION

It is widely accepted that faces are processed holistically – as an integration of all features (Maurer, Grand, & Mondloch, 2002; Rossion & Gauthier, 2002). In particular, when holistic processing is disrupted by inversion or presenting isolated facial features, response times in face recognition and perception tasks increase, and accuracy decreases (Rossion & Gauthier, 2002, Tanaka & Farah, 1993; Tanaka & Simonyi, 2016; Yin, 1969). For example, Tanaka & Farah (1993) demonstrated that adults were more accurate at recognizing features when presented in the context of a full face, compared to when the features were presented in isolation. Interestingly, the authors also found that recognition performance was disproportionately higher for eye judgements relative to nose or mouth judgements, suggesting the eyes may play a fundamental role in holistic face perception.

At the neuronal level, comparative regions of macaque cortex have been identified that respond preferentially to human faces and facial features (Freiwald, Tsao, & Livingstone, 2009; Meyers, Borzello, Freiwald, & Tsao, 2015; Perrett, Hietanen, Oram, Benson, & Rolls, 1992; Perrett, Rolls, & Caan, 1982). For example, Freiwald et al. (2009) demonstrated that individual neurons were specifically tuned to featural information. In fact, the authors found that iris size and inter-ocular distance were some of the most strongly coded featural attributes, highlighting the significance of eye cues. It is also noteworthy that these neurons coded for small combinations of facial features (e.g., left eye and nose), with no single neuron coding for an entire holistic percept. This led Freiwald et al. (2009) to propose that neurons may individually code for their optimal featural information, whereas the overall facial percept is constructed based on facilitatory and inhibitory signals between neurons.

The importance of the role of the eyes during early face perception also comes from scalp-recorded event related potentials (ERPs) – in particular from the N170, a neural marker of early face perception. The N170 is a face-sensitive ERP component recorded maximally over occipito-temporal regions between 120-200 ms post-stimulus onset (Bentin, Allison, Puce, Perez, & McCarthy, 1996; George, Evans, Fiori, Davidoff, & Renault, 1996; Rossion & Jacques, 2011). Faces elicit significantly larger N170 amplitudes and faster peak latencies compared to objects or body parts (Bentin et al., 1996; Eimer, 2000b; Itier, Latinus, & Taylor, 2006; Itier & Taylor, 2004c, 2004d; Kloth, Itier, & Schweinberger, 2013; Rossion, Gauthier, et al., 2000), implicating different underlying neural generators across categories. Furthermore, in line with a well-documented right-hemispheric lateralization for face processing (Haxby, Hoffman, & Gobbini, 2000; Hilliard, 1973; Rossion, Dricot, et al., 2000), the N170 response is often most pronounced over the right hemisphere (Rossion & Jacques, 2011; Rossion, Joyce, Cottrell, & Tarr, 2003).

The N170 ERP component has been deemed a neural marker of holistic face perception (Eimer, 2000a, 2000b; Rossion & Gauthier, 2002; Rossion & Jacques, 2011), due to peak amplitude and latency sensitivities to holistic disruptions. Specifically, face inversion delays N170 latencies and enhances peak amplitudes relative to upright, intact faces (Itier et al., 2006; Itier, Taylor, & Lobaugh, 2004; Itier & Taylor, 2002, 2004a, 2004b; Jacques, d' Arripe, & Rossion, 2007; Rossion & Gauthier, 2002; Rossion et al., 1999). This larger response to inverted faces is believed to be due to the disruption of holistic processing, resulting in a larger neuronal response from feature- and/or object-based cells, compared to the cohesive neural representation of upright faces (Itier et al., 2007; Nemrodov et al., 2014; Rossion & Gauthier, 2002).

The specificity of the N170 component to holistic processing remains controversial, however, due to a strong body of literature indicating that the N170 is also sensitive to eye

information. In particular, the N170 elicits increased amplitudes and delayed latencies for isolated eye regions compared to full faces (Bentin et al., 1996; Itier, Alain, Sedore, & McIntosh, 2007; Itier et al., 2006; Itier, Van Roon, & Alain, 2011; Kloth et al., 2013; Taylor, Itier, Allison, & Edmonds, 2001). The N170 eye sensitivity has further been deemed species-sensitive, with a greater sensitivity to human eyes compared to eyes of other species (Itier et al., 2011), and is not merely due to a part-whole effect since a similar pattern is not observed for cars and isolated car lights (Kloth et al., 2013). Recently, Rousselet, Ince, van Rijsbergen, and Schyns (2014) reported that the N170, and in particular the transition between the P1 and N170 peaks, codes for contralateral eye information. These findings suggest that each eye may be processed independently – an idea that requires further empirical investigation.

Recent studies have also shown that the N170 eye sensitivity is present within the context of a full face, such that fixation on the eyes or nasion yield larger N170 amplitudes relative to fixation on other features (de Lissa et al., 2014; McPartland, Cheung, Perszyk, & Mayes, 2010; Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Nemrodov, Anderson, Preston, & Itier, 2014). Collectively these findings demonstrate that the human brain is attuned to the early detection and processing of the eyes within a face, and suggest the presence of a neural eye detector mechanism. Furthermore, the existence of an eye sensitivity within a face opposes the generally accepted view that faces are processed in a purely holistic manner, and instead suggests that early face perception may involve a combination of featural and holistic mechanisms. In an attempt to integrate these opposing views, Nemrodov et al. (2014) proposed the Lateral Inhibition, Face Template, and Eye Detector (LIFTED) model of face perception.

In short, the LIFTED model claims that early face perception, as marked by the N170 ERP component, involves a complex interplay of foveal and parafoveal information, stipulating that

information presented in fovea¹ (and parafovea) influences the holistic percept. In particular, when features are fixated in fovea, these features are cortically over-represented in ventral visual regions. Thus, in order to achieve holistic processing, the LIFTED model postulates that neurons coding for parafoveal information will inhibit the neurons coding for the fixated feature. The model also suggests that various factors, such as distance from fovea and featural salience, may impact the strength of the inhibitory signal elicited by parafoveal features. In particular, the LIFTED model emphasizes the presence of an eye detector during early face perception, with the eyes providing strong inhibitory signals when other features are fixated, as well as the eyes requiring a large degree of inhibition from other features. The model proposes that when faces are far away (or smaller in size), then the eyes will be fully inhibited, resulting in complete holistic processing. Alternatively, at closer distances (or larger sizes), the eyes should be more difficult to inhibit (i.e., partial inhibition), resulting in an interplay between featural and holistic mechanisms, such that the N170 will be modulated by featural fixation.

In light of this recent evidence regarding the N170 eye sensitivity, the current study sought to clarify the impact of featural and holistic mechanisms as well as the role of the eyes in early face perception, by examining N170 peak amplitudes and latencies to facial features (left eye, right eye, nasion, nose, and mouth) fixated in isolation or within the context of a full face. Human eyes contain a high degree of local contrast and pixel intensity (Kobayashi & Kohshima, 1997), and although the impact of low-level factors, such as global contrast and pixel intensity are known to modulate the N170 component, their impact at the local (featural) level is, to the best of my

¹ Fovea is an anatomical region on the human retina responsible for high visual resolution, whilst the surrounding region (parafovea and periphery) is involved in lower-resolution and gist-based visual processing (Larson & Loschky, 2009). Vision scientists have defined fovea as extending $\sim 1^\circ$ eccentricity on either side of fixation (i.e., subtending a total of 2°), parafovea as extending $1-5^\circ$ eccentricity, and periphery as extending beyond 5° (Polyak, 1941; Rodieck, 1998). Thus, this study will adhere to these specifications for the remainder of the paper.

knowledge, unknown. The current study aimed to address this issue by equating all internal facial features (left eye, right eye, nose, and mouth) on pixel intensity and contrast, in order to measure the unique contribution of each feature when presented within the context of a face or in isolation. Furthermore, the N170 response to internal facial features is largely understudied, with most investigations focusing primarily on the isolated eye region. Specifically, all studies to date have only compared the isolated eye region to one category of faces (typically centred on the nasion or nose). However, given recent evidence highlighting that featural fixation within a face modulates neural responding (de Lissa et al., 2014; McPartland et al., 2010; Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Nemrodov et al., 2014), it is apparent that this is not a suitable control, and makes it difficult to compare the impact of isolation to other facial features (i.e., nose or mouth). Therefore, the current study compared enforced fixation on the same facial features in isolation and within the context of a full face. By keeping foveal content the same across categories, any modulations in N170 responding can only be attributed to the presence/absence of parafoveal (face) information. Finally, the eye region is special for a variety of reasons, one of the most salient being the presence of two symmetrical eyes. This raises the question of whether the eyes are special because there are two symmetrical eye features (compared to only one nose feature or one mouth feature), or because of properties inherent to each eye (e.g., structure and shape, social relevance, etc.), and thus requires a direct examination of a single eye versus the eye region.

To this end, three primary research questions were evaluated:

1. *Does the eye sensitivity within a face context persist even after low-level properties (pixel intensity and contrast) are controlled at the local (featural) level? (Chapter 3)* I predicted that enforced fixation to the left and right eyes of faces, controlled for local pixel intensity and contrast, would still yield significantly larger N170 amplitudes relative to all other

featural fixations, thereby demonstrating that the eye sensitivity is not merely due to differences in low-level properties, but instead reflects higher-level mechanisms.

2. *How do context (full face vs. isolated feature) and featural fixation modulate N170 amplitude and latency? (Chapter 4)* In line with previous research, it was predicted that isolated eyes would yield a larger N170 amplitude and faster latency relative to isolated mouth or nose categories, reflecting sensitivity to the eyes compared to other face features presented in isolation. Importantly, this effect was expected to persist even with single isolated eyes, a condition not tested before, demonstrating the importance of the eye as a unique feature. Based on the LIFTED model, it was further anticipated that partial neural inhibition would be invoked during early face perception, such that the N170 would be modulated by featural fixation. Furthermore, all fixations within a full face context were expected to elicit smaller and faster N170 responses relative to the same featural fixations in isolation due to the recruitment of neural inhibition mechanisms and the presence of parafoveal information in the full face conditions.
3. *How is the N170 response modulated by eye content (single isolated eye vs. eye region) a) when an eye is fixated? and b) when the nasion is fixated? (Chapter 5)* Based on the LIFTED model, foveal and parafoveal information interact differently depending on face context. In particular, when features are presented in isolation (as in the case of the eye region), featural processing is invoked. Therefore, neural inhibition mechanisms should not be recruited, and the neural activity recorded for foveal and parafoveal (eye) information should be cumulative. Within an isolated eye region, foveal fixation on one eye results in the other eye being in parafovea; alternatively, if the nasion is fixated then both eyes are situated in parafovea. Therefore, it was predicted that isolated eye regions

would elicit larger N170 amplitudes relative to single isolated eyes. These effects were expected to uphold for both eye and nasion fixations, albeit attenuated for nasion fixations due to the absence of foveal content (Nemrodov et al., 2014). Moreover, in accordance with the fact that visual information is processed maximally in the contralateral hemisphere, and recent ERP findings of contralateral eye (Rousselet et al., 2014) and face (Towler & Eimer, 2015) processing, it was expected that effects would be enhanced in the hemisphere contralateral to visual field presentation.

Chapter 2: METHOD

Participants

Thirty-four undergraduate students from the University of Waterloo participated in the current ERP study (19 females, 25 right-eye dominant, $M = 21.29$ years, $SD = 3.04$). All participants reported normal or corrected-to-normal vision, and had lived in Canada and/or the United States for at least ten years ($M = 19.32$ years, $SD = 3.33$). This criterion was used to ensure participants had adequate exposure to Caucasian faces (to reduce the impact of the other-race effect and maximize efficient processing of the experimental stimuli). All participants also reported no history of: a) head injury, neurological disease or psychiatric disorder, b) epilepsy, seizures or sensitivities to flashing lights, nor c) consumption of antipsychotic medications or medications containing cortisone. An additional three participants were tested, but were subsequently rejected from analyses: two participants did not complete the experiment due to an inability to acquire a robust eye-tracking signal, and one participant registered too few trials per condition due to eye movements and artifact rejection. This study was reviewed and approved by a University of Waterloo Human Research Ethics Committee. All participants provided informed written consent at the beginning of the experiment, and participated for Psychology course credit.

Stimuli

Thirty grey-scale identities (15 male, 15 female) were selected from the face database produced by Nemrodov et al. (2014), generated using FACES™ 4.0 by IQBiometrix Inc. One additional identity was also selected from this database for the practice phase and oddball trials. Each facial identity was cropped into an oval subtending a visual angle of 8.13° horizontally and 12.64° vertically, so as to only include the internal features of the face (eyes, eyebrows, nose, and mouth). Isolated feature stimuli were created by extracting a rectangular segment (subtending a

visual angle of 6.92° horizontally and 2.45° vertically) from each facial oval, such that either an isolated eye region, an isolated nose, or an isolated mouth was contained within the segment. Single isolated left/right eye stimuli were generated by airbrushing out the opposite eye from the respective isolated eye region stimulus. All stimuli were modified using the GNU Image Manipulation Program (GIMP 2.8) software. Visual fixation was enforced on specific features (left eye, right eye, nasion, nose, and mouth) using a gaze-contingent stimulus presentation (detailed below), generating a total of 14 conditions – 5 full face conditions and 9 isolated feature conditions (displayed in Figure 1A): i) full face-left eye fixation (FF-LE), ii) full face-right eye fixation (FF-RE), iii) full face-nasion fixation (FF-Na), iv) full face-nose fixation (FF-No), v) full face-mouth fixation (FF-M), vi) isolated eye region-left eye fixation (IEyes-LE), vii) isolated eye region-right eye fixation (IEyes-RE), viii) isolated eye region-nasion fixation (IEyes-Na), ix) isolated nose-nose fixation (INo), x) isolated mouth-mouth fixation (IM), xi) isolated left eye-left eye fixation (ILE-LE), xii) isolated left eye-nasion fixation (ILE-Na), xiii) isolated right eye-right eye fixation (IRE-RE), and xiv) isolated right eye-nasion fixation (IRE-Na).

All stimuli were mirror-flipped along the vertical axis to eliminate featural asymmetry effects, thereby doubling the number of stimuli. One identity was inverted 180° for all nine isolated feature conditions and three of the full face conditions (left eye, right eye, and nasion) to generate the inverted oddball stimuli. Each stimulus was then placed on a pixel-scrambled background, so that the final size of each image subtended 12.88° horizontally and 17.89° vertically (Figure 1B). For each stimulus condition, coordinates corresponding to five featural locations (left eye, right eye, nasion, nose, and mouth) were determined. Specifically, fixation crosses on the tip of the nose and just below the mouth line were aligned with one another along an axis passing through the midline of the face. Eye coordinates were determined by placing the cross on the centre of each

pupil, and nasion coordinates were determined by placing the cross between the eyes along an axis passing horizontally through the pupils. Each stimulus was then placed on the pixel-scrambled background so that the featural fixation (left eye, right eye, nasion, nose, and mouth) fell on the same location as the fixation cross.

To eliminate the possible influences of low-level factors on the N170 ERP component, all stimuli were equated on mean pixel intensity² (PI) and RMS contrast³ at both the local and global level. More specifically, within each facial identity, four regions of interest (ROIs) were created that subtended 1.92° visual angle vertically and horizontally around the centre of each facial feature (left eye, right eye, nose, and mouth; Figure 1B). The PI and RMS contrast values for each of these ROIs were adjusted using custom MATLAB scripts, so that the mean PI and RMS contrast across the ROIs were virtually identical (Table 1). The edges of each ROI were subsequently blended with the surrounding facial texture. All images were also adjusted at the global level to be equivalent in terms of mean PI (0.58) and RMS contrast (0.48), by manipulating the pixel-scrambled background using homemade MATLAB scripts based off the SHINE toolbox (Willenbockel et al., 2010).

² Calculated as the mean value for all pixels within the featural ROI (local) or across the entire image (global).

³ Calculated as the standard deviation value for all pixels within the featural ROI (local) or across the entire image (global).

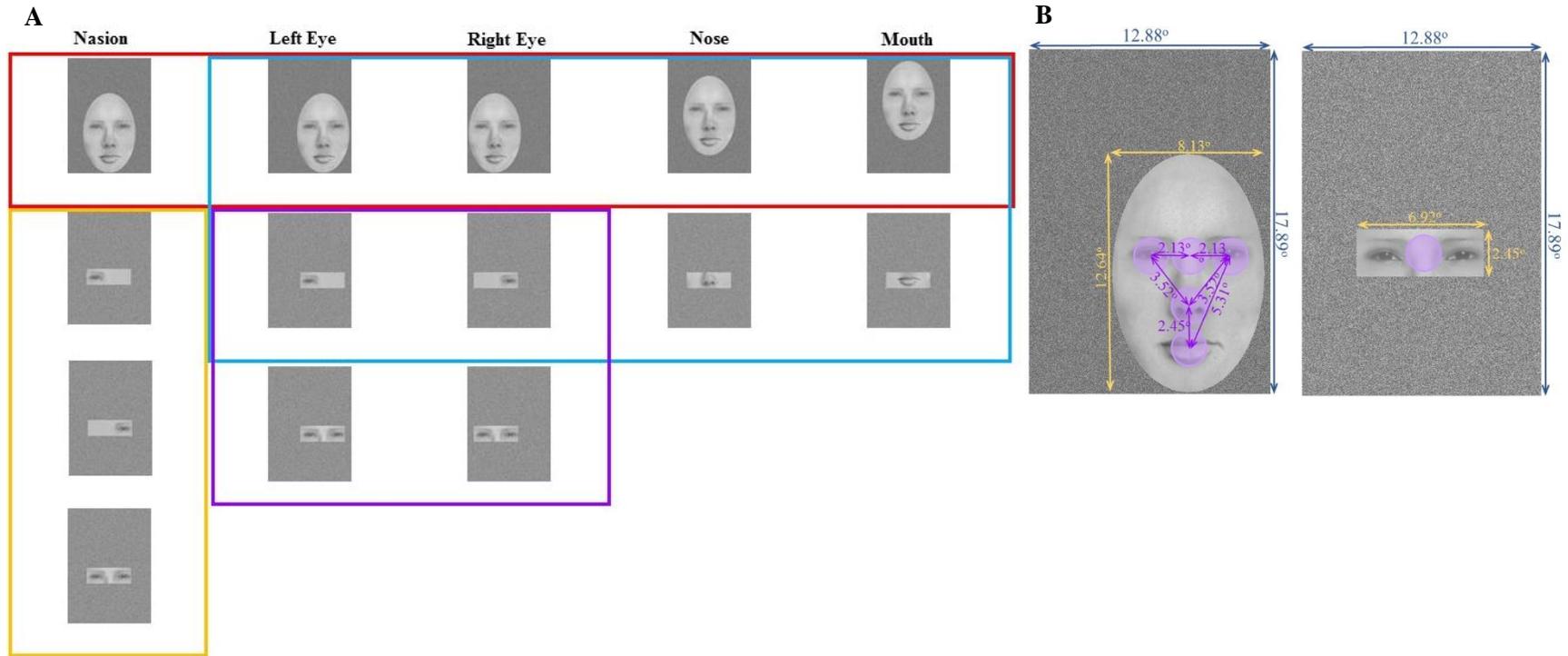


Figure 1. *Panel A:* Examples of the 14 study conditions. Participants always fixated on the same location of the computer screen, and each stimulus was presented offset to ensure the participant’s gaze landed on one of the five featural fixations (nasion, left eye, right eye, nose, or mouth). Note that eye positions are referenced from the observer’s perspective (i.e., left eye indicates the left eye of the image). Coloured boxes represent conditions included in each of the analyses: i) impact of low-level features on eye sensitivity in a full face context (research question #1; red box), ii) modulation of N170 responding to features in isolation and in a full face context (research question #2; blue box), iii) single eye vs. eye region with eye fixations (research question #3a; purple box), and iv) single eye vs. eye region with nasion fixation (research question #3b; yellow box). *Panel B:* Stimulus exemplars (one full face and one isolated eye region) with image size and angular distances between featural fixations. The purple circles represent the non-overlapping 1.92° ROIs centered on each feature, which were used to reject eye movements for each condition, and were identical in pixel intensity and RMS contrast.

Table 1. Mean pixel intensity and RMS contrast for each featural fixation based on a pre-defined 1.92° ROI. Standard deviations are in parentheses.

Fixation Location Region of Interest	Pixel Intensity	RMS Contrast
Left Eye	0.62 (0.002)	0.09 (0.001)
Right Eye	0.62 (0.002)	0.09 (0.001)
Nose	0.62 (0.004)	0.09 (0.002)
Mouth	0.62 (0.005)	0.10 (0.003)
Nasion	0.74 (0.012)	0.04 (0.022)

Design

The study was conducted in a dimly-lit sound-attenuated Faraday cage, in which participants were seated at a distance of 70 cm from the computer screen with their head supported in a chinrest. Participants were instructed to focus on the fixation cross, and that their gaze would trigger the appearance of a picture of a face or facial feature. Participants were further instructed to maintain this fixation when the picture appeared (i.e., no eye movements), even if they noticed they were not focused on anything in particular (e.g., nasion). Throughout the experiment, participants completed an oddball detection task (10% probability) to inverted faces and facial features⁴ in order to monitor attention, by pressing the spacebar to inverted images but making no response to upright images. All participants completed a short practice phase (18 trials) involving the same facial identity as the oddball stimuli, before beginning the experimental blocks. Five participants completed an additional practice phase due to eye-tracking difficulties or clarification of instructions.

An Eyelink 1000 remote system from SR Research, sampling at 1000 Hz, was used to measure eye position. At the beginning of each block the participant's dominant eye (as determined

⁴ The oddball face identity was different from those used in the experimental trials. Each experimental block consisted of fourteen oddball trials: nine isolated feature trials (IEyes-LE, IEyes-RE, IEyes-Na, INo, IMo, ILE-LE, ILE-Na, IRE-RE, and IRE-RE), two FF-LE trials, two FF-RE trials, and one FF-Na trial.

by the Miles test; Miles, 1930) was calibrated using a nine-point automatic calibration sequence. The non-dominant eye was recorded for three participants due to calibration issues with the dominant eye. Each experimental trial began with a gaze-contingent fixation trigger, during which participants had to maintain fixation within an ROI subtending $0.98^\circ \times 0.98^\circ$ visual angle centred on a cross (presented 15.95° horizontally and 11.86° vertically from the top-left corner of the computer monitor) for 306 ms. Due to variability in reorienting to the fixation cross after each trial, the average duration of this fixation trigger across participants was 553 ms ($SD = 128$ ms). This trigger activated stimulus presentation for 259 ms, followed by a response screen that remained until a button press was made, or for a maximum of 706 ms (Figure 2). If the fixation trigger was not activated within ten seconds (i.e. if the participant failed to fixate on the fixation cross for 306ms), the trial was aborted and a drift correct was recorded. Mid-block re-calibrations occurred following three sequential drift corrects or when the eye recording was clearly off-centre.

Each block of trials contained 140 experimental stimuli (10 stimuli – 5 of each gender – for each of the 14 conditions) and 14 oddball trials. Twelve blocks were included in this experiment, resulting in a total of 1848 trials overall⁵ (120 trials per condition \times 14 conditions = 1680 experimental trials; 168 oddball trials). However, due to time limitations⁶, not all participants completed the twelve blocks; participants completed an average of 9 blocks ($SD = 2$). The experiment was programmed under Experiment Builder 1.10.1385 (SR Research, <http://sr-research.com>) and stimuli were presented on a 1600 x 1200 pixel CRT computer monitor with a refresh rate of 85 Hz.

⁵ A large number of trials were included to maximize the signal-to-noise ratio and obtain a clear ERP signal, despite losing a number of trials to eye movements. Please see Appendix 1 for the average number of trials per condition.

⁶ The experimental session was restricted to a maximum of two hours (including EEG capping and clean-up). Thus, for some participants, especially those who experienced more eye-tracking difficulties and longer fixation trigger times, it was not possible to complete all blocks within this time frame. All participants completed a minimum of five blocks.

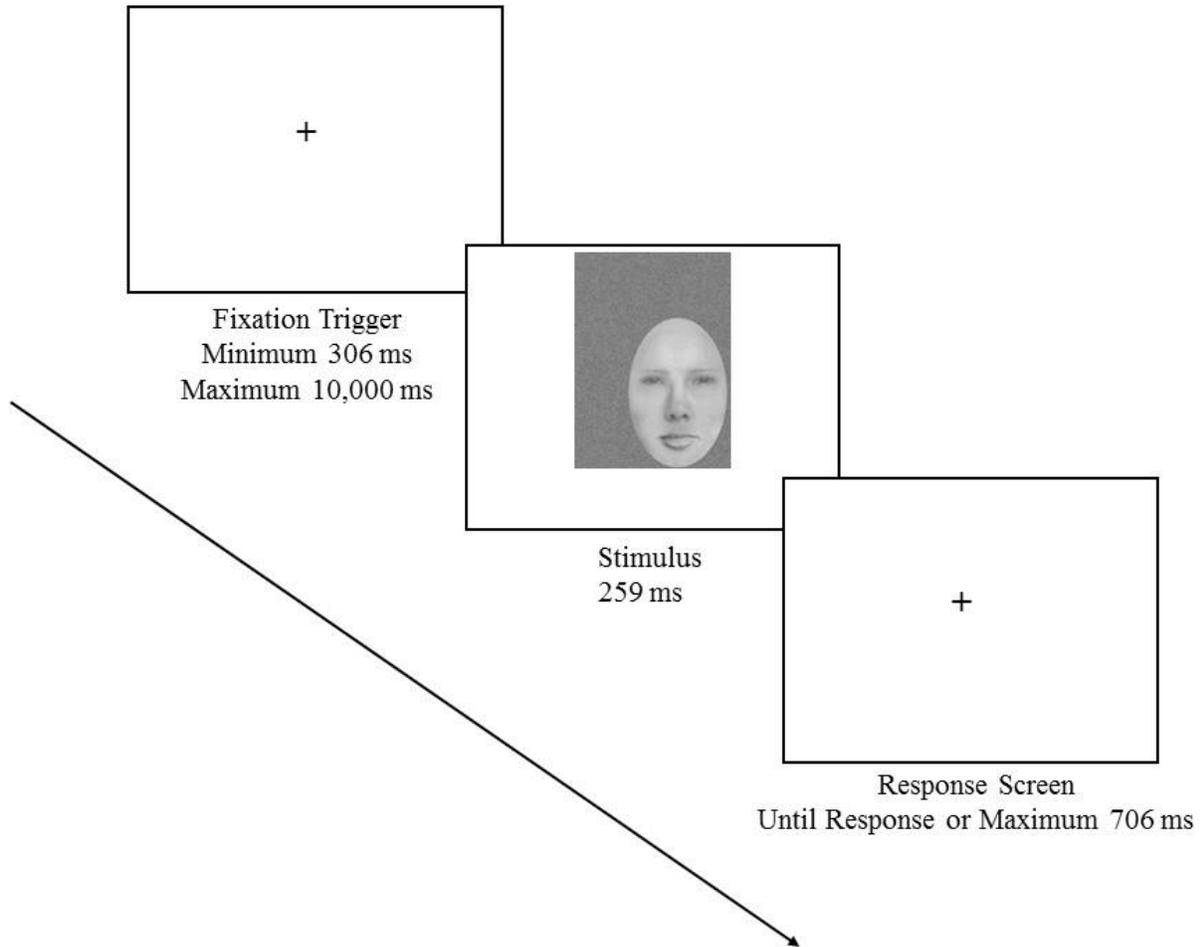


Figure 2. Trial example with left eye fixation on a face. First, the fixation cross was displayed on the screen as a fixation trigger for a minimum of 306 ms and a maximum of ten seconds ($M = 555$ ms \pm 122). If the trigger was not activated within this time period, the trial was aborted and a drift correct was initiated. Once the fixation trigger was activated, the stimulus was presented for 259 ms, followed by a response screen (with a fixation cross) for a maximum of 706 ms. Responses were only required for oddball trials (i.e., infrequent inverted stimuli).

Electroencephalogram recordings

Electroencephalogram (EEG) recordings were acquired using an Active-two Biosemi system with custom-made 72-electrode caps: 66 channels in an electrode cap under the 10/20 system extended (including CB1 and CB2 electrodes over the occipito-parietal region), and three pairs of face electrodes (two pairs of electrodes situated on the outer canthi and infra-orbital ridges to monitor horizontal and vertical eye movements, and one pair of electrodes situated over the mastoids). A Common Mode Sense (CMS) active-electrode and a Driven Right Leg (DRL) passive-electrode served as a ground during recording⁷. EEG data were collected continuously at 512 Hz, and electrode offset was kept below a value of $\pm 20\mu\text{V}$.

Data pre-processing

Only correctly rejected trials (i.e., upright face/feature trials for which no response was made) were included in the present analyses (0.28% of experimental trials were removed across participants due to miss and false alarm responses). EEG and ERP data were analyzed using EEGLab (Delorme & Makeig, 2004) and ERPLab (<http://erpinfo.org/erplab>) toolboxes in MATLAB.

All EEG data were average-referenced offline, and eye-tracking and EEG recordings were synchronized to ensure the maintenance of continuous fixation during the fixation trigger and stimulus presentation. Trials in which fixations extended beyond the 1.92° ROI for the centered feature were excluded from further analysis, resulting in removal of 3.38% of trials across all participants. Data were digitally band-pass filtered (0.01 Hz – 30 Hz) and epoched into time segments extending from -100ms pre- to 350ms post-stimulus presentation, using the pre-stimulus time as a baseline. Trials with artifacts above or below $\pm 70\mu\text{V}$ were automatically detected and

⁷ Please note that the Biosemi ActiveTwo system does not have an online reference during recording acquisition through the use of active electrodes (<https://www.biosemi.com/faq/cms&drl.htm>).

removed, and additional manual cleaning was conducted for one participant due to remaining artefacts, resulting in exclusion of 12.92% of trials across all participants. After trial rejection, participants provided an average of 76 trials per condition⁸ ($SD = 23$; Appendix 1).

Data Analysis

Each participant's average waveforms were individually inspected to determine the electrode at which the N170 amplitude was maximal for all conditions. This approach was taken, rather than the commonly used grand average approach, in order to be maximally sensitive to individual differences in N170 peaks (see also Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Rousselet & Pernet, 2011). The distribution of selected peak electrodes is presented in Table 2. The peak N170 amplitude and latency were measured at these electrodes between 120 ms and 215 ms post-stimulus onset.

Table 2. Number of participants who showed a maximal N170 peak at the left (PO7, P9, and CB1) and right (PO8, P10, CB2, and P8) hemisphere electrode locations.

	Left Hemisphere		Right Hemisphere
PO7	1	PO8	2
P9	27	P10	19
CB1	6	CB2	11
		P8	2

⁸ A lower number of trials were observed for the ILE-Na and IRE-Na conditions due to participants shifting their gaze towards the eye situated in parafovea. It is important to note, however, that these two conditions were only ever compared to the IEyes-Na condition (Figure 1, yellow box), which did not differ significantly in terms of the average number of trials. Thus, differences observed between conditions cannot be attributed to differences in the average number of trials included.

All analyses employed repeated measures analyses of variance (ANOVAs) conducted on the N170 peak amplitudes and latencies for a subset of conditions, depending on the question. The impact of low-level properties on the eye sensitivity within a full face (Chapter 3) was assessed by ANOVAs with Featural Fixation (5: nasion, left eye, right eye, nose, mouth) and Hemisphere (2: left, right) as within-subject factors, using the five full face conditions (Figure 1A, red box). Next, the modulation of the N170 across features presented in isolated or in the context of a full face (Chapter 4) was addressed by ANOVAs with Featural Fixation (4: left eye, right eye, nose, mouth), Context (2: full face, isolation), and Hemisphere (2: left, right) as within-subject factors, using the following conditions: FF-LE, FF-RE, FF-No, FF-M, IEyes-LE, IEyes-RE, INo, and IM (Figure 1A, blue box). The impact of parafoveal eye information for a single eye versus the eye region (Chapter 5) was evaluated for left and right eye fixations by conducting ANOVAs with Eye Fixation (2: left eye, right eye), Eye Content (2: single isolated eye, eye region), and Hemisphere (2: left, right) as within-subject factors, with the following conditions: ILE-LE, IRE-RE, IEyes-LE, and IEyes-RE (Figure 1A, purple box). Nasion fixations were evaluated by ANOVAs with Eye Content (3: isolated left eye, isolated right eye, eye region), and Hemisphere (2: left, right) as within-subject factors, using the following conditions: ILE-Na, IRE-Na, and IEyes-Na (Figure 1A, yellow box). All analyses were carried out using SPSS Statistics 23. Greenhouse-Geisser adjusted degrees of freedom were applied when Mauchley's test of sphericity was violated, and Bonferroni corrections were applied to all paired comparisons and follow-up analyses.

Chapter 3: EYE SENSITIVITY WITHIN A FACE

Low-level properties are known to impact early visual ERP components (e.g., Clark, Fan, & Hillyard, 1994). However, to the best of my knowledge, no studies to date have controlled for low-level visual properties at the local (featural) level when examining the N170 component. As such, it can be argued that increased neural responding to the eyes may be due to low-level sensitivities, rather than featural attributes. To this end, the current study controlled for local low-level properties (i.e., pixel intensity and contrast). Thus, any featural modulations observed on the N170 component would reflect properties inherent to the feature itself, rather than low-level factors.

I hypothesized that the N170 eye sensitivity is not merely due to low-level differences between the eyes and the other features, and thus the eye sensitivity would be observed within the context of a full face, even after equalizing low-level properties at the featural level. In particular, I predicted that fixation on the left and right eyes would yield significantly larger (more negative) N170 amplitudes relative to all other featural fixations, which in turn were not expected to differ from each other.

N170 peak amplitude

A main effect of Featural Fixation was due to left and right eye fixations yielding the largest N170 amplitudes ($F(4,132) = 21.61$, $MSE = 2.63$, $p < .001$, $\eta_p^2 = .40$; paired comparisons: $ps \leq .001$, except RE-nose comparison at $p = .062$), followed by nose fixation, itself larger than mouth fixation ($p = .002$). Nasion fixation did not differ from nose or mouth fixations ($ps \geq .681$), but was significantly attenuated relative to eye fixations ($ps < .001$), see Figure 3A. N170 amplitude was also enhanced in the right hemisphere relative to the left hemisphere (main effect of Hemisphere, $F(1,33) = 10.63$, $MSE = 48.08$, $p = .003$, $\eta_p^2 = .24$), although this varied with fixation

location (Hemisphere by Featural Fixation interaction: $F(3.07, 101.31) = 4.98$, $MSE = 2.57$, $p = .003$, $\eta_p^2 = .131$). In particular, enhanced N170 amplitudes were observed in the right hemisphere for the left and right eye fixations ($ps < .001$), as well as nasion fixation ($ps = .009$; Bonferonni-corrected significance threshold at $p \leq .01$). On the other hand, nose fixation only showed a trend for larger amplitudes in the right hemisphere ($p = .013$), and mouth fixation yielded similar amplitudes across hemispheres ($p = .034$; see Figure 3B).

N170 peak latency

The main effect of Hemisphere was not significant. A main effect of Featural Fixation was found ($F(3.06, 101.06) = 53.13$, $MSE = 18.07$, $p < .001$, $\eta_p^2 = .62$), but was further qualified by a Hemisphere by Featural Fixation interaction ($F(2.87, 94.54) = 20.07$, $MSE = 25.12$, $p < .001$, $\eta_p^2 = .378$). In both hemispheres, N170 latency was longer for mouth fixation relative to nasion, nose, and ipsilateral eye fixations ($ps < .001$), which did not differ from each other, but was not significantly different from the contralateral eye fixation (Figure 3A and 3C).

Bonferroni-corrected paired t -tests (significance threshold at $p \leq .01$) revealed significantly shorter N170 latencies for left eye fixation within the left hemisphere, and for right eye fixation within the right hemisphere ($ps < .001$). However, no hemispheric differences were found for nasion, nose, nor mouth fixations ($ps \geq .16$).

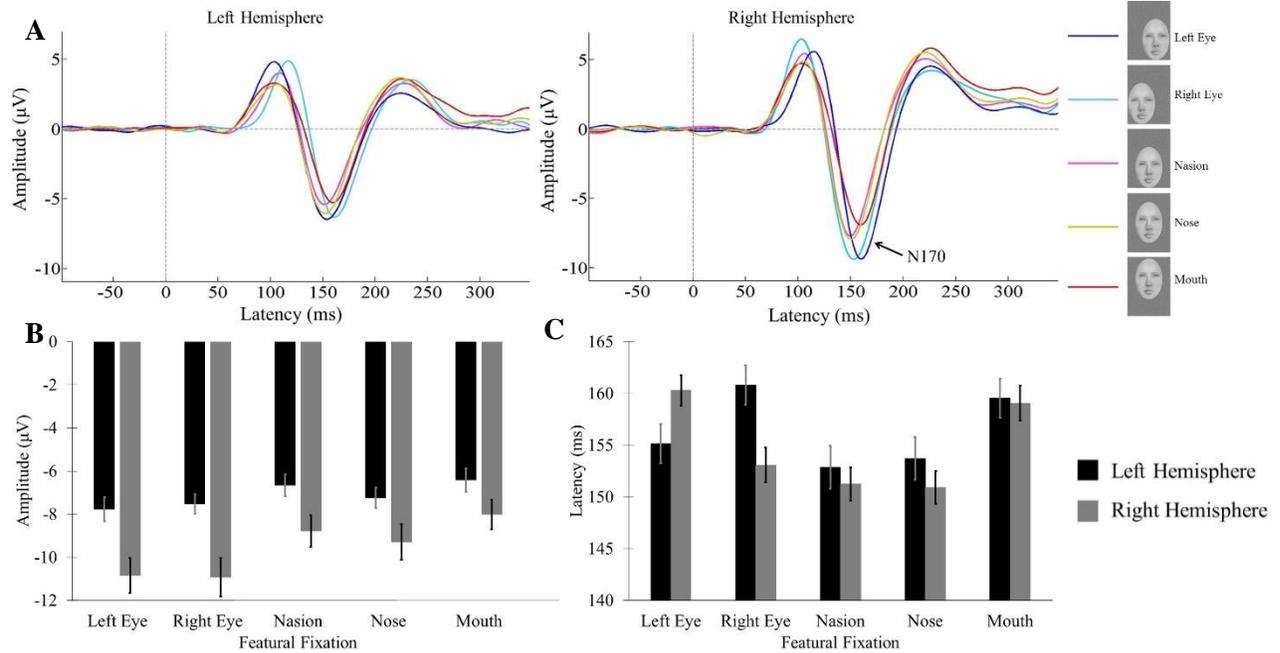


Figure 3. Peak N170 amplitudes and latencies for full face fixations. *Panel A:* Group ERP waveforms for each featural fixation within a full face (averaged across the electrodes at which the N170 was maximal for each participant). *Panel B:* Mean N170 peak amplitudes for each fixation location within a full face. Note the larger amplitudes in the right hemisphere. Left and right eye fixations yielded the largest N170 amplitudes, followed by nose and nasion fixations, with mouth fixation eliciting the smallest N170 amplitude. *Panel C:* Mean N170 peak latencies for each fixation location within a full face. Note the faster latencies for nasion and nose fixations, followed by ipsilateral eye fixations, with contralateral eye and mouth fixations producing the slowest latencies.

Discussion

The results of Chapter 3 demonstrate modulations on N170 amplitude and latency, dependent on featural fixation, that are not merely due to low-level visual properties of pixel intensity or contrast. In line with previous research (de Lissa et al., 2014; Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Nemrodov et al., 2014), the present results demonstrate a robust eye sensitivity within a full face, that persists even when features are controlled for local low-level properties. These findings support the LIFTED model (Nemrodov et al., 2014), and signify the importance of the eyes in early face perception. The present study also provides novel evidence for an additional attenuation in N170 amplitude for mouth fixations relative to nose and nasion fixations. In particular, the N170 amplitude was maximal when an eye was presented in fovea, and systematically decreased when the eyes were situated in parafovea – as in the case of nasion and nose fixations (2.13° and 3.52° from the centre of each eye, respectively; Figure 1B) – and peripheral vision, as in the case of mouth fixation (5.31° from the centre of each eye). Thus, N170 amplitudes showed a systematic decrease with increasing eccentricity of the eyes from fovea, supporting the conclusion that foveal eye information is critical to maximizing N170 responding.

It is also important to note that N170 amplitude responses showed hemispheric lateralization patterns consistent with this eye-eccentricity-from-fovea account. Specifically, left eye, right eye, and nasion fixations yielded strong right hemispheric responses (consistent with previous literature), whereas fixation on the nose only yielded a trend for a right hemispheric lateralization, and fixation on the mouth elicited no differences between hemispheres. If hemispheric lateralization was simply due to a visual field effect, then fixation on features situated along the face midline (i.e., nasion, nose, and mouth) should not show hemispheric differences in responding. However, the presence of a right hemispheric lateralization for nasion fixation, and trend for lateralization for the nose, point to an eye-eccentricity-from-fovea account, with

decreasing lateralization strength as the featural fixation moves further from the eyes. These findings are in line with the LIFTED model's implication that holistic processing is likely affected by the size of the face and the distance between features (Nemrodov et al., 2014). Thus, previous reports of equivalent N170 amplitudes for mouth and nose fixations (Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Nemrodov et al., 2014) may be due to the employment of smaller face sizes, thereby restricting the ability to discriminate between nose and mouth fixations, a factor we are currently examining in our lab. Therefore, the N170 peak amplitude findings reported here likely reveal a particular sensitivity of extrastriate visual areas to the location of eyes within the visual field, with a maximal sensitivity for eye information in fovea.

Chapter 4: FEATURAL FIXATION – ISOLATION VS. FULL FACE

The N170 is sensitive to eye information presented in isolation (Bentin et al., 1996; Itier et al., 2007, 2006, 2011; Kloth et al., 2013; Taylor et al., 2001) and within the context of a full face (de Lissa et al., 2014; McPartland et al., 2010; Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Nemrodov et al., 2014). However, issues remain. Specifically, no studies to date have controlled for visual fixation when examining the N170 sensitivity to isolated eyes. Furthermore, studies comparing isolated feature and full face categories only use one face category (often cued to the nasion), making comparisons to other features (e.g., nose or mouth) more difficult. Thus, it is necessary to re-evaluate these original studies with appropriate control categories and enforced fixation. To this end, the present study compared N170 modulations to internal facial features (left eye, right eye, nose, and mouth) when presented in isolation, or within the context of a full face. This method ensured that foveal information was preserved across feature-face conditions, such that modulations observed in N170 responding would be attributed to changes in parafoveal information, and thus featural integration into a holistic percept. Moreover, including single isolated eye conditions allowed for refined insight into the role of each eye in early face perception, and permitted suitable controls for the isolated feature categories.

In line with the neural inhibition account of face perception, I hypothesized that the N170 would be faster and attenuated in amplitude when features were fixated within a full face context, relative to fixation on the same features in isolation. Featural fixation was also expected to modulate the degree of neural inhibition invoked within a full face context. Furthermore, I predicted that the eye sensitivity would be preserved for isolated features, such that single isolated eyes would elicit enhanced N170 amplitudes relative to isolated mouth and nose conditions.

N170 peak amplitude

A main effect of Context was found, such that consistently larger N170 amplitudes were elicited when features were fixated in isolation relative to a full face context ($F(1,33) = 26.92$, $MSE = 28.24$, $p < .001$, $\eta_p^2 = .45$). Moreover, amplitudes were larger over the right than the left hemisphere (main effect of Hemisphere: $F(1,33) = 9.48$, $MSE = 87.18$, $p = .004$, $\eta_p^2 = .22$). Similar to that reported in Chapter 3, this right hemispheric lateralization was most pronounced for left eye, right eye, and nose fixations, and least pronounced for mouth fixation, as revealed by a Hemisphere by Featural Fixation interaction ($F(3,99) = 11.85$, $MSE = 2.26$, $p < .001$, $\eta_p^2 = .26$; Figure 4A). A main effect of Featural Fixation ($F(2.16, 71.31) = 9.14$, $MSE = 3.10$, $p < .001$, $\eta_p^2 = .22$) was also found, but as can be seen in Figure 4A-C, this was further qualified by a Context by Featural Fixation interaction ($F(3,99) = 27.18$, $MSE = 2.65$, $p < .001$, $\eta_p^2 = .45$).

N170 amplitude context difference scores (i.e., isolated feature – full face) were compared between featural fixations, revealing the largest score for mouth fixation ($ps < .001$) compared to eyes and nose fixations that did not differ (Figure 4C). As discussed in Chapter 3, when analyzed separately within a full face context, fixation on the left and right eyes yielded the largest N170 amplitudes, which were significantly larger than nose fixation, which were larger in turn than mouth fixation. In contrast, when isolated features were analyzed separately, nose fixation yielded a significantly smaller N170 amplitude relative to right eye and mouth fixations ($ps \leq .001$) that did not differ from each other. Thus, the largest context effect seen for mouth fixation was due to a reduction in N170 amplitude for mouth fixation compared to eye fixations within a full face context (Figure 4B).

All other interactions were not statistically significant.

N170 peak latency

A robust main effect of Context was due to significantly prolonged N170 latencies when features were fixated in isolation relative to a full face context ($F(1,33) = 443.25$, $MSE = 118.63$, $p < .001$, $\eta_p^2 = .93$), yielding an average delay of approximately 25 ms (Figure 4A). This delay varied between fixated features, as revealed by a Context by Featural Fixation interaction ($F(3,99) = 70.25$, $MSE = 16.31$, $p < .001$, $\eta_p^2 = .68$; Figure 4A and 4D). When context latency difference scores (isolated feature – full face) were calculated for each fixation location, the largest decrease in N170 peak latency was seen for nose fixation ($ps < .001$; Figure 4D). Mouth fixation also yielded a marginally larger latency decrease relative to eye fixations ($ps \leq .076$). As reported in Chapter 3, when faces were analyzed separately, latencies were most delayed for mouth fixation, while they did not vary between nose and the ipsilateral eye conditions (Figure 3C). However, when isolated features were analyzed independently, nose fixation yielded the longest latency relative to all other features ($ps < .001$), which did not differ from each other. Thus, nose fixation yielded the largest latency difference score due to prolonged latencies when presented in isolation (Figure 4D).

A main effect of Hemisphere was also found, with faster N170 latencies in the right compared to the left hemisphere ($F(1,33) = 6.52$, $MSE = 114.95$, $p = .02$, $\eta_p^2 = .17$). Moreover, a Hemisphere by Featural Fixation interaction ($F(3,99) = 10.19$, $MSE = 16.34$, $p < .001$, $\eta_p^2 = .24$) was qualified by the Hemisphere by Context by Featural Fixation interaction ($F(3,99) = 22.93$, $MSE = 18.09$, $p < .001$, $\eta_p^2 = .41$). Follow-up Bonferroni-corrected paired t -tests (significance level at $p \leq .013$) revealed that the three-way interaction was driven by larger context latency differences (isolated feature – full face) in the hemisphere contralateral to eye fixation ($ps < .001$; Figure 4D). Alternatively, no significant hemispheric differences were observed for nose or mouth fixations ($ps = .30$ and $.13$, respectively).

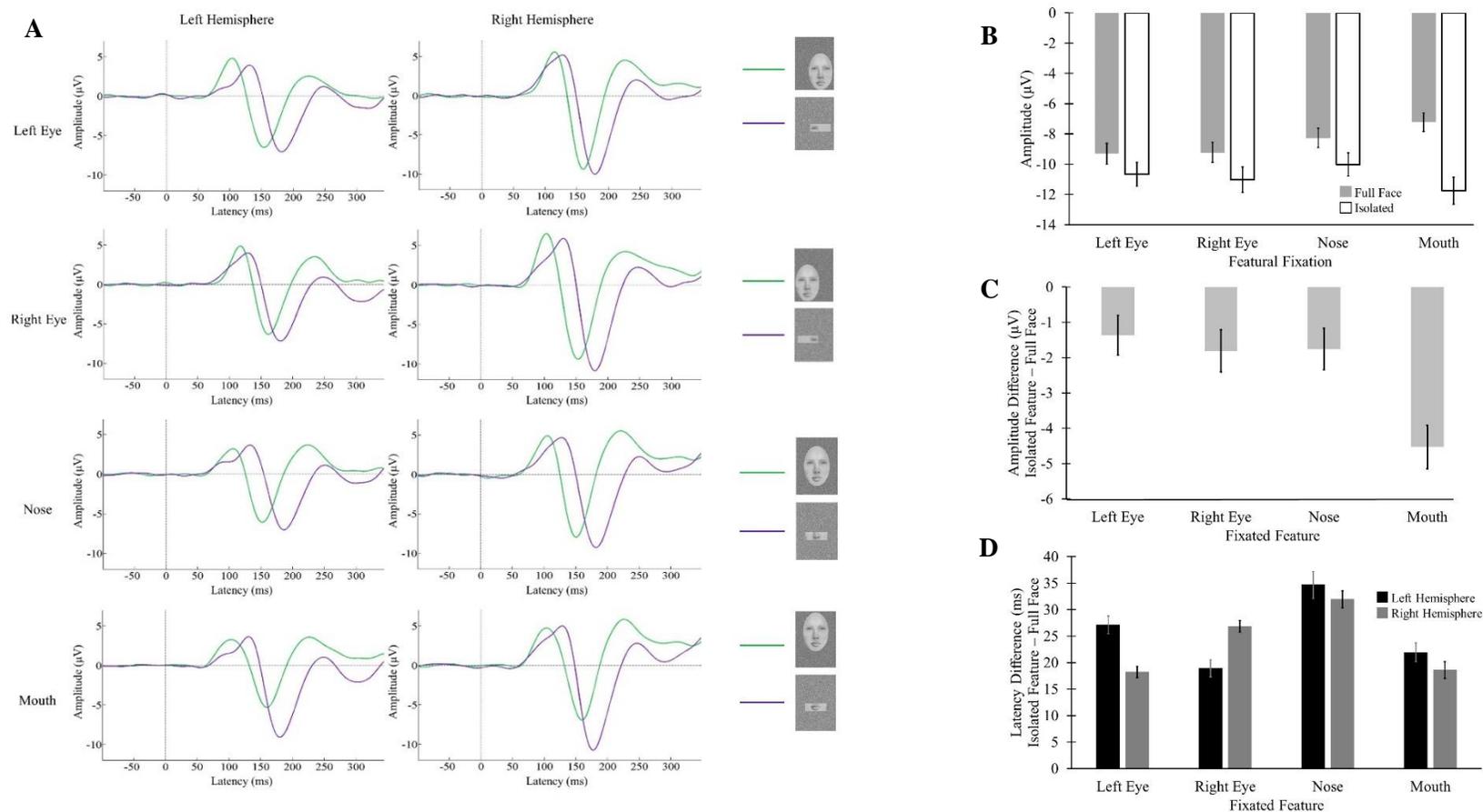


Figure 4: Peak N170 amplitudes and latencies for facial features fixated in isolation or within a full face context. *Panel A:* Group N170 ERP waveforms for each fixated feature presented in isolation (purple) or in a full face context (green), for each hemisphere (averaged across the electrodes at which N170 was maximal for each participant). *Panel B:* Mean N170 peak amplitudes for each fixated feature comparing isolated and full face conditions (averaged across hemispheres) *Panel C:* Mean N170 amplitude difference scores (isolated feature – full face) for each fixated feature, averaged across hemispheres. Note the larger amplitude difference for mouth fixation relative to all other featural fixations. *Panel D:* Mean N170 latency difference scores (isolated – full face) for each featural fixation, across each hemisphere. Note the significantly larger latency difference for nose fixation relative to all other featural fixations, as well as larger latency reductions for eye fixations in the hemisphere contralateral to visual field presentation.

Discussion

The results of Chapter 4 reveal robust reductions in amplitude and latency when all featural fixations were presented within a full face context, relative to featural fixation in isolation. These findings parallel Bentin et al.'s (1996) seminal reports of delayed N170 responses for isolated features compared to a full face, and extend these findings further by demonstrating that these patterns persist even when each feature is compared to its direct equivalent within a full face context (rather than comparison to only one face condition). It is important to highlight here that this technique permits direct comparison of the N170 ERP response when the same feature is in the fovea; thus, any modulations observed on the N170 are specific to the presence/absence of parafoveal information. These results provide strong evidence in favour of a neural inhibition account for early face perception (Nemrodov et al., 2014), demonstrating that full faces consistently generate N170s that are attenuated in amplitude and shorter in latency, despite modulations of the N170 response with featural fixation. These findings are also in line with single-cell recordings from macaque monkeys, in which individual neurons within face processing areas respond most strongly to single features, or combinations of features, rather than a full holistic percept, and it is through the integration of these excitatory and inhibitory neural signals that a holistic percept is accomplished (Freiwald et al., 2009).

The current study also provides new evidence of the context effect for single isolated eyes, rather than the commonly used eye region. However, it is important to note that an isolated eye sensitivity was not completely shown. In particular, N170 amplitudes and latencies were not significantly different for left eye, right eye, nor mouth fixations in isolation, although these three categories elicited significantly larger and faster N170 amplitudes than did nose fixations. These findings provide the first evidence of a lack of eye sensitivity at the individual feature level.

Within a featural diagnostic framework, the eyes are considered to be the most diagnostic features for various attributes of face processing (e.g. gender discrimination, face recognition), followed by the mouth, followed in turn by the nose (Arcurio, Gold, & James, 2012; Hills, Ross, & Lewis, 2011; Schyns, Petro, & Smith, 2007). Yet, it is the eye region that is commonly assessed in most experiments, and thus, the specific contribution of each individual eye is unclear. Within macaque cortex, specific neural populations have been identified that code featural face information. In particular, some attributes of eye information (e.g., inter-ocular distance, iris size) are coded by a large population of these cells, whilst other structural properties of the eye (e.g., eye size, eye eccentricity) and other facial features (e.g., nose base, mouth size) are coded less frequently (Freiwald et al., 2009). Thus, it is possible that when presented with only one eye, as in the present study, neural coding mechanisms may rely more on the smaller populations of eye-sensitive neurons since certain aspects of eye information (e.g., inter-ocular distance) cannot be coded. Therefore, the presence of both eyes within an eye region may be necessary to increase the perceptual and/or social significance of the stimulus at the amplitude level, sub-serving the widely reported isolated eye sensitivity (Bentin et al., 1996; Itier et al., 2007, 2006, 2011; Kloth et al., 2013; Taylor et al., 2001).

Importantly, the latency for single isolated eyes was also delayed by as much as 27 ms in the ipsilateral hemisphere, relative to fixation within a full face. Even within the contralateral hemisphere, where neural processing was the fastest for eye fixations, single eye latency delays (~18 ms) were nearly twice as long as previously reported for isolated eye region stimuli (Bentin et al., 1996; Itier et al., 2007, 2006, 2011; Kloth et al., 2013; Taylor et al., 2001). Neural processing of faces occurs extremely rapidly, and thus any delays in perceptual processing have significant impacts on overall perception, as well as other higher-order processing abilities (e.g., identity

recognition, gaze perception, etc.). Thus, significantly prolonged latencies (as in the case of the single isolated eyes presented here) have strong implications for severe face perception deficiencies due to ineffective speeds in neural processing. Furthermore, the prolonged latency for the isolated nose condition suggests that this stimulus may be processed more similarly to an object when in isolation. In fact, the isolated nose condition elicited an average N170 peak latency of 183 ms, in line with previous accounts of object processing latencies (Bentin et al., 1996; Itier et al., 2006; Kloth et al., 2013; Rossion, Gauthier, et al., 2000, 2003). Thus, when the nose is presented within a facial context, the parafoveal information provides valuable information, speeding the neural response and enabling effective perception strategies. Alternatively, the single isolated eyes and isolated mouth conditions may preserve some of their diagnostic relevance for the speed of neural responding, evidenced by faster N170 latencies relative to isolated noses.

Taken together these results highlight the importance of considering diagnosticity and social relevance for individual features and feature combinations, as well as implicating separate mechanisms for N170 amplitude and latency. Based on these findings, I also propose that the previously reported isolated eye sensitivity is likely due to the use of the eye region (containing two eyes) and may be more a product of an eye *region* detector (indexed by N170 amplitude) and the beginnings of holistic processing (indexed by N170 latency) – due to the binding of multiple features – rather than an eye sensitivity *per se*, an issue that is addressed further in Chapter 5.

It is also important to note that the degree of neural inhibition (indexed by amplitude and latency context difference scores) was modulated by featural fixation, supporting the idea of a complex interplay between featural and holistic mechanisms. Specifically, mouth fixation generated the largest decrease in N170 amplitude (an astonishing context difference of 4.53 μ V), with nose, left eye, and right eye fixations eliciting comparatively smaller amplitude reductions

(1.75 μV , 1.37 μV , and 1.81 μV , respectively; see Figure 4C). On the other hand, nose fixation elicited the largest N170 latency decrease, whereas fixation on the left eye, right eye, and mouth yielded comparatively smaller latency reductions. Taken together these findings highlight the salience of the eyes in early face perception, leading to partial inhibition during eye fixations, evidenced by small reductions in N170 amplitude and latency between isolated and full face contexts. Alternatively, fixation on the mouth and nose induce more complete neural inhibition mechanisms (with greater changes in amplitude or latency between isolated and full face fixations). These results highlight the powerful inhibitory role of the eyes on other features during early face perception.

Chapter 5: SINGLE EYE VS. EYE REGION

The eye region is structurally unique in that it contains two eye features, thus allowing for the neural coding of not only intra-ocular factors (e.g., iris size, eye width) but also inter-ocular properties (e.g., inter-ocular distance). This structure also ensures that when visual attention is directed to the eye region, at least one eye will be coded in parafovea – if fixation is on an eye, then the other eye will be situated in parafovea; likewise, if fixation is on the nasion, then both eyes will be situated in parafovea. Thus, it remains unclear whether previous reports of eye sensitivity (both with isolated eye regions and within the context of a face) are due to the increased neural coding for eye information in general (i.e., eyes are special), or if this sensitivity is due to neural coding of two symmetrical eye features. To date, this question has not been addressed, with almost all studies focusing exclusively on the eye region. However, Rousselet and colleagues (2014) recently concluded that the transition between the P1 and N170 components was maximally responsive to contralateral eye information, suggesting that the N170 is sensitive to individual eye information. These findings provide exciting preliminary insights into the N170 eye sensitivity and holistic processing, and call for replication and convergence with more commonly used ERP techniques in order to substantiate these claims. Furthermore, a direct comparison of single isolated eye and isolated eye region categories is necessary in order to clarify the independent role of each eye in early face perception.

To this end, the present study compared N170 modulations to single eye and eye region categories when fixation was enforced on the left and right eye, or on the nasion. I hypothesized that parafoveal eye information would be additive with foveal information, due to the reliance on featural mechanisms and the absence of neural inhibition, such that eye regions would elicit faster and larger N170 responses relative to single eyes, indicative of an eye region sensitivity. This

pattern was predicted to hold true irrespective of fixation, although patterns were expected to be attenuated when fixation was enforced on the nasion (due to a lack of foveal content).

Left and right eye fixations

N170 peak amplitude

A main effect of Hemisphere was driven by larger N170 peak amplitudes in the right hemisphere compared to the left hemisphere ($F(1,33) = 16.20$, $MSE = 57.97$, $p < .001$, $\eta_p^2 = .33$). This hemispheric difference was more pronounced for right eye than left eye fixation (Hemisphere by Eye Fixation interaction, $F(1,33) = 39.74$, $MSE = 1.64$, $p < .001$, $\eta_p^2 = .55$). Most importantly, a main effect of Eye Content was due to eye regions eliciting larger N170 amplitudes than single eyes ($F(1,33) = 12.53$, $MSE = 4.57$, $p = .001$, $\eta_p^2 = .28$; Figure 5A-C). This effect, however, was qualified with Hemisphere by Eye Content ($F(1,33) = 19.49$, $MSE = 1.24$, $p < .001$, $\eta_p^2 = .37$) and Hemisphere by Eye Fixation by Eye Content ($F(1,33) = 12.57$, $MSE = 1.83$, $p = .001$, $\eta_p^2 = .28$) interactions.

To quantify the three-way interaction further, Hemisphere by Eye Content ANOVAs were conducted for each eye fixation separately. For both eye fixations, simple effects of Hemisphere and Eye content were seen, confirming the main effects found in the omnibus ANOVA. In addition, the Hemisphere by Eye Content interaction was not significant for left eye fixation ($p = .95$), but was significant for right eye fixation ($F(1,33) = 33.92$, $MSE = 1.39$, $p < .001$, $\eta_p^2 = .51$). Bonferroni-corrected paired t -tests (significance level at $p \leq .025$) performed on the right eye fixation condition revealed larger amplitudes for eye regions compared to single eyes in the right hemisphere ($p < .001$), but no amplitude difference in the left hemisphere ($p = .38$). Thus, eye regions elicited larger amplitudes than single eyes in both hemispheres for left eye fixation but only in the right hemisphere for right eye fixation (Figure 5A-C).

N170 peak latency

A robust main effect of Eye Content was due to significantly faster N170 latencies for eye regions compared to single eyes ($F(1,33) = 274.86$, $MSE = 28.93$, $p < .001$, $\eta_p^2 = .89$), with an average difference of 11 ms (Figure 5A-B and 5D). This eye content effect was slightly more pronounced overall for the left eye fixation than for the right eye fixation (significant Hemisphere by Eye Fixation interaction, $F(1,33) = 8.85$, $MSE = 14.30$, $p = .005$, $\eta_p^2 = .21$), but most importantly, it was largest in the hemisphere contralateral to parafoveal information, as revealed by a significant Hemisphere by Eye Fixation by Eye Content interaction ($F(1,33) = 55.01$, $MSE = 13.61$, $p < .001$, $\eta_p^2 = .63$). Thus, as seen in Figure 5D, the latency difference between the eye region and single eyes was observed for both eye fixations but was most pronounced in the hemisphere ipsilateral to eye fixation, due to the presence of the other eye in the opposite visual field.

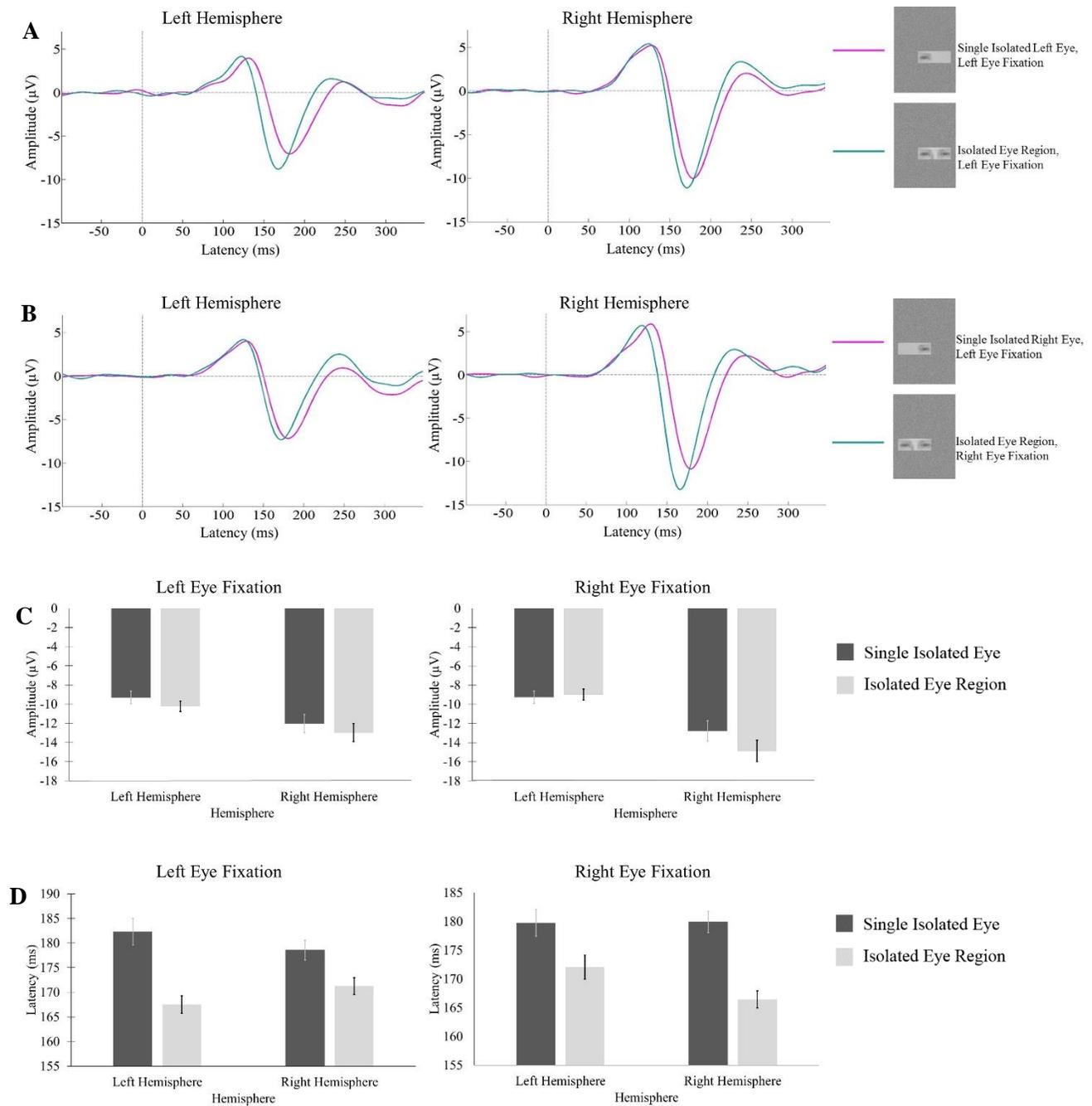


Figure 5. Peak N170 amplitudes and latencies for isolated eye conditions with left and right eye fixations. *Panel A:* Group ERP waveforms for isolated eye conditions with left eye fixations. *Panel B:* Group ERP waveforms for isolated eye conditions with right eye fixations. *Panel C:* Mean N170 amplitudes for isolated eye conditions with left and right eye fixations in each hemisphere. Note the larger N170 amplitudes for isolated eye regions compared to single isolated eyes. *Panel D:* Mean N170 latencies for isolated eye conditions with left and right eye fixations in each hemisphere. Note the significantly shorter N170 latencies to eye regions compared to single isolated eyes, an effect enhanced in the hemisphere contralateral to parafoveal eye information.

Nasion fixation

N170 peak amplitude

A main effect of Hemisphere was the result of larger N170 amplitudes in the right hemisphere compared to the left hemisphere ($F(1,33) = 13.78$, $MSE = 26.73$, $p = .001$, $\eta_p^2 = .30$). A main effect of Eye Content was also significant ($F(2,66) = 38.41$, $MSE = 3.83$, $p < .001$, $\eta_p^2 = .54$), but was further qualified by a Hemisphere by Eye Content interaction ($F(1.63, 53.80) = 10.99$, $MSE = 6.54$, $p < .001$, $\eta_p^2 = .25$). As shown in Figure 6A-B, the eye region yielded an N170 amplitude that was consistently enhanced relative to single eye conditions ($ps \leq .011$), with a trend for contralateral eyes to yield enhanced amplitudes relative to ipsilateral eyes ($ps \leq .094$). Bonferroni-corrected paired t -tests (significance level at $p \leq .016$) further revealed significant hemispheric effects for single left eye ($p < .001$) and eye region ($p = .001$) conditions, with consistently larger amplitude responses in the right hemisphere. However, there were no differences in N170 amplitude across hemispheres for the single right eye condition ($p = .43$).

N170 peak latency

The main effect of Eye Content was significant, demonstrating longer latencies for single eyes relative to the eye region ($F(2,66) = 53.96$, $MSE = 77.58$, $p < .001$, $\eta_p^2 = .62$). However, this effect was qualified further by a significant Hemisphere by Eye Content interaction ($F(1.49, 49.08) = 16.58$, $MSE = 152.36$, $p < .001$, $\eta_p^2 = .33$). Bonferroni-corrected paired t -tests (significance level at $p \leq .016$), revealed that this interaction was driven by faster N170 latencies in the left compared to the right hemisphere for the single right eye condition ($p = .005$), and faster N170 latencies in the right compared to the left hemisphere for the single left eye condition ($p = .001$; Figure 6A and 6C). The eye region condition yielded similar N170 latencies in both hemispheres ($p = .29$).

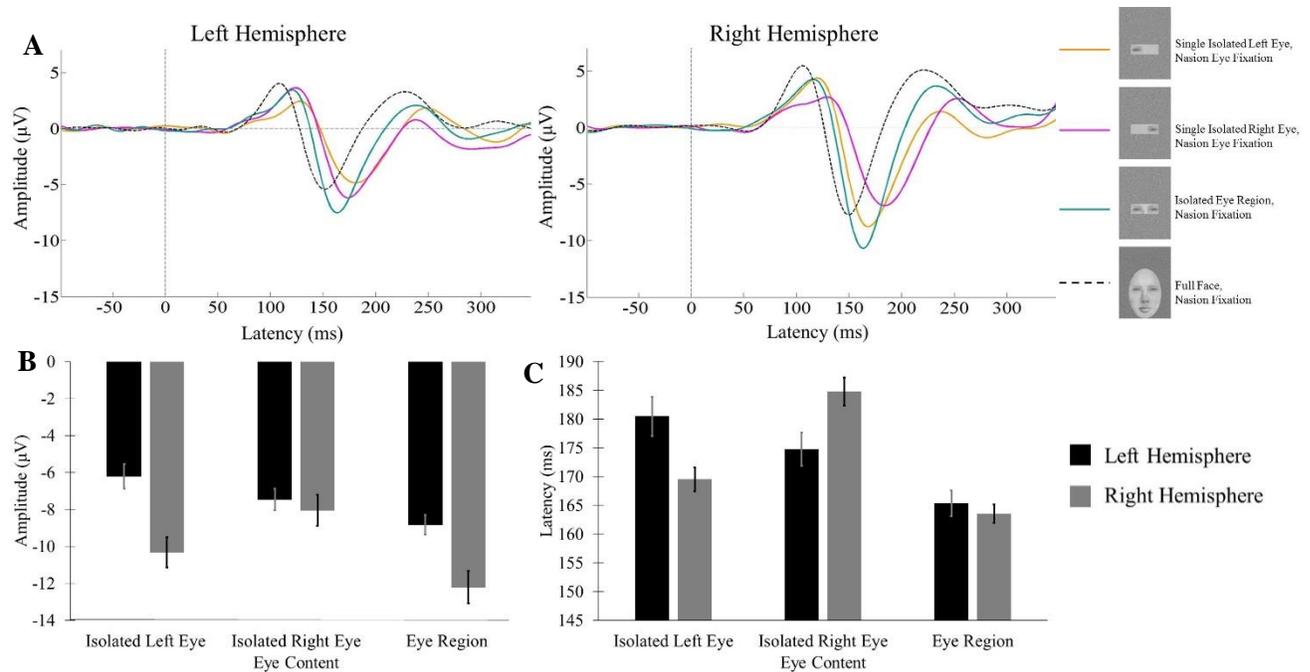


Figure 6. Peak N170 amplitudes and latencies for isolated eye conditions with nasion fixation. *Panel A:* Group ERP waveforms for isolated eye conditions with nasion fixation. The FF-Na condition (from Chapter 3) was added for visual comparison. *Panel B:* Mean N170 amplitudes for isolated eye conditions with nasion fixation in the left and right hemispheres. Note the enhanced N170 amplitudes for the eye region relative to single eyes, and the right-hemispheric lateralization for the eye region and single left eye. *Panel C:* Mean N170 latencies for isolated eye conditions with nasion fixation in the left and right hemispheres. Note the prolonged N170 latencies for single eyes compared to the eye region, particularly in the hemisphere ipsilateral to parafoveal eye information.

Discussion

The results of Chapter 5 revealed that the N170 was larger, and faster, for eye region conditions relative to single eyes, regardless of whether fixation was on an eye or on the nasion. Condition differences were further intensified in the hemisphere contralateral to eye presentation, such that an eye situated in left parafovea elicited faster and larger N170 responses in the right hemisphere, whereas an eye situated in right parafovea elicited faster and larger N170 responses in the left hemisphere. These findings parallel nicely with recent reports of N170 sensitivities to contralateral face (Towler & Eimer, 2015) and eye (Rousselet et al., 2014) information, supporting differential hemispheric involvement based on visual fixation and parafoveal content, and highlighting the sensitivity to, and coding of, eyes within both the left and right hemispheres. Enforced nasion fixation yielded similar results, although the overall patterns were attenuated relative to left and right eye fixations, signifying the importance of eye information in fovea.

Of particular interest, the eye region showed surprising latency differences relative to a single eye, speeding neural processing by as much as 15 ms in the contralateral hemisphere. It is also important to note that, as shown in Figure 6A, eye region latencies fell midway between latencies for contralateral single eyes and nasion fixation within a full face. Thus, it appears that N170 latencies to isolated eye regions may be indicative of early stages of holistic processing by integrating two symmetrical eye features. N170 amplitudes, on the other hand, responded in a manner more consistent with additive feature-based information. Specifically, the addition of an eye in parafovea significantly increased N170 peak amplitudes, consistent with the summation of foveal and parafoveal featural content suggested by the LIFTED model for featural processing. Evidence from macaque monkeys further indicates that particular cells within comparative face processing areas are particularly sensitive to eye information, and that some cells respond mostly

to inter-ocular cues, which would only be relevant for the perception of two horizontally symmetrical eyes (Freiwald et al., 2009). Thus, the additive effect observed here on N170 amplitude is likely representative of not only the enhanced neural activity elicited by coding for the presence of *two* eye features, but also the addition of neurons coding for eye region-specific information (e.g., inter-ocular distance).

Taken together these findings strongly implicate an eye region detector in early face perception, and provide compelling evidence for dissociative neural mechanisms sub-serving N170 amplitude and latency. In particular, amplitude appears to be more sensitive to featural (eye) information, whereas latency appears to be more sensitive to holistic integration. Therefore, the current results implicate a complex interplay between featural and holistic mechanisms in early face and eye perception, rather than a purely holistic account.

Chapter 6: GENERAL DISCUSSION

To date it has been well established that the eye region plays a vital role in early face perception. However, the impact of attributes inherent to the eye region (e.g., low-level properties, symmetrical eyes) and the unique contributions of each eye remains unclear. The current study aimed to address these issues through a systematic evaluation of N170 ERP modulations when featural fixations (left eye, right eye, nasion, nose, and mouth) were fixated in isolation and within the context of a full face. In summary, the results of Chapter 3 showed that the eye sensitivity within a full face was not due to differences in low-level properties at the local (featural level). Modulation of the N170 response within a full face context was also found to be related to the eccentricity of the eyes from fovea. In Chapter 4, I demonstrated a robust context effect, whereby N170 responses were faster and attenuated when features were fixated within a full face compared to fixation in isolation, in line with a neural inhibition account of early face perception. Moreover, in Chapter 5, I showed that the N170 response was enhanced in amplitude and faster in latency for eye region conditions, compared to single isolated eyes, highlighting the importance of two symmetrical eyes in guiding the commonly observed eye sensitivity effect.

In terms of N170 amplitude, the present results implicate a neural sensitivity to the eye region, rather than to a single eye *per se*. These findings suggest that the commonly reported eye detector may in fact be more accurately characterized as an *eye region* detector. Within an evolutionary context, the refined ability to perceive and detect two symmetrical eyes would be arguably more adaptive (Emery, 2000; Kobayashi & Kohshima, 1997). The perception of a single eye-like stimulus is not particularly beneficial for survival/interaction, as many objects contain similar characteristics (i.e., small, round shape, high local contrast). Alternatively, the presence of two horizontally symmetrical eye-like stimuli are more likely to be indicative of a pair of eyes,

thereby indicating the presence of another person or animal. Therefore, the easy detection of an eye region (rather than a single eye) can lead to more effective identification of evolutionary threat or social interaction, and thus it makes intuitive sense to conclude that an eye region detector would be present at the neural level.

The faster latencies observed for isolated eye regions relative to single eyes also suggests that the addition of parafoveal eye information may initiate early stage holistic processing by speeding neural responding and bringing the latency closer to what would be observed within the context of a full face. Alternatively, N170 amplitudes showed an additive effect, with larger amplitudes for eye regions relative to single eyes. To date, it has been largely accepted that faces are processed in a purely holistic manner, through the integration of internal features into a Gestalt percept. The current results, however, suggest that additional featural mechanisms are at play during early face perception, such that visual fixation within a face significantly impacts the degree of neural responding. In particular, the presence of an eye in fovea enhanced N170 responding within the context of a full face (Chapter 3), and the degree of neural inhibition initiated within a full face context was modulated by featural fixation (Chapter 4). Eccentricity of the eyes from fovea also appears to have significant effects on N170 amplitude, thereby signifying the importance of maintaining fixation on an eye for maximal neural responding, and highlights the powerful role of the eyes as an inhibitor for other facial features. All in all these findings implicate a complex interplay between featural and holistic mechanisms during early face perception that requires further refinement in future research studies.

The ability of the current study to unravel several new attributes of holistic and featural face processing can be partially attributed to the use of new, state-of-the-art ERP techniques. In particular, the current study focused on peak N170 responses for each participant, rather than the

commonly used grand average approach which focuses on the electrodes with the largest N170 responses for a group *on average*. The peak electrode approach used here provides maximal sensitivity to individual variations in N170 responding, not only allowing a more accurate representation of individual responding, but also permitting evaluation of fine-grained differences and paired comparisons that may be otherwise overlooked.

The present study also implemented simultaneous ERP and eye tracking methodologies in order to maximize clarity of the N170 signal. One may view the use of enforced fixation as a limitation of the current design, since it restricts naturalistic movements and exploration of the face; however, I argue that this is actually a strength of the technique. Although adults spend more time, on average, attending to the eyes of a face, several studies have reported idiosyncratic differences in scan-path patterns (e.g., Kanan, Bseiso, Ray, Hsiao, & Cottrell, 2015; Mehoudar, Arizpe, Baker, & Yovel, 2014). However, when a person engages in their preferred face-scanning behaviours, they are likely to bias their visual fixations to certain features over others, resulting in disproportionate samplings for each feature. Given recent evidence that foveal fixation modulates early ERP components of face perception (de Lissa et al., 2014; Neath & Itier, 2014; Neath-Tavares & Itier, 2016; Nemrodov et al., 2014), eye movements inherently change the foveal information and thus update the neural percept, introducing more noise in the ERP signal. Therefore, the incorporation of co-registered eye tracking with the ERP recording provides the refined ability to evaluate the underlying neural mechanisms without the contamination of micro eye movements, as well as providing opportunities for sampling less commonly fixated features (e.g., mouth or nose). It would be interesting for future studies, however, to evaluate the influence of individual differences in the neural response to preferred versus non-preferred features.

It is also of particular note that the current study is the first ERP investigation to incorporate face and feature stimuli that were controlled at both the local (featural) level, as well as at the global (image) level. This strict equalization of low-level properties permitted more refined evaluations of the contributions of each facial feature, and confirmed that featural effects observed on the N170 are not the result of differences in pixel intensity or contrast. As shown in Table 1, pixel intensity and RMS contrast values were relatively equated for all internal facial features (left eye, right eye, nose, and mouth), although it was not possible to equate the nasion without disrupting the integrity of the facial percept. Therefore, it is acknowledged that some condition differences may be attributed to minute variations between conditions in terms of pixel intensity or contrast; however, it is unlikely that these small variations in low-level properties have a major impact on the overall results. It should be noted, however, that the influence of spatial frequency and power spectra properties remain unclear, and should be further clarified in future studies.

In conclusion, the present study provides compelling new evidence for the persistence of an eye sensitivity within a full face context that is not dependent on low-level factors, and is subserved by an eye region detector that is maximally sensitive to contralateral eye information. In particular, fixation on the eyes enhances N170 amplitude and latency responding, and produces reliable right hemispheric lateralization patterns, consistent with optimized face processing mechanisms. The complex interplay observed between foveal and parafoveal information, as well as the location of eyes within the visual field and eccentricity from fovea, strongly suggests that early face perception mechanisms are not purely holistic in nature – contrary to previous beliefs. Taken together, it can be speculated that the N170 ERP component reflects sensitivity to a neural eye region detector – for the detection of two symmetrical eyes within space, in order to anchor a face template based on first-order relations (two eyes above a nose, above a mouth; Maurer et al.,

2002) – as well as the neural inhibition mechanisms proposed to facilitate holistic processing (i.e., integration of foveal and parafoveal face information into a holistic percept).

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Appendix 1

Table A1. Average number of trials per condition across all participants. Standard deviations are in parentheses.

Experimental Condition	Trials per Condition (SD)
Full Face, Nasion Fixation (FF-Na)	76.41 (21.85)
Full Face, Left Eye Fixation (FF-LE)	76.53 (22.33) †
Full Face, Right Eye Fixation (FF-RE)	76.88 (21.57)
Full Face, Nose Fixation (FF-No)	75.38 (21.67)
Full Face – Mouth (FF-M)	74.65 (22.01)
Isolated Eye Region, Nasion Fixation (IEye-Na)	77.41 (22.40)
Isolated Eye Region, Left Eye Fixation (IEye-LE)	78.03 (20.63) †
Isolated Eye Region, Right Eye Fixation (IEye-RE)	78.62 (22.04)* †
Isolated Left Eye, Nasion Fixation (ILE-Na)	68.56 (27.02)
Isolated Left Eye, Left Eye Fixation (ILE-LE)	77.76 (21.57) †
Isolated Right Eye, Nasion Fixation (IRE-Na)	66.12 (29.76)
Isolated Right Eye, Right Eye Fixation (IRE-RE)	78.56 (21.52)* †
Isolated Nose, Nose Fixation (INo)	78.18 (20.29)* †
Isolated Mouth, Mouth Fixation (IM)	78.91 (21.75)* †

* Conditions significantly different from the isolated left eye-nasion condition ($p \leq .05$)

† Conditions significantly different from the isolated right eye-nasion condition ($p \leq .05$)