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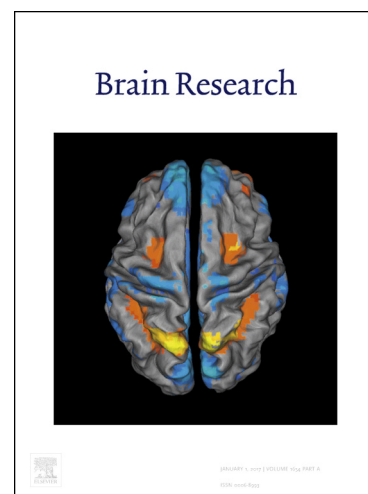
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From eye to face: The impact of face outline, feature number, and feature saliency on the early neural response to faces

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ABSTRACT

The LIFTED model of early face perception postulates that the face-sensitive N170 event-related potential may reflect underlying neural inhibition mechanisms which serve to regulate holistic and featural processing. It remains unclear, however, what specific factors impact these neural inhibition processes. Here, N170 peak responses were recorded whilst adults maintained fixation on a single eye using a gaze-contingent paradigm, and the presence/absence of a face outline, as well as the number and type of parafoveal features within the outline, were manipulated. N170 amplitudes and latencies were reduced when a single eye was fixated within a face outline compared to fixation on the same eye in isolation, demonstrating that the simple presence of a face outline is sufficient to elicit a shift towards a more face-like neural response. A monotonic decrease in the N170 amplitude and latency was observed with increasing numbers of parafoveal features, and the type of feature(s) present in parafovea further modulated this early face response. These results support the idea of neural inhibition exerted by parafoveal features onto the foveated feature as a function of the number and possibly the nature of parafoveal features. Specifically, the results suggest the use of a feature saliency framework (eyes > mouth > nose) at the neural level, such that the parafoveal eye may play a role in down-regulating the response to the other eye (in fovea) more so than the nose or the mouth. These results confirm the importance of parafoveal features and the face outline in the neural inhibition mechanism, and provide further support for a feature saliency mechanism guiding early face perception.

Keywords: N170, neural inhibition, feature saliency, face outline

1. INTRODUCTION

The ability to detect and perceive a face in one's environment is not only a critical evolutionary behaviour, but also an integral precursor to the extraction and interpretation of social cues (e.g., gaze direction, emotional expression, identity, gender; Itier, 2015; Itier & Batty, 2009; Kleinke, 1986). Humans are highly social beings and, as such, a distributed neural network exists, dedicated to the perception and processing of faces and social information (Haxby, Hoffman, & Gobbini, 2000; Ishai, 2008; Ishai, Schmidt, & Boesiger, 2005). Within this network, two primary brain hubs, the "occipital face area" (OFA) and the "fusiform face area" (FFA), have been implicated in featural processing and holistic integration of face information (Arcurio, Gold, & James, 2012; Haxby et al., 2000; Kanwisher & Yovel, 2006; Rossion, 2008). Intracranial recordings performed directly on the human cortical surface have also identified face- and feature-sensitive sites that respond more strongly to faces or facial features than to other objects (Allison, Puce, Spencer, & McCarthy, 1999; Engell & McCarthy, 2014; Halgren, Baudena, Heit, Clarke, & Marinkovic, 1994; McCarthy, Puce, Belger, & Allison, 1999; Puce, Allison, & McCarthy, 1999; Seeck, Michel, Blanke, Thut, Landis, & Schomer, 2001). In particular, face- and eye-region-specific sites are abundant on the occipitotemporal cortical surface (McCarthy et al., 1999; Engell & McCarthy, 2014), with eye-region-specific sites even more prevalent than face-specific sites (Engell & McCarthy, 2014), thereby implicating a particular sensitivity for the eyes at the cortical level.

In line with these findings, scalp-recorded event-related potentials (ERPs) support a special sensitivity to eye regions, which seems distinct from the sensitivity to whole faces. The N170, a face-sensitive ERP component recorded maximally around 120-200 ms post-face onset over posterior occipitotemporal cortex (Bentin, Allison, Puce, Perez, & McCarthy, 1996; George, Evans, Fiori, Davidoff, & Renault, 1996; for review see Rossion & Jacques, 2012), is

larger and delayed in response to isolated eye regions relative to full faces, a finding now well-documented in the field (Bentin et al., 1996; Itier, Alain, Sedore, & McIntosh, 2007; Itier, Latinus, & Taylor, 2006; Itier, Van Roon, Alain, 2011; Kloth, Itier, & Schweinberger, 2013; Nemrodov & Itier, 2011, 2012; Taylor, Edmonds, McCarthy, & Allison, 2001; Taylor, Itier, Allison, & Edmonds, 2001; Shibata et al., 2002). Importantly, a recent study revealed that this large response to eye regions is distinct from that to a single eye, with a stronger and faster N170 when two symmetrical eyes were presented, compared to the presentation of only one isolated eye (Parkington & Itier, 2018). This eye region sensitivity was not merely due to variations in contrast or pixel intensity, but rather reflected a higher-level sensitivity to the eye region information. It is noteworthy, however, that all features (left eye, right eye, nose, and mouth) showed a substantial increase in N170 amplitude and latency when presented in isolation, compared to when presented within the context of a full face. This finding, in agreement with human intracranial recordings (McCarthy et al., 1999; Engell & McCarthy, 2014), suggests a possible shift in the neural response between a response to features, a response to eye regions, and a response to whole faces. In other words, the scalp-recorded N170 could simply reflect the activation of different cortical sites (feature-sensitive, eye-region-specific or face-specific sites) depending on what is presented. What constitutes a face context, enough to promote this neural shift from feature to face response, however, remains unclear and is what the present study attempts to elucidate.

It is well accepted in the cognitive literature that face processing involves the integration of features into a holistic percept, whereby the structure and configuration of features are combined into an indecomposable whole (Maurer, Le Grand, & Mondloch, 2002; Rossion, 2008; Rossion & Gauthier, 2002; Tanaka & Farah, 1993; Yin, 1969). By and large holistic processing

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has been assumed to be a relatively rigid process, occurring irrespective of where one is looking on the face. However, neural recordings suggest that face processing may instead involve a complex interplay between holistic and featural processing mechanisms (Friewald, Tsao, & Livingstone, 2009; Nemrodov, Anderson, Preston, & Itier, 2014; Itier & Preston, 2018; Parkington & Itier, 2018; Schyns, Jentzsch, Johnson, Schweinberger, & Gosselin, 2003; Schyns, Petro, & Smith, 2007; Smith; Rousselet, Ince, van Rijsbergen, & Schyns, 2014). Face cells within the macaque cortex are sensitive to face parts and their combinations, do not require the presentation of a full face to elicit optimal responses, and show a high sensitivity to eye information (Friewald et al., 2009; Issa & DiCarlo, 2012). In humans, reverse correlation techniques suggest the contralateral eye is central to face processing regardless of task demands, with integration of other facial features occurring after this contralateral eye detection during the ascending part of the N170 component (Schyns et al., 2003, 2007; Rousselet et al., 2014). The N170 is also sensitive to eye colour, eye shape, face width, and face proportions (Zheng, Mondloch, Nishimura, Vida, & Segalowitz, 2011), and recent gaze-contingent investigations have further revealed that when an eye is fixated within an upright face, the N170 amplitude is consistently larger compared to fixation on the nasion, nose, mouth, or forehead (de Lissa, McArthur, Hawelka, Palermo, Mahajan, & Hutzler, 2014; Itier & Neath-Tavares, 2017; Itier & Preston, 2018; Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Nemrodov et al., 2014; Parkington & Itier, 2018). However, in addition to this eye-sensitivity during early face perception, recent findings also suggest that the N170 may vary with fixation on other face parts (Parkington & Itier, 2018) and with the presence or absence of non-fixated features (Itier & Preston, 2018; Nemrodov et al., 2014). These findings point towards a *malleable,* rather than

rigid, holistic process, at the level of the N170 component, whereby featural integration is modulated by which feature is fixated and which features are situated nearby.

The Lateral Inhibition, Face Template, and Eye Detector (LIFTED) model of early face perception (Nemrodov et al., 2014) posits that early face perception, as captured by the N170 component, first involves the activation of a neural eye detector – which we now suggest is an eye *region* detector (Parkington & Itier, 2018) – that permits the detection of two symmetrical eyes within the environment. From these anchor points, the relative positions and distances between features are coded. If the canonical face configuration (i.e., two eyes above a nose, itself above a mouth, all contained within a face outline) is detected, neural inhibition mechanisms are activated, such that the neurons coding for the fixated feature are down-regulated by inhibitory signals from neurons coding for parafoveal feature information. This neural inhibition permits the integration of all face parts into an integrated whole percept. If the typical canonical face configuration is not detected (e.g., if the face is inverted or if isolated features are shown), neural inhibition mechanisms are not recruited, resulting in the combined activity of neurons coding for foveal and parafoveal information, observed as larger scalp-recorded N170 responses.

While the original model proposed that the strength of the inhibition process was likely dependent on the distance between the parafoveal and foveal features (Nemrodov et al., 2014), more recent findings suggest that the degree of inhibition might rather be dependent on the *saliency* of both the feature fixated in fovea and the features in parafovea (Itier & Preston, 2018; Parkington & Itier, 2018). Behavioural studies have proposed a feature saliency hierarchy, whereby the eyes are deemed the most salient feature, followed by the mouth, followed in turn by the nose (Davies, Ellis, & Shepherd, 1977; Haig, 1985; Hills, Ross, & Lewis, 2011; Schyns, Bonnar, & Gosselin, 2002; for review see Shepherd, Davies, & Ellis, 1981). In line with this

saliency framework, these recent ERP findings suggest that the eyes might exert maximal inhibition on other features and may also be the most inhibited feature, although it is unclear whether this could be driven by the actual saliency of one eye or by the fact that there are two eyes, an idea that can be further refined with the present study. Here, we followed up on the LIFTED model and evaluated the impact of the presence/absence of different facial features on the proposed neural inhibition mechanism. In particular, we tested whether the neural inhibition of an eye might vary depending on the number and type of feature(s) presented in parafovea (see Figure 1 for the various conditions tested and Figure 2 for a trial example). This was accomplished through three primary goals.

First, we sought to elucidate the role of the face outline in early face perception (Goal #1). The face outline is an integral component of the face structure and is relied upon for behavioural face recognition and identification (Ellis, Deregowski, & Shepherd, 1975; Shepherd et al., 1989). Moreover, at the neural level, intracranial recordings in humans have revealed that, at face-specific ventral sites, the face contour alone (i.e., face outline with hair but no internal features) elicits a smaller amplitude response and delayed latency compared to full faces, and a smaller amplitude but similar latency compared to eye regions (McCarthy et al., 1999). Single-cell recordings in macaque cortex, on the other hand, have revealed that face-sensitive cells respond strongly to face shape cues (e.g., face aspect ratio) and outlines, in addition to their sensitivity to eye information (Friewald et al., 2009; Issa & DiCarlo, 2012). Similarly, a sensitivity to face width and proportion, as well as a sensitivity to eye colour and eye shape, have been reported at the level of the scalp-recorded N170 (Zheng et al., 2011). Overall, data converge towards the idea that both the eyes and face outline may be critical driving components in the modulation of early neural responses.

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Moreover, a smaller and earlier N170 has been reported for the presentation of full faces compared to the presentation of internal features (in their preserved first-order configuration) without a face outline (Shibata et al., 2002; Zion-Golumbic & Bentin, 2007). Similarly, faster and attenuated N170 responses have been shown for fixation on features within a full face relative to fixation on the same features presented in isolation (regardless of the feature; Parkington & Itier, 2018). These results point towards a possible shift from a featural neural response to a face neural response when features are contained within a face configuration including a face outline. Here, we directly tested the role of the face outline in this neural response shift by comparing the N170 response to fixation on a single isolated eye relative to fixation on the same eye within a face outline (with no other parafoveal features). We predicted that the simple presence of a face outline would significantly reduce the N170 latency and amplitude relative to fixation on the same eye presented in isolation, thereby providing evidence that the face outline plays a critical role in shifting the neural response towards more face-like processing mechanisms in early perception.

Next we sought to determine the impact of the number of parafoveal features on neural inhibition (Goal #2). One of the central ideas of the LIFTED model is that the strength of the neural inhibition response should be greater when more features are present in parafovea, and weaker when fewer parafoveal features are present. Here, we directly tested this hypothesis by comparing N170 responses to one fixated eye when presented alone in a face outline (i.e., with no parafoveal features) and when presented in face-like stimuli with one, two, or three parafoveal features. Based on the LIFTED model, we predicted that the N170 response would be largest for the one eye condition, attenuated with the presence of one parafoveal feature, attenuated further

with the presence of two parafoveal features, and smallest for the full face condition (with three parafoveal features).

Finally, we sought to determine the impact of the type of parafoveal feature(s) on the neural inhibition process (Goal #3). Here, the variations of the N170 recorded to fixation on an eye within a face outline were monitored as a function of the nature of the feature(s) presented in parafovea (an eye, a nose, or a mouth in the case of only one parafoveal feature; an eye and nose, an eye and mouth, or a nose and mouth combinations in the case of two parafoveal features). Based on recent findings suggesting that the strength of the inhibition may be related to feature saliency rather than distance to fovea (Itier & Preston, 2018; Parkington & Itier, 2018), we predicted that the presence of a second eye in parafovea would elicit the largest degree of inhibition, with the mouth eliciting an intermediate degree of inhibition, and the nose generating the weakest inhibition. Moreover, two-feature combinations with higher cumulative saliency (e.g., an eye and mouth) were expected to elicit greater degrees of inhibition than two-feature combinations with lower cumulative saliency (e.g., a mouth and nose). Alternatively, finding that the nose elicited a larger degree of inhibition relative to the mouth would provide support in favour of the distance-from-fovea account initially proposed by the LIFTED model (Nemrodov et al., 2014), as the nose was situated closer to the fixated eye than to the other eye or the mouth (Figure 1).

<Insert Figures 1 and 2 here>

2. RESULTS

2.1 Impact of the Face Outline

In order to elucidate the inhibitory role of the face outline in early face perception, peak N170 amplitudes and latencies were analyzed separately using repeated-measure ANOVAs with Hemisphere (2: left, right), Eye Fixation (2: left eye, right eye), and Stimulus Type (2: isolated eye, one eye) as within-subject factors. It is important to note that because fixation was enforced on the left/right eye of each face-like stimulus, thus presenting the majority of the visual image in the opposite hemifield, it was expected that neural activation for face-like stimuli would be strongest (and thus most representative) in the hemisphere contralateral to hemifield presentation (Figure 3, see Method Section for more details).

<Insert Figure 3 here>

2.1.1 N170 Peak Amplitude

Overall, N170 peak amplitudes were larger from right-side sites relative to left-side sites (main effect of Hemisphere: $F(1,44) = 28.78$, $MSE = 35.24$, $p < .001$, $\eta_p^2 = .40$). No effect of Stimulus Type was found ($p = .20$); however, there were significant Hemisphere x Fixated Eye ($F(1,44) = 37.93$, $MSE = 1.46$, $p < .001$, $\eta_p^2 = .46$) and Hemisphere x Fixated Eye x Stimulus Type ($F(1,44) = 57.36$, $MSE = 1.48$, $p < .001$, $\eta_p^2 = .57$) interactions. As seen in Figure 4 A-B, isolated eyes did not elicit an amplitude difference between left and right eye fixation in either hemisphere. In contrast, as predicted (Figure 3), an amplitude difference was found dependent on the eye fixated within a face outline (one eye condition), which showed opposite patterns across hemispheres. Specifically, within the left hemisphere, N170 peak amplitudes were marginally smaller for right eye fixation compared to left eye fixation ($p = .03$; Bonferroni paired *t*-tests significant at $p \leq .013$), whereas in the right hemisphere, N170 peak amplitudes were smallest for left eye fixation ($p = .001$). Because of this eye fixation effect for the one eye condition, N170 peak amplitudes within the right hemisphere were significantly smaller for the one eye condition,

compared to the isolated eye condition, when fixation was enforced on the left eye ($p = .001$; Bonferroni paired t-tests significant at $p \leq .013$), but not when fixation was enforced on the right eye ($p = .32$). Alternatively, the opposite pattern was observed within the left hemisphere, such that the one eye condition elicited marginally smaller amplitudes than the isolated eye with right eye fixation ($p = .03$), but not with left eye fixation ($p = .58$).

2.1.2 N170 Peak Latency

Isolated eyes elicited significantly delayed N170 peak latencies ($M = 182$ ms, $SD = 12$ ms) compared to an eye fixated within a face outline ($M = 157$ ms, $SD = 11$ ms; main effect of Stimulus Type: $F(1,44) = 573.10$, $MSE = 94.85$, $p < .001$, $\eta_p^2 = .93$; Figure 4A & 4C).[1] A main effect of Hemisphere was also present ($F(1,44) = 6.89$, $MSE = 60.92$, $p = .01$, $\eta_p^2 = .14$), but was qualified by a significant Hemisphere x Fixated Eye interaction ($F(1,44) = 4.00$, $MSE = 9.86$, $p = .05$, $\eta_p^2 = .08$). Specifically, latencies were faster in the right than in the left hemisphere for right eye fixation ($p = .003$; Bonferroni paired t-tests significant at $p \leq .013$) but not for left eye fixation ($p = 0.10$).

<Insert Figure 4 here>

2.1.3 Results Summary

The presence of a face outline around the fixated eyes elicited robustly faster N170 latencies compared to the eyes presented in isolation (Figure 4A-C). Moreover, when an eye was fixated within a face outline, N170 amplitudes were significantly attenuated for left eye fixations within the right hemisphere, as well as for right eye fixations within the left hemisphere. Taken

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[1] A Fixated Eye x Stimulus Type interaction ($F(1,44) = 4.92$, $MSE = 16.31$, $p = .03$, $\eta_p^2 = .10$) was also found. However, this was driven by a minute difference ($M_{difference} = 1.39$ ms) between eye fixations for the isolated eye conditions. Given the isolated eye conditions contained identical (albeit mirror-flipped) information (see ∂ 2.2), and this mean difference is within the realm of measurement error acquired with a 512 Hz recording, the implications of this interaction will not be discussed further.

together these findings provide evidence that the presence/absence of a face outline does play an important role during early face perception, as marked by the scalp-recorded N170 component.

2.2 Impact of the Number of Parafoveal Features

The LIFTED model postulates that the number of features present within parafovea should impact the degree of neural inhibition observed on the N170 component, such that inhibition should be stronger with increasing numbers of parafoveal features (Nemrodov et al., 2014). To test this idea, we compared N170 responses when zero, one, two, or three parafoveal features were visible within a face outline. The one eye (zero parafoveal features) and full face (three parafoveal features) conditions were compared to two aggregate categories: a *one feature* category consisting of the averaged N170 response across the one eye + nose, one eye + mouth, and two eyes conditions, and a *two feature* category consisting of the averaged N170 response across the one eye + nose + mouth, two eyes + nose, and two eyes + mouth conditions[2]. Separate repeated-measure ANOVAs for N170 peak amplitudes and latencies were conducted with Hemisphere (2: left, right), Eye Fixation (2: left eye, right eye), and Number of Parafoveal Features (4: zero, one, two, three) as within-subject factors.

2.2.1 N170 Peak Amplitude

N170 peak amplitudes demonstrated a consistent attenuation with increasing number of parafoveal features, such that zero parafoveal features (one eye condition) elicited the largest N170 amplitude, followed by one parafoveal feature, then two parafoveal features, with three parafoveal features (full face condition) eliciting the smallest N170 amplitude (main effect of

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[2] Note that these aggregate scores were computed averaging the original N170 peak amplitude and latency values extracted for each original condition separately (i.e. we did *not* first average the conditions at the ERP level and then extracted those values, as this would potentially create issues for amplitude measures given the slight variations in latencies between individual conditions).

Number of Parafoveal Features: $F(1.74, 76.35) = 25.11$, $MSE = 3.64$, $p < .001$, $\eta_p^2 = .36$; paired

comparisons: $ps \leq .02$; Figure 5B). Overall, right-side electrodes elicited larger N170 amplitudes

compared to left-side sites (main effect of Hemisphere: $F(1,44) = 27.39$, $MSE = 62.18$, $p < .001$,

$\eta_p^2 = .38$). Furthermore, in addition to the expected Hemisphere x Fixated Eye interaction

($F(1,44) = 50.94$, $MSE = 7.21$, $p < .001$, $\eta_p^2 = .54$), the three-way Hemisphere x Fixated Eye x

Number of Parafoveal Features interaction ($F(2.43, 106.93) = 5.92$, $MSE = 0.93$, $p = .002$, $\eta_p^2 =$

.12) revealed that the condition differences were clearer within the right hemisphere (for right

eye fixations) than in the left hemisphere (for left eye fixations; Figure 5A). Specifically, when

fixation was enforced on the right eye, right hemispheric amplitudes followed this gradient, with

all paired comparisons significant ($ps < .003$) except for the zero-one feature comparison ($p =$

.30). Alternatively, for left eye fixation within the left hemisphere, there were no amplitude

differences when two or three parafoveal features were present ($p = .18$), though these conditions

were attenuated relative to the presence of zero or one parafoveal features ($ps \leq .03$).

2.2.2 N170 Peak Latency

Mirroring that reported above, N170 peak latencies were fastest when three features were

present in parafovea (full face condition), followed by two features, followed in turn by one

feature, with zero parafoveal features (one eye condition) yielding the longest latencies overall

(main effect of the Number of Parafoveal Features: $F(1.65, 72.40) = 89.77$, $MSE = 41.99$, $p <$

.001, $\eta_p^2 = .67$; all paired comparisons: $ps < .001$; Figure 5C). N170 latencies were also shorter

within the right hemisphere compared to the left (main effect of Hemisphere: $F(1,44) = 5.78$,

$MSE = 155.80$, $p = .02$, $\eta_p^2 = .12$). Moreover, in addition to the expected Hemisphere x Fixated

Eye interaction ($F(1,44) = 32.01$, $MSE = 39.47$, $p < .001$, $\eta_p^2 = .42$), the significant three-way

Hemisphere x Fixated Eye x Number of Parafoveal Features interaction ($F(2.18, 96.04) = 10.97$,

$MSE = 8.51$, $p < .001$, $\eta_p^2 = .20$) indicated that the latency differences between conditions were stronger within the right hemisphere (for right eye fixations; $\eta_p^2 = .67$) than in the left hemisphere (for left eye fixations; $\eta_p^2 = .64$).

<center><Insert Figure 5 here></center>

2.2.3 Results Summary

Overall, both N170 peak amplitude and latency responses were significantly reduced as the number of features present in parafovea increased (Figure 5A-C), with zero parafoveal features (one eye condition) eliciting the slowest and largest response, and three parafoveal features (full face condition) yielding the fastest and smallest response. This response gradient was clearest within the right hemisphere for right eye fixation. In line with the LIFTED model (Nemrodov et al., 2014), and our initial predictions, the current findings support the idea that the strength of neural inhibition observed during early face perception is moderated by the number of features visible in parafovea.

2.3 Effect of Feature Type with One Parafoveal Feature

The original LIFTED model (Nemrodov et al., 2014) postulated that the strength of neural inhibition varies with features' eccentricity from fovea. This hypothesis predicts that the nose (located 3.52° from either fixated eye; Figure 1) should elicit the strongest degree of inhibition, with the other eye (4.25°) eliciting an intermediary degree of inhibition, and the mouth (5.31°) yielding the weakest inhibitory strength. Alternatively, if neural inhibition is instead a function of feature saliency, as suggested more recently (Itier & Preston, 2018; Parkington & Itier, 2018), then the N170 recorded to a fixated eye should be most reduced when

the other eye is present in parafovea, followed by the presence of a mouth, with the nose eliciting the weakest degree of inhibition.

N170 responses were compared when a single eye was fixated within a face outline relative to the presence of one parafoveal feature (eye, nose, or mouth). Peak N170 amplitudes and latencies were analyzed using repeated-measure ANOVAs with Hemisphere (2: left, right), Eye Fixation (2: left eye, right eye), and Parafoveal Feature Type (3: nose, mouth, eye) as within-subject factors. The conditions used were the one eye + nose, one eye + mouth, and two eyes conditions (Figure 1).

2.3.1 N170 Peak Amplitude

N170 peak amplitudes were significantly larger within the right hemisphere compared to the left (main effect of Hemisphere: $F(1,44) = 26.17$, $MSE = 49.69$, $p < .001$, $\eta_p^2 = .37$) and the expected Hemisphere x Fixated Eye interaction ($F(1,44) = 57.34$, $MSE = 5.94$, $p < .001$, $\eta_p^2 = .57$) was significant. There was no main effect of Parafoveal Feature Type ($p = .62$). However, a significant three-way Hemisphere x Fixated Eye x Parafoveal Feature Type interaction ($F(2,88) = 7.74$, $MSE = 0.96$, $p = .001$, $\eta_p^2 = .15$) revealed that while the simple effect of Parafoveal Feature Type was not significant within the left hemisphere when left eye fixation was enforced ($p = .14$), it was significant within the right hemisphere for right eye fixations ($F(2,88) = 3.33$, $MSE = 1.42$, $p = .04$, $\eta_p^2 = .07$), due to a slightly attenuated amplitude when an eye was visible in parafovea compared to when the nose was visible ($p = .08$; Figure 6A-B).

2.3.2 N170 Peak Latency

A main effect of Parafoveal Feature Type was found ($F(2,88) = 9.33$, $MSE = 15.47$, $p < .001$, $\eta_p^2 = .18$), such that the presence of an eye or mouth in parafovea elicited significantly shorter latencies relative to the presence of a nose ($ps = .002$), though they did not differ from

each other (p = .66). The main effect of Hemisphere was only marginally significant (p = .07) but, as expected, was moderated by eye fixation (Hemisphere x Fixated Eye interaction: $F(1,44)$ = 39.19, MSE = 25.34, p < .001, η_p^2 = .47). A significant Hemisphere x Fixated Eye x Parafoveal Feature Type ($F(2,88)$ = 16.51, MSE = 5.20, p < .001, η_p^2 = .27) interaction further revealed that the latency differences between parafoveal features was clearest for right eye fixations within the right hemisphere. Specifically, the presence of an eye in parafovea elicited significantly faster latencies relative to the presence of a nose or mouth in parafovea (ps ≤ .02), which did not differ from each other (p = 1.00). For left eye fixations within the left hemisphere, having an eye visible in parafovea also elicited shorter latencies, although only the eye-nose comparison reached significance (p < .001; all other paired comparisons ps > .10; Figure 6A & 6C).

<center>*<Insert Figure 6 here>*</center>

2.3.3 Results Summary

When fixation was enforced on an eye, the type of feature visible in parafovea did have an impact on N170 responses, though this pattern was clearer for peak latency responses than for amplitudes. Specifically, when the second eye was visible in parafovea, N170 latencies were shorter, and amplitudes were slightly attenuated, compared to the presence of a nose or mouth in parafovea, with effects clearest for right eye fixations within the right hemisphere. Although the variations observed were overall weak, these findings do not support an eccentricity-from-fovea account for the strength of inhibition observed, but instead are more in line with a feature saliency account, with the eye serving the strongest inhibitory role, followed by the mouth, with the nose producing the smallest inhibitory effect within a face outline.

2.4 Effect of Feature Type with Two Parafoveal Features

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When multiple parafoveal features are present, the inhibition strength should be a function of the sum or average[3] of their distances to the foveated feature or of their social saliency. If inhibitory strength is a function of parafoveal feature eccentricity, then a second eye and nose should elicit maximum inhibition, and thus smallest N170 amplitude, followed by the presence of a nose and mouth, with the presence of a second eye and mouth eliciting the least inhibition, and thus largest amplitude. Alternatively, if inhibition is related to feature saliency, then the N170 amplitude reduction should be maximal when the parafoveal features are the second eye and mouth, which should elicit maximum inhibition (one high-salience and one moderate-salience feature), followed by the presence of a second eye and nose (one high-salience and one low-salience feature), with a nose and mouth eliciting the least inhibition and thus largest N170 (one moderate-salience and one low-salience feature).

Repeated-measure ANOVAs were conducted on peak N170 amplitudes and latencies with Hemisphere (2: left, right), Eye Fixation (2: left eye, right eye), and Parafoveal Feature Combination (3: nose + mouth, eye + nose, eye + mouth) as within-subject factors, using the one eye + nose + mouth, two eyes + nose, and two eyes + mouth conditions (Figure 1).

2.4.1 N170 Peak Amplitude

N170 peak amplitudes were significantly larger within the right hemisphere relative to the left hemisphere (main effect of Hemisphere: $F(1,44) = 27.65$, $MSE = 46.74$, $p < .001$, $\eta_p^2 = .39$) and, as expected, this interacted further with eye fixation (Hemisphere x Fixated Eye interaction: $F(1,44) = 34.78$, $MSE = 6.97$, $p < .001$, $\eta_p^2 = .44$). The main effect of Parafoveal Feature Combination did not reach significance ($p = .10$), however, a significant Hemisphere x Fixated Eye x Parafoveal Feature Combination interaction ($F(2,88) = 5.18$, $MSE = 0.86$, $p = $

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[3] Note that the LIFTED model does not make any specific assumption as to whether the sum or average distances matter, but both lead to the same prediction.

.009, η_p^2 = .11) was found. As seen in Figure 7A-B, a small amplitude gradient was observed, with the largest amplitude elicited when a nose and mouth were visible in parafovea, followed by an eye and nose, with the presence of an eye and mouth eliciting the smallest amplitude. The three-way interaction highlighted that this gradient was not significant for right eye fixations within the right hemisphere (p = .11), but was significant for left eye fixations within the left hemisphere (simple effect of Parafoveal Feature Combination: $F(2,88)$ = 4.29, MSE = 1.81, p = .02, η_p^2 = .09), with a significant amplitude difference when an eye and mouth were visible in parafovea compared to the presence of a nose and mouth (p = .01; all other paired comparisons: ps ≥ .13).

2.4.2 N170 Peak Latency

As shown in Figure 7A & 7C, a main effect of Parafoveal Feature Combination ($F(1.13$, $50.22)$ = 8.17, MSE = 160.36, p = .005, η_p^2 = .16) was due to shorter N170 peak latencies when an eye and mouth or an eye and nose were visible in parafovea compared to the presence of a nose and mouth (ps ≤ .007). Latencies were also marginally faster when an eye and mouth were present in parafovea compared to an eye and nose (p = .08). Moreover, latencies were faster within the right hemisphere relative to the left (main effect of Hemisphere: $F(1,44)$ = 5.04, MSE = 147.91, p = .03, η_p^2 = .10), although this was only upheld for right eye fixations (Hemisphere x Fixated Eye interaction: $F(1,44)$ = 12.97, MSE = 85.11, p = .001, η_p^2 = .23; hemispheric difference for right eye fixations: p < .001; hemispheric difference for left eye fixations: p = .74; Figure 7A & 7D). The three-way interaction did not reach significance (p = .14).

<Insert Figure 7 here>

2.4.3 Results Summary

Overall, when fixation was enforced on an eye and two features were visible in parafovea, the type of features present modulated the N170 response. In particular, a slight response gradient was observed, such that the N170 was slightly smaller and faster when an eye and mouth were visible in parafovea, followed by the presence of an eye and nose, with the presence of a nose and mouth eliciting the largest and slowest N170 response. Similar to our findings above with one parafoveal feature (see ∂ 2.3), the N170 response pattern appears to be more in line with a feature-saliency account of inhibition strength, than with an eccentricity-from-fovea account. Specifically, the current results suggest that the presence of an eye (arguably the most salient facial feature) in parafovea elicits the strongest inhibitory signal when seen with a mouth (the second most salient facial feature), followed with moderately less inhibition when seen with a nose (the least salient facial feature), and the weakest inhibition observed when a mouth and nose are visible in parafovea.

3. DISCUSSION

With the present study, we aimed to elucidate the role of the face outline and internal facial features in early face perception and to further investigate the neural inhibition mechanisms proposed by the LIFTED model (Itier & Preston, 2018; Nemrodov et al., 2014; Parkington & Itier, 2018). Here, N170 responses were measured when fixation was enforced on an eye presented in isolation or within a face outline with zero, one, two or three parafoveal features (Figure 1). A series of analyses permitted an in-depth examination of the impact of individual features, and the number of features present, on these early neural mechanisms.

First, we confirmed that the face outline does play an integral role in early face perception (Goal #1). When fixation was enforced on an eye presented within a face outline, the

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N170 response occurred significantly earlier relative to fixation on the same eye presented in isolation (Figure 4A). It is unlikely that this finding was driven by mere differences in low-level factors (mean pixel intensity or contrast) between our two conditions, since this impressive (~25ms) latency shift was also found recently, when low-level factors were equated at the local (feature) and global (image) levels (Parkington & Itier, 2018). Rather, in line with the latter study, the present findings suggest that the mere presence of a face outline is sufficient to elicit a distinct shift in the neural response to a more face-like pattern (Figures 4A & 8). Indeed, in addition to the large latency shift, hemispheric effects (which interacted with the eye fixated; see Figure 3) emerged, in line with hemispheric lateralization responses commonly observed for faces (Dundas, Plaut, & Behrmann, 2014; Rossion & Jacques, 2012; Scott & Nelson, 2006). When presented in isolation, the left and right eyes elicited similar N170 responses in both hemispheres. However, as soon as the outline was present, interactions between hemisphere and the fixated eye appeared, such that amplitude reductions were seen in the hemisphere contralateral to the fixated eye. In other words, the face outline provided the boundary that allowed the visual system to anchor the eye in the face frame of reference: the left eye became the left eye because of its position toward the left of the face outline, and vice versa for the right eye. As such, the face outline may play a critical role in driving early face detection responses at the neural level, a conclusion supported by earlier reports of shorter and smaller N170s for full faces compared to the same internal facial features presented without a face outline (Zion-Golumbic & Bentin, 2007; Shibata et al., 2002), and by behavioural data (Ellis, Deregowski, & Shepherd, 1975; Shepherd et al., 1989; Fraser, Craig, & Parker, 1990). Although computational models (Tsao & Livingstone, 2008; Ullman, Vidal-Naquet, & Sali, 2002) and N170 recordings (Rousselet et al., 2014) highlight the importance of the eyes (especially the contralateral eye) in

face detection, the stimuli used in those studies were always full faces and it is likely that this face detection was facilitated by a combination of eye information in relation to face outline information.

Importantly, our results also dovetail with monkey single-cell and human intracranial and scalp-recorded neural responses (Engell & McCarthy, 2004; Friewald et al., 2009; Issa & DiCarlo, 2012; McCarthy et al., 1999; Seeck et al., 2001; Zheng et al., 2011). In particular, Issa and DiCarlo (2012) reported that the response of face-selective cells within the macaque posterior lateral face patch is driven by the presence of a single eye within a curved boundary context, mimicking the face outline. Moreover, face cells (Friewald et al., 2009) and the N170 (Zheng et al., 2011) respond strongly to eye and face shape information, compared to other featural traits (e.g., nose width, lip height), highlighting that the primate brain may be especially tuned to the combination of eye and face outline information. The detection and perception of the eyes within the environment has several critical evolutionary and social advantages (Emery, 2000; Kobayashi & Kohshima, 1997), and although the presentation of two symmetrical eyes (i.e., eye region) elicits a distinct neural response compared to the presentation of a single eye (Parkington & Itier, 2018), it appears that the simple presentation of one eye within an oval boundary or face outline is sufficient to shift the neural response from a featural pattern to a more face-like response.

Next, we sought to evaluate the impact of the number of internal facial features on the strength of the neural inhibition response (Goal #2) once the face outline was present. A monotonic decrease in N170 amplitude and latency was observed with an increase in the number of visible features (Figure 5), supporting the neural inhibition account (Itier & Preston, 2018; Nemrodov et al., 2014; Parkington & Itier, 2018). Fixation on a single eye within a face outline

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elicited the strongest and most delayed neural response. However, having one or two features visible in parafovea led to systematic decreases in latency and amplitude, with a full face (i.e., three features in parafovea) eliciting the smallest and fastest N170 response. Moreover, in line with a right-hemispheric dominance in face processing, these effects were most pronounced within the right hemisphere (Figure 8).

Interestingly, a recent fMRI study showed that within the OFA, the BOLD response was similar for isolated eyes, a mouth, a nose or the combination of two eyes, but decreased with increasing numbers of internal features (two eyes > two eyes + mouth > two eyes + nose + mouth). However, no response gradient was observed within the FFA (Arcurio et al., 2012). In addition to confirming the sensitivity of the OFA to individual facial features, this response gradient within the OFA also suggests an attenuated neural response for feature combinations closest to a full face, despite the absence of a face outline, and parallels our decrease in N170 amplitude with increasing number of features. Although the BOLD response seems to map better onto spectral perturbations in the frequency domain than onto ERP modulations (Engell, Huettel & McCarthy, 2012), these similar gradient results support the idea that the scalp-recorded N170 modulations might reflect activity emanating from the OFA. In any case, those fMRI results support the idea that at least one main node of the core face system is sensitive to the number of features visible and might also be subject to neural inhibition processes (possibly coming from the FFA, see Engell, Kim & McCarthy, 2018). Moreover, single-cell recordings in the non-human primate brain also suggest that neuron clusters within the face processing network respond optimally to combinations of features and accomplish an optimal whole-face response based on feature integration and inhibition networks (Friewald et al., 2009; Issa & DiCarlo, 2012). These findings are in line with the neural inhibition account proposed by the LIFTED

model (Itier & Preston, 2018; Nemrodov et al., 2014; Parkington & Itier, 2018), and support a holistic integration mechanism at the neural level – such that as more features are present within parafovea they can be more successfully integrated into a Gestalt-whole, leading to a more optimal face-like response.

Finally, consistent with recent reports (Itier & Preston, 2018; Parkington & Itier, 2018), the strength of the neural inhibition response appears to be weakly moderated by the *saliency* of the feature, rather than the feature's eccentricity from fovea, as originally proposed by the LIFTED model (Nemrodov et al., 2014; Goal #3). In the present study, when one feature was visible in parafovea, the response was faster and slightly attenuated if that parafoveal feature was the second eye but remained unchanged if the parafoveal feature was a nose or mouth (Figure 6), implicating the eye as an important "feature inhibitor" (see also Itier & Preston, 2018). These findings are in line with the feature saliency theory proposed within the behavioural literature (Davies et al., 1977; Fraser et al., 1990; Haig, 1985; Hills et al., 2011; Schyns et al., 2002; Shepherd et al., 1981) and provide support for the coding of feature saliency at the neural level. It is important to note, however, that these saliency findings were small and most evident within the right hemisphere. In accordance with intracranial recordings demonstrating a larger number of face- and eye-sensitive cell clusters within the right compared to the left hemisphere (Engell & McCarthy, 2014; McCarthy et al., 1999), and a right hemispheric dominance for face and social processing (Dundas et al., 2014; Haxby et al., 2000; Kanwisher, McDermott, & Chun, 1997; Rossion et al., 2000), the saliency and social significance of features may be most strongly coded within the right hemisphere, particularly for the eyes, although both hemispheres are involved in complex information coding involving eye features (Ince et al., 2016).

Our findings further suggest that the weighted saliency contribution of multiple features also appears to be taken into account at the neural level. Specifically, when two features were visible in parafovea, a response gradient was evident, especially for latency measures (Figure 7), such that the fastest and most attenuated response was elicited when an eye and mouth were present, moderate when an eye and nose were visible, with a nose and mouth yielding the largest and slowest N170 response. This gradient suggests that at the neural level, the combination of saliency weighting for each individual feature is coded and represented by modulations on the N170 component. It currently remains unclear, however, whether this combinatorial process would be linear or sublinear in nature, and requires further investigation to pin-point the origin and mechanism sub-serving this neural saliency coding. These saliency findings should also be interpreted with some caution pending further replication, due to the subtle nature of the effects, particularly at the scalp-level.

It is also important to consider that conditions in which two eyes were visible elicited N170 responses more similar to the full face category compared to conditions in which only one eye was visible (for a visual comparison of all conditions see the Supplementary Figure). These findings highlight the seemingly dual role that eyes may play, not only being a strong inhibiting parafoveal feature, but also a feature which requires a high degree of inhibition to down-regulate the salient foveal eye response. Consistent with previous research (Bentin et al., 1996; Eimer, 1998; Itier et al., 2006, 2007, 2011; Itier & Preston, 2018; Parkington & Itier, 2018; Shibata et al., 2002; Taylor et al., 2001), two eyes within a face outline seem necessary to elicit a more face-like response. Even when three features were visible within the face but the second eye was missing (i.e., eye + nose + mouth condition), the N170 response was not as strong as when two symmetrical eyes were present. These findings provide support in favour of the LIFTED model

according to which the detection of two eyes anchor the face percept, leading to an integration of all visible features through inhibition mechanisms. Without the presence of two symmetrical eyes, the face percept cannot be anchored as successfully, leading to weaker integration and inhibition mechanisms (evidenced by larger peak amplitudes). These results highlight that although the number of features present is an important factor for inhibitory mechanisms (Goal #2), it is not sufficient to elicit a complete face response. Rather it appears that it is a combination of the number *and* nature/saliency of the features that guides the neural response closer to the optimal face response.

Although the current study elucidates many components of the LIFTED model of early face perception, including a neural eye region detector, and the proposed neural inhibition mechanisms, the current study only examined modulations when fixation was enforced on an eye. Therefore, future investigations evaluating similar conditions with fixation enforced on other features (e.g., nose, mouth) are important next steps in clarifying the holistic versus featural underpinnings of early face perception.

4. CONCLUSION

In line with the LIFTED model of early face perception (Itier & Preston, 2018; Nemrodov et al., 2014; Parkington & Itier, 2018), we showed that the number and type of features visible in parafovea modulate early face neural response, and that the strength of the neural inhibition seems influenced by feature saliency. A distinct amplitude and latency shift was observed on the N170 component when an eye was fixated within a face outline compared to fixation on the same eye in isolation, suggesting that the face outline may facilitate a shift in neural generators from featural to holistic integration processing. A monotonic decrease in

amplitude and latency was observed with increasing numbers of parafoveal features, with a full face eliciting the smallest and fastest response. The presence of a second eye in parafovea was also shown to elicit a slightly stronger degree of inhibition, followed by the mouth, followed in turn by the nose, thereby supporting the idea that the neurons coding for the eyes not only require a high degree of inhibition from other features, but also elicit a strong degree of inhibition upon other features. All in all the present findings are in line with the neural inhibition mechanisms proposed by the LIFTED model, with support in favour of a feature-saliency account of inhibition strength.

5. MATERIALS AND METHOD

5.1 Participants

Forty-five (45) adults (20 males, M_{age} = 20.69 years, SD_{age} = 2.10, 41 right-handed) with no history of head injury, neurological disease, or psychiatric disorders participated in the present study for course credit or cash payment. Data for an additional 17 participants were collected, but were subsequently excluded from analyses due to eye-tracking difficulties (14), too few trials per condition after eye movement and artifact rejection (2), or technical issues during the electroencephalogram (EEG) recording (1). All participants reported normal or corrected-to-normal vision, did not have a personal or familial history of epilepsy, seizures, or flashing lights, and were not taking antidepressant or antipsychotic medications at the time of testing. The study was reviewed and approved by a University of Waterloo Human Research Ethics committee, and in accordance with the Declaration of Helsinki, all participants provided informed written consent prior to the start of the study.

5.2 Stimuli

Thirty grey-scale identities (15 male, 15 female) were created using FACES™ 4.0 by IQBiometrix Inc. Face stimuli (10.36º x 15.19º) were modified to create seven additional left eye[4] conditions within a facial outline in which only one, two, or three features were visible, by airbrushing out the unwanted features (Figure 1). An isolated eye condition was also created by extracting a rectangular segment (2.86º x 2.45º) centred on the left eye, from each full face identity. All stimuli were subsequently flipped along the vertical axis to generate the same conditions with right eye fixation. This resulted in a total of nine stimulus type conditions (Figure 1): a) isolated eye, b) one eye, c) one eye + nose, d) one eye + mouth, e) one eye + nose + mouth, f) two eyes, g) two eyes + nose, h) two eyes + mouth, and i) full face. All conditions were presented an equal number of times with left and right eye fixation. One additional female identity underwent the aforementioned transformations for use in the practice phase, and were inverted 180º to create oddball stimuli for the experimental phase.

5.3 Design

Participants were seated 70 cm from the computer screen in a dimly lit, sound-attenuated Faraday cage, with their heads supported in a chinrest. Participants were instructed to focus on the centrally-presented fixation cross, such that their gaze would trigger the presentation of an image, and to maintain this central fixation when the image appeared (i.e., no eye movements). Throughout the experiment, participants engaged in an oddball detection task (10% probability), by pressing the spacebar on a standard keyboard to inverted images. All participants completed a practice phase containing 16 experimental trials and four oddball trials prior to starting the experimental blocks. The experiment was initially presented on a 19" CRT monitor with a

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[4] Note that left/right eye fixations are referenced from the observer's perspective (i.e., left eye indicates the eye on the left-most part of the image).

refresh rate of 75 Hz; however, part-way through data collection an upgrade was made to a 21"

CRT computer monitor with a refresh rate of 85 Hz.

An Eyelink 1000 desk-mounted remote eye-tracking system (SR Research, http://sr-research.com), was used to monitor eye movements, recording at a sampling rate of 1000 Hz. A nine-point calibration sequence was initiated at the beginning of each block in order to calibrate the participant's dominant eye (as determined by the Miles test; Miles, 1930). Each trial began with a gaze-contingent fixation trigger, during which participants had to maintain fixation within a 1.24° diameter centered around the fixation cross for 250 ms[5]. Once the fixation trigger was activated, a stimulus – with either the left or right eye presented in the centre of the screen – was flashed for 250 ms. This was then followed by a response screen which remained until a button response was made, or for a maximum of 700 ms (Figure 2). If the fixation trigger was not activated within ten seconds (i.e., if the participant failed to fixate on the cross for 250 ms), the trial was aborted and a drift correct was recorded. Mid-block recalibrations were conducted following three sequential drift corrects or when the eye recording was clearly off-centre.

Three blocks of 180 experimental trials (10 identities [5 female, 5 male] x 9 conditions x 2 eye fixations) and 18 oddball trials (9 conditions x 2 eye fixations, all inverted) were created and repeated four times throughout the experiment, leading to a total of twelve blocks overall (120 trials per condition x 9 conditions x 2 eye fixations = 2160 experimental trials + 216 oddball trials). However, due to time limitations, participants only completed an average of 7 blocks (*SD* = 2). The experiment was programmed and presented under Experiment Builder 1.10.1385 (SR Research, http://sr-research.com).

5.4 EEG Recordings

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[5] Due to variability in reorienting to the fixation cross after each trial, the average duration of this fixation trigger across participants was 481 ms (*SD* = 100 ms).

An Active-two Biosemi system was used to acquire the EEG recordings with custom-made 72-electrode caps: 66 channels embedded in a cap under the 10/20 system extended (including PO9 and PO10 electrodes over the occipito-parietal region), and three pairs of face electrodes (two pairs placed on the outer canthi and infra-orbital ridges to monitor horizontal and vertical eye movements, and one pair placed over the mastoids). A Common Mode Sense (CMS) active electrode and Driven-Right Leg (DRL) passive electrode served as a ground during recording. EEG data were collected continuously at 512 Hz, and electrode offset was kept below ± 20 mV.

5.5 Data Processing

All EEG data were processed using the EEGLab (Delorme & Makeig, 2004) and ERPLab (http://erpinfo.org/erplab) MATLAB toolboxes. Only correct experimental trials (i.e., upright trials with no response) were analyzed. 0.23% of trials were removed across participants due to miss and false alarm responses.

EEG data were average-referenced offline, and were synchronized with the eye-tracking recordings, such that only trials in which participants maintained fixation within a pre-determined 1.80° region of interest (ROI), centered on the left or right eye of the stimulus (Figure 1), were included. This resulted in the removal of 2.32% of trials across all participants due to eye movements. Data were subsequently digitally band-pass filtered (0.01 – 30 Hz) and epochs were generated from -100 ms pre- to 350 ms post-stimulus presentation, with the 100 ms pre-stimulus time used as a baseline. EEG artifacts above or below ±70 µV were rejected using an automated detection procedure, with 12.18% of trials rejected across all participants. Overall, participants provided an average of 64 trials per condition (*SD* = 21; see Supplementary Table).

5.6 Data Analysis

As evident in Figure 8, all conditions elicited classic N170 topographies within the posterior occipito-temporal region. All participants showed this distribution, with one electrode in each hemisphere eliciting the strongest peak responses for all conditions. The N170 ERP component was maximal at different electrodes across participants (but within a participant, all conditions were maximal on the same electrode). As such, the averaged ERP waveforms were individually inspected for each participant, in order to determine the electrodes for which the N170 amplitude was maximal for all conditions (see also Itier & Neath-Tavares, 2017; McCrackin & Itier, 2018; Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Itier & Preston, 2018; Parkington & Itier, 2018). The distribution of peak electrodes across participants are presented in Table 1. N170 amplitude and latency were measured at these electrodes between 120 ms and 220 ms post-stimulus onset.

<Insert Figure 8 & Table 1 here>

To address our three primary research questions, a series of repeated measures analyses of variance (ANOVAs) were conducted on the N170 peak amplitudes and latencies, with a subset of conditions. For clarity, each analysis is described at the beginning of the associated Results subsection.

It is important to note that because fixation was enforced on the left/right eye of each face-like stimulus, thus presenting the majority of the visual image in the opposite hemifield, it was expected that neural activation would be strongest (and thus most representative) in the hemisphere contralateral to hemifield presentation (Figure 3). Attenuated activation was also expected in the ipsilateral hemisphere, with stronger activation anticipated in the right hemisphere for left eye fixation (compared to the left hemisphere for right eye fixation), in line with the right-hemispheric lateralization commonly observed in face perception (Dundas et al.,

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2014; Haxby et al., 2000; Kanwisher et al., 1997; Rossion & Jacques, 2012; Rossion et al., 2000; Scott & Nelson, 2006).

As demonstrated in Figure 8, these neural activation patterns were upheld, with bilateral activation for all face-like stimuli, and stronger activation in the hemisphere contralateral to the hemifield containing the most visual information. As such, significant Hemisphere by Eye Fixation interactions were expected (and found) for all analyses and are not elaborated on further. Follow-up analyses for significant three-way interactions (involving the stimulus categories) were focused within the contralateral hemisphere to unveil the most representative activation patterns.

All analyses were conducted using SPSS Statistics 25, with Greenhouse-Geisser adjusted degrees of freedom applied when Mauchley's Test of Sphericity was violated ($p < .05$), and Bonferroni corrections applied to all paired comparisons.

Acknowledgements

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Figure Legends

Figure 1. Stimuli exemplars and visual angle measurements. *Left Panel:* Examples of the nine stimulus types presented with left and right eye fixation. Note that left/right eye fixations are referenced from the observer's perspective (i.e., left eye indicates the eye on the left-most part of the image). Participants maintained central fixation on the computer screen, and each stimulus was presented offset to ensure the left or right eye landed in the centre. *Right Panel:* Full face and isolated eye stimulus exemplars with image size and angular distances between features. The blue circles highlight the 1.80^o regions of interest centred on the left or right eye, which were used to reject eye movements for each condition.

Figure 2. Sample trial progression with left eye fixation on a full face. Each trial started with a central fixation cross. Participants were required to activate a fixation trigger by maintaining fixation on the cross for 250 ms, which then initiated stimulus presentation for 250 ms. The average time taken to activate the trigger was 481 ms ± 100. If the trigger was not activated within 10 seconds the trial was aborted and a drift correct was implemented. Following stimulus presentation, a response screen with a central fixation cross was presented until a response was made or for a maximum of 700 ms. Oddball trials progressed in the same manner, with inverted stimuli.

Figure 3. A visual representation of hemispheric processing for faces with fixation enforced on the left and right eye. Darker red and orange circles indicate regions with higher expected activation. Lighter yellow circles indicate regions with lower expected activation. Note that faces with left eye fixation should be processed optimally in the left hemisphere, and faces with right eye fixation should be processed optimally in the right hemisphere.

Figure 4. Peak N170 amplitudes and latencies for isolated eye and one eye conditions, averaged across the electrodes at which the N170 was maximal for each participant. *Panel A:* N170 ERP waveforms across the left and right hemispheres for isolated eye (blue) and one eye (red) conditions with left (solid lines) and right (dashed lines) eye fixations. *Panel B:* N170 peak amplitudes across left (white) and right (grey) eye fixations for isolated eye and one eye conditions within the left and right hemispheres. Note the smaller N170 amplitudes for the one eye condition with right eye fixation within the left hemisphere, and for the one eye condition with left eye fixation within the right hemisphere, whereas the isolated eye condition did not elicit amplitude differences between eye fixations.

Figure 5. Peak N170 amplitudes and latencies as a function of the number of parafoveal features, averaged across the electrodes at which the N170 was maximal for each participant. N170 ERP waveforms (*Panel A*) for zero (red), one (purple), two (light blue), and three (black) parafoveal feature conditions with left eye fixation (solid lines) within the left hemisphere and right eye fixation (dashed lines) within the right hemisphere. N170 peak amplitudes (*Panel B)* and latencies *(Panel C)*, averaged across hemisphere and eye fixations, for zero, one, two, and three parafoveal features. Note the attenuation in amplitude and latency with increasing number of parafoveal features.

Figure 6. Peak N170 amplitudes and latencies when the left or right eye was fixated with one feature present in parafovea, averaged across the electrodes at which the N170 was maximal for

each participant. N170 ERP waveforms (*Panel A*) when a nose (green), mouth (fushia), and eye (orange) were present in parafovea with left eye fixation (solid lines) within the left hemisphere and right eye fixation (dashed lines) within the right hemisphere. N170 peak amplitudes (*Panel B*) and latencies (*Panel* C) when a nose, mouth, and eye were present in parafovea with left and right eye fixations across the left (grey) and right (black) hemispheres. Note the slightly attenuated amplitude and faster latency within the right hemisphere, when right eye fixation was enforced with a second eye visible in parafovea.

Figure 7. Peak N170 amplitudes and latencies when the left or right eye was fixated with two features present in parafovea, averaged across the electrodes at which the N170 was maximal for each participant. N170 ERP waveforms (*Panel A*) when a nose and mouth (brown), eye and nose (teal), and an eye and mouth (yellow) were present in parafovea with left eye fixation (solid lines) within the left hemisphere and right eye fixation (dashed lines) within the right hemisphere. N170 peak amplitudes (*Panel B*) and latencies (*Panel C*) when a nose and mouth, eye and nose, and eye and mouth were present in parafovea with left and right eye fixations across the left (grey) and right (black) hemispheres. Note the shorter latencies when an eye and nose or an eye and mouth were present in parafovea, compared to the presence of a nose and mouth. N170 peak latencies, averaged across parafoveal feature categories (*Panel D*), when fixation was enforced on the left and right eyes within the left (grey) and right (black) hemispheres. Note the significantly faster right hemispheric latencies when fixation was enforced on the right eye.

Figure 8. Grand-averaged scalp topographic maps (back-of-head view) for each condition with left and right eye fixation, at the peak N170 latency in the left (left eye fixations) and right (right eye fixations) hemispheres.
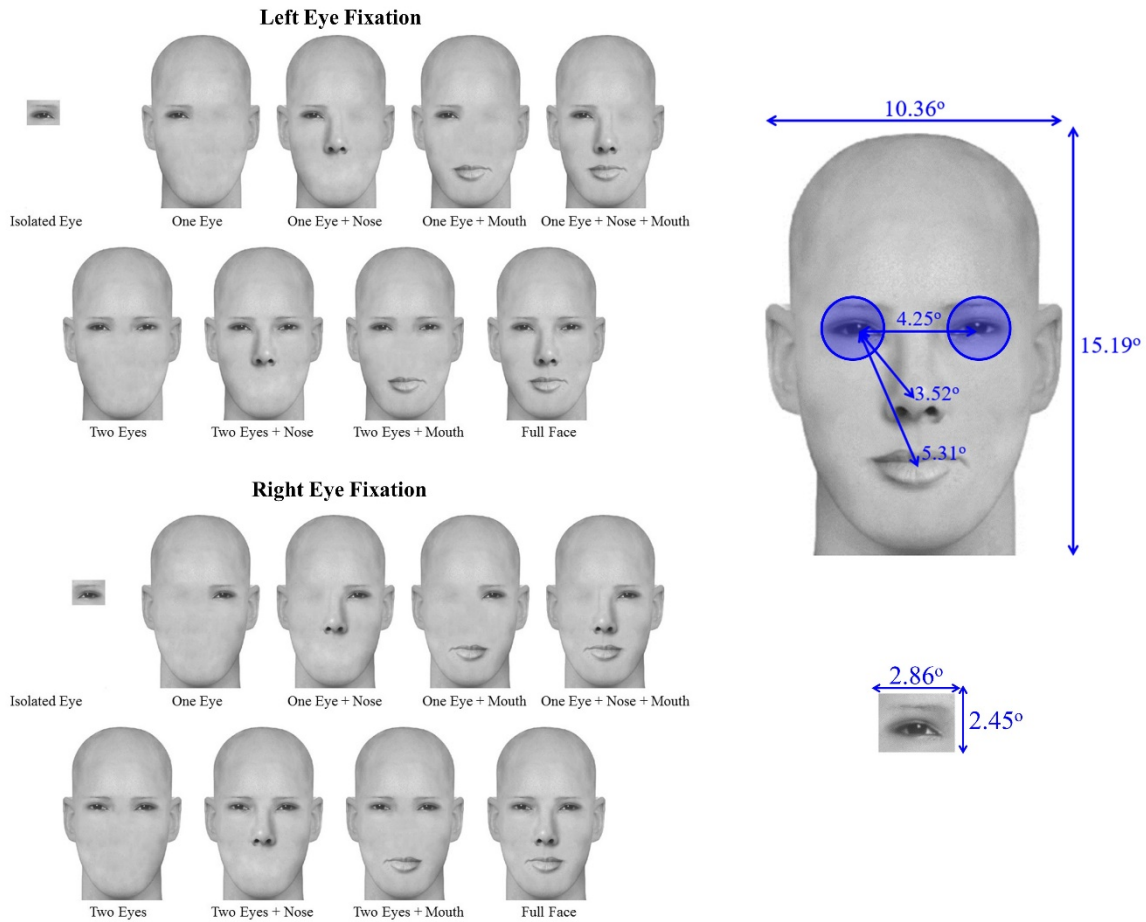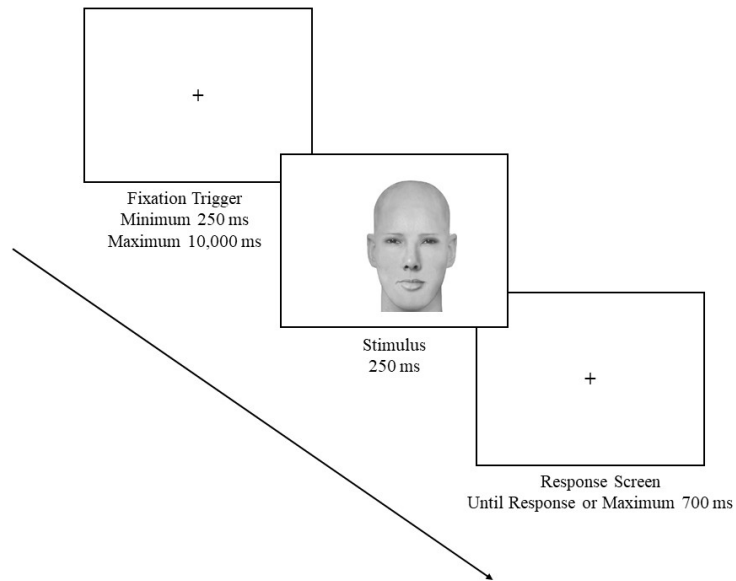
FACE OUTLINE, FEATURE NUMBER & SALIENCY
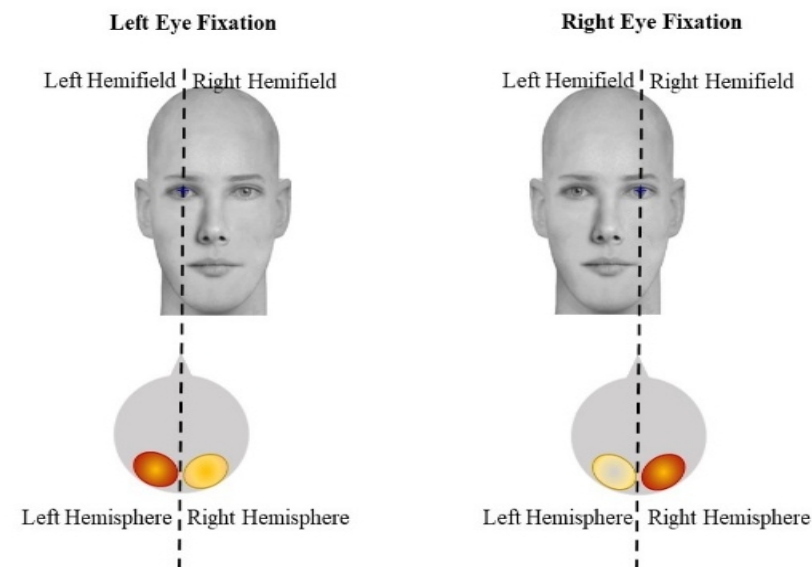
Figures

Figure 1

Figure 2

Fixation Trigger
Minimum 250 ms
Maximum 10,000 ms

Stimulus
250 ms

Response Screen
Until Response or Maximum 700 ms

Figure 3

Left Eye Fixation

Left Hemifield | Right Hemifield

Left Hemisphere | Right Hemisphere

Right Eye Fixation

Left Hemifield | Right Hemifield

Left Hemisphere | Right Hemisphere
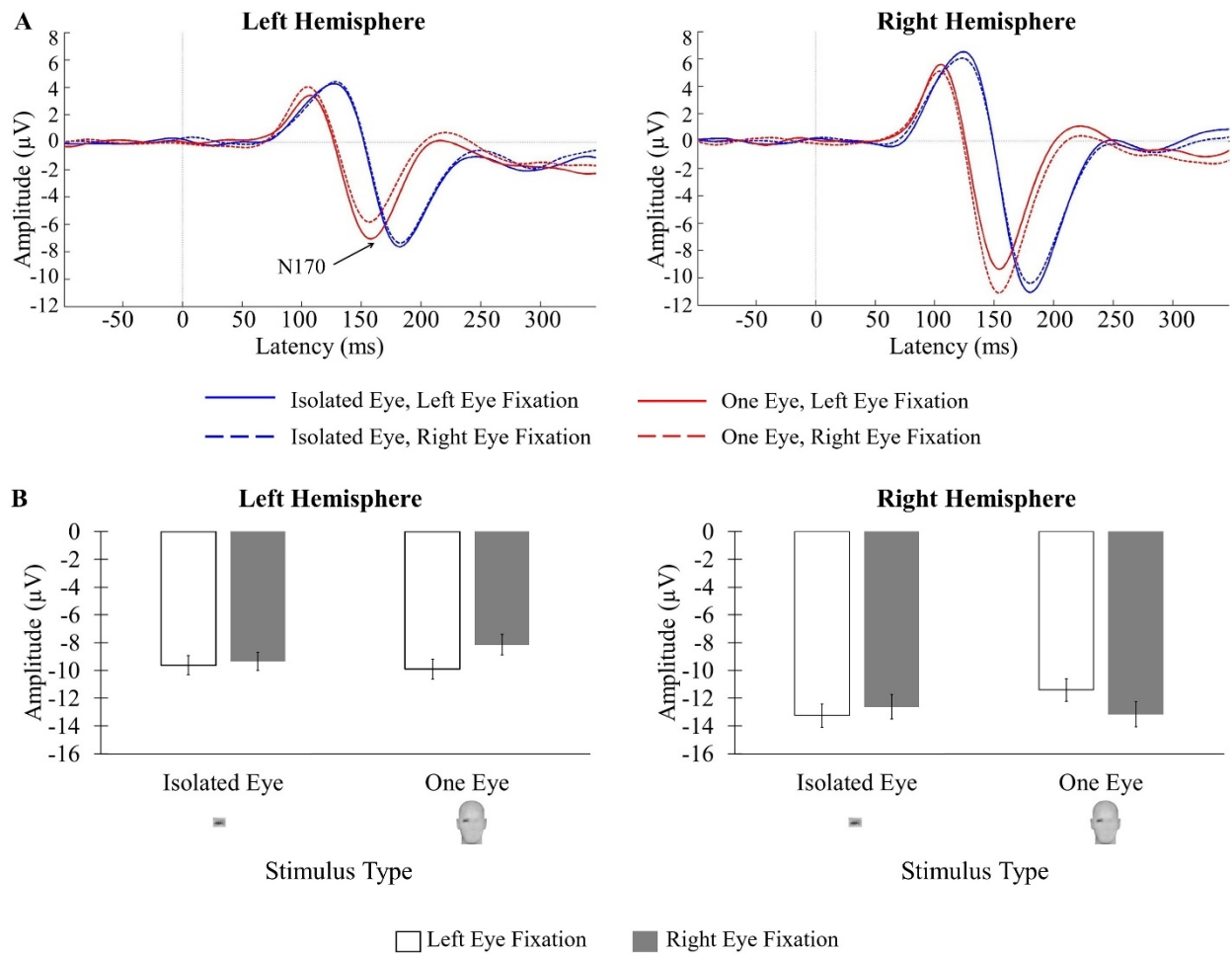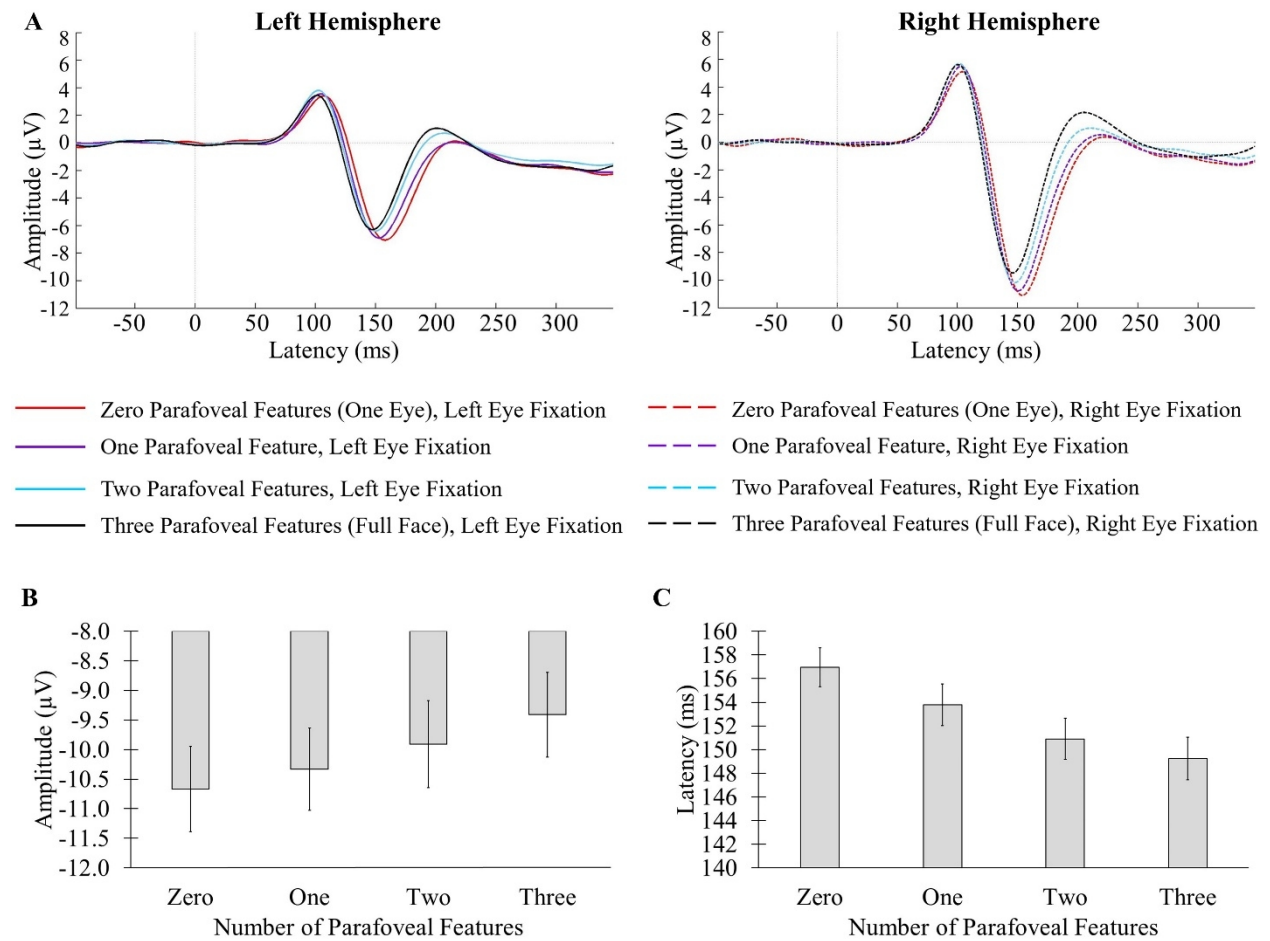
Figure 4

Figure 5

Figure 6

Figure 7
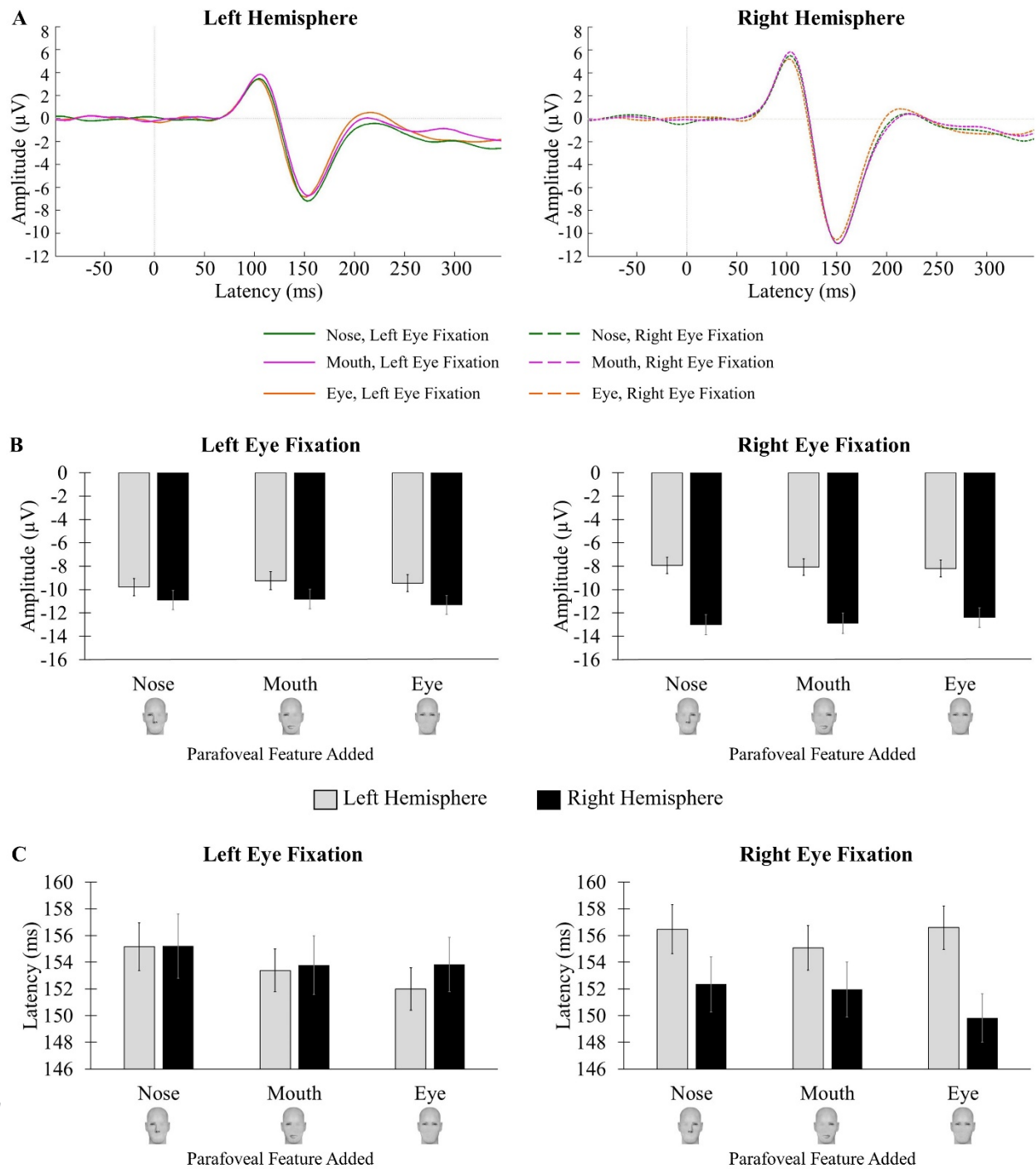
Figure 8

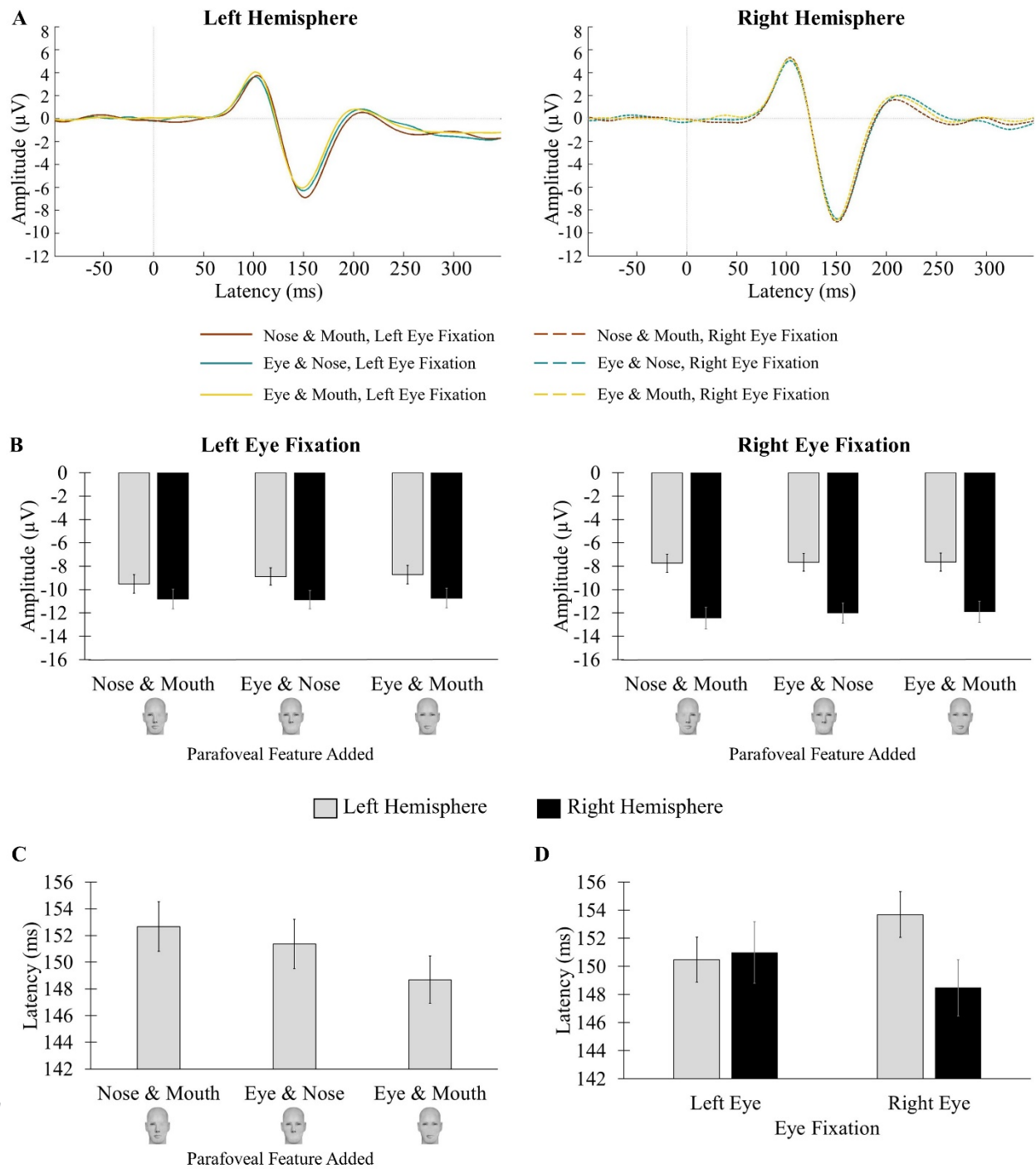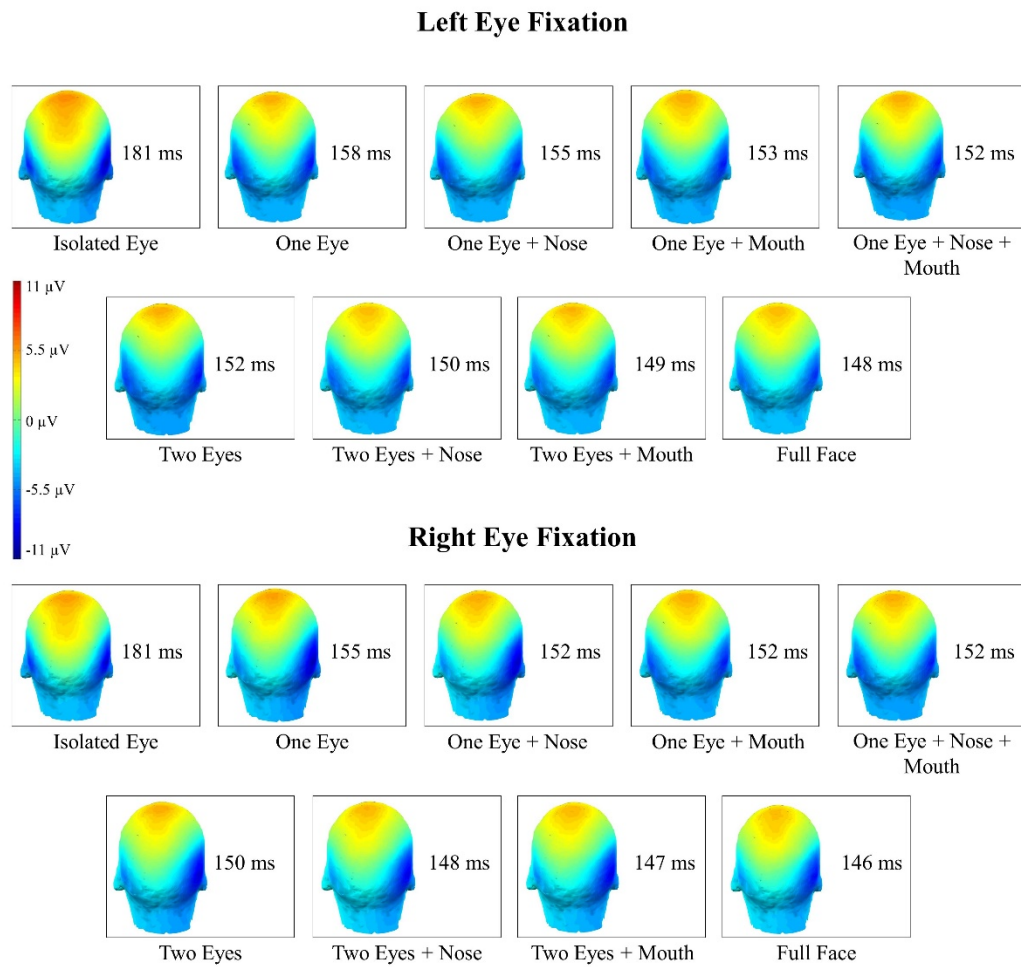**Left Eye Fixation**

Right Eye Fixation

Tables

Table 1. Electrode site locations selected for analysis based on maximal N170 amplitude responses for all conditions.

Left Side		Right Side	
Electrode	**# Participants**	**Electrode**	**# Participants**
PO7	7	PO8	7
PO9	23	PO10	10
P9	15	P10	27
		P8	1

Highlights

- The presence of a face outline shifts the N170 response to a more face-like pattern.

- The N170 is faster and attenuated with increasing numbers of parafoveal features.

- The N170 seems further modulated by feature saliency (eyes > mouth > nose).

- Support for feature saliency and neural inhibition mechanisms are discussed.