

Holistic face processing across neural and behavioral measures

by

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Author's Declaration

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Statement of Contributions

James Siklos-Whillans was the sole author for the General Introduction and the General Discussion, which were written under the supervision of Dr. Roxane Itier and were not written for publication.

This thesis consists in part of three manuscripts written for publication. As the COVID19 pandemic hit Ontario hard during the first 2.5 years of James Siklos-Whillans' PhD, the first manuscript was based on data collected pre-pandemic by other members of the Itier lab. They were re-analyzed entirely by James Siklos-Whillans. The other two chapters are based on original data collected post-pandemic. As lead author of these studies, James Siklos-Whillans was responsible for conceptualizing study designs, collecting data, carrying out data analyses, and drafting and submitting manuscripts.

As co-author and supervisor, Dr. Roxane Itier contributed intellectual input on study design and analyses and provided feedback and editing for each manuscript.

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Abstract

Holistic face processing is a fundamental aspect of human visual perception, distinguishing face processing from other visual stimuli processing. It involves the integration of various facial features into a whole face percept. This thesis investigates the cognitive and neural mechanisms underlying holistic face processing through a series of behavioral and electrophysiological experiments. Using event-related potentials (ERPs), this research explores the effects of stimulus orientation and fixation location on face and object processing. In addition, using accuracy and reaction time measures, the thesis explores the effects of face size on face recognition and gender discrimination.

The first two ERP studies focus on the face inversion effect and its modulation by fixation location for faces and houses. A gaze-contingent paradigm ensures precise control over where participants fixate on upright and inverted faces and houses. Results reveal that fixation location significantly influences ERP responses, particularly the N170 component, a key marker of early face processing, but the strongest effects were seen at earlier and later time periods. Notably, holistic processing appears flexible, with fixation on specific facial features exerting differential effects on neural activity. Importantly, we found a strong house inversion effect and similar modulations of the neural activity to houses with fixation location. The findings challenge the traditional view of holistic processing as a rigid, fixation-independent mechanism only at play for faces and not objects.

A third behavioural study examines the role of face size in recognition accuracy and reaction times across orientations and tasks. Behavioral results indicate that holistic face processing varies with size, orientation, and task with optimal processing occurring within a specific range between extreme face sizes. These results provide new insights into how face size modulates perception and recognition efficiency.

Together, these studies demonstrate that holistic face processing is dynamic and influenced by multiple factors, including fixation location, orientation, and size. By employing advanced statistical techniques such as mass univariate analysis of ERP data, this research provides a more nuanced understanding of the spatiotemporal dynamics of face perception. The findings have implications for models of face recognition, cognitive neuroscience, and applications in artificial intelligence and biometric technologies.

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Dedication

To my beloved parents and brother,

Your unwavering support, boundless love, and endless encouragement have been the foundation upon which I built this journey. From the late nights of doubt to the early mornings of uncertainty, you stood by me with patience and understanding. Your belief in me fueled my perseverance, and for that, I am eternally grateful.

To my dearest friends,

Thank you for your constant support, laughter, and friendship. You made the challenging moments bearable and the successes all the more joyous. Your companionship has been a source of strength throughout this journey.

In loving memory of Mark Francescutti, Doug Gomez, Basil Hammoud, Marissa Macciocchi, and my cherished grandmother Grace Whillans,

Marbo, your vibrant caring spirit and generosity will always be remembered. Your untimely passing is a profound loss, but your memory remains a beacon of inspiration.

Doug, your selflessness and heroism in saving a drowning child exemplifies the best of humanity. Your sacrifice will never be forgotten, and your courage continues to inspire me.

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This thesis is a testament to all of your influences on my life. I dedicate this work to you all, with my deepest and most sincere gratitude and love. Thank you

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List of Abbreviations

EEG - Electroencephalography

ERPs - Event Related Potentials

Exp. – Experiment

LIMO - LInear MOdeling MatLab toolbox

TFCE - Threshold-Free Cluster Enhancement

ANOVA - Analysis of Variance

RMS – Root Mean Square

M – Mean

SD – Standard Deviation

Yrs – years

CMS - Common Mode Sense

DRL - Driven Right Leg

MUA - Mass Univariate Analysis

FIE - Face Inversion Effect

HIE - House Inversion Effect

UW - University of Waterloo

HDI - Highest Density Interval

CI - Confidence Interval

CaD – Canadian dollar

List of Symbols

Hz – Hertz

° - Degrees of visual angle or orientation

μV – Microvolts

± - Plus-minus

≅ - Approximately equal to

~ - approximately

Δ – Delta (Difference)

α – Alpha (denotes significance level)

General Introduction

For decades research concerning visual processing has considered faces to be a special stimulus category as they are processed by dedicated neural networks (Haxby et al. 2000; Duchaine and Yovel 2015; Grill-Spector et al. 2017). Most research suggests that faces are processed holistically, meaning that the brain integrates facial features (eyes, nose, mouth) into a unified whole rather than processing each feature independently like other objects are believed to be processed. The study of holistic face processing has its roots in Yin's (1969) discovery of the Face Inversion Effect (FIE), which revealed that turning faces upside down disproportionately impairs their recognition compared to other stimuli. In contrast, non-face objects are generally processed in a more feature-based or part-based manner, with much less disruption caused by inversion (Maurer et al. 2002; Tanaka and Gordon 2011). This contrast with objects has been demonstrated with several other experimental paradigms that use different stimulus manipulations thought to address holistic processing more directly. For instance, Mooney faces (Mooney 1957) and the composite face task are experimental paradigms used to assess holistic face processing, with Mooney faces (faces made solely of black and white) testing the ability to perceive faces from high-contrast, degraded images, and the composite face task measuring the extent to which individuals process facial features as a unified whole rather than as independent parts (Robbins and McKone 2007; Toh et al. 2017). The part/whole task is also one of the earliest test of holistic processing (Tanaka and Farah, 1993) and shows that individual features of a face are better recognized in the context of the face than on their own, suggesting that memory of individual face parts are integrated into the holistic processing of the whole face (see Tanaka and Simonyi 2016 for a review of the use of this task). While memory for parts of faces is influenced greatly by the whole face, objects are thought to contain a greater proportion of parts that are more influential than whole representations.

At the behavioral level, studies show that faces are processed differently from other objects in terms of their response accuracy and reaction time, specifically with a larger discrepancy between upright and inverted stimuli for faces than objects. At the neural level, these differences are often attributed to the functioning of specific brain areas revealed by fMRI studies. Brain areas such as the Fusiform Face Area, which shows increased activation for faces,

is often compared with the Parahippocampal Place Area or the Lateral Occipital Complex that are associated with non-face categories such as locations (houses, etc.) or objects (wrist watches, etc.) respectively (Kanwisher et al. 1997; Haxby et al. 1999; Haist et al. 2010; Wang et al. 2019; Li et al. 2022). Similarly, faces differ from objects in the timing and amplitude differences seen in Event Related Potential (ERP) responses particularly when stimuli inversion is examined (Bentin et al. 1996; Haxby et al. 1999; Li et al. 2022). Despite this basic understanding of holistic processing, there is still debate on what exactly holistic processing means and how it should be interpreted (Farah et al. 1995; McKone and Yovel 2009; Matsuyoshi et al. 2015; Tanaka and Simonyi 2016). This thesis will demonstrate that holistic processing is more nuanced than the dichotomy discussed above. By using both neural and behavioral measures, this thesis examined understudied factors to elucidate the pliability of holistic processing in faces and objects perception.

Indeed, certain factors that influence holistic processing, particularly fixation location, remain understudied. While the Face Inversion Effect has been robustly examined, how fixation on specific facial regions influences the processing of upright and inverted faces at the neural level requires further exploration. Gaze-contingent studies using eye-tracking have begun to show that where people look on a face—whether it be the eyes, nose, or mouth—can influence the early neural processing of that face (Nemrodov et al. 2014; Itier and Preston 2018). Such findings suggest that the specific features under fixation can modulate the neural signatures of face perception, including the amplitude and latency of the ERP component that is associated with holistic processing, i.e. the N170 (Nemrodov et al. 2014; Itier and Preston 2018). Objects, on the other hand, are thought to be processed featurally, therefore each part of an object should be processed in a similar way (De Lissa et al. 2014). The comparison of how fixation location and inversion influence face processing as well as the processing of one category of objects, namely houses, was examined thoroughly in this thesis.

Another underexplored area is the role of face size in modulating holistic processing. Theoretical work in face perception suggests that larger or smaller faces might alter how features are integrated into a holistic percept. For instance, very large faces might overwhelm the visual system with the large amount of information provided, making feature integration potentially more difficult and the processing of the face more featural than holistic. In contrast, smaller faces

might reduce the visibility of key features and the distance between them which could disrupt holistic processing and impair recognition. On the other hand, the placement of the face and its features in the visual field changes with size. The entirety of the smaller faces is within the focal point of the visual field (e.g. the fovea) which should ease the integration of facial features into one percept and in turn increase recognition accuracy. Similarly, the larger faces contain more detailed information which could ease in recognition accuracy as features become more distinguishable. Importantly, the results of studies exploring the effect of face size on holistic processing have been mixed, suggesting that size modulates face perception in complex ways that might depend on the task at hand. The methodological and theoretical ramifications of these findings extend to practical applications, such as designing optimal conditions for face recognition technologies or understanding how face size influences social perception (Rossion 2009).

Throughout the past half century of research, behavioral and ERP methods have been used to better understand holistic face processing. Over such a long period of time it is understandable that improvements to the way data are measured and analyzed were made to better understand specific aspects of face processing. For instance, early studies of visual processing examined how fixation location can play a role in face processing, however they did not accurately measure fixation with eye trackers or use headrests to limit head movements (Jeffreys et al. 1992). With EEG studies it is important to ensure the participant is observing the stimuli the way it was intended to be observed without head movements, eye blinks, and with their fixation on the desired location (Nemrodov et al. 2014; Itier and Preston 2018). This is important for behavioral studies of face size as well as it ensures participants maintain the same distance from the stimuli. Additionally, the traditional ERP analyses of these studies have been criticized for focusing too narrowly on pre-selected components and time windows, potentially missing effects occurring outside those intervals (Pernet et al. 2015; Luck and Gaspelin 2017; Delorme 2023). To address these limitations, more advanced statistical techniques, such as Mass Univariate Analysis (MUA) or Linear Modeling (LIMO) statistics, have been employed (Pernet et al., 2011). These methods analyze the entire time course of ERP data across all electrodes, offering a more comprehensive view of when and where on the scalp fixation location interacts with orientation to shape face processing. By using these methods, the current thesis aimed to

provide a more nuanced understanding of the temporal dynamics involved in holistic face processing. As such, it is important to note that these methodological concerns have theoretical implications. For example, many of the studies examining holistic face processing have used objects as a control stimulus since they seemingly do not experience the same level of disruption as faces when inverted. As the traditional analysis of ERP data has only focused on singular time points at specific electrodes, it is possible that objects show a similar inversion effect as faces at earlier or later time points that have not been analyzed or reported. By addressing these methodological and statistical issues in the field we hope to get a more accurate understanding of holistic processing and its malleability across faces and objects.

In this thesis, the investigation of holistic face processing is divided into three chapters, the first two using the ERP technique and the last one using behavioral measures. Chapter 1 employed advanced neural analysis techniques to examine how orientation and fixation location affect the early neural processing of both face and house stimuli in two separate groups of participants. Chapter 2 builds on Chapter 1 by increasing the statistical power through a larger sample size and trial numbers while also comparing face and house processing within the same participants using MUA. Both Chapter 1 and 2 challenge the traditional claim that objects do not exhibit an inversion effect and, therefore, are not processed holistically. They also show the importance of fixation location on neural responses and how similar or distinct these responses can be across both face and house stimuli. Chapter 3 focuses on the role of face size in shaping holistic processing. Here we looked at the effect of inversion, task and face size on face recognition using behavioral measures. These experiments demonstrated that there is an ideal range of sizes at which face processing is holistic and that task influenced this process. Together, these chapters provide a comprehensive analysis of how orientation, fixation location, and size influence holistic face processing across behavioral and neural measures.

Chapter 1

House and Face neural processing

1.1 Introduction

Decades of research have shown that face and object processing rely on different specialized neural networks and cognitive processes (Haxby et al. 2000; Rossion and Gauthier 2002; Duchaine and Yovel 2015; Grill-Spector et al. 2017). One of the hallmarks of this face specificity is holistic processing, the integration of facial features into an indecomposable perceptual whole, while objects would be processed essentially on the basis of their components or features (Tanaka and Farah 1993; Maurer et al. 2002; Rossion 2009; Tanaka and Gordon 2011). Plane inversion, the rotation of images by 180°, is one manipulation that has been studied intensively, as it majorly disrupts face perception and recognition, but impacts object processing and recognition only mildly (Yin 1969; Valentine 1988; Farah 1996; Rossion 2009). This “Face Inversion Effect” (FIE) has been interpreted as reflecting the disruption of holistic processing that upright faces enjoy while no such disruption exists for upright objects, being mainly processed on the basis of their features, leading to less or no inversion effect for objects (Rossion 2009).

Event Related Potentials (ERP) recording neural activity on the scalp have tracked the timing of the FIE. ERP studies have focused on an early negative component maximal between 130-200ms post-face onset at a few lateral posterior electrodes. This N170 component (George et al. 1996; Bentin et al. 1996b) is considered the earliest reliable neural marker of face perception and is assumed to reflect holistic processing (Eimer 2000; Rossion and Jacques 2011). This assumption stems in part from the impact of stimulus plane inversion on the N170, which is delayed and enhanced for inverted compared to upright faces (Rossion 1999; Rossion et al. 2000; Itier and Taylor 2002, 2004a, b, c, d). Importantly, some inversion effects have been reported for language related items like Chinese characters and visual scenes (e.g. Wang et al. 2011; Van Helden and Naber 2023), however most studies have found no effect of inversion on the N170 recorded for objects such as cars, chairs, houses, shoes, mugs or even novel objects like Greebles (Bentin et al. 1996; Eimer 2000; Rossion et al. 2000, 2003; Rebai et al. 2001; Stekelenburg and de Gelder; Nihei et al., 2018). A few studies, however, have reported a small delay with

inversion for cars, houses, words, animal faces or chairs, but without an inversion effect on amplitude (Rossion et al. 2003; Itier et al. 2006, 2011; Kloth et al. 2013). The systematic lack of amplitude difference between upright and inverted objects contrasts sharply with the systematic and clear FIE on face N170 amplitude, one of the most replicated findings in the face ERP field.

This difference in N170 inversion effect supports the view that faces and objects are processed differently early on. The “face specificity” has been argued to reside in an early holistic processing mechanism that occurs around the N170 timing (Eimer 2000; Rossion and Jacques 2011). However, recent studies have cast doubt on the idea that this holistic processing is a “perceptual snapshot” where features are glued together in an indecomposable percept. Indeed, the N170 amplitude varies depending on which facial feature is in fovea or in parafovea, and on whether some features are missing from the face (Nemrodov et al. 2014; Itier and Preston 2018; Parkington and Itier 2018, 2019; Winward et al. 2022). These ERP experiments used eye tracking and gaze-contingent procedures to ensure participants were fixated on the desired area of the face when it appeared on the screen. They showed that fixation on the eyes elicited a larger N170 than fixation on any other area (Zerouali et al. 2013; Nemrodov et al. 2014; De Lissa et al. 2014; Neath and Itier 2015; Neath-Tavares and Itier 2016; Itier and Preston 2018; Parkington and Itier 2018). The fact that fixation location influences the N170 demonstrates the malleability of holistic face processing. As far as we know, only one experiment has examined the effect of fixation location on object processing and found no effect for wristwatch, the category studied (De Lissa et al. 2014). This study only had about 20 trials per condition for this object category (before artefact rejection), making the results unreliable. Whether fixation location could affect early neural processing of objects in the same way as it does for face processing remains largely unclear. The present study sought to fill this gap using a gaze-contingent approach and house stimuli, an object category that has already been investigated in previous ERP studies as a control object category for faces.

It is important to highlight that most face ERP studies have used a traditional analysis approach focusing on the N170 component analyzed during a restricted time window at a subset of electrodes, and/or have decided which time frames and electrodes to include in the analysis based on the group grand average visual inspection. This approach increases the likelihood of both false positives (type I errors) and false negatives (type II errors) (see details in Bürki et al.,

2018; Grope et al., 2011; Kiebel and Friston, 2004; Rousselet and Pernet 2011; Pernet et al., 2011; Luck and Gaspelin 2017). To reduce these errors, more stringent statistics such as Mass Univariate Analysis (MUA) are recommended (e.g., Luck and Gaspelin 2017; Fields and Kuperberg 2020). MUA decreases both error types as it examines all timepoints and electrodes in a data-driven approach, using strong corrections for family-wise errors (Oostenveld et al. 2011; Rousselet and Pernet 2011; Groppe et al. 2011, b; Stropahl et al. 2015). The present study used the hierarchical Linear Modeling (LIMO) toolbox for the analysis of EEG data (LIMO, Pernet et al. 2011), which has already been used in a few face processing ERP studies (Rousselet et al. 2008b; Pernet et al. 2011; Rousselet and Pernet 2011; Turano et al. 2017; Durston and Itier 2021; Hudson et al. 2021; Winward et al. 2022; Itier and Durston 2023). MUA is different from the traditional analysis in that it focuses on amplitude differences at individual timepoints, where traditional analysis techniques would examine latency shifts and amplitude differences at ERP peaks. In this regard the two analysis techniques are in some ways complementary as the traditional technique helps elucidate the delay in response and the effect on the waveform peaks whereas MUA shows where on the scalp and at which one time points the statistical differences occur between conditions in terms of amplitude.

Recent studies that used MUA have revealed that large significant effects are often found in-between amplitude peaks, suggesting that focusing on the N170 component risks missing additional important findings. In particular, the inversion and fixation location effects for both faces and objects may be seen reliably at other time points and electrodes than the N170 peak measured at posterior electrodes. For instance, earlier studies reported face inversion effects on the P1 component preceding the N170 (Linkenkaer-Hansen et al. 1998; Halit et al. 2000; Itier and Taylor 2002, 2004; Itier et al. 2004; Taylor et al. 2004) although this finding was controversial, not always replicated and argued to reflect low-level stimuli differences (Rossion and Jacques 2011). Similarly, two studies reported that the largest P1 amplitude occurred when fixation was on the mouth (Neath and Itier 2015; Neath-Tavares and Itier 2016), suggesting the effects of fixation location starts earlier than the N170. Itier and Durston (2023) recently confirmed these early effects using MUA and reported strong and widespread effects of fixation location from 50-350ms post-face onset. These results confirm the necessity of analyzing the entire time course to uncover new inversion and fixation location differences which could have

important consequences for the conceptualization of when objects and faces differ during early visual processing.

The present study sought to investigate the effects of orientation and fixation location on the processing of house (Above Windows, Between Windows, Center, Beside-the-Door, Door, Left, and Right Windows) and face stimuli (Forehead, Nasion, Nose, Mouth, Left and Right Eyes) using a data-driven approach (all time points and electrodes) and robust MUA. The first experiment focused on the perception of fixation location across upright and inverted houses (Data from unpublished work). The other two experiments investigated the processing of fixation location in upright and inverted whole faces using identical stimuli and procedures that were initially developed to examine the N170 component (Data from two published papers: Nemrodov et al. 2014; Itier and Preston 2018). The two face data sets were first compared to ensure the lack of experiment group effect and then combined into one large group to increase statistical power. All three experiments employed a gaze-contingent approach wherein an eye tracker ensured gaze fixation location within a 1.8° circle around the center of a given area of interest, with areas matched between faces and houses (e.g., left eye/left window; right eye/right window; nasion/in between windows etc.). All experiments also included a similar number of trials per fixation location compared to previous studies (~50 trials per condition), contributing to good power.

As far as we know, no study has systematically investigated the effects of inversion, fixation location and their interaction, on the entire neural time course recorded to face and house stimuli. We anticipated replicating the original published N170 peak results reviewed earlier regarding orientation and fixation location effects. Mainly that there will be a larger and more negative ERP wave for inverted faces compared to upright faces. In terms of fixation location, we expected to replicate the larger more negative ERP wave for the nasion and eye fixations at bilateral posterior electrodes. Whether the FIE would vary with fixation location was unclear given the inconsistent results on N170 in the original studies (lack of clear modulation of the FIE by fixation location in Nemrodov et al., 2014, but largest FIE for nasion in Itier and Preston, 2018). If houses, like objects in general, are truly processed featurally, then no effect of orientation would be expected on the house N170, although it was possible that early or later effects could be seen (e.g. Rousselet et al., 2008 reported an inversion effect for houses around the P2 component). The gaze contingent approach changes the position of the stimulus in the visual

field to put the desired feature at the fovea. Therefore, we expected to see retinotopic effects at early time points as seen in retinotopic mapping studies using checkerboards (Di Russo et al. 2005, 2012; Hagler et al. 2009; Capilla et al. 2016), including largest C2 and P1 for mouth fixation (Neath and Itier 2015; Neath-Tavares and Itier 2016; Itier and Durston 2023) and largest P1 for ipsilateral eye fixation (Winward et al. 2022; Itier and Durston 2023). The fixation location effect on the face N170 (largest N170 to eye fixations than other face fixation locations) is argued to reflect a high-level and eye specific sensitivity due to eyes being biologically and socially relevant (Nemrodov et al. 2014; Itier and Preston 2018). Therefore, we did not expect to find a similar effect for house windows which are not biologically or socially relevant. Finding different effects of fixation location for houses than faces would further support the early specificity of face processing and could help understand face and object processing further.

1.2 Materials and Methods

The present study included three experiments involving different participant samples, one novel experiment on house perception and two experiments on face perception (Nemrodov et al. 2014; Itier and Preston 2018; Exp. 2 and 3 respectively).

1.2.1 Participants

All three experiments included undergraduate students from the University of Waterloo (UW) who received course credit for their participation. The UW Research Ethics Board approved the three experiments, and all participants provided written informed consent before participating. Participants reported having no history of neurological disorders or head injuries, were not taking medication at the time of study, and had normal or corrected-to-normal vision. The house perception study included 20 participants (Mean age = 20yrs, SD = 2yrs, 9 females, 11 males). Out of the 55 participants available from Exp. 2 & 3, three participants were removed due to too low trial numbers necessary for MUA (1 out of the 21 participants from Exp.2; 2 out of the 34 participants from Exp.3), leaving a final sample size of 52 participants (Mean age = 20yrs, SD = 1.4, 33 or 34¹ female) for the face perception study.

¹ The gender information for Exp.2 was lost making identifying the gender of the removed participant from that pool impossible.

1.2.2 Stimuli

The house stimuli were created to match the face stimuli as best as possible. Nine (9) different images of houses were created using a unique house template (Fig. 1.1A) and only altering the windows and doors (slightly different sizes, shapes, and luminance of these features).

Both Exp. 2 and 3² used the identical 40 bald face stimuli (20 male) created using FACESTM 4.0 by IQBiometrix. Faces were of a neutral expression; gaze directed forward and were presented in grey scale on a white background. All faces had the same face outline with different facial features (nose, mouth, eyes, etc.) that created different identities (Fig. 1-1B).

All images (houses and faces) were rotated by 180° to create inverted houses and inverted faces, all subtending 9.5° horizontally and 13.6° vertically. For each category, mean pixel intensity ($M=195.3$, $SD = 0.68$), and mean Root Mean Square (RMS) contrast ($M= 0.17$, $SD = 0.01$) were calculated using custom matlab scripts.

1.2.3 Design and Procedure

In the house perception experiment, participants pressed a button when they saw images of flowers (oddball task or go/no go task; flower trials not analyzed) and were asked to not respond to but pay attention to the upright and inverted houses. In the face perception experiments, participants performed an Orientation-detection task using a game controller, discriminating between upright and inverted faces (with button press order counterbalanced across participants). Each experiment took between 1.5-2h including EEG set-up.

All stimuli were presented in the same dimly lit and sound attenuated room on a CRT monitor situated 70cm away from participants' head resting in a chinrest to restrict head movements. The experiment began with practice trials repeated until participants verbalized that they felt comfortable with the task. Each trial began with a jittered fixation cross on a white screen for 1-100ms (Fig. 1-1C). An eye tracker permitted the use of a gaze contingent procedure in which participants were required to fixate on the cross for 250ms before the stimulus could be presented for 250ms, followed by a white response screen presented for 900ms.

² Please note that the original studies included eyeless (Nemrodov et al., 2014 or Exp. 2) and mouthless (Itier & Preston, 2018 or Exp. 3) faces in addition to intact faces. Here, we only focus on intact upright and inverted faces, common to both experiments.

The fixation cross was always presented in the center of the screen, and the stimuli were presented offset so that a specific feature was presented at the fovea. For faces, 6 fixation locations were created while for houses, 7 Fixation Locations were created that matched as closely as possible the face Fixation Locations: fixation Above windows (forehead), Between windows (nasion), Left window (left eye), Right window (right eye)³, house Center (nose), Beside the door (Mouth), and on the Door (no face equivalent) (see Fig. 1-1A, 1-1B). A total of 12 conditions were generated for faces (6 Fixation Locations x 2 Orientations) with 80 trials per condition (960 trials total) and 14 house conditions in total (7 Fixation Locations x 2 Orientations) with 80 trials per condition (total of 1120 house trials). Appendix table 1 contains the number of trials per condition that were analyzed within this chapter.

³ Left eye/window refers to the eye/window on the left side of the face/house, whether the stimulus is upright or upside down. Same for right eye/window (see Fig. 1.1).

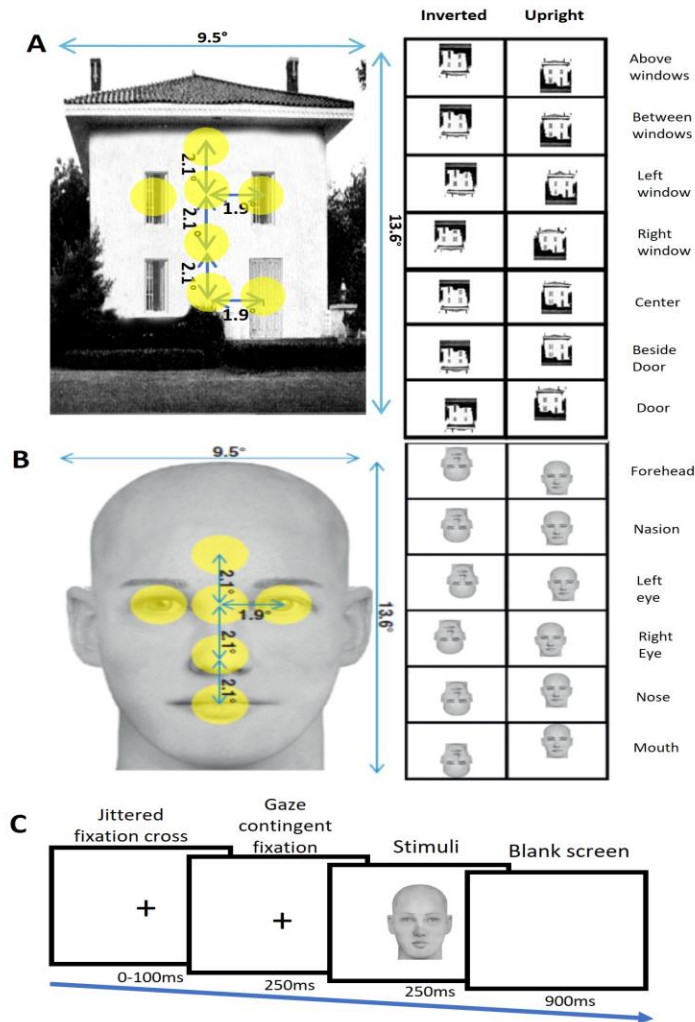


Figure 1-1. Stimuli and procedure

(A) Left panel: an example of the house stimuli with stimulus size and the various distances (in visual angles) between fixation location centers. The yellow circles represent the size of the regions of interest (1.8°) centered on each location; on a given trial, any fixation situated beyond those ROIs resulted in the trial being discarded (see text for details). Right panel: all the House Fixation Location conditions with corresponding house stimuli positions on the screen depending on the house orientation. Six fixation locations directly correspond to the face fixation locations (i.e. Above Windows is the equivalent of the Forehead condition; Between Windows is the equivalent of Nasion location etc.). The Door condition is the only condition with no face equivalent. (B) Left panel: an example of the face stimuli with the various angular distances between the fixation location centers, with regions of interests centered on each location. Right panel: all the Face Fixation Location conditions with corresponding face stimuli positions on the screen depending on face orientation. (C) Example of a trial progression. Each trial started with a 0-100ms jittered fixation cross. Once the eye-tracker registered and confirmed participants' fixation for a minimum of 250ms (gaze-contingent fixation), the stimulus was presented for 250ms. Finally, a blank white screen was presented for 900ms during which participants responded.

1.2.4 Electrophysiological and eye tracking recordings

In each experiment, the EEG was recorded continuously at 516 Hz using a 64 channel Active-two Biosemi system. Two extra electrodes were custom added to these caps (PO9 and

PO10 sites) creating a 66 electrodes cap according to the extended 10/20 system. Three pairs of extra electrodes were also placed at the outer canthi and infra-orbital ridges to monitor eye movements and on the mastoids, for a total of 72 recording sites. The ground was a Common Mode Sense (CMS) active-electrode and a Driven Right Leg (DRL) passive-electrode. As per manufacture recommendations electrode direct current offsets were kept under 20mV. The signal was then average-referenced offline.

Correct fixation during trial presentation was ensured using an SR Research EyeLink 1000 eye-tracker sampling at 1000Hz. A nine-point automatic calibration was used with participants' dominant eye (as determined by the Miles test) before every block. If after 10 seconds, participants could not fixate properly on the fixation cross for 250ms, a drift correction was performed, and recalibration of the eye tracker was executed mid-block after 2 drift corrections.

1.2.5 Data analysis

1.2.5.1 Preprocessing of EEG data

All incorrect trials and/or trials with micro-saccades outside the pre-defined area of interest around the fixation cross (1.8° diameter visual angle) were removed from the analysis. Data preprocessing was done using the toolboxes EEGLab version 2023.1 (Delorme and Makeig 2004) running under MATLAB 2022b with the latest LIMO version at the time⁴. Any trials with $\pm 70 \mu\text{V}$ artifacts were removed by an automated procedure; ERP data were further visually inspected and remaining artifacts were manually removed. The data were digitally band-pass filtered (0.01Hz-30Hz) and -100ms to +350ms epochs were generated to focus on the early neural responses. After trial rejection any participant with lower than 40 trials out of the original 80 trials per condition were removed from the analysis (3 participants from the face experiments were lost at this stage)⁵. The final average number of artefact-free trials per conditions per participant across all 3 experiments was 56.93 (SD = 11.57).

⁴ Version “limo_eeg-master” from the LIMO [GitHub: http://github.com/LIMO-EEG-Toolbox/](http://github.com/LIMO-EEG-Toolbox/)

⁵ Although somewhat arbitrary, this decision was based on simulations data suggesting that the TFCE correction works best with 50 trials per conditions (Pernet et al., 2015).

1.2.5.2 Statistical analyses of ERP

The LInear MOdeling of EEG data toolbox (LIMO, Pernet et al., 2011; Pernet et al., 2015) running under MATLAB 2022b was used to perform a Mass Univariate Analysis of the data, focusing on the -100-350ms epoch. First, for every subject, LIMO uses a General Linear Modeling (GLM) approach to create parameter estimates using Weighted Least Square for every timepoint, condition, and electrode. This first step allows obtaining one parameter per condition, accounting for between trial variance. In a second step, the data are analyzed at the group level. LIMO performs a statistical test at every data point (every timepoint at every electrode; Pernet et al., 2011). For repeated measure ANOVAs, as used here, Hotelling T^2 -tests are used to account for the covariance between measures so there is no need to adjust for sphericity. We used a customized version of the default electrode neighbourhood matrix generated by LIMO for our montage.

For the house experiment, parameter estimates were examined using a 2 (Orientation) x 7 (Fixation Location) repeated measures ANOVA. For the face experiment, we first compared the two experiments using a 2 (Orientation) x 6 (Fixation Location) x 2 (Exp. 2 + Exp. 3) mixed model ANOVA. Tests used an alpha of 0.05 and the recommended 1000 bootstraps. The lack of significant main effects or interaction across experiments, allowed us to pool the participants from Exp. 2 and 3 together in one single group. This combined data set was then analyzed using a 2 (Orientation) x 6 (Fixation Location) repeated measures ANOVA. Given the significant Orientation by Fixation Location interaction obtained for faces, we then ran two separate follow-up analyses to better appraise this complex interaction. The first analysis focused on the effect of Fixation Location run separately for upright and inverted faces. In the second analysis, we performed 6 *F*-contrasts testing for the effect of Orientation at each Fixation Location (using a Bonferroni-corrected α level).

For all analyses, the Cluster Mass spatio-temporal clustering and the Threshold-Free Cluster Enhancement (TFCE) correction techniques were implemented (Maris and Oostenveld 2007; Groppe et al. 2011, b; Pernet et al. 2015). These corrections use bootstrapping clustering techniques to control for multiple comparisons in EEG and fMRI research and group together data from various electrodes that are related spatially and temporally (a minimum of 2 channels is needed to create a cluster in LIMO). The results of each effect are then compared to the effect

null distribution to determine significance. Clusters are deemed significant if the sum of all their F values falls in the $1-\alpha$ portion of a customized null distribution (Maris and Oostenveld 2007; Smith and Nichols 2009; Groppe et al. 2011). In this way the results can be seen as more arbitrary depending on the α chosen beforehand. It is also possible for this technique to miss statistically significant effects if the effect does not meet the threshold requirements for cluster size but is still statistically significant. On the other hand, TFCE correction treats the data points individually, the significant results should still be interpreted as “clusters” and understood as groups of significance rather than individual data points (Pernet et al. 2015, 2019). Simulations have shown that TFCE correction works best with at least 50 trials per condition (Pernet et al. 2015), which is what we had in most of our conditions. TFCE is also a more data driven correction technique as it is by definition threshold free, building clusters based on where the differences are the strongest and most extensive. Given the lack of direct comparison between correction techniques on the same data, we used both techniques. The TFCE corrected data were used in all figures and some of the Cluster mass corrected data can be found in Appendix A.

1.3 Results

1.3.1 House perception study

Exp.1 was analyzed in LIMO using a 2 (Orientation) x 7 (Fixation Location) repeated measures ANOVA ($\alpha = 0.05$) with TFCE correction. Only the main effect of Orientation reached the significance threshold (Fig. 1-2A).

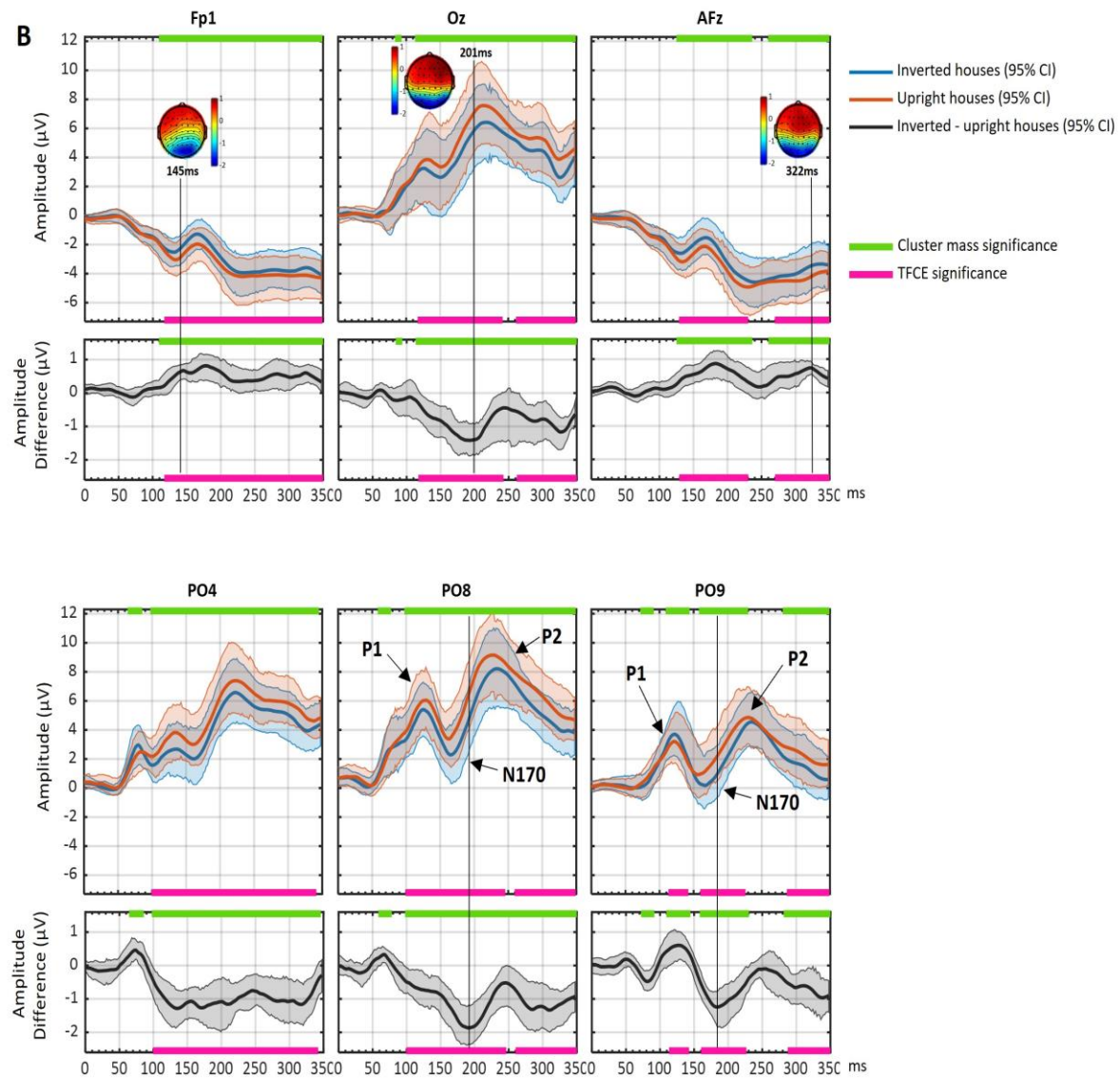
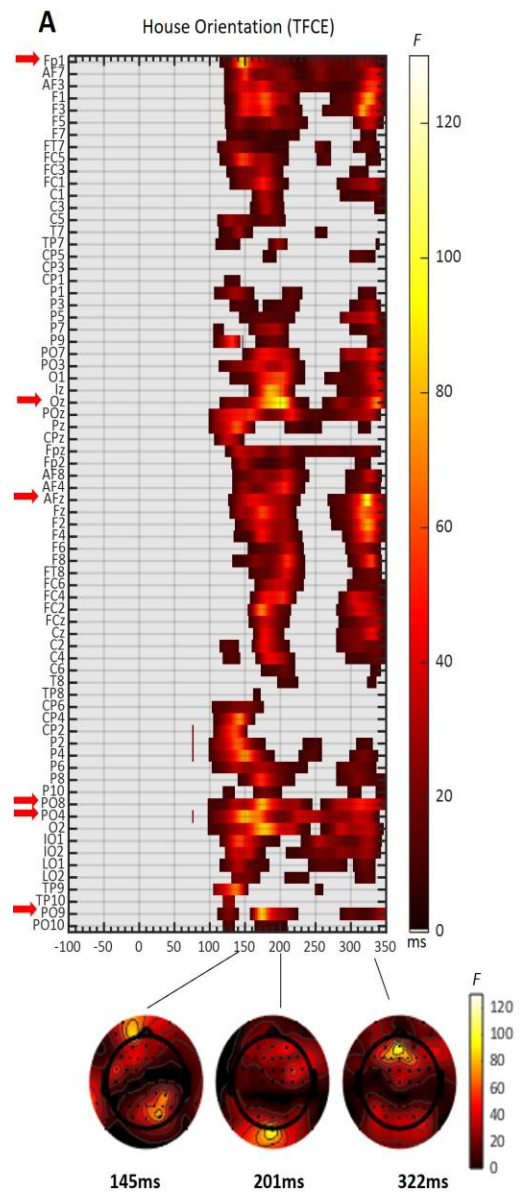


Figure 1-2. House perception study results.

(A) Main effects of Orientation with $\alpha = .05$ and TFCE correction applied. The raster plot depicts the significant F -values of the various effects at every electrode (72, y axis) and time-point (-100 pre-house onset to +350ms post-house onset) analyzed (magnitude of the F -values according to the coloured scale). The topographic maps of the unthresholded and uncorrected F -values are displayed at 145ms, 201ms, and 322ms when the F -value local maxima were registered for the house orientation effect after TFCE correction (see text for details). (B) ERPs (inverted houses in blue, upright houses in red) and amplitude difference plots (inverted minus upright houses in black), with their respective confidence intervals, illustrating the main effect of Orientation on three relevant electrodes (outlined by the red arrows on (A)). The vertical lines highlight that the maximum House Inversion Effect was found during the N170-P2 interval. The topographic maps on electrode Fp1, Oz, and AFz display the voltage difference between the upright and inverted conditions across the scalp (according to the small colour bar scale beside that goes from $-2\mu\text{V}$ to $+1\mu\text{V}$) at the same time point at which respective maxima in F values were found in (A). The green bar at the top of the plots represents the time points at which the main effect of Orientation was significant for these electrodes after cluster-mass correction, while the pink bar at the bottom illustrates the significant time points after TFCE correction. For all ERP plots, the ERPs represent the central tendency computed using raw means for single subject trials and 20% trimmed means across subjects; the difference waves were created with a 95% Bayesian Highest Density Interval (HDI) confidence interval (CI) so that if the CI includes 0, we can be confident that there is no effect then.

Table 1-1. Main effect of orientation for the house perception study.

Electrodes included in the three “bands” of activation and their timing. The effect peak electrode and statistics are also displayed.

House perception study (N=20)	Timing	Electrodes	Effect Peak
Orientation Main Effect	76ms - 155ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C5, T7, TP7, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F8, C2, C4, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	Fp1 at 145ms ($F(1, 19) = 87.81, p < .001$)
	160ms - 240ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, C5, T7, TP7, CP5, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP4, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, PO9, PO10	Oz at 201ms ($F(1, 19) = 96.64, p < .001$)
	260ms - 350ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, T7, TP7, CP5, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, PO9	AFz at 322ms ($F(1, 19) = 96.68, p < .001$) (peak of entire effect)

1.3.1.1 Main Effect of Orientation for Houses

The main effect of Orientation showed significant differences between upright and inverted house stimuli from 76ms to 350ms with the largest F value occurring at 322ms on electrode AFz ($F(1, 19) = 96.68, p < 0.001$; Fig. 1-2B). Three disjointed “bands” of significance appeared in the raster plots. The first one spanned $\cong 76$ -155ms, the second spanned $\cong 160$ -240ms and the third started at $\cong 260$ ms and continued until the end of the epoch. Local F value maxima were also seen at 145ms on FP1, at 201ms on Oz, and at 322ms on AFz (Table 1-1, Fig. 1-2A-B). The ERP amplitude and amplitude difference wave graphs show the extent of the cluster mass (green line) and TFCE (pink line) significance on the electrodes at which local F value maxima were seen (see Table 1-1). When looking at electrodes at which the N170 was clearly visible (e.g. PO8 and PO9, Fig. 1-2B), the largest amplitude difference (inversion effect) was seen around 200ms (as seen at Oz), corresponding to the ramping part from the N170 peak toward the P2, although the significant points covered the P1-N170-P2 complex at most posterior sites. At these sites, the inversion effect was in the typical direction with more negative N170 amplitudes for inverted than upright houses. Around the P1 and P2 components, amplitudes were more positive for upright than inverted items although at some sites like PO9, the P1 was larger for inverted than upright houses. The pattern was seen polarity reversed at frontal sites (e.g. Fp1, AFz, Fig.1-2B).

1.3.1.2 Main effect of Fixation Location for Houses

There was no significant timepoint for the main effect of Fixation Location with TFCE or Cluster Mass correction. When uncorrected, the effect was scattered with very low F values (<20 ; see Appendix Fig.1A) although a few denser points were seen, which did not survive corrections.

1.3.1.3 Interaction between Orientation and Fixation Location for Houses

The Interaction between Fixation Location and Orientation also did not reach the threshold of significance with TFCE or Cluster Mass correction. The significant F values were low (<20) with a band of significant values from $\cong 70$ -140ms which did not survive correction, and scattered timepoints outside this band (see Appendix Fig.1A).

1.3.2 Face perception study

1.3.2.1 Face experiments Comparison

The direct comparison of the two face Data Sets using a 2 (Stimulus Orientation) x 6 (Fixation Location) x 2 (Experiments) mixed model ANOVA did not reveal any main effect of Experiment nor interactions between the main factors and Experiment. This lack of effect was due to similar patterns found for each data set analyzed separately, despite their difference in sample size ($n=20$ vs. $n=32$). Separately, each experiment displayed similar significant main effects of Stimulus Orientation, Fixation Location, and their interaction. Therefore, Exp. 2 and 3 were combined and reanalyzed as one large group to increase the power of the analysis, using a 2 (Orientation) x 6 (Fixation Location) repeated measures ANOVA. The remainder of the results section will focus on the combined experiments ($N=52$).

1.3.2.2 Main effect of Orientation for Faces

A significant main effect of Orientation was seen across the scalp, from 82ms to 350ms, with the largest F value occurring at 170ms on electrode PO10 ($F(1, 51) = 238.24, p < .001$; Fig. 1-3). Three “bands” of significance were seen, with very similar pattern whether TFCE (Fig.1-3A) correction was applied, and the pattern was already clearly there in the uncorrected analysis. The F values observed in this analysis were large with many timepoints exceeding values of 100. The ERP amplitude and amplitude difference wave graphs in Fig.1-3B show the extent of the Cluster Mass (green line) and TFCE (pink line) significance on a few electrodes of interest, chosen for their local F value maxima (see Table 1-2).

The first band was seen from 82-142ms with a local F value maximum at 125ms on FC1 (Table 1-2, Fig.1-3B) where amplitudes were more negative for inverted than upright faces after the frontal N1, during the ramping part towards the VPP (Vertex Positive Potential, opposite of the N170 at fronto-central midline electrodes, see Joyce and Rossion 2005). At posterior sites (e.g. PO10), this corresponded to a larger (and later) P1 for inverted than upright faces. The second band from 148-204ms encompassed the middle of the P1-N170 transition, the N170 peak (larger and later for inverted faces) and most of the N170-P2 transition at posterior sites. The local F maximum for this band was seen at 170ms on PO10, that is, *after* the N170 peak (which occurred around 150ms) in the middle of the N170-P2 interval (Fig.3B, vertical lines on PO9 &

PO10; Table 1-2). This pattern was seen polarity reversed at frontal electrodes with the VPP showing more positive amplitude for inverted than upright faces (also seen on FC1, Fig.1-3B). The last band of significance occurred from 222-350ms across most of the scalp with a local F maximum on P10 at 322ms (Table 1-2). At posterior electrodes this timeline coincided with the peak of the P2 which was larger for inverted faces, while during the rest of the epoch amplitudes were more negative for inverted than upright faces (Fig.1-3B).

1.3.2.3 Main effect of Fixation Location for Faces

A significant main effect of Fixation Location was also observed with TFCE (Fig. 1-4, left panel), which was overall less strong (F values < 50) than the Orientation main effect and was again clearly seen without correction. The effect was observed from 68ms to 350ms with the peak of the effect occurring at 180ms on electrode Fz ($F(5, 47) = 43.99, p < .001$; Fig. 1-4, left panel). Again, three “bands” of significance were seen with local F value maxima (see Table 1-2 for details). As Fixation Location interacted significantly with Orientation, we focus on the interaction below.

1.3.2.4 Interaction between Orientation and Fixation Location for Faces

The interaction was significant using TFCE correction (Fig.1-4, right panel) across the scalp from 59ms until 350ms, with the largest F value occurring at 119ms on electrode Oz ($F(5, 47) = 51.25, p < .001$; Table 1-2). We followed-up with two different post-hoc contrasts to better understand this complex Interaction.

Figure 1-3. Face perception study results.

(A) Main effects of Orientation with $\alpha = .05$ and TFCE correction applied. The raster plot depicts the significant F -values at every electrode (72, y axis) and time-point (-100 to +350ms) analyzed (magnitude of the F -values according to the coloured scale). The topographic maps of the unthresholded and uncorrected F -values are displayed at 125ms, 170ms, and 322ms when the F -value local maxima were registered for the face orientation effect after TFCE correction (see text for details). **(B)** Main effect of Orientation on ERP amplitudes displayed at 5 relevant electrodes (outlined by the red arrows on (A)), showing ERPs for inverted faces in blue, upright faces in red and their difference (inverted minus upright faces in black in the lower panels), with their respective confidence intervals. The topographic maps on electrode FC1, PO10, and P10 display the voltage difference between the upright and inverted conditions across the scalp (according to the $-2\mu\text{V}$ to $+1\mu\text{V}$ small colour bar scale) at the same time point at which respective maxima in F values were found in (A). The green bar at the top of the plots represents the time points at which the main effect of Orientation was significant for these electrodes using the cluster-mass correction while the pink bar at the bottom illustrates the same effect using the TFCE correction (see text for details and Appendix fig. 1 for uncorrected effects). The vertical black lines show the correspondence between the peak of the FIE and where it is temporally on the actual ERPs. Note that FIE peaks are seen between the P1-N170 and N170-P2 components, while the FIE was weaker at the peak of the N170. For all ERP plots, the ERPs represent the central tendency computed using raw means for single subject trials and 20% trimmed means across subjects; the difference waves were created with a 95% Bayesian Highest Density Interval (HDI) confidence interval (CI) so that if the CI includes 0, we can be confident that there is no effect then.

Table 1-2 Main effect of orientation, fixation location and their interaction, for the faces.

Electrodes included in the “bands” of activation obtained for each effect and their timing. The electrode and time point at which the largest F values were seen for each band are also displayed.

	Timing	Electrodes	Effect local F value maxima
Orientation Main Effect	82ms - 142ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, C5, T7, TP7, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	FC1 at 125ms ($F(1, 51) = 174.34, p < .001$)
	148ms - 204ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, C5, TP7, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO2, LO2, TP9, TP10, PO9, PO10	PO10 at 170ms ($F(1, 51) = 238.24, p < .001$) (peak of the entire effect)
	222ms - 350ms	AF3, F1, F3, FC3, FC1, C1, C3, T7, TP7, CP3, CP1, P1, P3, P7, P9, PO7, PO3, Iz, Oz, POz, Pz, CPz, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO2, LO2, TP9, TP10, PO9, PO10	P10 at 322ms ($F(1, 51) = 83.83, p < .001$)
Fixation Location Main Effect	68ms - 148ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, C5, T7, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	TP9 at 138ms ($F(5, 47) = 33.65, p < .001$)
	150ms - 240ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, C5, T7, TP7, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	Fz at 180ms ($F(5, 47) = 43.99, p < .001$) (peak of the entire effect)
	246ms - 350ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, CP1, P1, P3, P5, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	Oz at 336ms ($F(5, 47) = 15.22, p < .001$)
Orientation X Fixation Location	59ms - 170ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, C5, T7, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	Oz at 119ms ($F(5, 47) = 51.25, p < .001$) (peak of entire effect)
	210ms - 327ms	Fp1, AF7, AF3, F3, F5, F7, FT7, FC5, FC3, C1, C3, C5, T7, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, Cz, C2, C4, C6, T8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	O1 at 302ms ($F(5, 47) = 20.79, p < .001$)

1.3.2.4.1 Follow-up contrasts #1: Main Effect of Fixation Locations for upright and inverted Faces analyzed separately.

We first ran two repeated measures ANOVA analyses using the factor Fixation Location (6 levels) separately on the upright and inverted face data (using $\alpha=0.025$).

For upright faces, the effect of Fixation Location was significant with TFCE correction between 68-350ms (Fig.1-5A). The largest F value for this effect was seen at 119ms on electrode Oz ($F(5, 47) = 52.31, p < 0.001$; Fig. 1-5A). When looking at the ERP waves, two different components showed strong variations with fixation locations. First, at POz, the equivalent of a C2 component was seen, with positive amplitude for mouth fixation and negative amplitudes for forehead and nasion fixations. At occipital sites, the P1 ERP component showed a clear amplitude gradient with smallest and earliest P1 peak amplitude for Nasion fixation, followed by the Forehead and Nose, then Left and Right eye, with the largest amplitude seen for the mouth fixation (Fig.1-5B occipital sites, top row). The Left and Right eye fixations exhibited the largest P1 at posterior lateral electrodes (PO9/PO10) followed by the Nasion (similar P1 to Right Eye), Nose, Mouth, and Forehead (Fig.1-5B). After the P1, the N170 ERP component consistently showed largest amplitudes for eye fixations with an even larger amplitude for the Right eye fixation at PO10. While the effect was significant until 350ms at some electrodes, no clear pattern emerged during the later time points.

Similarly, the effect of Fixation Location was significant for inverted faces using TFCE correction between 59ms and 350ms after stimulus presentation. The largest F value for this effect was on electrode FC1 at 182ms ($F(5, 47) = 43.44, p < 0.001$; Fig. 1-6A). When looking at the ERP waves at POz, C2 amplitudes were negative for mouth fixation and positive for forehead fixation, i.e. in opposite polarity of what was seen for upright faces. At occipital sites, P1 amplitudes were also lowest for mouth fixation and largest for forehead fixation but no clear amplitude gradient was seen in between these two conditions (Fig. 1-6B top row). The Left and Right eye fixation exhibited largest P1 and N170 amplitude peaks at parieto-occipital electrodes, with largest amplitudes for Left eye at left site PO9 and largest amplitudes for Right eye at right site PO10.

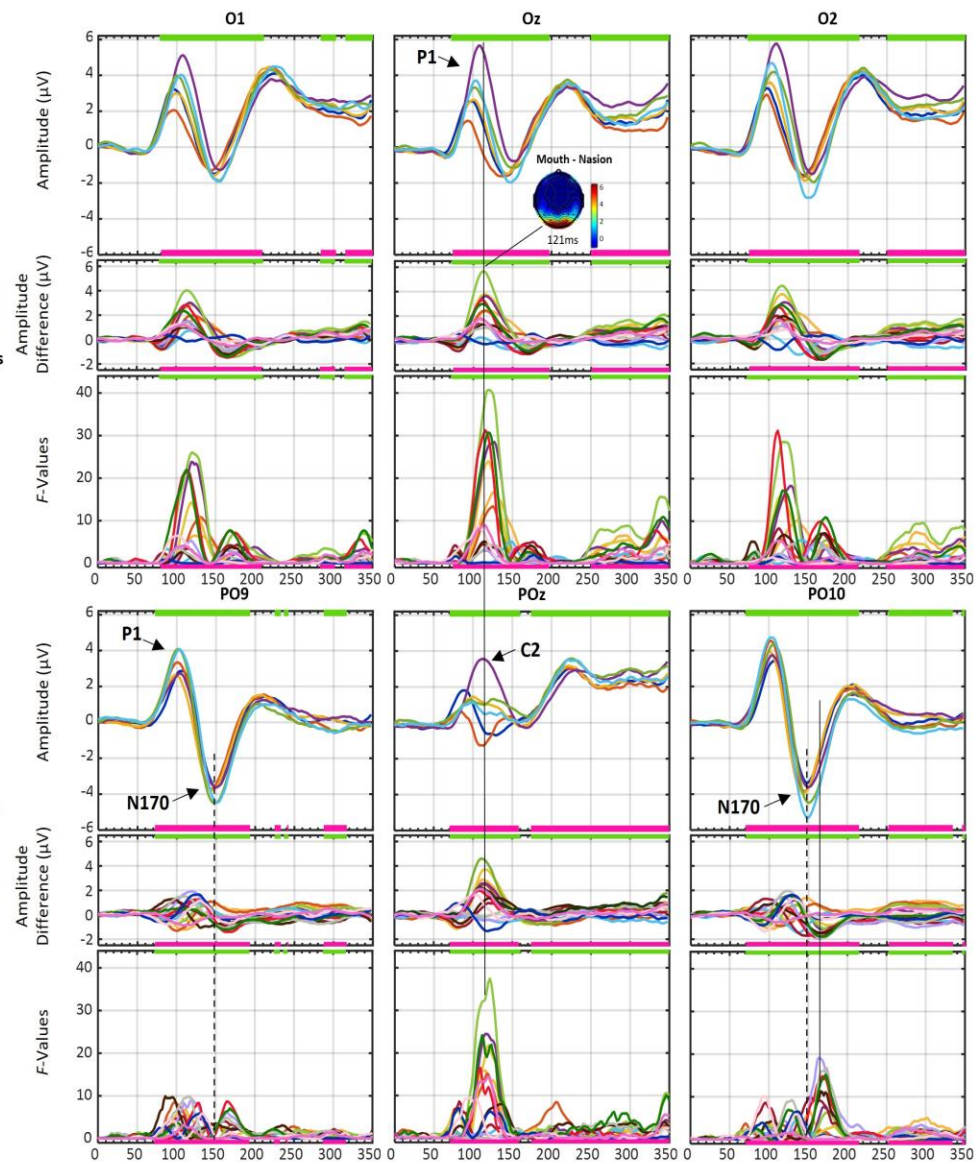
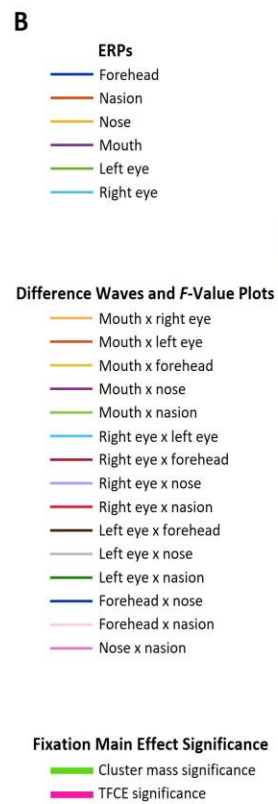
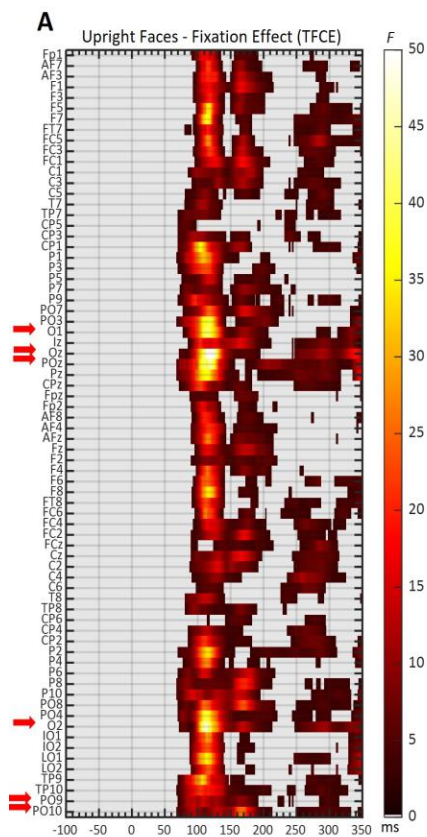


Figure 1-5. Analysis of fixation location for upright faces only.

(A) Raster plot of the main effect of Fixation Location with a TFCE correction ($p < 0.025$). **(B)** The 6 Fixation Location conditions are displayed at 6 posterior electrodes where the largest F values were seen. For each electrode, 3 plots are displayed. The top plots display the group average ERPs for each fixation location (central tendency computed using raw means for single subject trials and 20% trimmed means across subjects). The middle plots display the difference waves between two conditions at a time. The green bar at the top of the plots represents the time points at which the main effect of fixation location was significant for these electrodes using the cluster-mass correction while the pink bar at the bottom represents the time points at which the main effect was significant using the TFCE correction. The bottom plots display the time courses of the F -values obtained for each contrast comparing two fixation locations at a time. The topographic maps on electrode Oz display the amplitude difference between the mouth and nasion fixations across the scalp (according to the $0\mu\text{V}$ to $+6\mu\text{V}$ small colour bar scale) at 121ms where that difference was maximum. The vertical black lines show the correspondence between the peak of the paired contrasts and where it is temporally on the actual ERPs, Falling on the C2 at POz and on the P1 at Oz. The dashed vertical black line highlights that at the peak of the N170, weak F values were found.

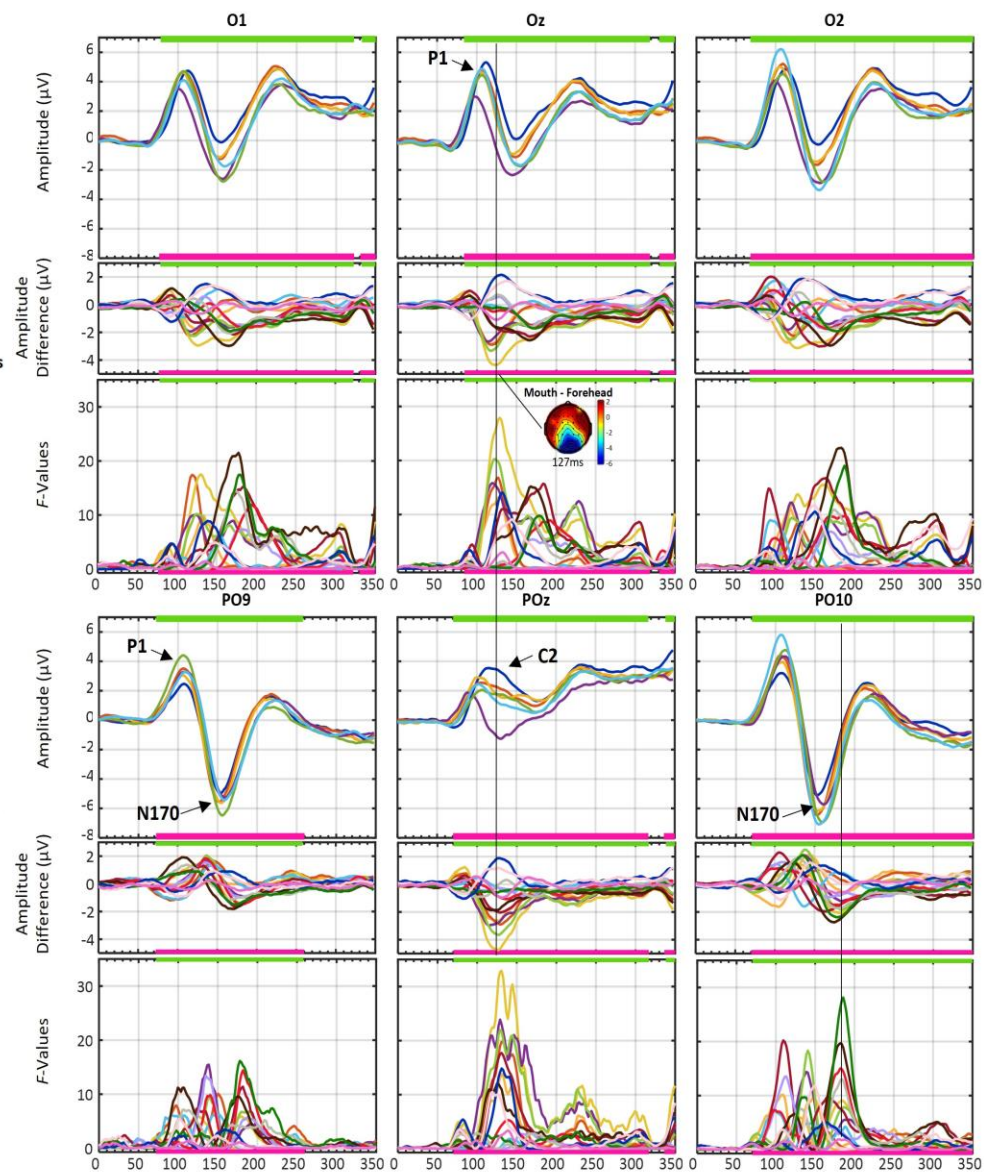
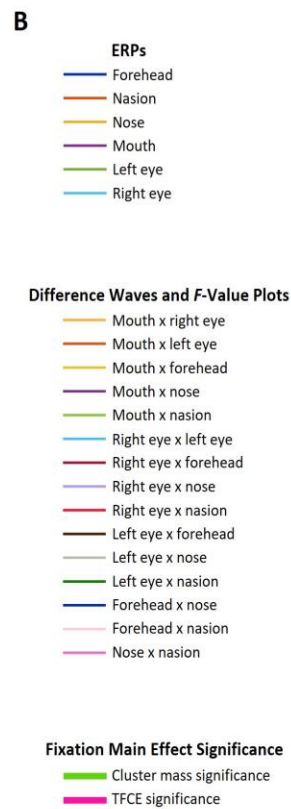
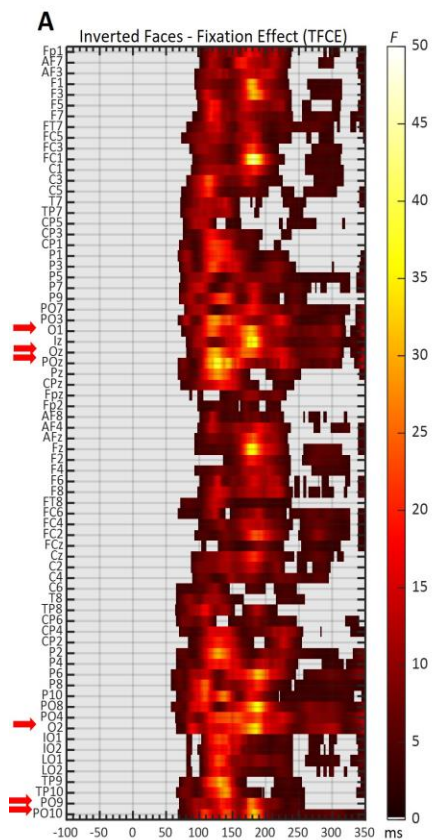


Figure 1-6. Analysis of fixation location for inverted faces only.

(A) Raster plot of the main effect of Face Fixation Locations with a TFCE correction ($p < 0.025$). **(B)** The 6 Fixation Location conditions are displayed at 6 representative posterior electrodes. For each electrode, 3 plots are displayed. The top plots display the group average ERPs for each fixation location (central tendency computed using raw means for single subject trials and 20% trimmed means across subjects). The middle plots display the difference waves between two conditions at a time. The green bar at the top of the plots represents the time points at which the main effect of fixation location was significant for these electrodes using the cluster-mass correction while the pink bar represents the time points at which the main effect was significant using the TFCE correction (see text for details). The bottom plots display the time courses of the F -values obtained for each contrast comparing two fixation locations at a time. The topographic maps on electrode Oz display the amplitude difference between the mouth and forehead fixations across the scalp (according to the $-6\mu\text{V}$ to $+2\mu\text{V}$ small colour bar scale) at 127ms where that difference was maximum. The vertical black lines show the correspondence between the peak of the F -values paired contrasts and where it is temporally on the actual ERPs, falling on the C2 at POz and on the P1 at Oz. Note the opposite effects here compared to what is seen for upright faces on Figure 5.

1.3.2.4.2 Follow-up contrast#2 - Face Inversion Effect at each Fixation Location

We also performed 6 *F*-contrasts using a significance threshold of $p < 0.0083$ (to account for the number of contrasts performed), assessing the FIE separately at each Fixation Location (Fig.1-7). The FIE was largest around 115-120ms at parieto-occipital and occipital sites. At POz, the FIE was seen as a positive C2-like component for forehead and nasion fixations, with a negative C2-like component for mouth fixation, due to opposite polarity of the C2 between upright and inverted conditions for these fixation locations. At occipital sites, larger P1 was seen for inverted than upright faces for all fixations except mouth fixation for which the opposite was seen; this resulted in a positive FIE deflection for all fixations (and maximally so for nasion and forehead fixations) except for mouth fixation for which the FIE elicited a negative deflection (Fig. 1-7; see Table 3 for details). At that time and electrodes, the FIE was strongest for nasion fixation, as reflected by largest contrast *F*-values, followed by forehead fixation, mouth fixation and then nose fixation, while the smallest *F* values were seen for eye fixations (Fig. 1-7, *F*-value time courses). The Left and the Right eye fixations elicited larger FIE at lateral parietal sites, where the N170 is typically measured (e.g., P9/P10), than at midline occipital sites, with a peak of contrast *F*-values corresponding to the N170-P2 interval. The FIE was larger at P9 for Left eye (*F*-values green line on Fig. 1-7) than Right eye fixation (light blue line) while at P10 the FIE was equally large between the two eye fixations. Nasion fixation (red line) elicited a FIE at these lateral sites as large as the FIE elicited by eye fixations.

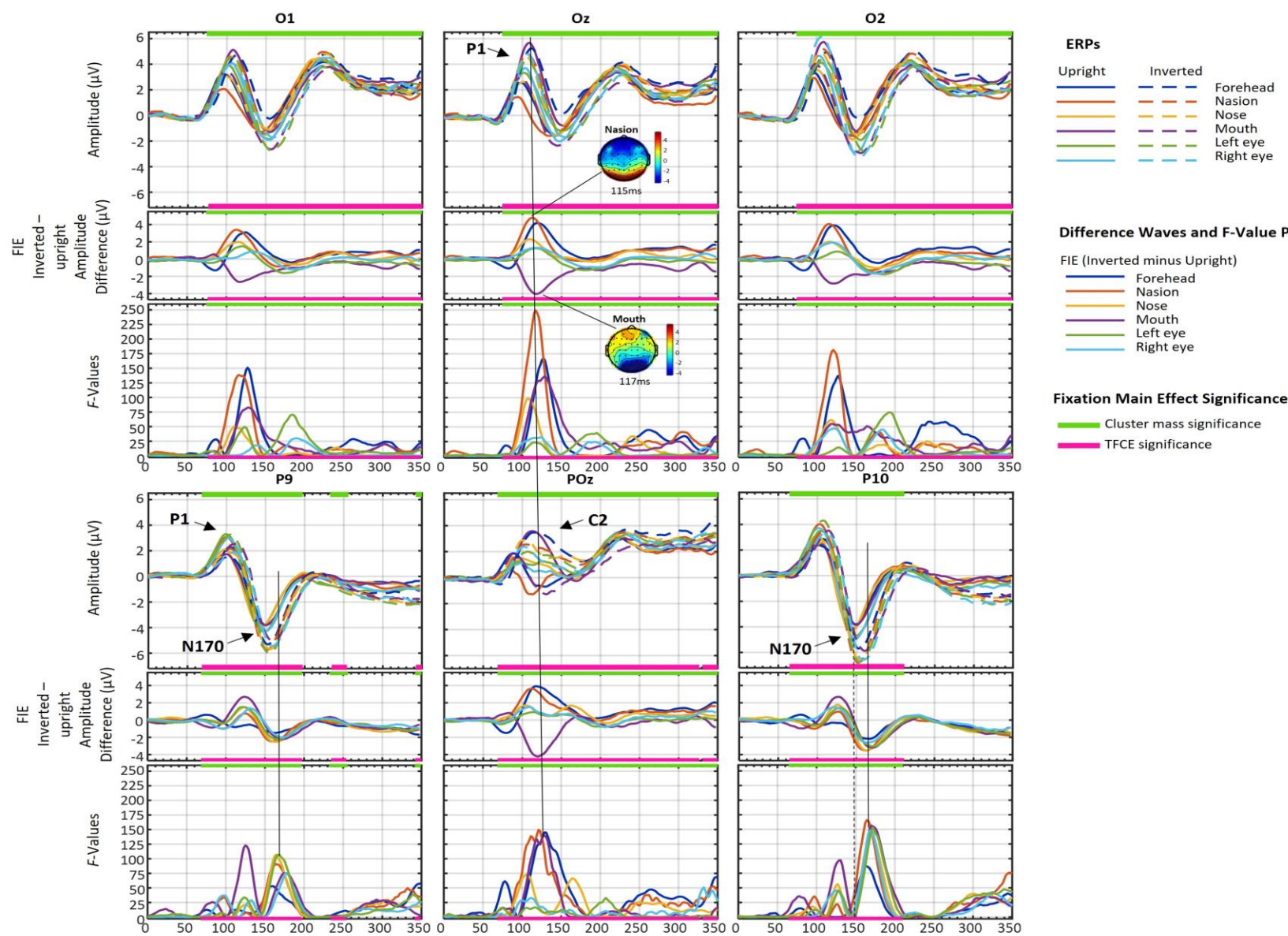


Figure 1-7. Face inversion effect.

Six representative posterior electrodes (outlined by the red arrows on Fig.1-4) are focused on. The top graphs display the ERPs for upright (plain lines) and inverted faces (dotted lines) for each fixation location. The middle plots display the actual FIE (i.e. the amplitude difference between the inverted and upright faces at each fixation location). The topographic maps on electrode Oz display the FIE across the scalp (according to the $-4\mu\text{V}$ to $+4\mu\text{V}$ small colour bar scale) at the time point at which the FIE was largest for the nasion fixation (at 115ms, top map) and for the mouth fixation (at 117ms, bottom map). Note how opposite the effects are for nasion and mouth fixations. The green bar at the top of the plots represents the time-points at which the Orientation by Fixation Location interaction was significant for these electrodes using the cluster-mass correction while the pink bar at the bottom represents the time-points at which the interaction was significant using the TFCE correction (see text for details and Appendix fig. 1 for uncorrected effects). The bottom plots display the time courses of the F -values obtained for each fixation location contrast (inverted vs. upright conditions) at these electrodes. Note how the FIE varies with fixation location (and electrodes) and is largest for fixation on the nasion at occipital sites (see text for details)

Table 1-3. Face inversion effect.

For each fixation location, the timing “bands” of the FIE are reported, with the electrode at which a local F value maxima (and its latency) was found, along with the statistics (inverted versus upright).

FIE contrasts (inv-up) for each Fixation location	Timing	Max electrode – local maximum latency	Local maximum F -value and FIE amplitude difference, at the local maximum latency.
Forehead	64ms - 92ms 97ms - 198ms 203ms - 350ms	POz - 76ms Oz - 125ms POz - 345ms	$F(1, 51) = 61.50, p < .001, \Delta -1.5 \mu V$ $F(1, 51) = 168.02, p < .001, \Delta 4.00 \mu V$ $F(1, 51) = 68.74, p < .001, \Delta 2.05 \mu V$
Nasion	84ms - 142ms 140ms - 197ms 220ms - 350ms	Oz - 115ms PO10 - 164ms P10 - 343ms	$F(1, 51) = 249.08, p < .001, \Delta 4.71 \mu V$ $F(1, 51) = 184.84, p < .001, \Delta -3.62 \mu V$ $F(1, 51) = 75.97, p < .001, \Delta -1.77 \mu V$
Nose	82ms - 142ms 138ms - 197ms 224ms - 350ms	Oz - 105ms PO10 - 164ms P10 - 296ms	$F(1, 51) = 99.57, p < .001, \Delta 2.22 \mu V$ $F(1, 51) = 161.03, p < .001, \Delta -3.89 \mu V$ $F(1, 51) = 40.04, p < .001, \Delta -1.35 \mu V$
Mouth	97ms - 146ms 145ms - 220ms 257ms - 350ms	POz - 127ms PO10 - 172ms CPz - 314ms	$F(1, 51) = 139.50, p < .001, \Delta -3.93 \mu V$ $F(1, 51) = 174.50, p < .001, \Delta -3.26 \mu V$ $F(1, 51) = 41.11, p < .001, \Delta 0.93 \mu V$
Right Eye	87ms - 141ms 145ms - 208ms 300ms - 350ms	PO10 - 123ms PO10 - 168ms POz - 330ms	$F(1, 51) = 72.94, p < .001, \Delta 1.75 \mu V$ $F(1, 51) = 155.35, p < .001, \Delta -2.90 \mu V$ $F(1, 51) = 50.90, p < .001, \Delta 0.95 \mu V$
Left Eye	89ms - 139ms 145ms - 217ms 262ms - 350ms	PO9 - 121ms PO10 - 172ms PO9 - 337ms	$F(1, 51) = 82.52, p < .001, \Delta 1.83 \mu V$ $F(1, 51) = 180.83, p < .001, \Delta -3.57 \mu V$ $F(1, 51) = 47.91, p < .001, \Delta -1.21 \mu V$

1.4 Discussion.

The present ERP study examined the effects of plane inversion (orientation), fixation location and their interaction, on the early neural responses to house and face stimuli. Inversion is a well-studied manipulation in the ERP face processing literature, which has been instrumental in revealing the early processing difference between faces and objects. In contrast, the effect of fixation location has received little attention in face perception and is simply unexplored in object perception. In this study we examined the effects of inversion and fixation location on early face and house processing. We used a mass-univariate analysis (MUA) with powerful corrections for statistical errors to examine every timepoints and electrodes, allowing to assess not only the N170 effects reported previously but also the rest of the epoch across the whole scalp. In contrast to the classic idea that inversion effects on the N170 are not seen in objects, we found a clear and widespread effect of orientation for houses that spanned most of the epoch, including the N170 component. The effects of fixation location and their interaction with

orientation did not pass the threshold of significance for houses, while these effects were strong and widespread for faces. We discuss these findings below and their implication for house and face perception.

1.4.1 General inversion effect

The extensive research on plane inversion suggests that faces are processed holistically/configurally, integrating features into a perceptual whole, whereas objects are processed analytically or featurally (Yin 1969; Valentine 1988; Tanaka and Farah 1993; Maurer et al. 2002; Rossion 2009; Tanaka and Gordon 2011). The FIE indicates a disruption of this holistic processing, captured by variations of the N170 ERP component. The N170 peak is larger and delayed for inverted faces, however, only its latency seems affected by object inversion (Rossion et al. 2003; Itier et al. 2006, 2011; Kloth et al. 2013).

In contrast to these earlier reports, the current study found that inversion affected the N170 for faces and houses similarly, with both categories showing increased N170 amplitude for inverted items. Although latencies were not formally measured, a visual comparison of Fig. 1-2 and Fig. 1-3 suggests that a latency delay with inversion also exists for both categories. Faces and houses were tested in different samples, so the effects were not directly comparable between the two categories. Nevertheless, our results point towards a possibly stronger inversion effect for faces than houses based on the strength of the *F* values (compare Fig.1-2 and 1-3 raster plots).

The present results suggest that holistic/configural processing occurs not only for faces, but also for houses, although important differences can be noted. First, the use of MUA to examine the entire epoch revealed that the maximum statistical difference for houses occurred after the N170 peak, during the N170-P2 interval. Second, the house inversion effect (HIE) showed variations in strength and temporal distribution of significant timepoints that were quite different from those seen for the FIE, suggesting a more nuanced mechanism in how faces and houses are processed. For instance, while the amplitude FIE was largest around 170ms at posterior bilateral sites, the amplitude HIE was largest around 200ms at medial occipital sites. The HIE also encompassed the P2 component, similar to what Rousselet et al. (2008) reported (while they did not report HIE on the N170). These different topographies and timing of activation suggest different underlying generators for the two categories, with different time course of inversion

effect. Direct comparison between faces and houses in terms of the strength of the inversion effect, its topographical distribution and its time course, will have to be investigated in future MUA work using within-subject gaze-contingent designs. Furthermore, whether other object categories than houses can elicit similar widespread inversion effects at the neural level requires empirical demonstration.

Additionally, the results suggest that holistic processing starts early and encompasses the P1 component, sensitive to low-level factors such as mean image contrast, luminance, and spatial frequencies. Indeed, for both categories, the inversion effect started way earlier than the N170, around 76ms for houses and 82ms for faces, with first local maxima occurring soon after the P1 peak (145ms for houses and 125ms for faces). As inverted and upright items are identical in terms of low-level factors, these early inversion effects around the P1 suggest that face and house configuration, considered a high-level process, impacts early neural activity and feature integration. Face inversion effects on the P1 have been reported before (e.g. Linkenkaer-Hansen et al. 1998; Itier and Taylor 2002, 2004; Nihei et al., 2018), but not consistently and were argued by some to be driven by low-level factors of contrast and luminance due to the hair. The present study employed digitally created pictures with the same bald face outline and no hair, differing only by the shape of their features. Therefore, the present early inversion effects can only be attributed to neuronal computation differences in feature integration between upright and inverted faces. Whether low-level cues (local contrast and luminance etc.) contribute to this feature integration does not undermine the fact that the features and their relationships in space (i.e. the face configuration, which is a high-level process) starts to be coded at that time. The results imply a broader impact of face and house orientation on neural processing, affecting earlier but also later ERP components than the N170. As we discuss below, these early inversion effects also varied with fixation location for face stimuli.

1.4.2 Fixation location effects and their Interaction with Orientation

The main effect of Fixation Location and its interaction with Orientation showed significant early effects across the scalp for the face category, including during the N170 component. A handful of gaze-contingent studies have reported larger N170 to eye fixations compared to other feature fixations (Zerouali et al. 2013; Nemrodov et al. 2014; De Lissa et al. 2014; Neath and Itier 2015; Neath-Tavares and Itier 2016; Itier and Preston 2018; Parkington and Itier 2018) and

the present MUA confirmed this finding. This result argues against the idea that the N170 reflects a strict holistic face processing stage in the sense of a perceptual snapshot where features would be perceptually “glued” in a whole face representation. Rather, the fact that this component varies with fixation location and orientation, and with the presence or absence of surrounding features (Nemrodov et al. 2014; Itier and Preston 2018; Parkington & Itier, 2019; Winward et al., 2002), suggests it reflects a malleable feature integration process. However, an important new finding revealed by the MUA, was that the statistical effect of fixation was weak at the N170 peak, and much stronger at earlier time points.

Indeed, the largest interaction effects were seen during the first “band” of activation between 59-170ms, with the maximal *F*-value seen posteriorly around 119ms (Fig.1-4). This interaction reflected differences in fixation effects between upright and inverted faces. Examination of upright faces separately revealed a similar first band of activation for the fixation effect, with maximal *F*-value also at 119ms at posterior sites and corresponding to an amplitude gradient starting around the C2 and P1 component and largest after the P1 peak, during the P1-N170 interval. This fixation effect reflected retinotopic effects driven by the different face positions with fixation location. At POz, the C2 component, also called P125/N135 in prior work (Di Russo et al. 2005, 2012; Capilla et al. 2016), was indeed largest and positive for mouth fixation, when most of the face was in the upper visual field, and negative for forehead and nasion fixations, when most of the face was in the lower visual field (Fig.1-5). At occipital sites, P1 was largest (and delayed) for mouth fixation and smallest (and earliest) for nasion fixation, with P1 amplitude for the other fixation locations falling in between (Fig.1-5). The exact opposite patterns were seen for inverted faces: largest positive C2 for forehead and nasion fixations, most negative C2 for mouth fixation; largest P1 for forehead fixation and smallest P1 for mouth fixation, although the P1 gradient for the other fixations was not as clear as for upright faces (Fig.1-6). These variations led to a strong FIE at POZ during the C2 timing, along with a strong FIE at occipital sites during the P1-N170 interval (Fig.1-7).

One recent MUA study looking at fixation location on upright faces with emotional expressions (including neutral faces) reported a very similar band of activation with similar amplitude gradients for C2 and P1, reflecting the same early retinotopic effects (Itier and Durston 2023). To our knowledge, no other prior ERP study has reported such a retinotopic

mapping effect for face stimuli. Prior ERP studies on retinotopy essentially focused on checkerboard stimuli and did not use eye tracking to ensure participants were fixated where they were supposed to (Di Russo et al. 2005, 2012; Capilla et al. 2016). Here, using a gaze-contingent approach, we report similar early retinotopic effects for upright face ERPs and further show how these effects change when faces are upside-down. Whether the C2 and P1 strong responses to the upper visual field information (when fixation was on the mouth) might relate to downstream behavioural advantages for the upper visual field when processing face gender (Quek and Finkbeiner 2014) or gaze direction (Palanica and Itier 2017), will have to be investigated by future studies.

We also replicated the larger P1 for ipsilateral eye fixations (Zerouali et al. 2013; Nemrodov et al. 2014; De Lissa et al. 2014; Neath and Itier 2015; Neath-Tavares and Itier 2016), reflecting the fact that, when one eye is fixated, most of the face is situated in the contralateral hemifield, eliciting stronger amplitudes on the hemisphere contralateral to that visual field and thus ipsilateral to the fixated eye. These lateralized retinotopic effects were also reported by recent MUA (Winward et al. 2022; Itier and Durston 2023) although in the present study they were clearest for inverted faces.

Another new important finding of the present study is that the FIE varied with fixation location. Discrepant results had been reported in the original studies on the N170, with Nemrodov et al. (2014) reporting no variations of the FIE with fixation location but Itier and Preston (2018) reporting largest FIE for nasion fixation on the N170 amplitude (for intact faces). The combination of the two samples into a large one and the MUA enabled to confirm that the FIE indeed varied with fixation location and was strongest (in terms of contrast F values) for nasion fixation. However, this strongest FIE was seen earlier than the N170, right after the P1, and more occipitally (Fig. 1-7). Again, if the FIE reflects holistic processing, i.e. the perceptual integration of features into a whole, then our results support the view that holistic processing is malleable and varies depending on fixation location. It is thus not strictly holistic.

The change in fixation location affects the position of the face in the visual field but also that of the parafoveal features. Indeed, depending on which feature is fixated, the position of the other parafoveal features in the visual field will vary. For instance, if the face is upright, fixation on the mouth implies the other features are in the upper visual field, just like the majority of the

face outline itself. Therefore, we prefer talking in terms of feature integration. The fact that nasion fixation elicits the strongest FIE highlights the importance of this face area for optimal feature integration, an idea that fits with eye tracking studies showing that this face area is one of the preferred fixation spots during face exploration as it is typically the face center of gravity (Barton et al. 2006; Bindemann et al. 2009; Peterson and Eckstein 2011, 2012). Thus, maximum feature integration seems to occur during the P1-N170 interval when faces are upright, leading to maximum disruption when faces are inverted and hence, to a maximal FIE.

Importantly, the second strongest F -value maxima in paired contrasts were seen *after* the N170, during the N170-P2 interval, for the nasion and for the eye fixations (as reflected by the peaks of F values at P9/P10, for these contrasts, see Fig.1-7). These second maxima have also been reported by Itier and Durston (2023) although in that study the nasion fixation was not tested and the second maxima were driven by eye fixation locations. Around the N170 peak, the FIE was small with weaker F values (see vertical dash line on Fig.1-7). The data overall suggest that the N170 might be an inflexion point between two processes (Itier and Durston 2023), rather than the peak of a holistic process as suggested in the literature (Eimer 2011; Rossion and Jacques 2011). The P1-N170 interval has been argued to reflect feature integration with the N170 peaking when that integration is complete (Schyns et al. 2007; Rousselet et al. 2014; Ince et al. 2016). The fact that a second strong FIE maxima was found after the N170 and towards the P2, suggests that feature integration is still on-going past the N170 peak, and until 350ms. The N170-P2 interval is involved in the coding of the ipsilateral eye (Ince et al. 2016) and the number of parafoveal features (Winward et al. 2022) while the P2 component has been suggested to be involved in the processing of feature type (Winward et al. 2022) and face typicality, with larger P2 for more typical faces (Wiese and Schweinberger 2008; Stahl et al. 2010; Kaufmann and Schweinberger 2012). This latter idea fits with the continued feature coding around that time, given face typicality inherently implies computation of features, their distances and their comparison to norms or templates (Valentine 1991; Schulz et al. 2012).

In contrast to the strong effect of fixation location seen for faces, and its interaction with orientation, no significant impact of fixation location, and no interaction with inversion, were found for house stimuli, indicating that fixation location may not be critical for this object category. This outcome is notable, as it implies an absence of early retinotopic effects for houses,

in contrast to a strong retinotopic mapping for faces and even for checkerboards, based on previous studies. However, the uncorrected analyses suggested a potential fixation location interaction with inversion, but these were too weak to be statistically significant after correction for multiple comparisons, possibly due to the limited sample size in the house study. Further research with larger sample sizes is necessary to determine whether feature integration for houses is truly immune to fixation position or if fixation location effects, akin to those observed with faces, might emerge with more statistical power.

1.4.3 Conclusion

In conclusion, MUA revealed that, in this chapter, the N170 peak, which is the focus of most past and present research, is the time point at which some of the weakest *F*-values were found, while the strongest *F*-values were seen 20-30ms (up to 50ms) earlier. MUA also uncovered significant differences after the N170 suggesting a more complex face processing dynamic than previous research suggests. Overall, the present data support the idea of a protracted, malleable feature integration process during the first 350ms of vision, that varies with which feature is in fovea and where the other features are situated in parafovea. This feature integration was maximal during the P1-N170 interval, around 120ms, and strong again during the N170-P2 interval, around 170ms. The chapter also demonstrated that houses elicit a strong and widespread orientation effect though more sporadic than that seen for face stimuli. These findings suggest a feature integration process for house stimuli, rather than a strict analytical process as widely discussed in the literature, although specific differences in effect strength and underlying generators compared to faces still need further investigation. More research comparing these two categories in a within-subjects design with greater trial number and increased sample size is required. Overall, the present results advocate for a more systematic use of statistics such as MUA (see also Kiebel and Friston, 2004; Luck and Gaspelin, 2017) to analyze all time points and all electrodes in a data-driven way, and for the abandonment of sole ERP peak analysis, to gain a better and more comprehensive understanding of the processing time course of faces and objects. Direct comparisons of MUA and various multivariate approaches (e.g. Principal Component Analysis, (Donchin and Heffley 1979); Independent component Analysis, (Makeig et al. 1999); Partial Least Square analysis, (Lobaugh et al. 2001)) are also important avenues for future research. In particular, the location of the effects on the scalp is dependent on the

reference used to compute the ERP signal and approaches that are reference-independent like the global field power and global dissimilarity measures (see e.g. (Murray et al. 2008; Brunet et al. 2011)), will help in effect generalizability.

Chapter 2

House versus Face neural processing

2.1 Introduction

The MUA results in Chapter 1 demonstrated a clear face inversion effect (FIE), however, the statistical peak occurred earlier than previous peak analyses suggested. Surprisingly, there also was an inversion effect for houses, which is a novel finding. This house inversion effect (HIE) appeared at different times and seemed weaker than the FIE, however no statistical comparison was made to confirm these differences. This work highlights that holistic processing is not merely a ‘perceptual snapshot’ but rather reflects a more nuanced feature integration process that continues over time. The implication of these results is that houses are processed holistically/configurally to some degree and not just featurally.

A significant effect of fixation location and its interaction with orientation was also seen for faces, whereas no such effect was found for house stimuli after familywise error correction. With the use of MUA, Chapter 1 confirmed amplitude modulations by fixation location and inversion for faces. The effects were strong, widespread across the scalp and spanned the entire epoch (70-350ms post face onset). The early effects of fixation location found only for faces imply that there is a strong retinotopic mapping effect for faces but not for houses. The only previous gaze contingent experiment with objects reported no effect of fixation location (De Lissa et al. 2014), however, this study was underpowered in both trial numbers and sample size. The lack of early fixation effects for objects is surprising given retinotopic mapping effects have been observed even for checkerboards (Di Russo et al. 2005, 2012; Capilla et al. 2016). The uncorrected analysis for houses in Chapter 1 indicated a potential trend towards a significant fixation location effect and interaction with orientation. It is possible that the limited sample size and trial numbers for this analysis limited the strength of these results after correction for multiple comparisons. Furthermore, the results of Chapter 1 did not include a statistical comparison between faces and houses which were tested in different samples.

The present study sought to investigate the effects of inversion and fixation location on the processing of house and face stimuli within the same participants using MUA. Chapter 1 results confirmed the necessity of analyzing the entire time course of ERPs using MUA with an increased sample size to uncover when differences occurred and at which electrodes. The same statistical analysis tool as Chapter 1 was used (LIMO; Pernet, et al. 2011). The experimental paradigm of the current experiment matched the one used in the Face study of Chapter 1 as closely as possible and included the same orientation discrimination task. The main differences included an increased trial number per condition, an increased sample size (4 times larger than the sample size of the House study in Chapter 1), one fewer fixation location and the use of well-matched face and house stimuli from another research group. The goal of this research was to replicate and extend the results of Chapter 1. Unlike chapter 1, the same number of fixation locations was used between face and house stimuli so they would be statistically, spatially, and featurally comparable (e.g., left eye/left window; right eye/ right window; mouth/beside door; nasion/between windows, and nose/center, with the distance between these features identical within each category).

We anticipated replicating the orientation effect for faces and finding a FIE for each fixation location with the largest FIE for nasion fixation. The same visual field/retinotopic effects as seen in Chapter 1 were expected for upright faces, with largest P1 seen for mouth fixation and smallest P1 seen for nasion fixation. Since the house experiment in Chapter 1 included a relatively small sample size ($n=20$), with a much larger sample size ($n=80$), we expected to replicate the strong inversion effect for houses but still expected it to be weaker and to show a different time course as the FIE (as suggested by the visual comparison between face and house results in Chapter 1). If the lack of fixation effect for houses in Chapter 1 was due to statistical power, as suggested by the uncorrected results (Appendix. Fig 1), then we anticipated that an effect of fixation location for houses would survive TFCE correction with our increased sample size. Retinotopic effects should then be seen at early time points around the C2 and P1 as seen in Chapter1, for both faces and houses. However, the effect should be weaker and present slightly differently than that seen for faces. In

particular, ERPs for window fixations should differ from eye fixations, since houses are stable, non-biologically and less socially relevant stimuli than faces.

2.2 Materials and Methods

2.2.1 Participants

Participants in this study included undergraduate students from the University of Waterloo (UW) who received course credit for their participation as well as some paid participants who were recruited outside of the university (\$CAD15/hour). The experiment was approved by the UW Research Ethics Board with written informed consent forms read and signed before the experiment. Participants were included if they self-reported no history of neurological disorders or head injuries, no use of antipsychotic medication or recreational drugs at the time of study and had normal or corrected-to-normal vision. The experiment tested 96 participants, however, 16 participants had to be removed due to issues with recording the eye tracker or EEG, low trial numbers (<20 per condition), and/or issues with data processing. A total of 80 participants were included in the analysis of this study (Mean age = 21.36, SD = 4.93; 51 female, 29 male; 32 left-handed, 48 right-handed).

2.2.2 Stimuli

The stimuli were adapted from the unaltered raw images used by (Gold et al. 1999)) and variants of these stimuli have been used for two decades to compare object and face processing (Rousselet et al. 2005, 2007, 2008). In total there were 10 unique faces (5 females, 5 males) and 10 unique house stimuli (Fig. 2.1). The faces were greyscale photographic images of faces in a neutral expression cropped in an oval frame. The house stimuli were greyscale photographic images of a base house image with the windows and doors altered. The face and house images were resized so that the face and houses themselves subtended 9.5° horizontal x 13.6° vertical angle to match Chapter 1 stimuli dimensions. Both face and house images were centered in the grey homogeneous background of the monitor

(averaged luminance:20.2cd/m²). Each category's average pixel intensity was 128.01 and their average RMS contrast was 0.10 (faces) and 0.13 (houses).

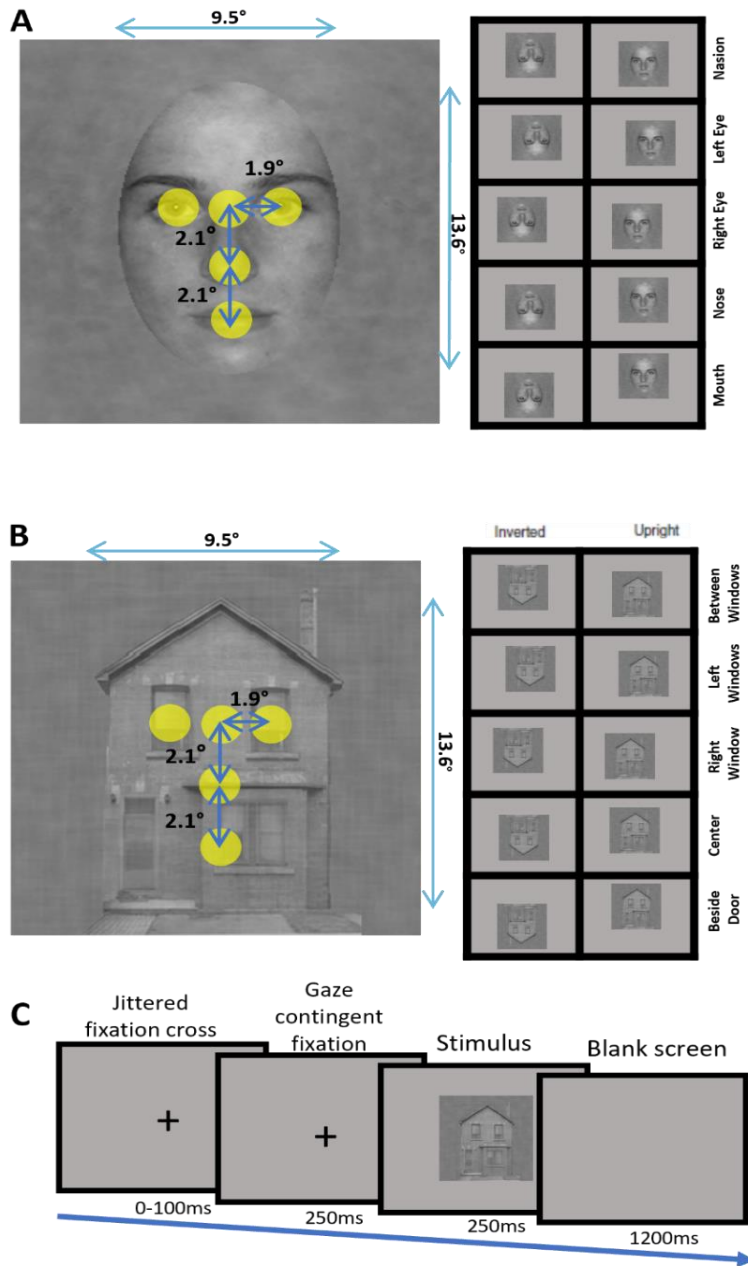


Figure 2-1. Stimuli and procedure

(A) Top left panel: Example of Face stimuli including stimulus size and various distances (measured in visual angles) between fixation location centers. Yellow circles indicate the regions of interest (1.8°) centered on each location; any fixation beyond these regions resulted in the trial's exclusion (refer to details in the text). **Top right panel:** Face Fixation Location conditions with corresponding face stimuli positions on the screen, varying by orientation. Specific fixation locations map directly with face regions (e.g., Beside-the-Door corresponds to the Mouth condition; Between Windows corresponds to the Nasion location, etc.). **(B) Middle left panel:** Example of House stimuli with various angular distances between fixation location centers, each centered within designated regions of interest. **Middle right panel:** Depicts all House Fixation Location conditions with respective house stimuli positions on the screen, varying by orientation. **(C) Bottom panel:** Trial sequence. Each trial began with a jittered fixation cross lasting 0-100ms. Once the eye-tracker confirmed participant fixation for a minimum of 250ms (gaze-contingent fixation), the stimulus appeared for 250ms. The trial concluded with a 1200ms blank screen during which participants provided their responses.

2.2.3 Design and Procedure

The same gaze-contingent paradigm and orientation discrimination task as the Face study from Chapter 1 were used (see section 1.2.3 for more detail).

Both face and house stimuli included 5 fixation locations: Left window (left eye), Right window (right eye), Between-windows (nasion), house Center (nose), and Beside-door (Mouth) (see Fig. 2.1). Participants completed 10 blocks each with 200 trials within it: 100 face trials and 100 house trials (for each category: 50 upright, 50 inverted; 10 per each fixation location per orientation). In total this experiment included 20 conditions created by a 2 Stimulus Type x 2 Orientations x 5 Fixation Locations within-subject design, with 100 trials per condition (2000 trials total). The task was an orientation discrimination task (press button 1 for upright items, button 2 for inverted items, with button assignment counterbalanced across participants). The study took 2 hours.

2.2.4 Electrophysiological and eye tracking recordings

The same EEG and eye tracker systems were used for recording as in Chapter 1, as well as the same recording parameters (section 1.2.4 for more details).

2.2.5 Preprocessing of EEG data

The preprocessing of the data followed the same steps as in Chapter 1, including removing incorrect trials and trials where fixation deviated by 1.8° or more from the fixation

location interest area center (section 1.2.5). After artefact rejection, the average number of trials per conditions per participant was 70.63 (SD = 11.03; Appendix Table 2 for trial number per condition). Participant with trial numbers lower than 20/100 trials in a single condition were removed from the analysis (2 participants were lost at this stage).

2.2.6 Statistical analyses of ERP data

As in Chapter 1, LIMO was used to perform mass univariate ANOVAs at each time point and electrode (same Matlab and LIMO versions used; section 1.2.6). The parameter estimates for this study were first examined using a 2 (Stimulus type) x 2 (Orientation) x 5 (Fixation Location) repeated measures ANOVA using $\alpha = 0.05$ and TFCE correction. We report below the main findings and interactions, followed by separate analyses for face and house stimuli.

2.3 Results

2.3.1 Omnibus analysis with Face and House stimuli

The 2 (Stimulus type) x 2 (Orientation) x 5 (Fixation Locations) repeated measures ANOVA revealed that all main effects (Appendix Fig.1b) and interactions (Fig.2.2) reached the threshold of significance using the TFCE correction.

Given the significant Stimulus Type by Orientation by Fixation Location three-way interaction and given our goal to replicate the effects described in Chapter 1, the face and house stimuli were analyzed separately first; we discuss the three-way interaction next.

2.3.2 Face stimuli analyzed separately.

Face stimuli were analyzed separately in LIMO using a 2 (Orientation) x 5 (Fixation Location) repeated measures ANOVA (Bonferroni corrected $\alpha = 0.025$) with TFCE correction (Fig. 2.3).

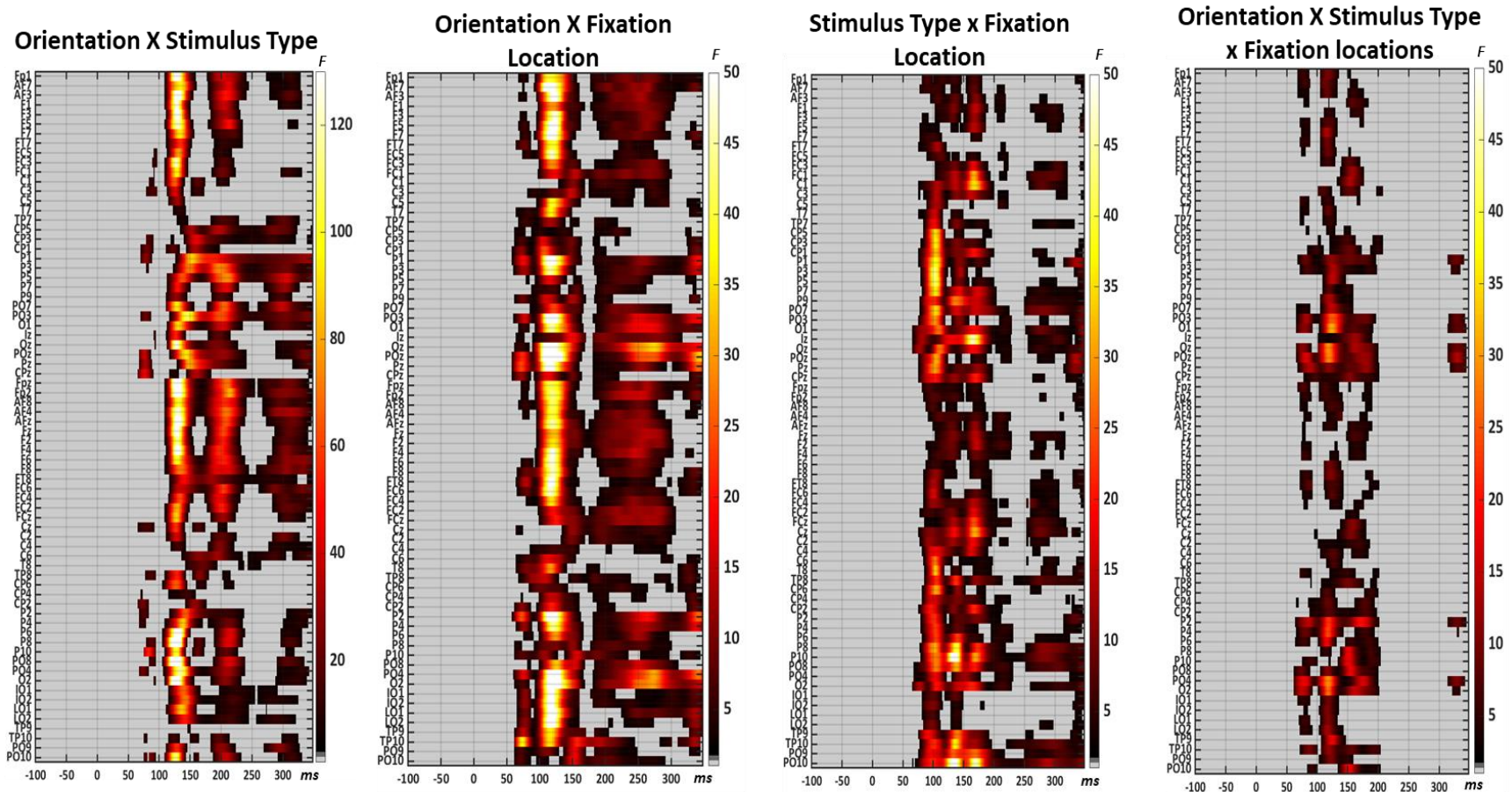
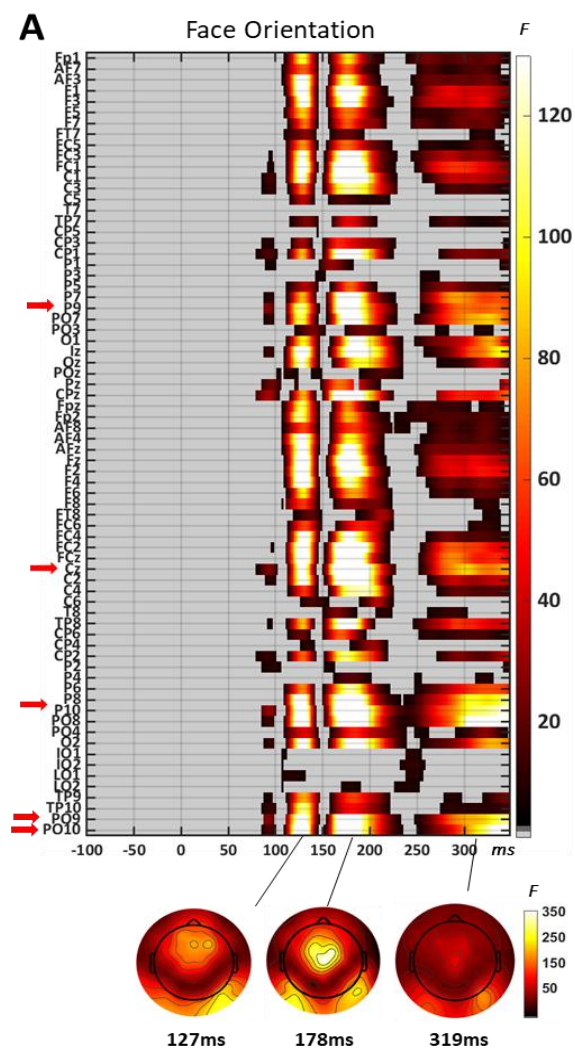


Figure 2-2. All interaction effects between Orientation, Stimulus type, and Fixation Location.

Each of these raster plots were created with an $\alpha = .05$ and TFCE correction applied. The raster plots depict the significant F -values at every electrode (72, y axis) and time-point (-100 to +350ms) analyzed (magnitude of the F -values according to the coloured scale).

2.3.2.1 Main effect of Orientation for Faces

The effect of Orientation was significant across the scalp from 78ms to 350ms, with the peak of this effect occurring at 178ms on electrode Cz ($F(1, 79) = 349.49, p < .001$; Fig. 2.3A). Three prominent “bands” of significance were seen across the scalp with a small early band that covered central and posterior electrodes. The first small, early and sparse band was seen from 78-106ms with a local maximum at 94ms on CPz ($F(1, 79) = 34.92, p < .001$). During this timeframe, amplitudes were more negative for inverted than upright faces just before the ramping part of the P1 peak. The next band was the first of the three prominent bands and spanned 106-153ms, encompassing the P1-N170 transition and the N170 peak, with larger and later N170 peak for inverted faces. The local maximum for this band was seen at 127ms on PO10, that is, *before* the N170 peak, in the middle of the P1-N170 interval ($F(1, 79) = 219.67, p < .001$; Fig 2.3B., first vertical lines on PO9/PO10; Table 2.1). Frontal and central electrodes showed the reversal of this N170 pattern with the Vertex Positive Potential (VPP). The VPP is seen on fronto-central midline electrodes which exhibited more positive amplitudes for inverted than upright faces (Fig. 2.3B, Cz). The second prominent band spanned 149-235ms across the scalp with the statistical peak at 178ms on electrode Cz. This band corresponded to the N170-P2 interval *after* the N170 peak with inverted faces eliciting more negative amplitudes than upright faces at posterior sites (second vertical line on PO10). The final band of significance appeared from 240ms until the end of the epoch across most of the scalp. The local maximum of this band occurred on PO8 at 319ms ($F(1, 79) = 219.67, p < .001$; Table 1), where amplitudes were most negative for inverted faces (Fig. 2.3B).



B

- Inverted Faces (95% CI)
- Upright Faces (95% CI)
- Inverted - upright Faces (95% CI)
- Cluster mass significance
- TFCE significance

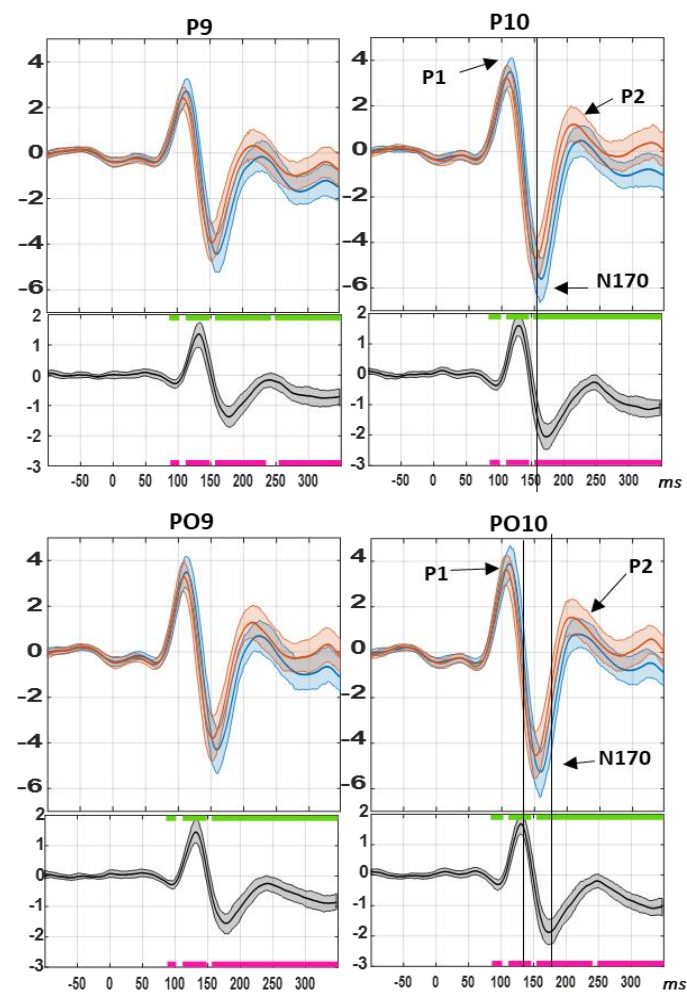
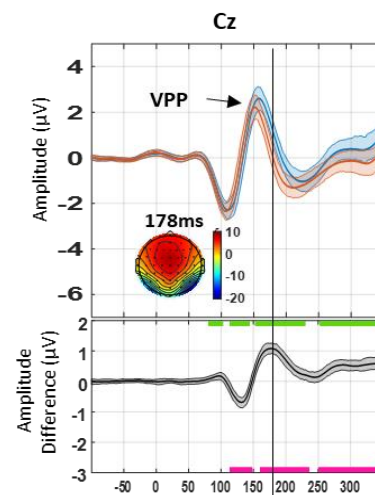


Figure 2-3. Face Inversion Effect (FIE).

(A) This section displays a raster plot of the main effect of orientation, with a significance threshold set at $\alpha = .025$ and TFCE correction applied. The raster plot illustrates significant F -values across 72 electrodes (represented on the y-axis) and over time (ranging from -100 to +350ms) with the magnitude of the F -values indicated according to the colour scale. Below the raster plot are topographic maps showing the uncorrected and unthresholded F -values at three specific time points (127ms, 178ms, and 319ms) where the local maxima for the FIE were observed. Red Arrows on the side of the Raster plot indicated the electrodes seen in the ERP plots to the right. **(B)** ERP amplitudes at five key electrodes, which are highlighted by red arrows in part (A). The ERP waveforms for inverted faces are displayed in blue, while those for upright faces are shown in red. The difference between the inverted and upright faces is depicted in black in the lower panels, and each line is accompanied by their respective 95% confidence intervals. The topographic map on electrodes Cz presents the voltage differences between the upright and inverted conditions across the scalp at 178ms (colour scale ranging from -20 μ V to +10 μ V). The green bar at the top of the difference wave plots indicates the time points where the main effect of orientation for faces was significant for these electrodes, as determined by cluster-mass correction. The pink bar at the bottom of the plots shows the same significant time points as determined by TFCE correction (see text for details and Appendix fig. 1 for uncorrected effects). Vertical black lines highlight the correlation between the peak of the FIE and its temporal position on the actual ERPs. Notably, the FIE peaks are observed during the transition periods between the P1-N170 and N170-P2 components.

Table 2-1. All Interaction effects between orientation, stimulus, and fixation location.

Electrodes included in the “bands” of activation and their timing. The electrode and timing of local *F*-value maxima are also displayed.

Interaction (N=80)	Timing	Electrodes	Local <i>F</i> -value Maxima
Orientation X Stimuli	66ms- 96ms	FC5, FC3, FC1, C1, C3, CP3, CP1, P1, P3, PO3, Iz, Oz, POz, Pz, CPz, Cz, TP8, CP4, CP2, P2, P4, P8, P10, PO8, PO4, O2, TP10, PO10	P10 at 83ms ($F(1, 79) = 53.36, p < .001$)
	105ms- 166ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP10, PO9, PO10	P8 at 129ms ($F(1, 79) = 186.58, p < .001$) (peak of the entire effect)
	179ms- 255ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP10, PO9, PO10	FP2 at 212ms ($F(1, 79) = 82.01, p < .001$)
	257ms- 350ms	Fp1, AF7, AF3, F1, F5, FC1, TP7, CP5, CP3, P1, P3, P5, P7, P9, PO7, PO3, O1, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, C2, C4, C6, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO2, TP10, PO9, PO10	P5 at 302ms ($F(1, 79) = 42.55, p < .001$)
Orientation X Fixation Location	59ms–170ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, C5, T7, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	POz at 119ms ($F(4, 76) = 56.75, p < .001$) (peak of the entire effect)
	175ms–350ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, C5, T7, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	Oz at 272ms ($F(4, 76) = 34.59, p < .001$)
Stimuli X Fixation Location	66ms- 225ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, C5, T7, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2,	P10 at 135ms ($F(4, 76) = 61.22, p < .001$)

		AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	(peak of the entire effect)
	251ms–350ms	Fp1, AF7, AF3, F1, F3, F5, FC3, FC1, C1, C3, TP7, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, Fz, F2, F4, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	PO10 at 288ms ($F(4, 76) = 14.21, p < .001$).
Orientation X Stimuli X Fixation Location	63ms- 92ms	Fp1, AF7, AF3, F1, F5, F7, FT7, FC5, C5, T7, TP7, CP5, CP1, P1, P3, PO7, PO3, O1, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F8, FT8, FC6, FC4, T8, TP8, CP4, CP2, P2, P4, P6, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP10, PO10	P2 at 78ms ($F(4, 76) = 18.24, p < .001$)
	101ms- 143ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, C3, C5, T7, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, F2, F4, F6, F8, FT8, FC6, FC4, C2, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9	O1 at 123ms ($F(4, 76) = 31.5, p < .001$) (peak of entire effect)
	148ms– 208ms	Fp1, AF7, AF3, F1, F3, F5, FC5, FC3, FC1, C1, C3, C5, CP5, CP3, CP1, P1, P3, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, TP10, PO9, PO10	Oz at 171ms ($F(4, 76) = 19.89, p < .001$).
	314ms– 344ms	P1, P3, PO3, O1, Oz, POz, Pz, P2, P4, PO4, O2	POz at 328ms ($F(4, 76) = 14.1, p < .001$).

2.3.2.2 Main effect of Fixation Location for Faces

The effect of Fixation Location was significant with TFCE (Fig. 2.4). The Fixation effect appeared less strong (F values < 50) than the Orientation main effect. The differences between fixations were observed from 55ms until the end of the epoch with the peak of the effect occurring at 139ms on electrode P10 ($F(4, 76) = 88.82, p < .001$; Table 2.2). The raster plot appears as two very interconnected bands of significance. The first band spanned $\cong 55$ -226ms and included the statistical peak. The second band occurred from 218ms until the end of the epoch with the local maxima at 346ms on electrode O2 ($F(4, 76) = 32.85, p < .001$).

2.3.2.3 Interaction between Orientation and Fixation Location for Faces

The Interaction between Stimulus Orientation and Fixation Location reached the threshold of significance using TFCE correction (Fig.2.4) and was seen across the scalp from 57ms until the end of the epoch, with the effect maximum occurring at 117ms on electrode POz ($F(4, 76) = 93.17, p < .001$; Table 2.2). The raster plot appears with one prominent band surrounded by two disjointed weaker bands. The first weak band spanned $\cong 57$ -92ms across most of the scalp with its local maxima at 73ms on electrode P2 ($F(4, 76) = 35.94, p < .001$). The second and most prominent band begins $\cong 95$ ms until 175ms with the statistical peak of the effect on electrode POz at 117ms. Finally, the last disjointed band spanned from 175ms until the end of the epoch with its local maxima at 273ms on electrode Oz ($F(4, 76) = 30.03, p < .001$).

We followed-up with two different post-hoc contrasts to better understand this complex interaction. The first follow-up analysis assesses the effect of fixation location separately for upright and inverted faces. The second follow up analysis focuses on the face inversion effect (FIE) at each of the five fixation locations.

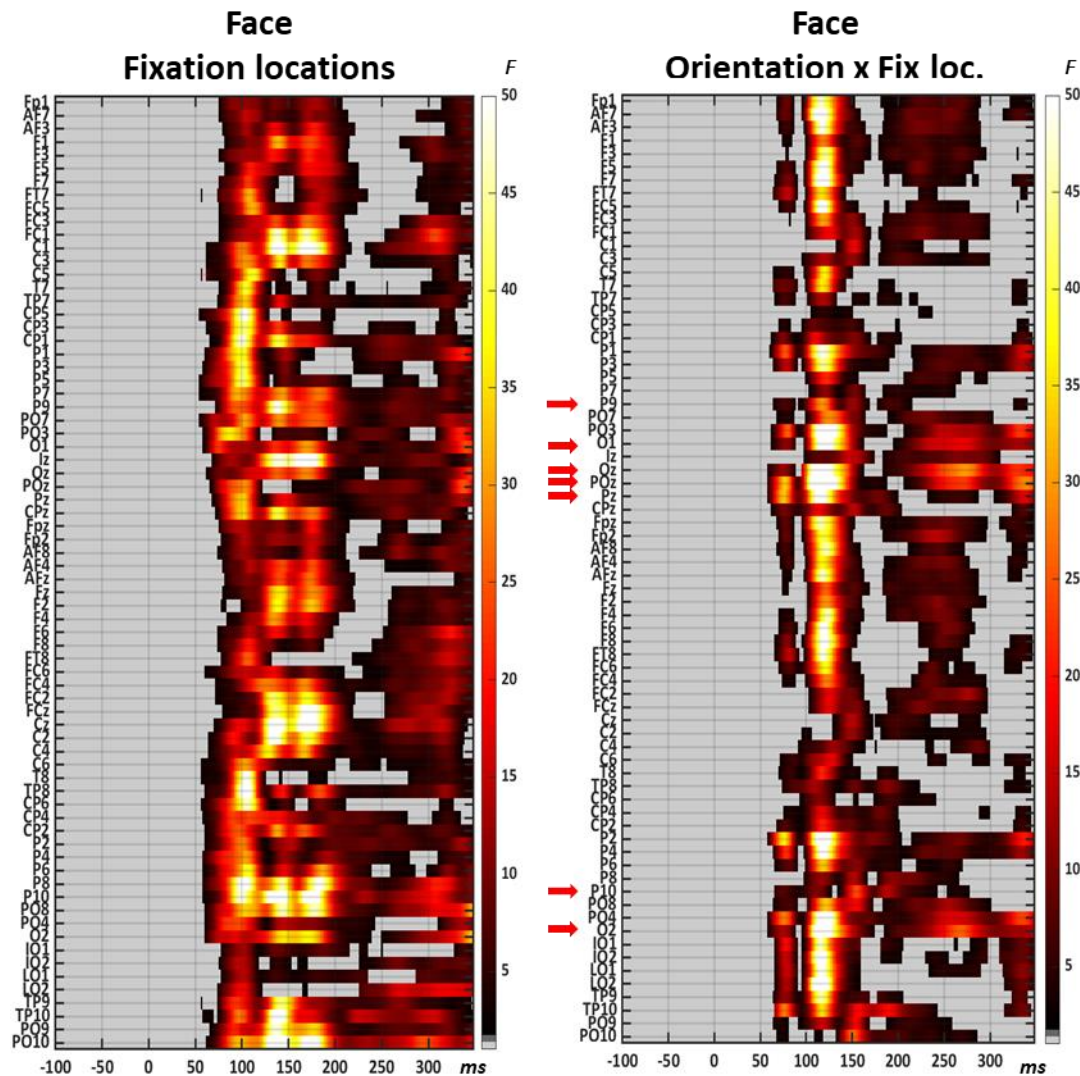


Figure 2-4. Results of the face alone analysis.

The main effects of Fixation Location (**Left panel**) and the interactions between Orientation and Fixation Location (**Right panel**). Both analyses used a significance threshold of $\alpha = .025$ and were subjected to TFCE correction (see text for details and Appendix fig. 1 for uncorrected effects). The raster plots illustrate the significant F -values for each effect across all electrodes (72 in total, shown on the y-axis) and time points (from -100 to +350ms, shown on the x-axis), with the magnitude of these values depicted by the color scale. The arrows on the plots point to specific electrodes that are further examined in Figure 2-7, which focuses on the FIE at each fixation location.

Table 2-2. Main effect of orientation, fixation location and their interaction, for the face only analysis.

Electrodes included in the “bands” of activation obtained for each effect and their timing. The electrode and timing of local *F*-value maxima are also displayed.

Face perception (N=80)	Timing	Electrodes	Local <i>F</i> -value Maxima
Orientation Main Effect	78ms - 106ms	FC3, FC1, C1, C3, CP3, CP1, P1, P7, P9, PO7, Iz, POz, Pz, CPz, FC2, Cz, C2, TP8, CP2, P2, P10, PO8, O2, TP9, TP10, PO9, PO10	CPz at 94ms ($F(1, 79) = 34.92, p < .001$)
	106ms - 153ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, C5, TP7, CP5, CP3, CP1, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, TP8, CP6, CP4, CP2, P2, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	PO10 at 127ms ($F(1, 79) = 219.67, p < .001$)
	149ms - 235ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, C5, TP7, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, LO2, TP9, TP10, PO9, PO10	Cz at 178ms ($F(1, 79) = 349.49, p < .001$) (peak of the entire effect)
	240ms - 350ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, TP7, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, T8, TP8, CP6, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	PO8 at 319ms ($F(1, 79) = 219.67, p < .001$)
Fixation Location Main Effect	55ms - 226ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, C5, T7, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	P10 at 139ms ($F(4, 76) = 88.82, p < .001$) (peak of the entire effect)
	218ms – 350ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, C5, T7, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	O2 at 346ms ($F(4, 76) = 32.85, p < .001$).

Orientation X Fixation Location	57ms - 92ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, C5, T7, TP7, CP3, CP1, P1, P3, P9, PO7, PO3, O1, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F4, F6, F8, FT8, FC6, FC4, C6, T8, TP8, CP4, CP2, P2, P4, P6, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	P2 at 73ms ($F(4, 76) = 35.94, p < .001$)
	95ms - 175ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, C5, T7, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	POz at 117ms ($F(4, 76) = 93.17, p < .001$) (peak of entire effect)
	175ms – 350ms	Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, T7, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, IO1, IO2, LO1, LO2, TP9, TP10, PO9, PO10	Oz at 273ms ($F(4, 76) = 30.03, p < .001$).

2.3.2.3.1 Follow-up contrast#1 - Main Effect of Fixation Location for upright and inverted Faces analyzed separately.

Two repeated measures ANOVA analyses examined the effect of Fixation Location (5 levels) separately for upright and inverted faces (using a Bonferroni corrected $\alpha=0.0125$).

When looking at the effect of Fixation Location for upright faces alone, a significant difference was observed between 57-350ms after face presentation with TFCE correction (Fig. 2-5A). The statistical peak of this effect occurred at 113ms on electrode POz ($F(4, 76) = 108.09, p < 0.001$). At Pz, a C2 component was seen, with positive amplitude for mouth followed by nose fixations, negative amplitude for nasion fixation, and amplitude around zero for the eye fixations (Fig. 2-5B). At Oz and especially POz, this amplitude gradient was seen even more clearly on the P1 component, with the smallest and earliest P1 peak for Nasion fixation followed by Eyes, then Nose and finally latest and largest P1 for Mouth fixation (Fig. 2-5B occipital sites, top row, and POz). At posterior lateral electrodes (PO9/PO10) the eye fixations exhibited the largest P1 amplitude ipsilaterally followed by the Nasion, Nose, and Mouth (Fig. 2-5B). After the P1, these eye fixations consistently showed the largest N170 amplitudes, followed by nasion, nose and mouth. More negative amplitudes for eyes than other fixations continued during the N170-P2 interval, including the P2 peak, with the difference being largest around 170ms, i.e. *after* the N170 peak (see second peak of F values on PO9/PO10, amplitude difference graph and vertical line on Fig. 2-5B). After the P2, less defined significant amplitude differences were seen until the end of recording, although amplitudes for mouth fixation were largest overall.

Figure 2-5. Fixation Location effect for Upright Faces analyzed separately.

(A) The raster plot shows the main effect of fixation location with a TFCE correction ($p < 0.0125$). The raster plot illustrates the significant F -values across all electrodes (72 in total, shown on the y-axis) and time points (from -100 to +350ms, shown on the x-axis), with the magnitude of these values depicted by a colour scale. Red Arrows on the side of the Raster plot indicate the electrodes seen in the ERP plots to the right. **(B)** The five fixation location conditions are displayed at seven representative posterior electrodes. For each electrode, three types of plots are presented. The top plots display the group average ERPs for each fixation location, with central tendency computed using raw means for single-subject trials and 20% trimmed means across subjects. The middle plots show the difference waves between pairs of conditions. The green bar at the top of these plots indicates the time points where the main effect of fixation location was significant using the cluster-mass correction, while the pink bar at the bottom indicates significant time points using the TFCE correction (see text for details and Appendix fig. 1 for uncorrected effects). The bottom plots illustrate the time courses of the F -values obtained for each contrast comparing pairs of fixation locations. The topographic map on electrode POz shows the amplitude difference between mouth and nasion fixations (M-N) across the scalp, with a $-2\mu\text{V}$ to $+6\mu\text{V}$ colour scale, at 113ms where this difference is maximal. Solid vertical black lines indicate the temporal correspondence between the peaks of the paired contrasts and their locations on the actual ERPs, corresponding to the C2 at POz and the P1 at Oz. The dashed vertical black line highlights that weak F values were observed at the peak of the N170.

For inverted faces, a significant effect of Fixation Location was observed between 59ms and 350ms after stimulus presentation using TFCE correction (Fig. 2-6A). The statistical peak was seen on electrode TP8 at 102ms ($F(4, 76) = 97.1, p < 0.001$). At Pz, a C2 component was again seen, this time with negative amplitude for mouth fixation and positive-going amplitudes for the other fixations (Fig 2-6B). The occipital electrodes showed a gradient of amplitude across fixations on the P1, in the opposite direction as seen with upright faces, with the smallest and earliest P1 seen for Mouth followed by Nose, contralateral Eye, Nasion, and ipsilateral Eye (Fig. 2-6B top row). The larger P1 for the ipsilateral than contralateral eye at O1 and O2 was more pronounced for inverted than for upright faces. Largest N170 peaks were also seen for eye fixations, again more pronounced for the ipsilateral eye, followed by the other fixations with smallest N170 seen for mouth fixation. Again, more negative amplitudes were seen during the N170-P2 interval for eye fixations at PO9/PO10 while mouth fixation elicited the smallest amplitude at occipital and Pz/POz sites until the end of the epoch.

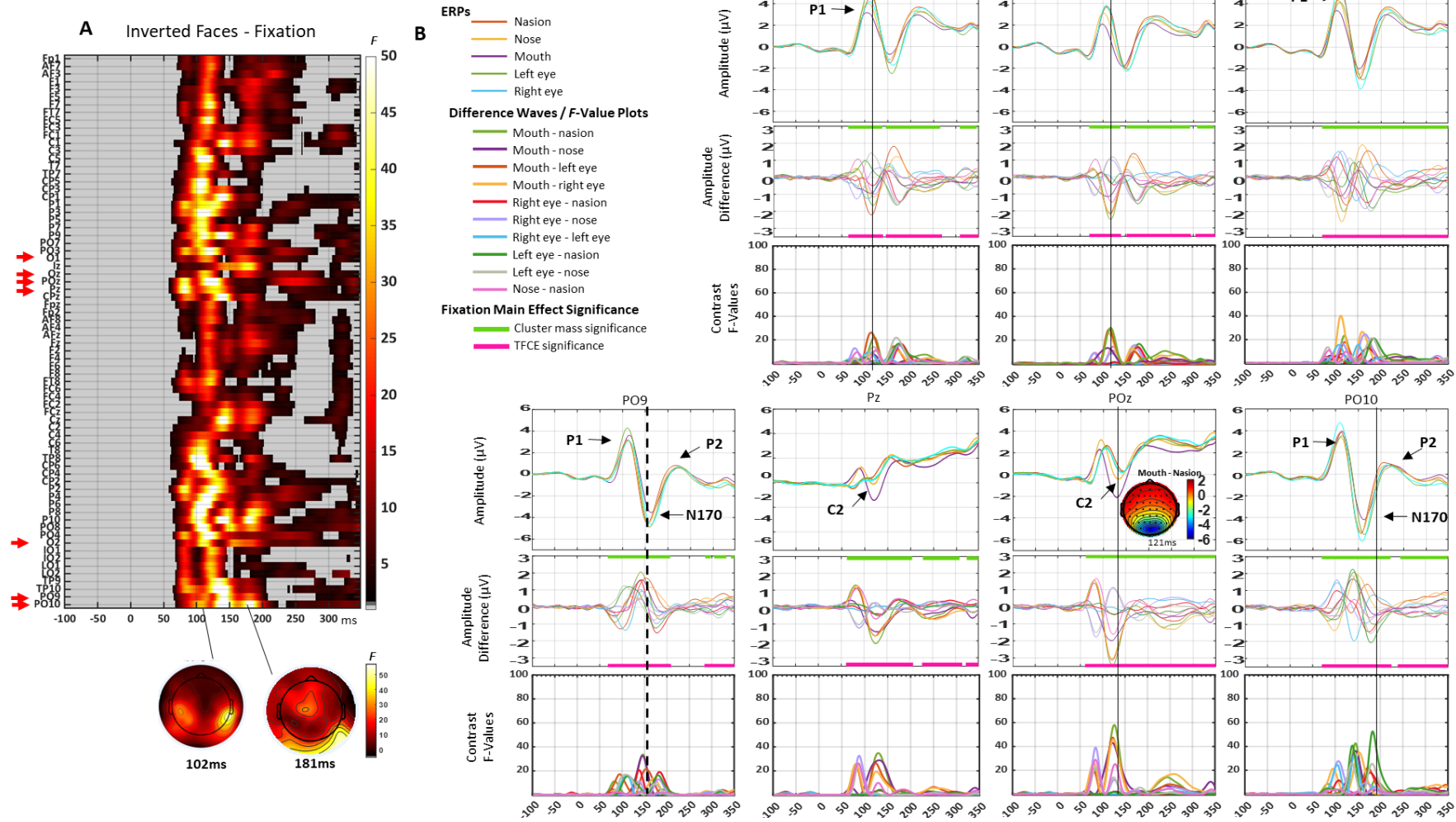


Figure 2-6. Fixation Location effect for Inverted Faces analyzed separately.

(A) The raster plot shows the main effect of fixation location with a TFCE correction ($p < 0.0125$). The raster plots illustrate the significant F -values for each effect across all electrodes (72 in total, shown on the y-axis) and time points (from -100 to +350ms, shown on the x-axis), with the magnitude of these values depicted by a colour scale. Red Arrows on the side of the Raster plot indicated the electrodes seen in the ERP plots to the right. **(B)** The five fixation location conditions are displayed at seven representative posterior electrodes. For each electrode, three types of plots are presented. The top plots display the group average ERPs for each fixation location, with central tendency computed using raw means for single-subject trials and 20% trimmed means across subjects. The middle plots show the difference waves between pairs of conditions. The green bar at the top of these plots indicates the time points where the main effect of fixation location was significant using the cluster-mass correction, while the pink bar at the bottom indicates significant time points using the TFCE correction. The bottom plots illustrate the time courses of the F -values obtained for each contrast comparing pairs of fixation locations. The topographic map on electrode POz shows the amplitude difference between mouth and nasion fixations (M-N) across the scalp, with a $-6\mu\text{V}$ to $+2\mu\text{V}$ colour scale, at 121ms where this difference was maximal. Solid vertical black lines indicate the temporal correspondence between the peaks of the paired contrasts and their locations on the actual ERPs, corresponding to the C2 at POz and the P1 at Oz. The dashed vertical black line highlights that weak F values were observed at the peak of the N170.

2.3.2.3.2 Follow-up contrasts #2: Face Inversion Effect at each Fixation Location

Five *F*-contrasts evaluating the FIE for each fixation location were created using a significance threshold of $p < 0.01$ to account for the number of contrasts performed.

For most fixation locations, the FIE showed a statistical peak around 115-127ms at parietal and occipital sites. At Pz, the FIE was seen as a positive C2-like component for nasion fixation, with a negative C2-like component for mouth fixation, due to opposite polarity of the C2 between upright and inverted conditions for these fixation locations. At occipital sites, the 115-127ms timing corresponded to the P1 peak which amplitude was larger for inverted than upright faces for all fixations except for mouth fixation, for which the inverse pattern was seen, with larger amplitude for upright than inverted faces (Fig. 2.7). At POz, where the statistical peak of the interaction was found (at 117ms, see earlier section), the FIE showed the largest *F*-values for mouth fixation, followed by nasion fixation and then the eye fixations, while the smallest *F* values were seen for the nose fixation (Fig. 2.7). At occipital sites, especially O2, nasion elicited the strongest FIE *F* values. At lateral parietal sites where the N170 is typically measured (e.g., P9/P10), the FIE was weaker during the P1-N170 interval compared to occipital sites. However, during the N170-P2 interval (i.e. between 150-230ms), the FIE showed a second peak of *F* values where the nose and contralateral eye fixations elicited strongest FIE. The FIE remained small until the end of the epoch (200-350ms) and was still seen in opposite direction for mouth and nasion fixations at POz.

Face ERPs



FIE Difference Waves and F-Value Plots



Fixation Main Effect Significance

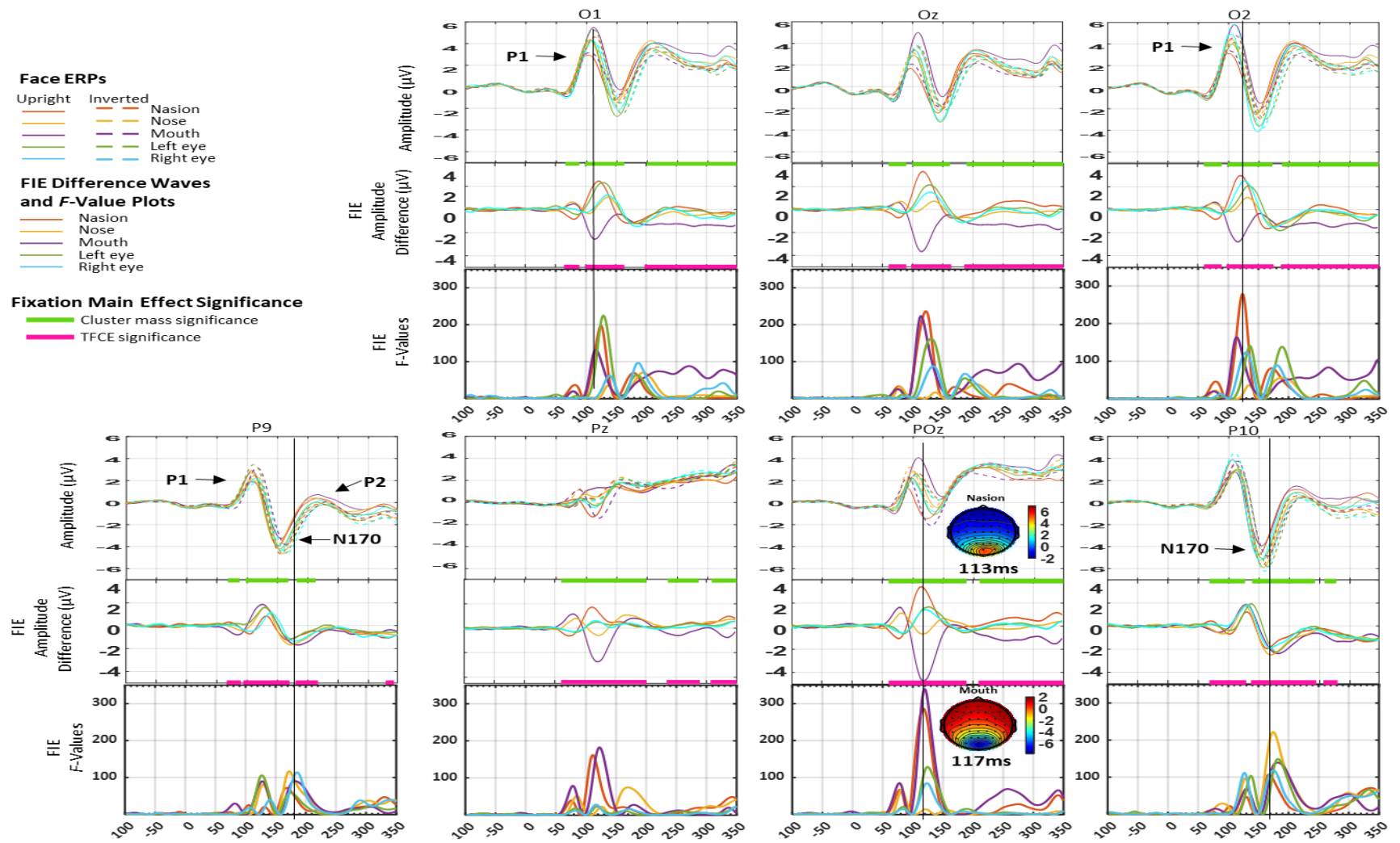
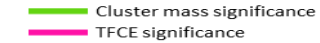


Figure 2-7. Face Inversion Effect (FIE) Across Individual Fixation Locations.

This analysis focuses on seven representative posterior electrodes (outlined by the red arrows in Figure 2-4). The top graphs display the ERPs for upright (solid lines) and inverted faces (dotted lines) for each fixation location. The middle plots show the actual FIE, represented as the amplitude difference between inverted and upright faces at each fixation location. The green bar at the top of these plots indicates the time points where the Orientation by Fixation Location interaction was significant using the cluster-mass correction, while the pink bar at the bottom indicates significant time points using the TFCE correction (see text for details and Appendix fig. 1 for uncorrected effects). The topographic maps on electrode POz illustrate the FIE across the scalp at the time points where the FIE was largest: 113 ms for the nasion fixation (-2 μ V to +6 μ V colour scale; top map) and at 117 ms for the mouth fixation (-6 μ V to +2 μ V colour scale; bottom map). Note the opposite effects observed for nasion and mouth fixations. The bottom plots display the time courses of the *F*-values obtained for each fixation location contrast (inverted vs. upright conditions) at these electrodes. Note how the FIE varies with fixation location and electrodes, with the largest effect observed for fixation on the nasion at occipital sites (see text for further details).

2.3.3 House stimuli analyzed separately.

2.3.3.1 Main effect of Orientation for House

House stimuli were analyzed separately in LIMO using a 2 (Orientation) x 5 (Fixation Location) repeated measures ANOVA ($\alpha = 0.025$) with TFCE correction.

A significant difference between upright and inverted house stimuli was observed from 66ms to 350ms with the difference peak occurring at 191ms on electrode FC2 ($F(1, 79) = 415.91, p < 0.001$; Fig. 2.8A). The LIMO raster plot revealed 2 prominent bands with a third band that was very sparse. The sparse band occurred first and spanned $\cong 66$ -84ms, the second prominent band spanned $\cong 106$ -244ms and the third started at $\cong 246$ ms and continued until the end of the epoch. Local maxima were also seen at 76ms on POz ($F(1, 79) = 51.67, p < 0.001$), at 191ms on FC2 ($F(1, 79) = 415.91, p < 0.001$), and at 325ms on PO8 ($F(1, 79) = 249.57, p < 0.001$, Table 2.3, Fig. 2-8A-B). The ERP amplitude and amplitude difference wave graphs show the extent of the TFCE corrected significance (pink line) on the electrodes at which local F value maxima were seen (see Table 2.3; Fig. 2-8B). When looking at the ERP waves at posterior sites, the significant differences included the P1 peak (e.g. at PO8) and continued until the end of the epoch, encompassing the N170 and P2 components. At these sites, the inversion effect was in the typical direction with more negative N170 amplitudes for inverted than upright houses. Around the P1 and P2 components, amplitudes were more positive for upright than inverted items at some sites (e.g. PO8) although at other sites like PO9, the P1 was larger for inverted than upright houses. The pattern was seen polarity reversed at frontal sites (e.g. FC2 showing a VPP-like component, Fig. 2-8B).

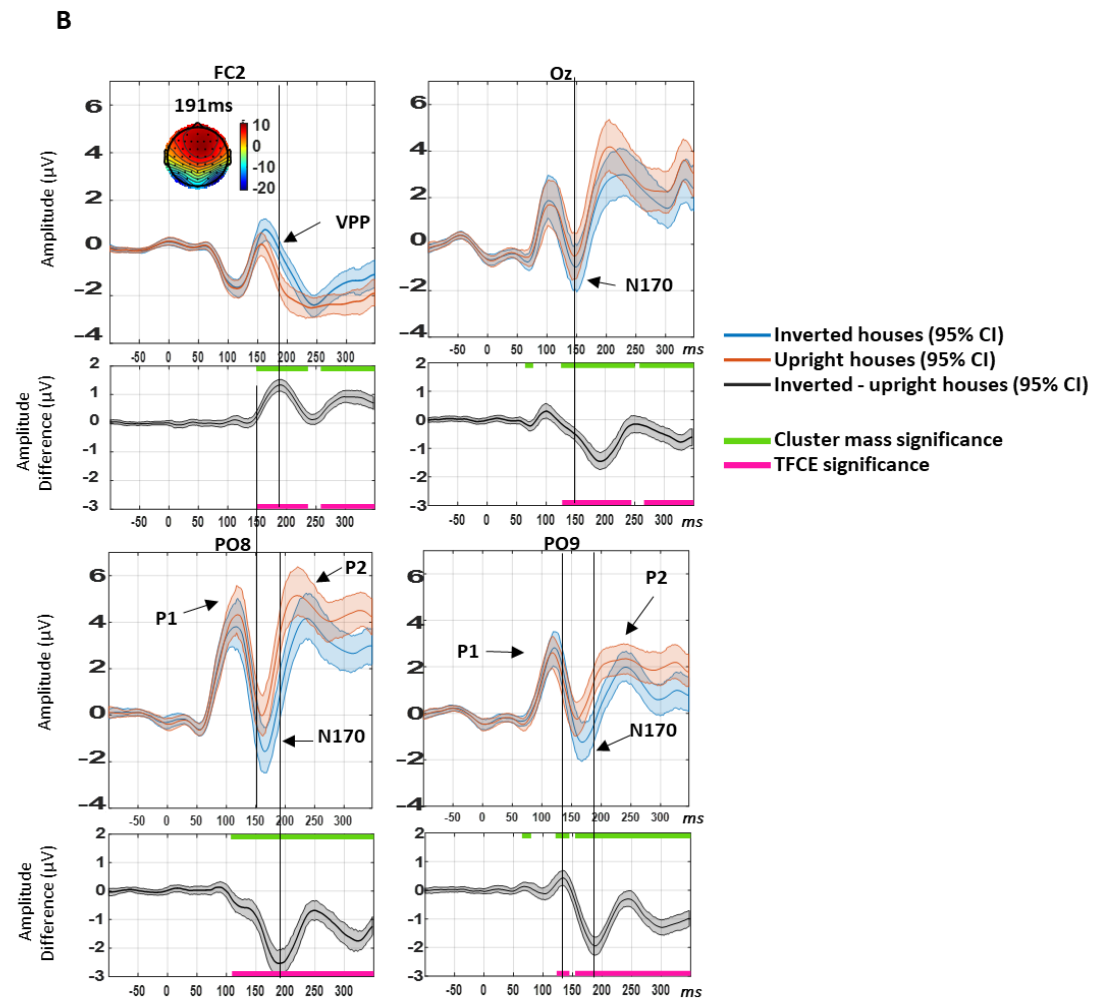
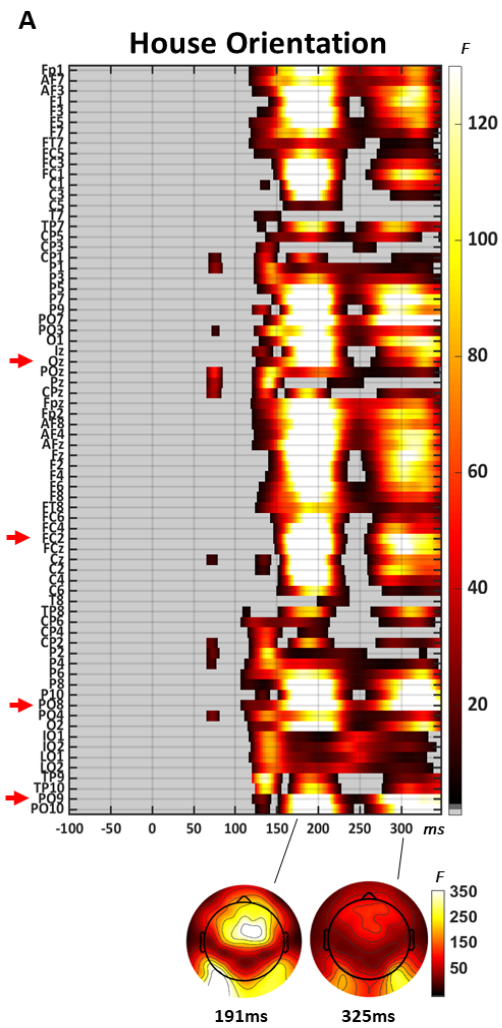


Figure 2-8. House Inversion Effect (HIE).

(A) This section displays a raster plot of the main effect of orientation, with a significance threshold set at $\alpha = .025$ and TFCE correction applied. The raster plot illustrates significant F -values across 72 electrodes (represented on the y-axis) and over time (ranging from -100 to +350ms) with the magnitude of the F -values indicated according to the colour scale. Below the raster plot are topographic maps showing the unthresholded and uncorrected F -values at two specific time points (191ms and 325ms) where the local maxima for the HIE were observed. Red Arrows on the side of the Raster plot indicate the electrodes seen in the ERP plots to the right. **(B)** This image displays the HIE on ERP amplitudes at four key electrodes, which are highlighted by red arrows in part (A). The ERP waveforms for inverted houses are displayed in blue, while those for upright houses are shown in red. The difference between the inverted and upright houses is depicted in black in the lower panels, and each line is accompanied by their respective 95% confidence intervals. The topographic map on electrodes FC2 presents the voltage differences between the upright and inverted conditions across the scalp at the local maxima at 191ms (colour scale ranging from -20 μ V to +10 μ V). The green bar at the top of the difference wave plots indicates the time points where the main effect of orientation for houses was significant for these electrodes, as determined by cluster-mass correction. The pink bar at the bottom of the plots shows the same significant time points as determined by TFCE correction (see text for details and Appendix fig. 1 for uncorrected effects). Vertical black lines highlight the correspondence between the peak of the HIE and its temporal position on the actual ERPs. Notably, HIE peaks are observed during the transition periods between the P1-N170 and N170-P2 components.

Table 2-3. Main effect of orientation, fixation location and their interaction, for the house only analysis.

Electrodes included in the “bands” of activation obtained for each effect and their timing. The electrode and timing of local F -value maxima are also displayed.

House perception (N=80)	FIE contrasts (inv-up) for each Fixation location	Timing	Max electrode - peak latency	Peak statistics and amplitude difference
	Between Windows	66ms - 142ms	TP9 - 136ms	$F(1, 79) = 84.52, p < .001, \Delta 1.1\mu V$
		139ms - 235ms	PO7 - 188ms	$F(1, 79) = 239.07, p < .001, \Delta -2.32\mu V$
		253ms - 350ms	PO8 - 317ms	$F(1, 79) = 101.72, p < .001, \Delta -1.68\mu V$
	Center	111ms - 241ms	PO7 - 193ms	$F(1, 79) = 209.61, p < .001, \Delta -2.32\mu V$
		243ms - 350ms	PO8 - 327ms	$F(1, 79) = 149.54, p < .001, \Delta -1.8\mu V$
	Beside-the-Door	94ms - 350ms	PO4 - 121ms	$F(1, 79) = 245.9, p < .001, \Delta -3.35\mu V$
	Right Window	65ms - 118ms	POz - 75ms	$F(1, 79) = 56.55, p < .001, \Delta -0.93\mu V$
		124ms - 252ms	PO7 - 193ms	$F(1, 79) = 182.75, p < .001, \Delta -2.17\mu V$
		247ms - 350ms	PO7 - 308ms	$F(1, 79) = 126.08, p < .001, \Delta -1.64\mu V$
	Left Window	94ms - 118ms	Pz - 107ms	$F(1, 79) = 44.67, p < .001, \Delta 1.04\mu V$
		132ms - 237ms	PO7 - 190ms	$F(1, 79) = 208.91, p < .001, \Delta -2.17\mu V$
		250ms - 350ms	P7 - 295ms	$F(1, 79) = 121.35, p < .001, \Delta -1.32\mu V$

2.3.3.2 Main effect of Fixation Location for Houses

There was a significant main effect of Fixation Location for houses with TFCE correction. The significant differences were observed from 41ms until the end of the epoch across the scalp (Fig. 2-9). Just like for faces, the Fixation location effect was weaker than the effect seen for orientation ($F < 50$). The peak of this effect was seen at 199ms on electrode PO8 ($F(4, 76) = 41.02, p < .001$; Fig. 2-9). No clear pattern emerged from the raster plot. Once again, the Fixation Location significantly interacted with Orientation for houses which is discussed in further detail below.

2.3.3.3 Interaction between Orientation and Fixation Location for Houses

The Interaction between Fixation Location and Orientation showed significant differences with TFCE correction from 61ms until the end of the epoch across the scalp. The peak of this effect was observed at 117ms on electrode POz ($F(4, 76) = 56.75, p < .001$; Fig. 2-9). The raster plot is characterized by a single prominent band followed by a disjointed and weaker band. The prominent band spanned 61-170ms and included the statistical peak of the interaction. The second disjointed band spanned from about 155ms until the end of the epoch with the local maxima occurring on POz at 249ms ($F(4, 76) = 17.71, p < .001$; Fig. 2-9). Just like for the face analysis, we followed-up with two different post-hoc contrasts to better understand this complex interaction.

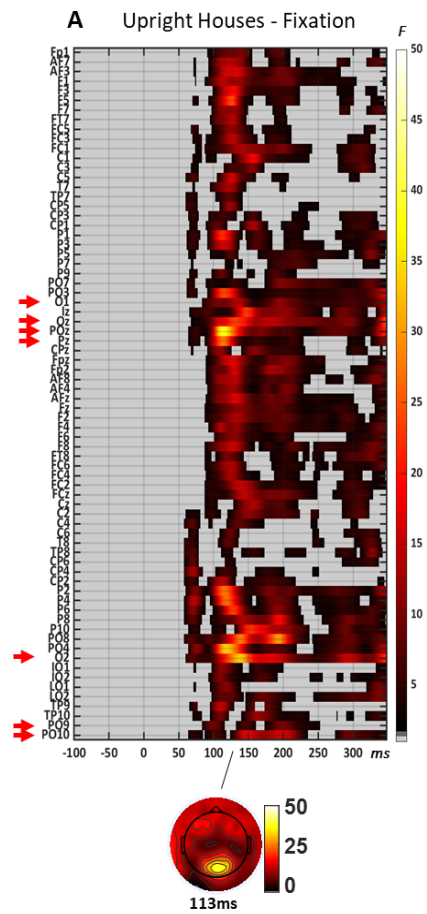
2.3.3.3.1 Follow-up contrast#1 - Main Effect of Fixation Locations for upright and inverted Houses analyzed separately.

Two repeated measures ANOVA using the factor Fixation Location (5 levels) were run separately for the upright and inverted house data (using $\alpha=0.0125$).

For upright houses, the effect of Fixation Location was significant with TFCE correction between 59-350ms (Fig. 2-10A). The statistical peak of this analysis was observed at 113ms on electrode POz ($F(4, 76) = 38.83, p < 0.001$; Fig. 2-10A), corresponding to the C2 component. At Pz, C2 was positive for the Beside-Door fixation and negative for the other fixations. At occipital sites, P1 was largest and latest for the Beside-Door fixation followed by the Right Window, Center, Left Window, with the smallest amplitude seen for the Between-Windows fixation (Fig. 2-10B, occipital sites, top row). The amplitude gradient was visible at occipital sites but attenuated at POz. Next, the N170 ERP component at posterior lateral sites also showed somewhat of a gradient. At PO10, largest N170 amplitudes were seen for Right Window and Between-Windows, followed by Left Window and Center, and the smallest N170 peak was seen for the Beside-Door fixation. At PO9, the N170 was largest for Between-Windows, followed by Left Window, Right Window, Center, and again smallest for Beside-Door fixation. This gradient largely held up for the N170-P2 interval although differences were seen between electrodes. Around the P2 component, amplitudes were consistently largest for Beside-Door and Center fixations; the pattern was less consistent after the P2.

Similarly, the effect of Fixation Location was significant for inverted houses using TFCE correction, between 57ms and 350ms after stimulus presentation, and was a bit less extant than for upright houses. The peak of this effect also occurred on electrode POz at 113ms ($F(4, 76) = 54.54, p < 0.001$; Fig. 2.11A). At Pz, the C2 was most negative for the Beside-Door fixation (i.e. the opposite of what was seen for upright houses) but less negative for the other fixations. At POz and occipital electrodes, the ERP waves consistently showed that P1

was smallest for the Beside-Door fixation, followed by Center fixation, however, no other clear pattern emerged from the other fixation locations.



B

ERPs

- Between-Windows (BW)
- Center
- Beside-Door (BD)
- Left Window
- Right Window

Difference Waves / F-Value Plots

- Beside-Door - Between Windows
- Beside-Door - Center
- Beside-Door - Left Window
- Beside-Door - Right Window
- Right Window - Between Windows
- Right Window - Center
- Right Window - Left Window
- Left Window - Between Windows
- Left Window - Center
- Center - Between Windows

Fixation Main Effect Significance

- Cluster mass significance
- TFCE significance

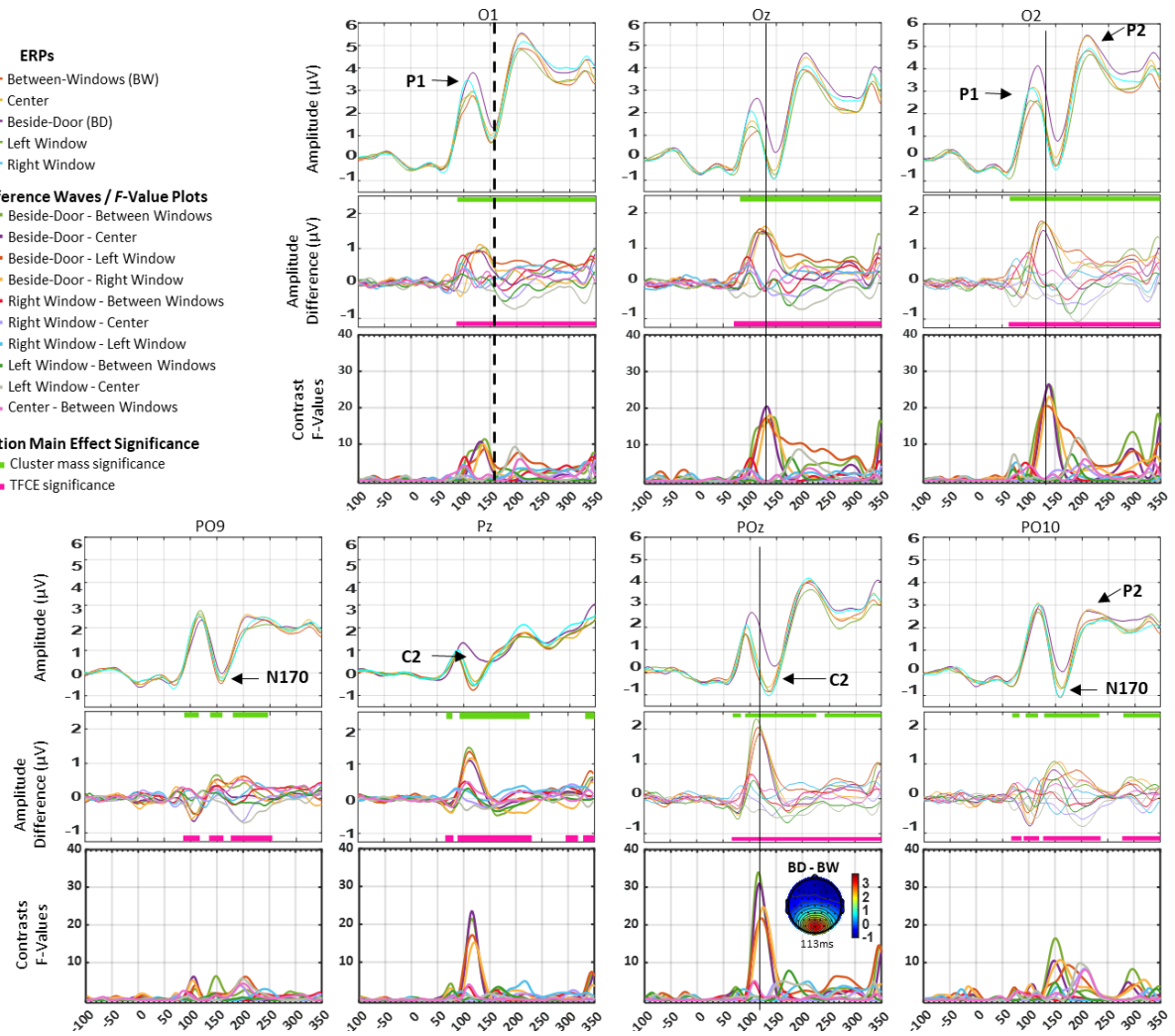


Figure 2-10. Fixation Location effect for Upright Houses analyzed separately.

(A) The raster plot shows the main effect of fixation location with a TFCE correction ($p < 0.0125$). Red Arrows on the side of the Raster plot indicate the electrodes seen in the ERP plots to the right. (B) The five fixation location conditions are displayed at seven representative posterior electrodes. For each electrode, three types of plots are presented. The top plots display the group average ERPs for each fixation location, with central tendency computed using raw means for single-subject trials and 20% trimmed means across subjects. The middle plots show the difference waves between pairs of conditions. The green bar at the top of these plots indicates the time points where the main effect of fixation location was significant using the cluster-mass correction, while the pink bar at the bottom indicates significant time points using the TFCE correction. The bottom plots illustrate the time courses of the F -values obtained for each contrast comparing pairs of fixation locations. The topographic map on electrode POz shows the amplitude difference between Beside-the-Door and Between-Windows fixations (BD-BW) across the scalp, with a $-1\mu\text{V}$ to $+3\mu\text{V}$ colour scale, at 113 ms where this difference is maximal. Solid vertical black lines indicate the temporal correspondence between the peaks of the paired contrasts and their locations on the actual ERPs, corresponding to the C2 at POz and the P1 at Oz. The dashed vertical black line highlights that weak F values were observed at the peak of the N170.

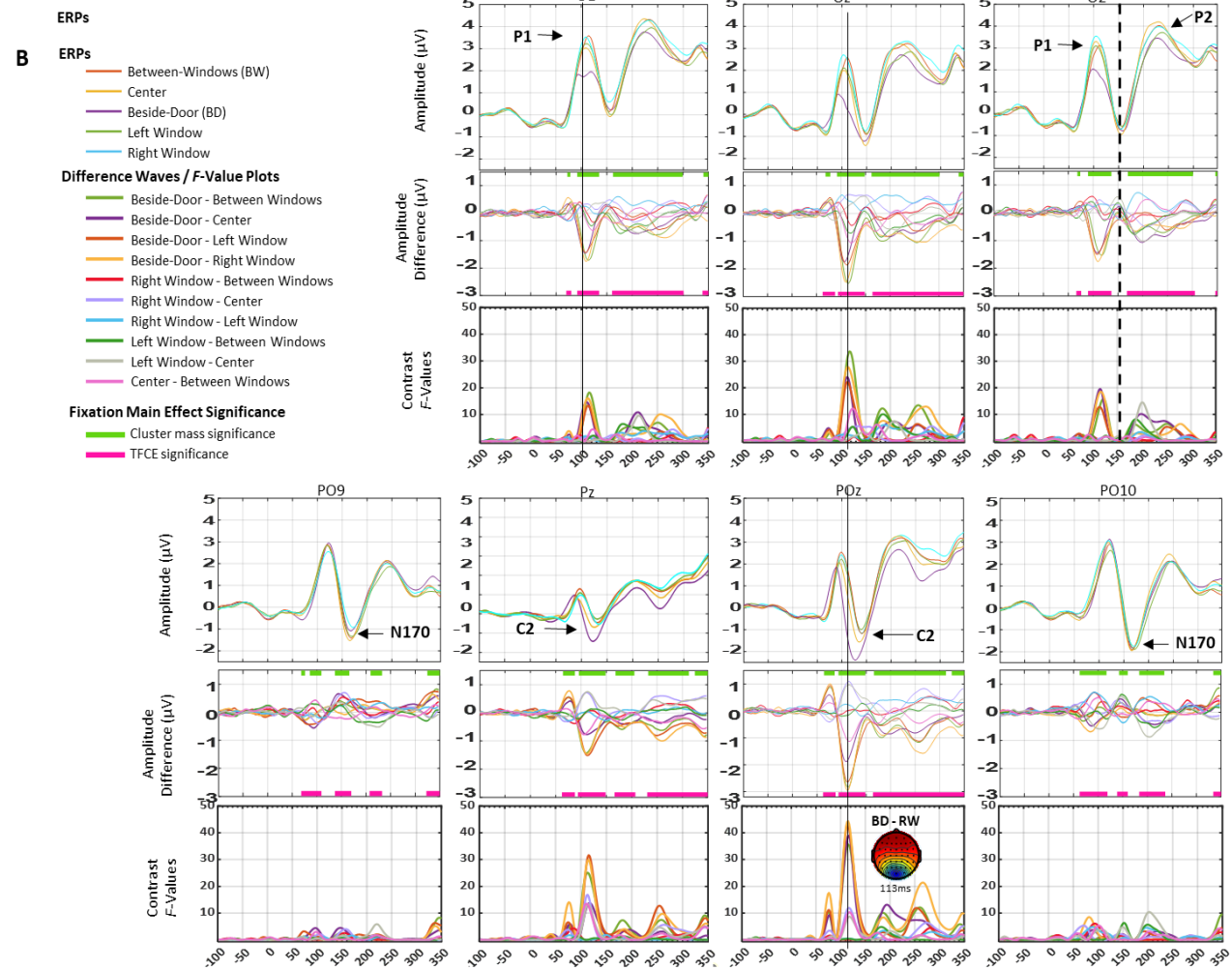
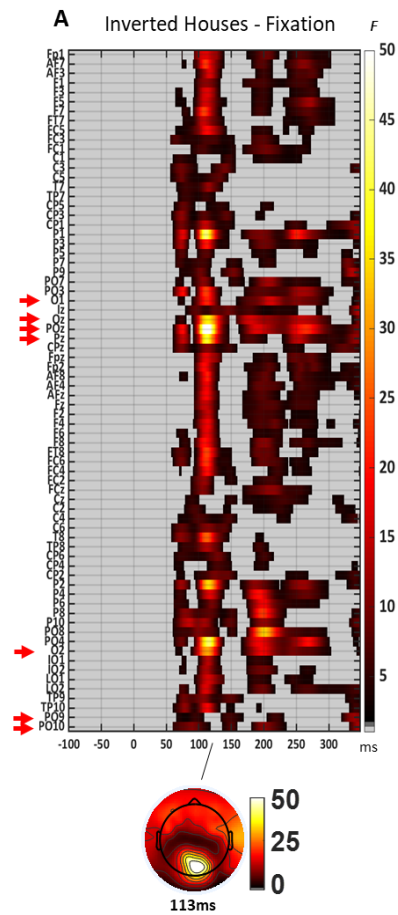


Figure 2-11. Fixation Location effect for Inverted Houses analyzed separately.

(A) The raster plot shows the main effect of fixation location with a TFCE correction ($p < 0.0125$). Red Arrows on the side of the Raster plot indicate the electrodes seen in the ERP plots to the right. (B) The five fixation location conditions are displayed at seven representative posterior electrodes. For each electrode, three types of plots are presented. The top plots display the group average ERPs for each fixation location, with central tendency computed using raw means for single-subject trials and 20% trimmed means across subjects. The middle plots show the difference waves between pairs of conditions. The green bar at the top of these plots indicates the time points where the main effect of fixation location was significant using the cluster-mass correction, while the pink bar at the bottom indicates significant time points using the TFCE correction. The bottom plots illustrate the time courses of the F -values obtained for each contrast comparing pairs of fixation locations. The topographic map on electrode POz shows the amplitude difference between Beside-the-Door and Between-Windows fixations (BD-BW) across the scalp, with a $-3\mu\text{V}$ to $+1\mu\text{V}$ colour scale, at 113 ms where this difference is maximal. Solid vertical black lines indicate the temporal correspondence between the peaks of the paired contrasts and their locations on the actual ERPs, corresponding to the C2 at POz and the P1 at Oz. The dashed vertical black line highlights that weak F values were observed at the peak of the N170.

2.3.3.3.2 Follow-up contrasts #2: House Inversion Effect at each Fixation Location.

Again, 5 *F*-contrasts using a significance threshold of $p < 0.01$ were used to assess the House Inversion Effect (HIE) at each Fixation Location separately (Fig. 2-12). First, like the results above for faces, the HIE demonstrated a positive C2-like component for the Between-Windows and a negative C2-like components for the Beside-Door fixation on electrode POz and on Pz to a lesser degree (Fig. 2-12), due to opposite polarity of the C2 between upright and inverted conditions for these fixation locations (around 115ms). This effect coincided with the statistical peak of the interaction on POz (see earlier section) where the Beside-Door fixation exhibited the largest HIE *F*-values followed by the Between-Windows, center, and the Windows fixations (Fig. 2-12). Second, the HIE for each fixation showed a peak around 180-200ms at parieto-occipital and occipital sites, corresponding to a more negative N170-P2 interval for inverted houses, creating negative difference waves (Fig. 2-12). At right parieto-occipital sites (e.g. PO8), the largest HIE during the P2 rise was seen for the Beside-Door fixation, followed by the window fixations (see contrast *F*-value peaks on Fig. 2-12). At left sites, however (e.g. P9), this effect was not seen.

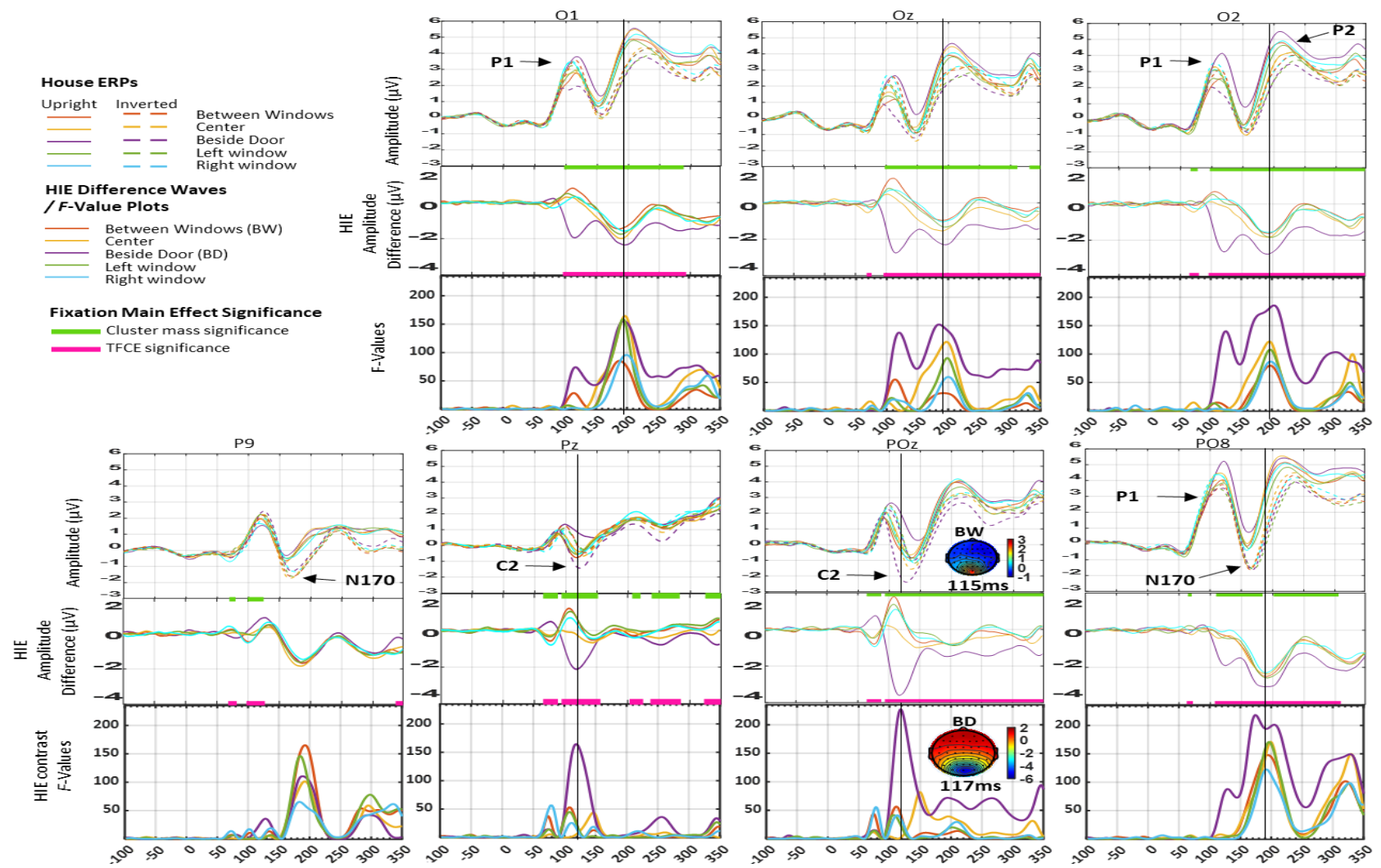


Figure 2-12. House Inversion Effect (HIE) Across Individual Fixation Locations.

This analysis focuses on seven representative posterior electrodes (outlined by the red arrows in Figure 2-9). The top graphs display the ERPs for upright (solid lines) and inverted houses (dotted lines) for each fixation location. The middle plots show the actual HIE, represented as the amplitude difference between inverted and upright houses at each fixation location. The green bar at the top of these plots indicates the time points where the Orientation by Fixation Location interaction was significant using the cluster-mass correction, while the pink bar at the bottom indicates significant time points using the TFCE correction (see text for details and Appendix fig. 1 for uncorrected effects). The topographic maps on electrode POz illustrate the HIE across the scalp at the time points where the HIE was largest: 115ms for the Between-Windows fixation ($-1\mu\text{V}$ to $+3\mu\text{V}$ colour scale; top map) and at 117ms for the Beside-the-Door fixation ($-6\mu\text{V}$ to $+2\mu\text{V}$ colour scale; bottom map). Note the opposite effects observed for Between-Windows and Beside-the-Door fixations. The bottom plots display the time courses of the F -values obtained for each fixation location contrast (inverted vs. upright conditions) at these electrodes. Note how the HIE varies with fixation location and electrodes, with the largest effect observed for the Beside-the-Door fixation at occipital sites (see text for further details).

2.3.4 Interaction effects.

All interactions were significant with TFCE correction and an alpha of $p < 0.05$. We focus below on the most meaningful interactions.

2.3.4.1 2-way Interaction between Orientation and Stimulus Type

The interaction between Orientation and Stimulus Type was significant from 66-350ms with the peak statistical effect occurring at 129ms on electrode P8 ($F(1, 79) = 186.58, p < .001$). The raster plot displayed one sparse early band followed by three prominent and at times interconnected bands of significant activity (Fig. 2-13A). The early sparse band spanned $\cong 66$ -96ms across central and posterior electrodes with its local maxima on P10 at 83ms ($F(1, 79) = 53.36, p < .001$). At these posterior sites, the effect corresponded to the rise of the P1 ERP component where a small inverse FIE emerged while no HIE was yet seen (Fig. 2-13B, PO8, blue arrows). The next band occurred from $\cong 105$ -166ms and included the statistical peak of the entire effect. This effect was driven by a difference in the inversion effect between faces and houses, with a strong FIE corresponding to the middle of the P1-N170 interval and a very small *inverted* HIE at the same time (ex. PO8 & P8, red arrows). The second prominent band in the raster plot was found from $\cong 179$ ms to $\cong 255$ ms with its local maxima at 212ms on electrode FP2 ($F(1, 79) = 82.01, p < .001$). At this site, the interaction was driven by stronger HIE than FIE, which included the VPP (i.e. the VPP was larger for inverted than upright items, but this difference was more pronounced for houses than faces). At posterior sites, this timing corresponded to the N170-P2 interval where the effect was polarity reversed and the HIE was larger than the FIE. Finally, the third band started around 257ms and continued until the end of the epoch with its local maxima at 302ms on electrode P5 ($F(1, 79) = 42.55, p < .001$).

Thus, the inversion effect was positive or negative depending on timing and scalp location and was largest for faces during the P1-N170 interval but largest for houses during the N170-P2 interval.

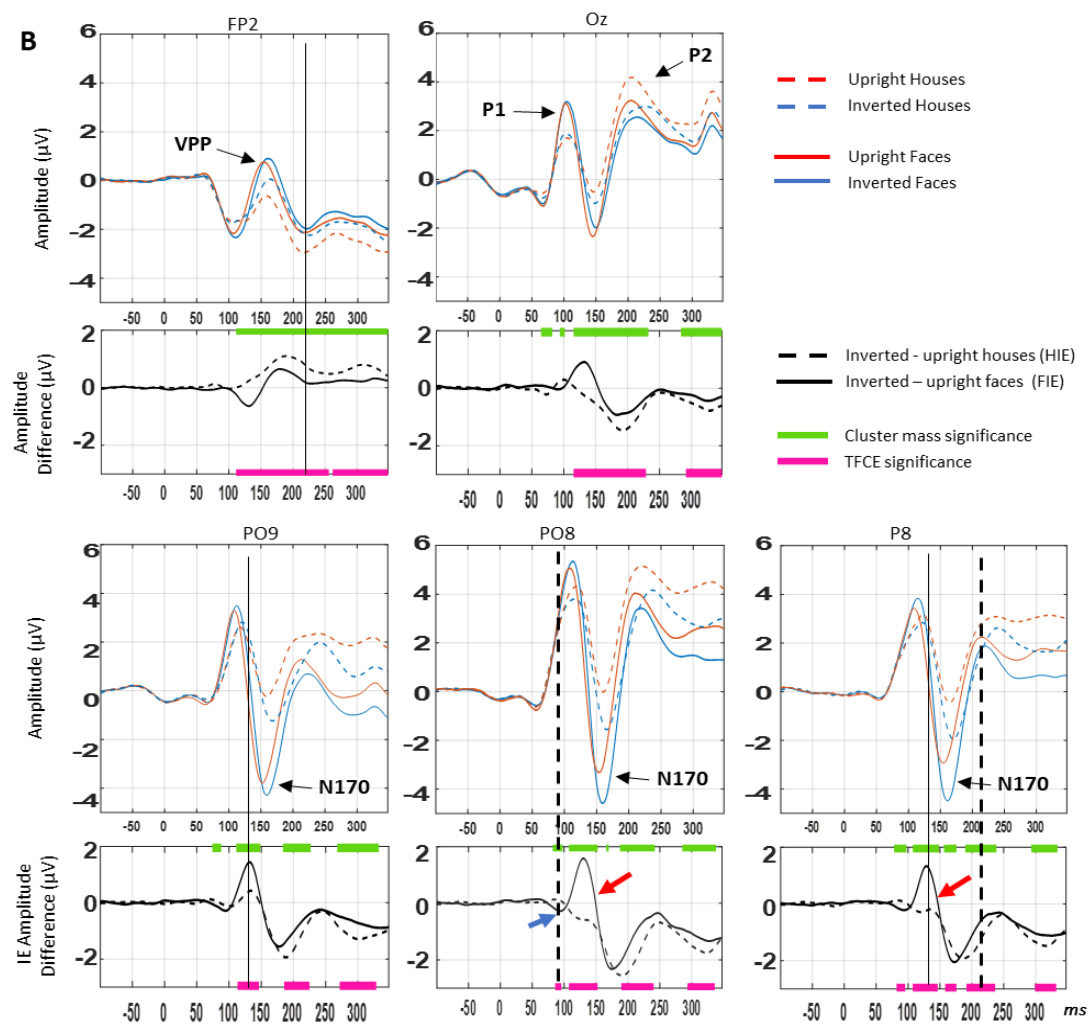
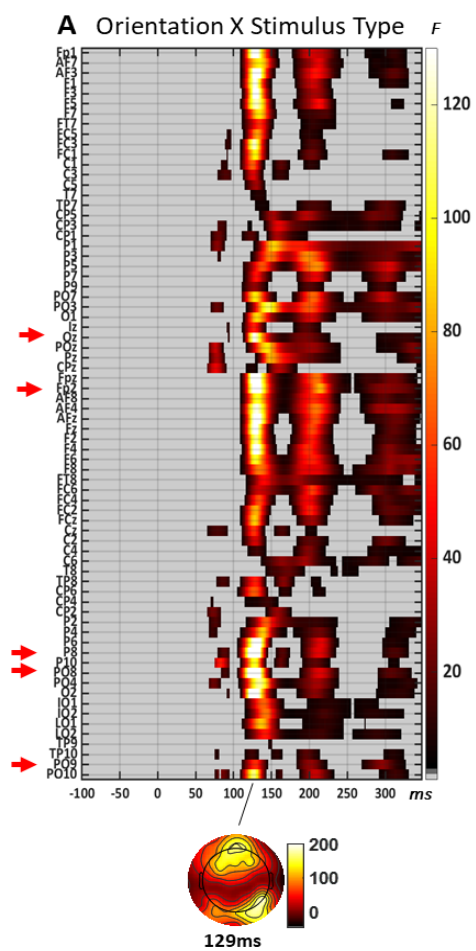


Figure 2-13. Orientation by Stimulus type interaction

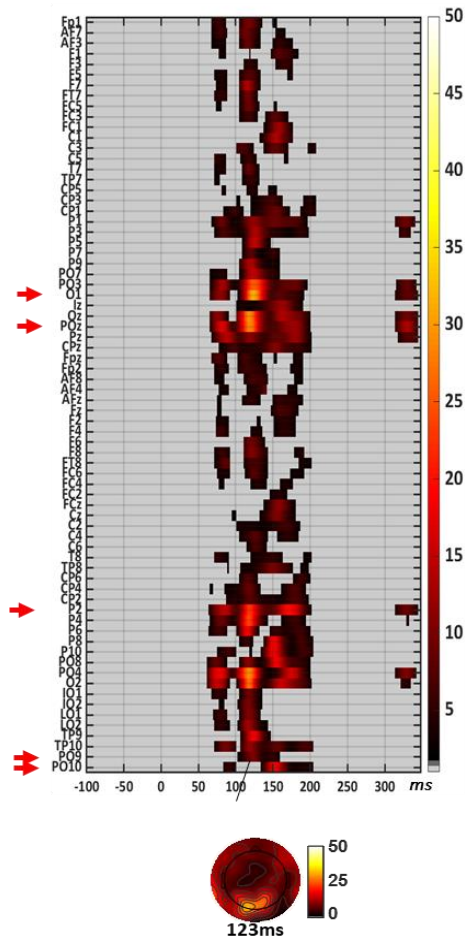
(A) The raster plot shows the Orientation by Stimuli Type interaction with a TFCE correction ($p < 0.05$). The raster plots illustrate the significant F -values for each effect across all electrodes (72 in total, shown on the y-axis) and time points (from -100 to +350ms, shown on the x-axis), with the magnitude of these values depicted by the colour scale. Red Arrows on the side of the Raster plot indicate the electrodes seen in the ERP plots to the right. **(B)** The upright (Red lines) and inverted (Blue lines) conditions are displayed at five representative frontal, occipital, and posterior electrodes with the face (solid lines) and house (dashed lines) stimuli. For each electrode, two types of plots are presented. The top plots display the group average ERPs for each fixation location. The bottom plots show the difference waves between upright and inverted stimuli. The green bar at the top of these plots indicates the time points where the main effect of fixation location was significant using the cluster-mass correction, while the pink bar at the bottom indicates significant time points using the TFCE correction. Solid vertical black lines indicate the temporal correspondence between the peaks of the paired contrasts and their locations on the actual ERPs. Blue arrows show the small inverted FIE where no HIE exists before the ramping up to the P1. Red arrows show large FIE and a very small inverted HIE during the P1-N170 interval.

2.3.4.2 Three-way Interaction between Orientation, Stimulus Type and Fixation Location

The 3-way interaction between all three factors was significant between 63-208ms across the scalp, with some isolated significant timepoints from 314-344ms in posterior regions (Fig. 2.14A). A sparse band spanned $\cong 63-92$ ms with a local maxima at 78ms on electrode PO4 ($F(4, 76) = 18.24, p < .001$), corresponding to the rise of the P1. The 3-way interaction at that time was due to the fact that for faces, both mouth and nose fixations elicited a positive FIE while nasion and eye fixations elicited a negative FIE. In contrast, for houses, only the beside-door fixation elicited a positive HIE while all other fixations elicited a small negative HIE (Fig. 2-14, blue arrow on POz).

Next, the middle and most prominent band occurred between $\cong 101-208$ ms. The peak of the interaction was seen on electrode O1 at 123ms ($F(4, 76) = 31.5, p < .001$) which corresponded to the middle of the P1-N170 interval but also to the C2 at POz electrode. At these sites, the 3-way interaction was due to a negative inversion effect for mouth/beside-door fixations, while concurrently the inversion effect was positive for the other fixation locations (vertical bars on O1 and POz, Fig. 2-14). However, the main difference between stimulus type was a clear gradient for faces, with larger FIE for nasion, followed by eyes and nose fixations, while the HIE gradient was much attenuated (although in the same direction: Between-windows > Windows > Center). Another local maximum was seen at 171ms on electrode P2 ($F(4, 76) = 19.89, p < .001$), corresponding to the N170-P2 interval. At this time on P2, the FIE was positive for nose and mouth fixations while their equivalent (center and beside-door fixations) elicited a negative HIE (Fig. 2-14). At PO10 during this time, the FIE peaked earlier for nasion fixation and later for mouth fixation while the HIE did not show latency shift but an overall larger HIE for Beside-door fixation.

A Orientation X Stimulus Type X Fixation Location



B

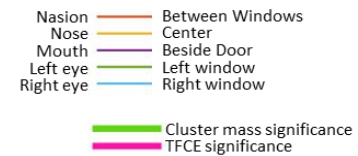
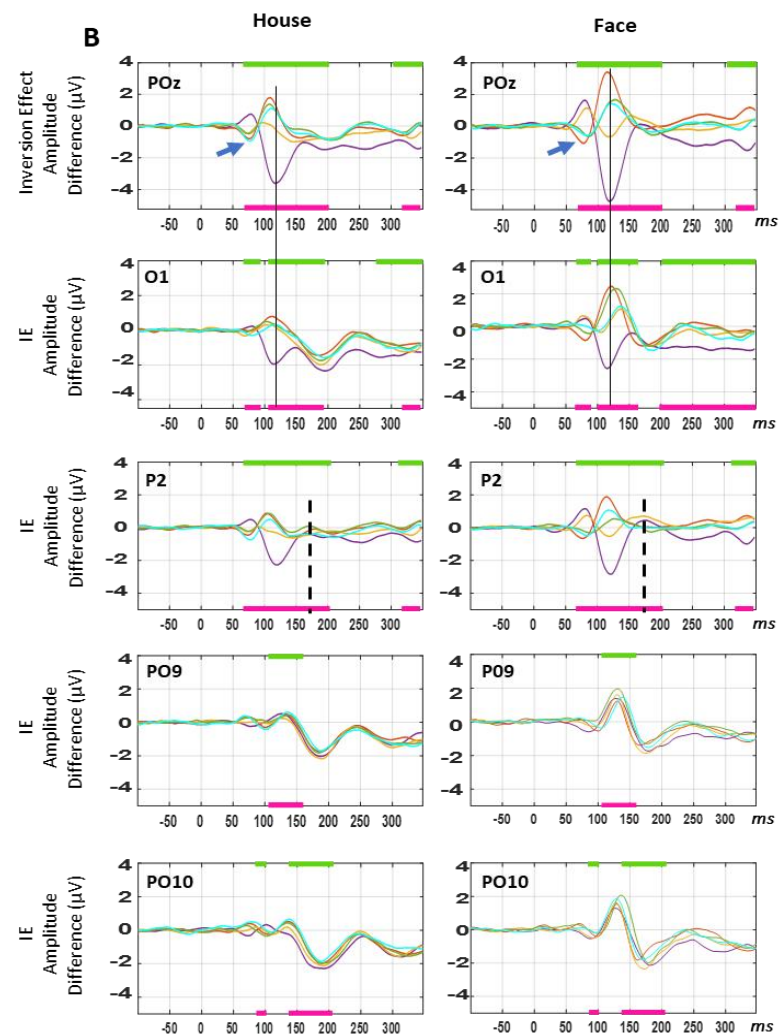


Figure 2-14. Orientation by Stimulus type by Fixation Location interaction.

(A) The raster plot shows the three-way interaction with a TFCE correction ($p < 0.05$). The raster plot illustrates the significant F -values for each effect across all electrodes (72 in total, y-axis) and time points (from -100 to +350ms, x-axis), with the magnitude of these values depicted by a colour scale. Red Arrows on the side of the Raster plot indicate the electrodes seen in the ERP difference wave plots to the right. **(B)** The five fixation location difference waves representing the HIE and FIE, are displayed at five representative occipital and posterior electrodes for both house (left) and face (right) stimuli. The green bar at the top of these plots indicates the time points where the main effect of fixation location was significant using the cluster-mass correction, while the pink bar at the bottom indicates significant time points using the TFCE correction. Solid vertical black lines indicate the temporal correspondence between the peaks of the paired contrasts, corresponding to the C2 at POz and the P1 at Oz. Blue arrows on POz highlight the differences between Nasion and Nose FIE and Between-the-Windows and center HIE during the rise of the P1 (see text for details). The dashed vertical black line highlights the timing of the third local maximum at P2.

2.4 Discussion

The current study examined the influence of plane inversion (orientation), fixation location and their interaction on early neural processing of face and house stimuli within the same participants. The purpose of this study was to confirm the differences between face and house stimuli seen in Chapter 1 in two different samples, using a within-subject design with well controlled stimuli, a large sample size, and large trial numbers. Many of the same findings seen in Chapter 1 were replicated within this analysis including the inversion effects for both faces and houses, as well as the fixation location effect and interaction effect for faces alone. Unlike Chapter 1, however, a fixation location effect and its interaction with orientation were also found for houses. Below, we highlight the similarities and discuss the differences between the studies findings and their implications for face and object perception.

2.4.1 General inversion effects between faces and houses

Much of the past research concerning faces and objects has used the inversion manipulation to demonstrate the processing difference between these stimuli and attributed this difference to a disruption in holistic processing. It is generally agreed that faces are processed holistically/configurally, i.e. as wholes, while objects are processed featurally (Farah et al. 1995; Haxby et al. 1999; Maurer et al. 2002; Sekuler et al. 2004; Tanaka and Gordon 2011; Richler et al. 2012; Richler and Gauthier 2014). This view stems mainly from behavioural findings of strong inversion effect for faces but smaller or no inversion effect for objects (Yin 1969; Tanaka and Farah 1993). At the brain level, the face sensitive N170, often conceived as a marker of holistic processing, is impacted by inversion for faces but not for objects (Rossion et al. 2000; Itier et al. 2006; Kloth et al. 2013). In contrast, replicating the first chapter's findings, the current study confirmed, with greater statistical power, that the inversion effect exists for objects such as houses.

Many of the amplitude and latency changes observed with inversion of each stimulus type in Chapter 1 were replicated in this within-subject study. This includes the effects on the P1, N170, and P2 ERP components. The raster plots for both faces and houses remained consistent across chapters with 3 prominent bands of significance for faces and 2 disjointed bands for houses (Appendix Fig. 1). Both chapters' orientation effect for faces appears as 2 early bands of

significance followed by a 3rd band, corresponding to the transition periods between ERP components (i.e. P1-N170, N170-P2, and P2 to baseline). The orientation effects for houses also occurred during the transition stages (i.e. N170-P2 and P2 to baseline), however the significant effects did not all begin at the same time for each electrode resulting in a disjointed band of significance. The strongest F values for faces occurred roughly at the same time between chapters (Ch.1: 170ms vs Ch.2: 178ms) during the N170-P2 interval while the N170 amplitude peak ($\cong 150$ ms) displayed some of the weakest statistical effects. The current study also shows an earlier and more prominent FIE compared to the disjointed HIE which is consistent across chapters.

In contrast to Chapter 1 and to our predictions, houses did not exhibit a smaller inversion effect than faces, but rather a similar and sometimes larger inversion effect than face stimuli, with a larger statistical HIE peak (at 191ms on electrode FC2, $F \cong 415$) compared to the FIE peak (at 178ms on electrode Cz, $F \cong 349$). The largest F -value for houses also occurred earlier than the one seen in Chapter 1 (Ch.1=322ms vs. Ch.2=191ms). This suggests that the combination of increased statistical power and the improved stimuli of the current study impacted the timing at which the statistical peak difference occurred. Interestingly, the timing of the statistical peak for houses in the present study appeared within the same N170-P2 transition phase as the effect for faces. Regardless, both chapters confirmed that the largest effect of orientation for houses occurred later than the largest effect for faces. It is important to note that Chapter 1 only visually compared the results of the two categories as they were obtained in different participants while the current within-subject study directly compared these differences statistically.

The 2-way interaction between Orientation and Stimulus Type included the largest statistical differences of all the interactions ($F \cong 186$; compare F values between interactions on Fig. 2-2). When looking at the ERP waves, the P1 for inverted faces was consistently larger and delayed compared to upright faces. This difference was less pronounced with houses and at some electrodes upright houses even elicited larger P1 than inverted houses, resulting in a negative HIE (e.g. PO8, Fig. 2-13B, red arrows). The largest significant differences between the FIE and the HIE were seen in the middle of the P1-N170 transition where the FIE was positive and larger than the HIE which was in the opposite direction (Fig. 2.13B, red arrows).

During the P1-N170 transition there was a clear lateralization effect for faces with right hemisphere electrodes showing a more pronounced inversion effect on the N170 amplitude peak than the left hemisphere electrodes. This lateralization effect was partially visible for house stimuli around this time; however, it was not as pronounced or consistent as for faces (e.g. Fig. 2-13, N170 peak amplitude difference PO8 vs PO9). No statistical comparison between hemispheres was performed on these data, however, the ERP waves appeared to follow a similar pattern as previous work on faces. Right hemispheric lateralization is expected for faces, however, objects such as houses have not always shown a consistent hemispheric effect across the literature (Haxby et al. 1999; Rebai et al. 2001; Itier and Taylor 2006; Rousselet et al. 2008).

During the N170-P2 interval, the latency delay and amplitude difference elicited by inversion was larger for houses than for faces (e.g. at PO8, $\cong 13\text{ms}$ and $\cong 0.5\mu\text{V}$ difference in the peak of the HIE compared to the FIE amplitude peak). This suggests that in some ways house processing was more influenced by inversion than face processing, just at later timepoints and different electrodes. It is possible that this difference in amplitude and timing accounts for the lack of effects reported for object inversion in past research that essentially focused on the N170 peak. In general, the ERP waveforms for the house stimuli appeared more delayed with overall smaller amplitudes than the waveforms seen for the face stimuli, which is typically seen in the literature. Despite this difference in ERP amplitudes and timing, the difference waves between upright and inverted stimuli were similar in magnitude, suggesting some qualitative and quantitative differences in processing these stimuli. While there are similarities in the magnitude of the inversion effect at some electrodes, there are some key differences in timing, statistical significance, and amplitude that distinguishes the processing of both stimulus types. These results call into question previous research which has described the effect of inversion as a quantitative effect (Sekuler et al. 2004). While there are quantitative differences due to inversion that affect houses and faces in similar ways (i.e. amplitude and latency effects), there appears to be some qualitative differences in how early and for how long inversion influences face processing compared to objects such as houses (Rossion 2008).

According to past research, the presence of a HIE would suggest that houses are processed holistically. The differences in amplitudes and timing of the HIE and FIE suggest that house stimuli may take longer and involve different underlying neural mechanisms to be processed

compared to faces. It is possible that the homogenous nature of face stimuli compared to the relative heterogenous nature of houses in the real world (houses can take many different shapes) could account for some of the observed differences. This study attempted to mitigate this factor by using well studied stimuli that have comparable features (windows and eyes, etc.), but did not look face-like. Despite these efforts there is still a gap in the amount of experience humans have in viewing faces compared to houses. All faces have the same configuration and general appearance (2 eyes above a nose above a mouth in an oval contour) whereas all houses/buildings do not, which could lead to differences in timing and processing of these different stimuli when upright or inverted.

Several studies have observed inversion effects with stimuli resembling faces, such as those composed of fruits and vegetables in Arcimboldo-style portraits (Caharel et al. 2013; Nihei et al. 2018). These studies noted that ratings of face-likeness were associated with the P1 inversion effects (Nihei et al. 2018). While it might be speculated that a similar mechanism could explain inversion effects in our house stimuli, this seems improbable. Our house stimuli featured a sidewalk, stairs, triangular roof with a chimney, bay windows (bottom right), and a door (bottom left) positioned in a way that disrupted the typical inverted triangular shaped configuration (eyes above nose, above mouth) of facial features (Fig. 2-1). Furthermore, other non-face-like stimuli, including car fronts that attempt to resemble faces, have not shown consistent inversion effects, while various non-face objects like compound Chinese characters and natural scenes have shown such inversion effects (Wang et al. 2011; Kloth et al. 2013; Nihei et al. 2018; Van Helden and Naber 2023). These findings suggest that inversion effects are more likely tied to the neural processes involved in integrating disparate features into a cohesive percept, as is necessary to perceive faces in Arcimboldo's artwork (Caharel et al. 2013) or gaining meaning in compound Chinese characters, than to face-likeness. To gain a more robust understanding of the processing differences between faces and houses, the effects of fixation location and how they vary with stimulus type and inversion need to be discussed.

2.4.2 Fixation effects and their Interaction with Orientation

Again, this study confirmed what was found in Chapter 1, with a Fixation Location effect that also interacted with Orientation for faces across the scalp at early and late timepoints. The

results for faces appear remarkably similar across Chapters with the results from the current study showing stronger *F*-values at more timepoints (compare Fig.1.4 and Fig.2.4), likely due to the increased sample size and trial numbers. Indeed, the maximal effects observed for the face Orientation by Fixation Location interaction in both chapters were seen at roughly the same time (Ch.1=119ms vs. Ch.2=117ms) and in the same region of the scalp (Ch.1=Oz vs. Ch.2=POz). Similarly, the retinotopic mapping seen for faces in Chapter 1 was also replicated in Chapter 2 with some interesting new distinctions.

One interesting distinction comes from the maximal fixation location effect for faces, which occurred at different timepoints (Ch.1=180ms vs. Ch.2=139ms) and scalp sites (Ch.1=Fz vs. Ch.2=P10) across chapters, suggesting that these earlier timepoints at posterior sites are critical for processing different face fixation locations. More importantly, a significant fixation location effect and its interaction with orientation was found for houses, which is a novel finding in this field and a major distinction between Chapters 1 and 2. Interestingly, the uncorrected results for houses in Chapter 1 showed an Orientation by Fixation Location interaction similar in timing to what was found in the current study (compare Appendix Fig. 1 and the band of largest *F*-values in Fig. 2-9). In Chapter 1, the interaction (and the main effect of Fixation Location) did not survive the corrections. This finding suggests that sample size (*N*=20 in Chapter 1 compared to *N*=80 in Chapter 2) and trial numbers (on average 56 trials/condition in Chapter 1 vs. 70 trials/condition in Chapter 2) were important factors in uncovering significant fixation location and interaction effects for houses. For faces, it seems that a sample size of 80 elicited a very similar set of results as a sample size of 52 (Chapter 1).

An important new finding compared to Chapter 1 is the presence of a C2 ERP component not just for faces but also for houses. This component is sensitive to the stimulus position in space in a retinotopic way: C2 is positive when most of the stimulus is in the upper portion of the visual field (with gaze position at the fovea) and negative when most of the stimulus is in the lower portion of the visual field. This effect is in line with previous research on retinotopic mapping which has shown that checkerboard patterns produce an effect on C2 around these early time points (Di Russo et al. 2005, 2012; Capilla et al. 2016). Similar retinotopic effects have been observed in another face processing study which also demonstrated a large effect for nasion fixations in upright faces and mouth fixations in inverted faces (Zerouali et al. 2013). The

presence of a similar pattern of early retinotopic responses for houses and faces is a novel finding. The lack of such early responses for houses in Chapter 1 was again most likely driven by the low power we had with 20 participants. Both faces and houses showed a similar fixation gradient, although larger differences between fixation locations were seen for faces.

The similarity in retinotopic effects during the processing of both stimulus types can be seen in opposite effects of the same fixation location between upright and inverted images, similarly for faces and houses. For example, fixation on the Mouth/Beside-the-Door elicited the largest amplitude in upright stimuli, but the smallest amplitude in inverted stimuli for C2 and P1; Nasion/Between-Windows fixation elicited the smallest amplitude in upright stimuli, but the largest amplitude in inverted stimuli. The amplitude gradient between fixation locations was clearly visible for faces and continued through much of the wave form whereas the gradient for house fixations was not as clear and was only consistent during the P1-N170 transition. These results suggest that retinotopic mapping is important around the C2 and P1 regardless of stimuli. They also suggest that this retinotopic information may still be used for face processing throughout the entire examined epoch whereas it appears less important for houses later in processing. Regardless, the gradient pattern demonstrates clear retinotopic effects in visual processing of houses, possibly through a similar, yet not identical holistic mechanisms than the one used in face processing.

Differentiation between stimuli processing can nevertheless be seen by comparing Nasion and Between-Windows fixations. Nasion seems to influence the C2 and P1 components more drastically than Between-windows fixation. Across both Chapters the Nasion fixation has shown some of the largest statistical differences. This suggests that the Nasion may be an optimal fixation location for face processing that is not shared with houses and possibly other object stimuli. One possible explanation is that the Nasion is the “center of mass” of a face which people tend to prefer because it facilitates feature integration even when the face is inverted, making it easier to process. It is also important to note that from the N170 onward the Eyes appear to elicit the most negative or positive ERP waves (upright and inverted respectively). This pattern is not as clearly observed for the window fixations for house stimuli. These differences could be seen as evidence for an eye processor mechanism in face perception as eyes provide a large amount of continually changing social information. Since the eyes of a face provide some

of the largest amount of this continually changing information (e.g. openness or squinting of the eyes depending on the facial expression, direction of gaze, etc.), it seems likely that the nasion, which is between the two eyes, would be the ideal fixation location for holistic processing. On the other hand, houses are stable, non-biologically relevant stimuli, which suggests that their processing would not require the continual updating of information in that area of the object. This could explain why the statistical effect of fixation location and its interaction with orientation is reduced with house stimuli in general, and why this effect was not found with the reduced statistical power in Chapter 1.

Additional evidence of processing differences between stimulus types can be seen in the maximal effects for fixation location. While the raster plots of the fixation location effect for each stimulus type analyzed separately appear similar, the maximal F values for houses (199ms) and faces (139ms) occurred at drastically different timepoints ($\cong 60$ ms difference). This difference is further accentuated when looking at the FIE and HIE at each individual fixation location. The maximal statistical difference in the FIE occurred during the P1-N170 interval whereas that for the HIE occurred during the N1-P2 interval, and this pattern was seen for all fixation locations (compare Fig. 2.7 and 2.12). This finding aligns with previous research that only observed a significant inversion effect for houses around the P2 (Rousselet et al. 2008). These transition stages between ERP component peaks contain more information about the processing differences between house and face stimuli than has been previously reported, a finding that suggests holistic processing is not merely a perceptual snapshot where features are glued together in a single percept at the N170 peak. Rather, feature integration into a percept is dynamic, protracted, and dependent on gaze fixation location.

Indeed, feature integration of faces and houses depends on where one is fixating but still differs between the two stimulus types. The brain may prioritize the feature integration of certain stimuli such as faces, possibly due to the increased amount of everchanging information elicited by a face that requires continual updating to be successful when interacting socially. According to the 3-way interaction, as early as 64ms and until 208ms, both the face and house stimuli elicited significantly different responses depending on where one is fixating and whether the stimulus is upright or upside down. These results demonstrate the qualitative and quantitative differences between these stimuli. At early timepoints the differences seem qualitative with the

nasion and eyes fixations eliciting some unique effects while at later points the differences are mostly a result of different response magnitude (amplitude) or the delay of the amplitude peaks between stimuli. Without the use of MUA to examine all the timepoints across all electrodes with proper family-wise correction techniques, these differences would be difficult to observe.

The similarities and differences between the face and house stimuli are better elucidated in the current study thanks to its increased statistical power, controlled stimuli, and within-subjects design. The use of MUA across all timepoints was crucial in uncovering these effects and should be used in ERP research over classical analyses. Following these results, the data seem to suggest some similarities between how humans process faces and houses along with some drastic differences. Some of these differences are temporal with the maximal effects for houses occurring much later than the effects for faces. Other differences are related to amplitude differences seen between stimuli across orientations and fixation locations. Clearly the combination of both differences suggests that while both stimuli share basic visual processing mechanisms such as the retinotopic effects discussed above, faces are processed in a fundamentally different way than objects such as houses. This could be attributed to any number of factors such as expertise/experience, biological or social relevancy, or the relative homogenous nature of faces compared to the large variety of objects within other categories. The current data can only demonstrate that there is a difference between these two stimuli in early visual processing across the scalp and epoch. The increased statistical power of the current study was required to elucidate this effect.

2.4.3 Conclusion

In summary, the traditional peak oriented statistical analysis of ERPs greatly limits the examination of the data and their interpretation. Using MUA allowed us to examine all timepoints and electrodes in a data driven manner that is inherently less biased than the traditional approach. By replicating the research paradigm in Chapter 1 and directly comparing the neural responses between the stimulus categories within the same participants, the current study replicated many of the findings seen for faces in Chapter 1. In particular, during face processing, some of the weakest statistical effects were seen during the N170 peak while the strongest statistical differences were seen during the P1-N170 interval. We also found that

significant differences continued after the N170 peak, and that the face feature integration process is malleable as it varies with which feature is in fovea, where the other features are situated in parafovea, and with face orientation. The study also replicated the strong orientation effect seen for houses in Chapter 1 and additionally uncovered, for the first time, a significant effect of fixation location for house stimuli which interacted with orientation. These findings suggest that houses are not processed just featurally but that their features are also integrated into a whole percept, like faces. Nevertheless, this feature integration differs between face and house stimuli, especially throughout the P1-N170-P2 transitions across the scalp. Further investigation on the mechanism underlying these scalp differences is required, along with the testing of other object and non-human face categories to allow generalizability of the findings.

Chapter 3

Face processing under various sizes

3.1 Introduction

Research on face processing in humans has generally suggested that faces are processed in a holistic, as opposed to feature-based, manner. As discussed in the previous chapters face inversion has been shown to interfere with this holistic integration of facial features (Maurer et al. 2002). As a result of this disruption, when viewing an inverted face, processing of feature-specific components (e.g., mouth shape, eye color) is enhanced (Barton et al. 2001, 2006). In addition, recognizing a whole face becomes challenging when inverted, whereas identifying individual facial features becomes easier (Tanaka and Farah 1993).

One additional factor that may influence whether a face is processed holistically or in a featural manner is the size of the image itself. This is potentially important given the variety of circumstances in which faces are processed in everyday life. As just one example, different mechanisms may be at play in seeing a friend from a distance walking towards you compared to when interacting with that same friend face-to-face a few feet away. Some studies have indicated that size might not significantly affect face recognition. For instance, in one study, face recognition was comparable whether the face was large ($15^{\circ} \times 10^{\circ}$ of visual angle) or smaller ($7.5^{\circ} \times 5^{\circ}$; Van Belle et al. 2010). When a wider range of stimulus sizes was employed, data suggested that there may be a specific range within which faces are processed holistically, with sizes outside this range engaging in more feature-based processing (Blakemore and Campbell 1969; Loftus and Harley 2005; McKone 2009; Ross and Gauthier 2015). However, there is a discrepancy between these studies concerning this optimal size range. One face recognition task study using upright and inverted faces found that upright face sizes larger than 6° of horizontal visual angle ($<1\text{m}$ distance) were processed holistically, with accuracy linearly increasing with face size; in contrast, inverted faces were not better recognized with face size (Yang et al. 2014). Another study using Mooney and superimposed faces found that faces were processed holistically between 3° (2m distance) and 0.713° (10m distance) of vertical visual angles (McKone 2009). This discrepancy is all the more difficult to quantify as these studies provide different visual angle dimensions (either vertical or horizontal).

Furthermore, some research has suggested that the extent of holistic versus featural processing may be task-dependent with several different recognition tasks displaying different results across sizes (Loftus and Harley 2005). There is evidence that holistic processes dominate recognition tasks, whereas featural processes become more relevant for gender identification tasks (Barton et al. 2001; Rule and Ambady 2008; Rule et al. 2009; Tabak and Zayas 2012; Yokoyama et al. 2014). As such there is a gap in the literature concerning the impact of face size across distinct real-world tasks. It is possible that the contradicting results across the previous size studies could be due to their various task differences (Pitcher et al. 2007).

To address this gap, we had participants perform a recognition memory-based task and a gender discrimination task using unfamiliar faces that varied across a range of face sizes. In Experiment 1, a memory-based task employed both upright and inverted faces to determine the optimal size range for holistic processing. Experiment 2 included both memory-based and gender discrimination tasks with only upright faces. Here, we wanted to determine whether there were different effects of size depending on the task used. We thought it was important to do this without also disrupting holistic processing using inverted faces.

We hypothesized that gender discrimination would be less size-dependent due to the salience of gender-differentiating features (e.g., lips, eyes; Brown and Perrett, 1993). That is, gender discrimination has been shown to rely more heavily on featural processing than other face processing tasks, and therefore it is possible that gender processing could be less sensitive to changes in face size since features stand out more easily (Loftus and Harley 2005). In contrast, face recognition, which involves representing both gender and identity, might be more sensitive to size variations. Larger faces may be expected to be more accurately identified than smaller sizes, given that larger visual angles increase the amount of visible information, which helps facilitate integration of features into a whole (i.e., holistic processing; Vuilleumier et al. 2003; Loftus and Harley 2005; Goffaux and Rossion 2006; Aguado et al. 2010; Yang et al. 2014). While it may be intuitive that processing smaller faces may be more efficient at integrating features together since they are closer together, the difficulty in identifying the fine details that distinguish one face from another is increased. However, a similar issue at very large face sizes may exist as participants could have more difficulties integrating the features that are farther from one another or too much detail to interpret in a short time (McKone 2009). It is important to

note that accuracy reported for recognition tasks is generally lower than accuracy for the gender discrimination tasks. Accuracies are also analyzed in different ways, with recognition tasks generally including a *d prime* (d') score for signal detection theory while raw accuracy is generally what is examined in gender discrimination tasks (Wixted 2007, 2020). In the current study, accuracy was analyzed as both a raw accuracy score, with only correct responses being analyzed, and as a d' .

Concerning face size, we hypothesized that holistic processing might be optimized within a specific size range, with deviations from that optimal range leading to a greater reliance on feature-based processing, possibly affecting face judgment tasks differently at the extremes of the size range. This would be in line with McKone (2009) which found a range of sizes at which holistic processing was most influenced (equivalent to ~2m-10m distance). In contrast, other works have suggested that past a certain size, holistic processing is no longer influenced by size (Yang et al., 2014). Based on these results it is possible that accuracy will increase with face size, however, at the extremely large sizes it is likely that there are some diminishing returns.

3.2 Experiment 1 Materials and Methods

3.2.1 Participants

All participants were students from the University of Waterloo (UW) who received course credit for their participation or \$15 CaD for this hour-long experiment. The UW Research Ethics Board approved this experiment, and all participants provided written informed consent before participating. Participants reported having normal or corrected-to-normal vision with no congenital prosopagnosia and they confirmed that they were not currently taking drugs (e.g. Cocaine, Cannabis, Alcohol). The age range of participants was 18-35 years, and they had lived in Canada for at least 5 years to ensure they all had a familiarity with Caucasian faces. In total 106 participants (Mean age = 19.4yrs (SD = 1.5), 77 female, 1 non-binary, 36 white/Caucasian) were included in this experiment and none were rejected.

3.2.2 Stimuli

The stimuli were adapted from the Radboud Face database and the Face generator application (Langner et al. 2010; Face generator). The stimuli were created by cropping an oval shape around each face image so that only the mouth nose and eyes were visible (ears, hair, neck, etc. were cropped out). All faces were of Caucasian-looking individuals of various age (18-60 years) that did not have beards, makeup, or other gender specific markers or paraphernalia included. They all maintained a neutral expression with their gaze directed forward and were presented in grey scale on a white background with only the face oval. In total there were 800 unique faces (400 male, 400 female) presented.

The face sizes were achieved using the size function within Psychopy at the following 5 sizes: 0.9°(0.7cm) horizontally x 1.4° (1cm) vertically; 2.0°(2.1cm) x 3.1°(3.2cm); 5.5° (5.8cm) x 8.2° (8.7cm); 8.7° (9.2cm) x 12.9° (13.6cm); 15.3° (16.2cm) x 22.3° (23.7cm) on a LED computer monitor (i.e. Size 1, 2, 3, 4, 5 respectively). Stimuli were presented at 60cm distance from a chinrest which was the distance used to calculate the approximate visual angle of each face size.

3.2.3 Design and Procedure

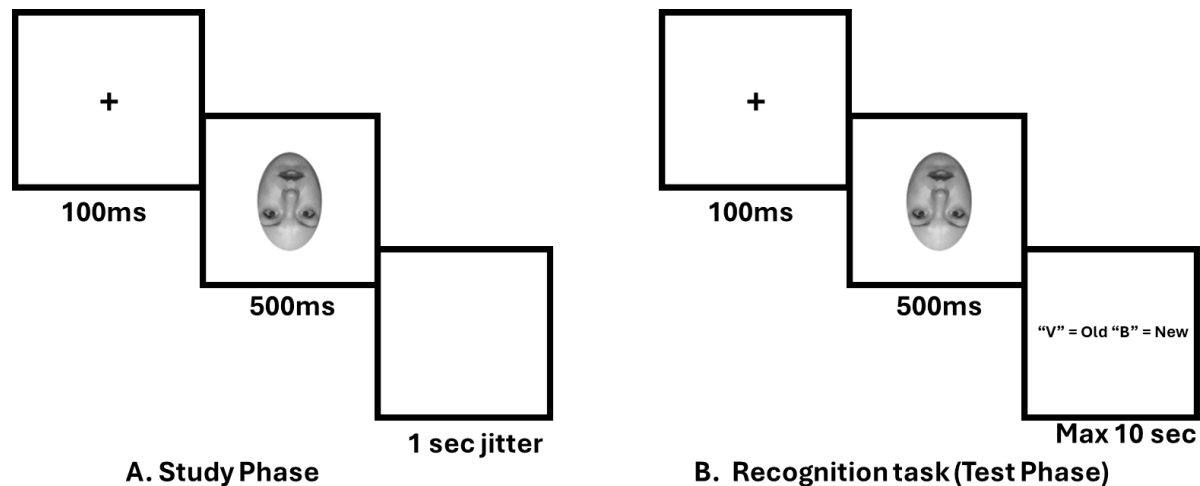


Figure 3-1 Experiment 1 procedure.

Depiction of the study phase of the recognition task where 20 faces were presented in each block (either upright or inverted). B. Progression for the test phase of the task, where the 20 "old" faces from the study phase were intermixed with 20 new faces and participants had to press a button for "old" faces and another one for "new" faces.

This experiment was split into 20 blocks of two consecutive phases: a Study phase and a Face Recognition test phase. In each block faces were either upright or inverted and of one

unique size. There were 2 blocks per face size within the upright and inverted conditions for a total of 10 conditions (2 orientations X 5 face sizes). In each block, the study phase contained 20 unique faces while the recognition phase included 40 trials (the 20 “old” faces just seen in the study phase and 20 additional unique “new” faces). Thus, there were 80 recognition trials per each of the 10 conditions.

In the study phase participants were instructed to view carefully the faces presented (Fig. 1A) and keep them in mind as in the second phase they would be asked to judge whether they had seen the face before or if it was new to them. Participants were instructed to make these judgments as quickly and accurately as possible (Fig 1B.; OLD v. NEW faces). The “V” and “B” buttons on the computer keyboard were used to indicate if the face they saw was “Old” or “New” and key assignment was counterbalanced across participants. Participants were instructed to only use their dominant hand when responding (index and middle fingers).

All stimuli were presented on a 53cm x 30cm digital monitor with a refresh rate of 60Hz, in a well-lit room. Participants used a chinrest to restrict head movements and maintain a 60 cm distance from the screen. The experiment began with practice trials repeated until participants felt comfortable with the task. In each trial, for both phases, a fixation cross was always presented in the center of the screen for 100ms. The face was then flashed on the screen for 500ms, centered and replacing the fixation cross. In the test phase, the faces were presented for 500ms after which an instruction screen would appear with the two button options during which participants answered as fast as possible using the keyboard (Fig. 1). The next trial began upon response. Trials without a response after 10sec were skipped and the next trial would then begin.

3.2.4 Data analysis

Trials which participants failed to respond to, or which contained technical issues (e.g. multiple responses at once) were removed from the analysis (this occurred for 7 participants with an average of 7 trials not responded to - 46 trials total). Accuracy in this study refers to the average number of correct responses for each of the 10 conditions (i.e. correctly identified old/new faces divided by the total number of recognition trials for that condition, i.e. 80 or less for the 7 participants).

The D prime (d') was calculated for each size and orientation to demonstrate the effects of orientation and size on recognition according to the signal detection theory. The z-transformed False alarm rates (incorrectly identified new faces as old) were subtracted from the z-transformed Hit rates (correctly identified old faces). There were 4 d' scores that rose above 3 SD from the mean across participants, which were also Winsorized. Hit and false alarm rates for the 7 participants who did not respond to several trials were adjusted accordingly.

Participants' reaction times were cleaned so that only correct responses within 2.5 SD from each participant's mean were used to create mean RT scores for each condition. Participants' mean accuracy and RTs that were above 3 SD from the group mean for a given condition were Winsorized (only 2 scores for accuracy and 2 scores for RTs).

Mean accuracy, d' scores and mean RT were each subjected to a repeated measures ANOVA with 2 orientation (upright, inverted) and 5 size (S1, S2, S3, S4, S5) within-subject factors. If the assumption for sphericity was violated (Mauchly's test significant at $p < 0.05$), Greenhouse-Geisser correction to the degrees of freedom were used.

3.2.5 Results

3.2.5.1 Recognition Accuracy

The main effect of Orientation was significant for accuracy ($F(1, 105) = 138.5, p < .001, \eta_p^2 = 0.569$). Participants were significantly more accurate at recognizing upright faces ($M = 0.59, SD = 0.06$) than inverted faces ($M = 0.54, SD = 0.06$; Fig. 3-2, Table 3-1). The d' for orientation was also significant ($F(1, 105) = 146.89, p < .001, \eta_p^2 = 0.583$) with again larger d' for upright ($d' = 0.54, SD = 0.03$) than inverted faces ($d' = 0.21, SD = 0.02$; Fig. 3-3, Table 3-1).

The Main Effect of Size was significant for accuracy ($F(3.652, 383.464) = 135.59, p < .001, \eta_p^2 = 0.261$) and d' ($F(4, 420) = 34.2, p < .001, \eta_p^2 = 0.246$) but both were qualified by a significant interaction between orientation and size (accuracy: $F(4, 420) = 4.91, p < .001, \eta_p^2 = 0.045$; d' : $F(4, 420) = 5.07, p < .001, \eta_p^2 = 0.046$), suggesting that the effect of size on recognition performance was different for upright and inverted faces.

To further investigate this interaction, the effect of face size on accuracy was examined separately for each orientation and was found to be significant for both upright ($F(4, 420) = 32.34, p < .001, \eta_p^2 = 0.235$) and inverted faces ($F(4, 420) = 9.41, p < .001, \eta_p^2 = 0.082$).

Bonferroni-corrected (threshold $p=0.05/10 = 0.005$) pairwise comparisons across the 5 upright sizes (10 paired comparisons) revealed that accuracy was significantly lower for Size 1 compared to all other face sizes (all paired comparisons $p < .00125$). The scores for the other 4 sizes were not significantly different from each other. An independent T-test conducted between chance level (test value = 0.5) and size 1 ($M = 0.54$ $SD = 0.07$) was significant ($t(105) = 6.66$, $p < 0.001$), suggesting that participants' performance was above chance even at the smallest upright face size. A curve fit analysis suggested that both linear ($R^2 = 0.081$) and quadratic ($R^2 = 0.125$) models were significant. For inverted faces, none of the comparisons survived the Bonferroni-corrected p -value threshold of 0.005. The independent T-test between chance level (test value = 0.5) and inverted size 1 accuracy ($M = 0.51$ $SD = 0.06$) was not significant ($t(105) = 2.31$, $p = .018$). The curve fit analysis for inverted faces also showed that both linear ($R^2 = 0.028$) and quadratic ($R^2 = 0.053$) models were significant.

The effect of size on d' was also significant for upright ($F(4, 420) = 29.72$, $p < .001$, $\eta_p^2 = 0.221$), and inverted faces ($F(4, 420) = 8.43$, $p < .001$, $\eta_p^2 = 0.074$) analyzed separately. Bonferroni-corrected pairwise comparisons across face sizes within each orientation elicited identical results to those reported above for accuracy. Similarly, a T-test with chance level for d' (test value = 0) also showed that d' were significantly above chance at Size 1 for upright faces ($t(105) = 5.73$, $p < 0.001$), but not for inverted faces ($t(105) = 2.31$, $p = .018$ – Bonferroni threshold $p=0.005$). All other sizes for upright and inverted faces were significantly above chance level ($p < 0.01$). Curve fit analysis suggested that linear and quadratic models were significant for upright ($R^2 = 0.072$; $R^2 = 0.114$) and inverted ($R^2 = 0.024$; $R^2 = 0.049$) faces.

With the analysis above suggesting that size 1 appears to be driving the interaction, another ANOVA was conducted removing size 1 to determine if the interaction effect remained significant. Both main effects of Orientation ($F(1, 105) = 147.2$, $p < .001$, $\eta_p^2 = 0.584$) and Size ($F(3, 315) = 5.54$, $p < .001$, $\eta_p^2 = 0.05$) remained significant, however, their interaction did not reach significance ($F(3, 315) = 0.829$, $p = .479$, $\eta_p^2 = 0.008$). Bonferroni-corrected pairwise comparisons between the remaining sizes revealed that Size 2 was significantly less accurate than size 4. The same analysis without size 1 was conducted on the d' with similar results. Again, both Orientation ($F(1, 105) = 151.42$, $p < .001$, $\eta_p^2 = 0.591$) and Size ($F(3, 315) = 4.42$, $p < .01$, $\eta_p^2 = 0.04$) were significant while the interaction was not ($F(3, 315) = 0.71$, $p = .549$, $\eta_p^2 =$

0.007). The pairwise comparisons for the d' matched the accuracy analysis above. These results suggest that once Size 1 is no longer included, the effect of size is much reduced and no longer differs between upright and inverted faces. Across both orientations, Size 4 elicited the highest accuracies (Table 3-1).

Table 3-1. Means, d' , and SDs for Experiment 1

Up: upright faces; Inv: inverted faces; S1-5: sizes, H: horizontal visual angle, V: vertical visual angle.

Size/orientation	Mean Accuracy	SD Accuracy	Mean RT	SD RT	D'	D' SD
UP S1 (H0.7° x V0.9°, $\cong$ 13.7m)	0.54	0.065	855ms	275ms	0.22	0.38
UP S2 (H2° x V3.1°, $\cong$ 4.3m)	0.59	0.076	880ms	225ms	0.54	0.47
UP S3 (H5.5° x V8.3°, $\cong$ 1.58m)	0.61	0.085	884ms	211ms	0.64	0.5
UP S4 (H8.7° x V12.3°, $\cong$ 1m)	0.62	0.086	880ms	211ms	0.67	0.48
UP S5 (H15.3° x V22.3°, $\cong$ 0.6m)	0.61	0.077	908ms	216ms	0.61	0.45
INV S1 (H0.7° x V0.9°, $\cong$ 13.7m)	0.51	0.054	828ms	305ms	0.07	0.31
INV S2 (H2° x V3.1°, $\cong$ 4.3m)	0.54	0.059	867ms	257ms	0.23	0.35
INV S3 (H5.5° x V8.3°, $\cong$ 1.58m)	0.54	0.066	902ms	255ms	0.25	0.38
INV S4 (H8.7° x V12.3°, $\cong$ 1m)	0.56	0.063	911ms	256ms	0.32	0.35
INV S5 (H15.3° x V22.3°, $\cong$ 0.6m)	0.54	0.065	916ms	241ms	0.22	0.35

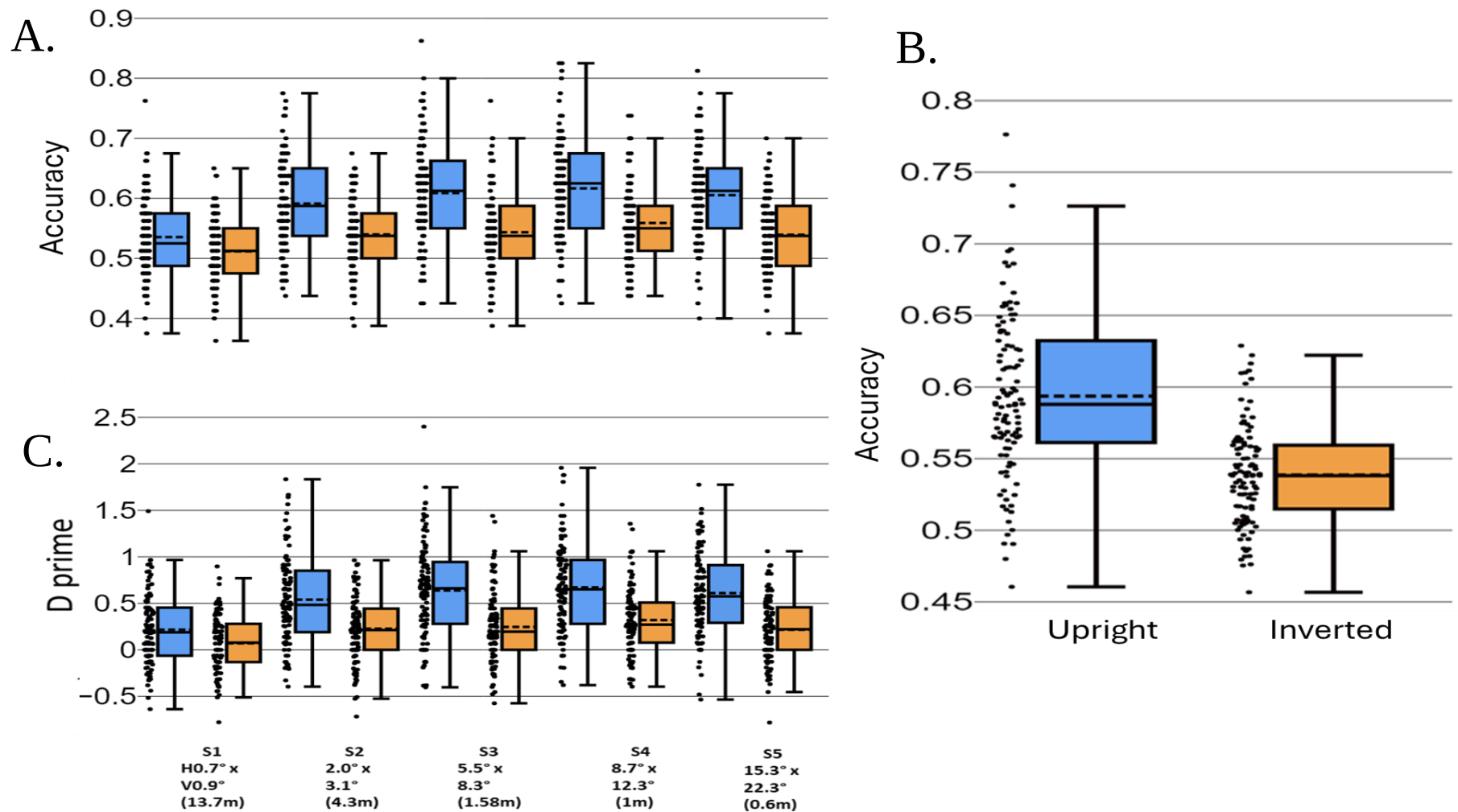


Figure 3-2. Experiment 1 raw accuracy and d'

A) Box and whisker plot for accuracy across all sizes and orientations with Upright faces in Blue and Inverted faces in Orange. The box plot limits represent the upper and lower quartiles. The median is marked by a solid horizontal line within the box and the mean is marked by the dotted line. B) Box plot for accuracy across upright (Blue) and inverted (Orange) faces. C) d' across all sizes and orientations with upright faces in Blue and inverted faces in Orange. For all graphs, black dots to the left of the boxplot represent individual participant means for that boxplot

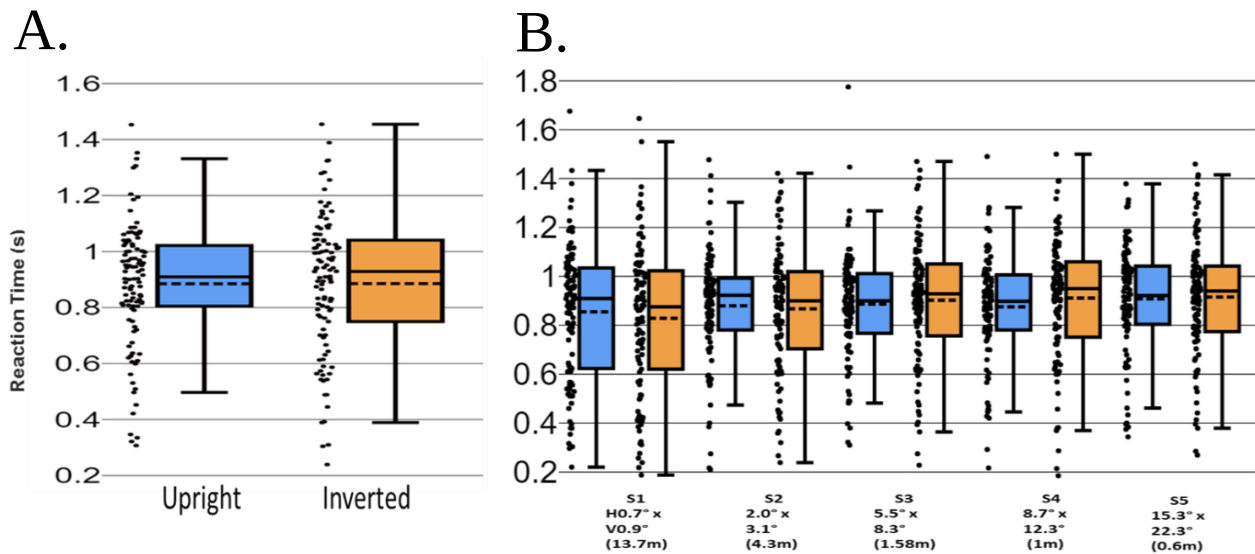


Figure 3-3. Experiment 1 reaction time

Box plot for RT across upright (Blue) and inverted (Orange) faces. The box plot limits represent the upper and lower quartiles. The median is marked by a solid horizontal line within the box and the mean is marked by the dotted line. B) Box and whisker plot for RT across all sizes and orientations with Upright faces in Blue and Inverted faces in Orange. For all graphs, black dots to the left of each boxplot represent individual participant means for that boxplot

3.2.5.2 Reaction Time

The main effect of Orientation was not significant ($F(1, 105) = 0.307, p = 0.58, \eta_p^2 = 0.003$). The main effect of Size was significant ($F(2.903, 304.856) = 12.803, p < .001, \eta_p^2 = 0.109$). Finally, the interaction between orientation and size was also significant ($F(3.509, 368.436) = 3.371, p < .05, \eta_p^2 = 0.031$), indicating that the effect of size on reaction times varied between upright and inverted faces.

Further investigation of the interaction was examined by testing for the effect of size separately for each orientation. The effect of size was significant for upright ($F(2.836, 297.276) = 4.509, p < .05, \eta_p^2 = 0.041$) and inverted faces ($F(3.46, 363.27) = 11.49, p < .001, \eta_p^2 = 0.099$). Bonferroni-corrected pairwise comparisons between upright face sizes were not significant. Similarly, Bonferroni-corrected paired comparisons for inverted faces were not significant. Curve fit analysis found that linear and quadratic models were not significant for upright faces ($R^2 = 0.004$; $R^2 = 0.004$ respectively) but were significant for inverted faces ($R^2 = 0.013$; $R^2 = 0.015$).

As with the accuracy analysis above, another ANOVA was conducted without size 1 to determine its influence on the interaction between Orientation and Size. The removal of Size 1 did not impact the results much, as the main effect of Orientation was still not significant ($F(1,$

105) = 1.94, $p = .166$, $\eta_p^2 = 0.018$) while the effect of Size ($F(2.627, 275.857) = 6.49$, $p < .001$, $\eta_p^2 = 0.058$) and the interaction remained significant ($F(3, 315) = 2.72$, $p = .044$, $\eta_p^2 = 0.025$).

3.2.6 Experiment 1 Summary

The results of experiment 1 showed that participants were significantly more accurate and sensitive (d') at recognizing upright faces compared to inverted faces although reaction times did not differ between the two orientations. Face size also played a role, and its interaction with face orientation highlighted that face size had a greater impact on recognition for upright than inverted faces. Importantly, this interaction was driven by the influence of size 1 as it was no longer significant once size 1 was taken out of the analysis and the remaining effect of size was severely diminished. Reaction times showed that participants generally responded faster to smaller faces, especially when upright.

These findings suggest that both orientation and size significantly influence face recognition. Size seems to be more impactful at extremely small and possibly extremely large face sizes. These results confirm our hypothesis and are in line with McKone (2009) which found a range (2-10m distance) at which faces are processed holistically; the present results show that this size range also applies for everyday face judgment tasks. To extend this investigation, the next experiment compared this face size effect across face judgment tasks to further investigate any task-related differences in face processing.

3.3 Experiment 2 Materials and Methods

3.3.1 Participants

None of the participants from Exp.1 were included in this experiment. The same participant criteria as in Experiment 1 were used. Participants were UW students who received \$15 or course credit, they provided informed consent that was approved by the UW Research Ethics Board, and they all had normal to corrected vision with no neurological disorders or current drug use. In total there were 107 participants (Mean age = 19.7, SD = 2.25, 79 female, 1 non-binary, 43 white/Caucasian) in this experiment, none were rejected.

3.3.2 Stimuli

The stimuli were the exact same upright faces as in Exp. 1 at the same sizes.

3.3.3 Design and Procedure

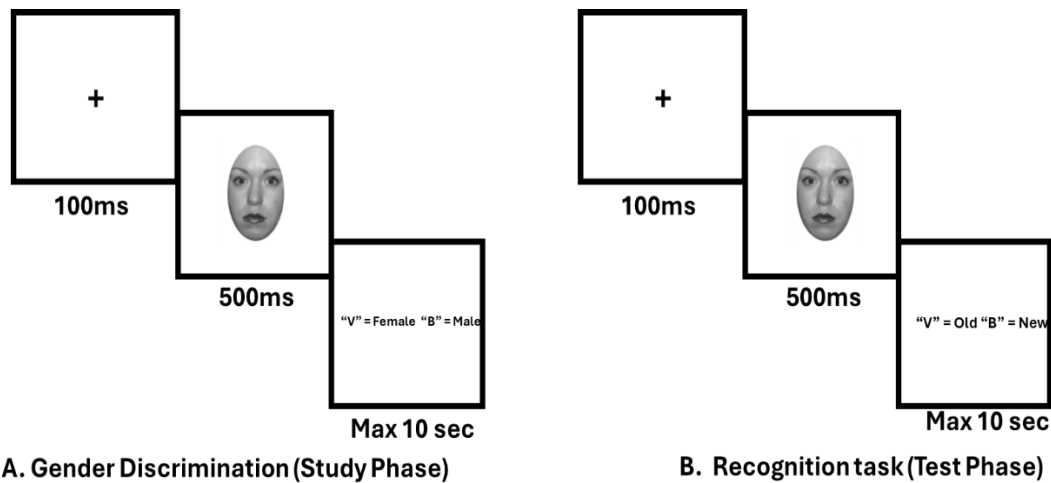


Figure.3-4 Experiment 2 Procedure.

A) Depiction of the first task: Gender Identification, which served as the encoding phase (20 trials). B) Progression of the second task: Face Recognition, where the 20 old faces were presented alongside 20 new ones (40 trials). The final screens show the button layout that was different for each task.

This experiment was split into two consecutive tasks: a Gender discrimination task followed by a Face Recognition task, with five face sizes (2 tasks X 5 face sizes). The gender discrimination task acted as the encoding phase and included 20 trials per block while the recognition task had 40 trials per block (the same 20 from the gender task plus 20 new faces). There were 10 blocks total (2 of each size) with, for each size, 200 trials for the gender identification task and 400 trials for the recognition task.

In the first task participants were instructed to judge the gender of the face presented as quickly and accurately as possible (Fig. 3-4a.; MALE v. FEMALE faces) using the “V” and “B” buttons on a computer keyboard to indicate if the face they saw was “Female” or “Male” (counterbalanced across participants). Participants were instructed to only use their dominant hand when responding.

They were told to keep these faces in mind as in the second task they would be asked to judge whether they had seen the faces before or if they were new to them, again as quickly and accurately as possible (Fig 3-4b.; OLD v. NEW faces).

All stimuli were presented on a digital monitor in a well-lit room. Participants used a chinrest to restrict head movements and maintain a 60 cm distance from the screen. The experiment began with practice trials repeated until participants felt comfortable with the task. In

each trial for both tasks a fixation dot was always presented in the center of the screen for 100ms. The face was then flashed on the screen for 500ms with its center where the fixation dot was. After the face was presented, some instructions were presented on the screen for a maximum of 10sec at which point the next trial began.

3.3.4 Data analysis

For this analysis data cleaning followed the same steps as Experiment 1. For 9 participants an average of 2 trials per participant (16 trials total) were not responded to within the allotted 10 seconds and were thus not included in the analyses. For RTs, incorrect trials and correct trials that surpassed 2.5 SD from a participant's average were eliminated. Accuracy and RT were further cleaned across participants with mean scores above 3 SD from the group mean being winsorized. There were 10 scores for accuracy and 7 scores across RTs that were winsorized this way. D prime (d') scores were calculated for each size in the recognition task in the same way as in Experiment 1 ($d' = Z(\text{hits}) - Z(\text{FA})$) and 3 d' that were 3 SD outside of the group mean were winsorized.

Accuracy and RTs were analyzed with a 2 Task (Gender, Recognition) x 5 Size repeated measures ANOVA. In addition, the d' for the recognition task was analyzed using a one-way ANOVA with size as the within-subject factor. Again, if the assumption for sphericity was violated (Mauchly's test significant at $p < 0.05$), Greenhouse-Geisser correction to the degrees of freedom was used.

3.3.5 Results

3.3.5.1 Accuracy

The main effect of task was significant for recognition accuracy ($F(1, 106) = 3589.1, p < .001, \eta_p^2 = 0.971$), due to participants discriminating the gender of faces ($M = 0.86, SD = 0.05$) significantly better than recognizing faces ($M = 0.58, SD = 0.04$; Fig. 3-5; Table 3-2).

The Main Effect of Size was also significant ($F(4, 424) = 47.79, p < .001, \eta_p^2 = 0.311$), but was qualified by the interaction between task and size ($F(4, 424) = 2.68, p < .05, \eta_p^2 = 0.025$). Post-hoc comparisons indicated that size S3 ($H5.5^\circ \times V8.3^\circ$) yielded the highest accuracy for both Gender identification ($M = 0.91, SD = 0.06$) and Recognition tasks ($M = 0.62, SD = 0.07$).

Again, to better understand this interaction, both tasks were analyzed separately. The effect of size on the Gender discrimination task was significant ($F(3.448, 365.467) = 37.34, p < .001, \eta_p^2 = 0.261$). Looking at the Bonferroni corrected pairwise comparisons for the gender discrimination task revealed that size 1 was significantly less accurate than all other sizes while size 3 was more accurate than size 5 ($p < .00125$). A curve fit analysis for the gender discrimination task found that both linear ($R^2 = 0.037$) and quadratic ($R^2 = 0.142$) models were significant. The effect of size on the Recognition task was also significant ($F(4, 424) = 16.67, p < .001, \eta_p^2 = 0.136$). The Bonferroni corrected pairwise comparisons showed that participants were significantly less accurate when responding to size 1 faces compared to all other face sizes ($p < .001$) which did not differ from each other. The curve fit analysis for the Recognition task found that both linear ($R^2 = 0.031$) and Quadratic ($R^2 = 0.08$) models were significant.

When examining the d' for the recognition task, the effect of size was significant ($F(4, 424) = 15.46, p < 0.001, \eta_p^2 = 0.127$). Bonferroni corrected pairwise comparisons mirrored the accuracy results with the exception that size 3 did not have a larger d' than size 5 (Fig. 3-5, Table 3-2).

Much like in Experiment 1, another ANOVA was conducted without size 1 to test its influence on the interaction effect. Both Task ($F(1, 106) = 3334.65, p < .001, \eta_p^2 = 0.969$) and Size ($F(3, 318) = 8.73, p < .001, \eta_p^2 = 0.076$) were significant while the interaction ($F(4, 424) = 1.19, p = .312, \eta_p^2 = 0.011$) was not. This again suggests that size 1 drove the significant interaction effect. In other words, the effect of size is the same for the two tasks for faces larger than Size 1.

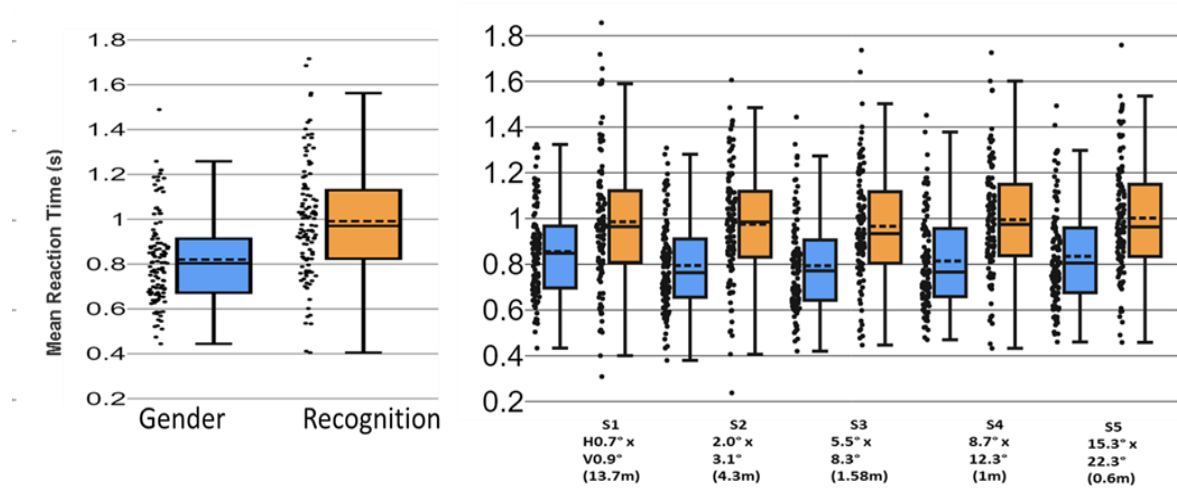


Figure 3-5. Experiment 2 reaction time

A) Box plot for RT across Gender discrimination (Blue) and Recognition (Orange) tasks. The box plot limits represent the upper and lower quartiles. The median is marked by a solid horizontal line within the box and the mean is marked by the dotted line. B) Box and whisker plot for RT across all sizes and tasks with the Gender discrimination task in Blue and the Recognition task in Orange. For all graphs, black dots to the left of each boxplot represent individual participant means for that boxplot.

Table 3-2. Experiment 2: Mean accuracies and d' with SDs for both tasks

Gen: Gender task; Rec: old/new recognition task, S1-5: sizes, H: horizontal visual angle, V: vertical visual angle.

Size/orientation	Mean Accuracy	SD Accuracy	Mean RT	SD RT	D'	D' SD
Gen S1 (H0.7° x V0.9°, ≅13.7m)	.81	.093	855ms	198ms	N/A	N/A
Gen S2 (H2° x V3.1°, ≅4.3m)	.88	.073	794ms	197ms	N/A	N/A
Gen S3 (H5.5° x V8.3°, ≅1.58m)	.90	.069	794ms	204ms	N/A	N/A
Gen S4 (H8.7° x V12.3°, ≅1m)	.88	.068	814ms	209ms	N/A	N/A
Gen S5 (H15.3° x V22.3°, ≅0.6m)	.87	.071	835ms	219ms	N/A	N/A
Rec S1 (H0.7° x V0.9°, ≅13.7m)	.55	.052	986ms	289ms	.27	.29
Rec S2 (H2° x V3.1°, ≅4.3m)	.59	.069	976ms	249ms	.49	.4
Rec S3 (H5.5° x V8.3°, ≅1.58m)	.61	.077	966ms	246ms	.61	.44
Rec S4 (H8.7° x V12.3°, ≅1m)	.60	.072	995ms	241ms	.54	.41
Rec S5 (H15.3° x V22.3°, ≅0.6m)	.59	.073	1000ms	249ms	.49	.4

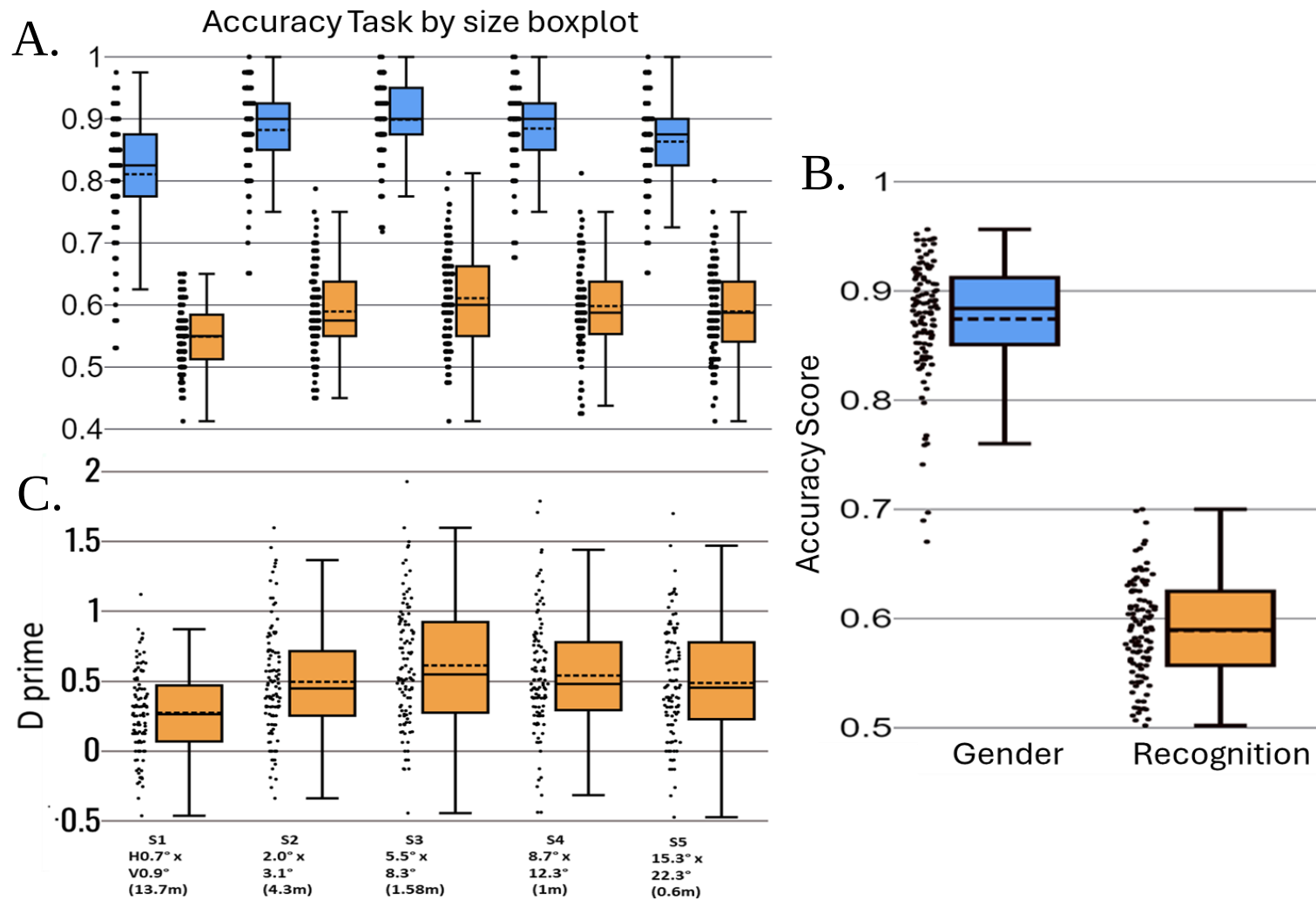


Figure 3-6 Experiment 2 accuracy and d'

A) Box and whisker plot for accuracy across all sizes and tasks with Gender discrimination task scores in Blue and Recognition task scores in Orange. The box plot limits represent the upper and lower quartiles. The median is marked by a solid horizontal line within the box and the mean is marked by the dotted line. B) Box plot for accuracy across face Gender discrimination (Blue) and Recognition (Orange) tasks. C) d' across all sizes for the Recognition task only. For all graphs, black dots to the left of the boxplot represent individual participant means for that boxplot.

3.3.5.2 Reaction Time

The main effect of Task was significant on reaction time ($F(1, 106) = 172.98, p < 0.001, \eta_p^2 = 0.62$). Participants responded to the gender identification task ($M = 819\text{ms}$, $SD = 190\text{ms}$) significantly faster than to the face recognition task ($M = 985\text{ms}$, $SD = 230\text{ms}$; Fig. 3-6).

The main effect of size was also significant ($F(3.643, 386.057) = 8.73, p < .001, \eta_p^2 = 0.076$) and was qualified by a significant interaction between task and size ($F(3.308, 350.64) = 5.34, p < .001, \eta_p^2 = 0.048$). This indicated that the effect of size varied across face judgment tasks.

The effect of size was significant for the gender ($F(3.44, 364.684) = 14.65, p < .001, \eta_p^2 = 0.121$) and recognition tasks ($F(3.363, 356.523) = 2.87, p < .05, \eta_p^2 = 0.026$) analyzed separately. Bonferroni corrected pairwise comparisons between face sizes within the gender discrimination task revealed that participants were slower when responding to size 1 faces ($M = 855\text{ms}$, $SD = 198\text{ms}$) compared to all other face sizes ($p < 0.05$) except size 5. Similarly, participants responded slower to size 5 ($M = 835\text{ms}$, $SD = 204\text{ms}$) compared to size 2 ($M = 794\text{ms}$, $SD = 197\text{ms}$) and size 3 ($M = 794\text{ms}$, $SD = 204\text{ms}$). A curve fit analysis revealed that only the quadratic model ($R^2 = 0.012$) reached significance. When looking at the recognition task, participants were significantly faster at responding to size 3 faces ($M = 966\text{ms}$, $SD = 246\text{ms}$) than size 5 ($M = 1002\text{ms}$, $SD = 249\text{ms}$), see Table 2. The curve fit analysis revealed that neither linear nor quadratic models were significant.

One final ANOVA was conducted on the RTs without size 1 to determine its influence on the interaction effect. Just like the results for the accuracy scores the main effect of Task ($F(1, 106) = 206.53, p < .001, \eta_p^2 = 0.661$) and Size ($F(3, 318) = 9.27, p < .001, \eta_p^2 = 0.08$) were significant while their interaction was not ($F(3, 318) = 0.79, p = .007, \eta_p^2 = 0.007$). This provides strong evidence that only at the extreme small size does task demands influence face processing.

3.3.6 Experiment 2 Summary

Experiment 2 revealed that participants were significantly more accurate when discriminating face gender compared to recognizing upright faces. Face size significantly affected performance, with larger faces leading to higher accuracy, particularly in the gender discrimination task. An interaction between face judgment task and size indicated that face size had a greater effect on gender discrimination than on upright face recognition, although this was uniquely driven by the smallest face size. Reaction times followed a similar pattern, showing significant effects and interactions. Crucially, this interaction was influenced by the smallest face size (size 1); when this size was excluded from analysis, the interaction effect disappeared.

Overall, these findings show that both face judgment task and face size significantly impact accuracy and reaction time, with face size exerting a more substantial influence at very small sizes. These results support our hypothesis and align with McKone's (2009) findings on an optimal size range for accurate face processing.

3.3.7 Comparison of upright faces in recognition tasks for Exp.1 and Exp.2

In order to examine the differences between the two slightly different experimental paradigms of the recognition tasks across each experiment, a between-subject analysis was performed on the upright faces of Exp. 1 and Exp. 2. It is important to note that in addition to the different paradigm participants in Exp. 1 also had double the number of trials and therefore, depending on the order of the blocks for each condition, could be more practiced in the task as well as more fatigued. The between subjects analysis of the accuracy scores (2 Experiments x 5 sizes mixed model ANOVA) yielded no significant effect of Experiment ($F(1, 211) = 0.35, p = 0.555, \eta_p^2 = 0.002$), however the Experiment by Size Interaction did reach significance ($F(4, 844) = 2.64, p = 0.033, \eta_p^2 = 0.012$). When looking at the between subjects analysis of the d' , there was also no significant difference observed ($F(1, 211) =$

1.16, $p = 0.205$, $\eta_p^2 = 0.008$), however, the Experiment by Size Interaction was significant ($F(4, 844) = 2.71$, $p = 0.029$, $\eta_p^2 = 0.013$). While the interpretation of this effect was difficult to rationalize, one possible explanation was the different peak accuracy for Exp 1 which occurred at size 4 while the peak accuracy for Exp 2 was at size 3. The analysis of the RT demonstrated a significant difference between the experiments ($F(1, 211) = 10.98$, $p < 0.001$, $\eta_p^2 = 0.049$). On average participants responded faster during Exp. 1 ($M=881\text{ms}$, $SD=22\text{ms}$) than they did in Exp. 2 ($M=986\text{ms}$, $SD= 22\text{ms}$) with Bonferroni pairwise comparisons between all sizes revealing they were significantly different from Exp. 1 to Exp. 2.

3.4 Chapter 3 discussion

The present study set out to address several gaps in the literature concerning the effects of face size across two face judgment tasks. Previous research has primarily focused on the effect of size on face holistic processing, often neglecting the role that face size may play in real-world scenarios. Moreover, existing studies have varied significantly in terms of the tasks used, the range of face sizes evaluated, how performance and stimuli size were measured, leading to inconsistent findings. Many of these studies have employed small sample sizes and trial numbers, limiting the generalizability of their results. Furthermore, while the importance of holistic processing has been well-documented, relatively little attention has been paid to how face size may affect different types of face processing tasks, such as gender discrimination, that rely more on featural processing.

In Experiment 1, we aimed to assess the effects of face size on recognition memory using both upright and inverted faces, to identify an optimal size range for holistic face processing. Experiment 2 extended these findings by focusing on how face size impacts performance on both a recognition memory task and a gender discrimination task, using only upright faces. This design allowed us to examine whether size influences tasks that are either dominant in holistic (face recognition) or featural (gender discrimination) processing differently across

tasks. By doing so, we sought to provide a clearer understanding of how face size affects face processing in a variety of tasks and whether certain sizes may enhance or decrease performance in real-world face judgment contexts.

The results of experiment 1 provide valuable insights into the impact of face orientation and size on recognition accuracy and reaction time. Our findings largely align with previous research by Mckone (2009), that reinforced the notion that face processing is a complex interplay between holistic and feature-based mechanisms, influenced significantly by orientation and size. The results of experiment 2 further elucidate the influence of face size on different face judgment tasks, specifically gender discrimination and face recognition. Our findings extend the understanding of how holistic and feature-based processing mechanisms operate under varying conditions, offering insights that could inform both theoretical perspectives and practical applications.

3.4.1 Effect of orientation on accuracy and reaction time

In Experiment 1, a significant main effect of orientation was observed on recognition accuracy, consistent with prior studies (Tanaka and Farah 1993; Barton et al. 2001; Maurer et al. 2002). Upright faces were recognized with greater accuracy than inverted faces, reaffirming the face inversion effect (FIE), which reflects the disruption of holistic processing when faces are inverted. This finding supports the notion that inversion interferes with the integration of facial features, forcing participants to rely more on feature-based processing, which is less efficient for face recognition (Tanaka and Farah 1993). However, even for upright faces the mean accuracy of the participants did not rise above 62% (Tables 3-1 & 3-2) at face sizes typical of human interaction (~1-2m distance). This is a marked drop in recognition accuracy compared to previous work which has shown accuracy levels above 80% (Lewin and Herlitz 2002; Jiang et al. 2011; Liu et al. 2013; Kok et al. 2017). This could possibly be a result of the paradigm used in the current experiment with more participants than most previous studies, a larger number of trials, all unique faces, and same presentation time during both study and test phases of the recognition task (Table 3-3). It is also important

to note that the images in this experiment were highly controlled only showing an oval of the face and only Caucasian faces. Previous research has shown that with added context such as hair, shoulders, scenery, etc. participants are more accurate in recognizing faces (Lewin and Herlitz 2002; Gruppuso et al. 2007; Hayes et al. 2010; Liu et al. 2013). Taken together, all these factors make the current experiment more difficult and cognitively demanding than previous work.

Despite the significant effect on accuracy, orientation had no significant effect on reaction time (RT) in Experiment 1. This contrasts with previous findings that suggest participants take longer to recognize inverted faces (Jiang et al. 2011; Mundy and Sadusky 2014). The lack of FIE on RT may be due to the experimental paradigm, in which faces were presented for 500ms for both study and test phases. In previous work, the paradigm for the recognition tasks presented the face in the test phase until the participant responded, allowing them to examine the faces for much longer than in the current studies (Loftus and Harley 2005; McKone 2009; Yang et al. 2014). This limited exposure time for participants in the current study might have led to them responding at a similar pace for both upright and inverted faces and across tasks. The instructions emphasizing speed may have further minimized differences in RT between orientations and tasks.

3.4.2 Task differences in accuracy and reaction time

The main effect of task on both accuracy and reaction time was highly significant in Experiment 2, illustrating a clear distinction between gender discrimination and face recognition tasks. Participants achieved significantly higher accuracy and faster RTs in the gender discrimination task compared to the recognition task. This effect can be explained by the relatively simpler nature of gender discrimination, which some research has suggested relies on feature-based processing of salient gender-specific facial features such as the eyes and lips (Brown and Perrett 1993). Indeed, accuracy scores for the gender discrimination task in the current experiment were quite high across all face sizes, including the smallest and largest faces, demonstrating the ease of the task even in more challenging visual conditions.

One criticism of this paper could be that the face recognition task was more difficult in Exp. 2 than Exp. 1. This difficulty may be attributed to the nature of the experimental paradigm, wherein participants performed the gender discrimination task during the learning phase. Such multitasking may have interfered with their ability to fully encode the faces for subsequent recognition trials, as the cognitive load during encoding was higher. This criticism can be assuaged by the fact that both Exp.1 and 2 elicited similar accuracy scores for upright faces despite different encoding tasks, hovering significantly above chance level, but not reaching past 65%. Another key distinction between the two experiments relates to the trial number. Exp. 1 included twice the number of faces and trials as Exp.2 which would increase participants' fatigue, boredom, and task experience. A statistical comparison between the upright faces in the recognition tasks across the two experiments revealed no difference for accuracy or d' , suggesting that this increased task difficulty for Exp.2 did not significantly impact the recognition results. The analysis of the RT was significantly different between experiments suggesting that participants' response times across the sizes varied between the experiments possibly due to the discrepancy in difficulty or fatigue. It is important to note that the interaction between Experiment and Size for upright faces was significant across accuracy and d' analyses, but not the RT analysis, making the interpretation of these results complex. While there seems to be no significant difference between the samples across experiments in terms of accuracy, there appears to be some difference across the sizes.

3.4.1 Effect of Face Size

Both experiments revealed a statistically significant main effect of size on recognition accuracy and reaction time, reinforcing the notion that face size plays a role in face processing efficiency. The highest accuracy for face recognition was observed at size 4 (8.7° h x 12.3° v) in Experiment 1, while size 3 (5.5° h x 8.3° v) yielded the best performance across tasks in Experiment 2. These results are consistent with previous research suggesting that holistic face processing is most effective within a specific size range, closely mirroring

the sizes at which people typically interact with faces in everyday life, approximately 1-2 meters away (Blakemore and Campbell 1969; Loftus and Harley 2005; McKone 2009).

In Experiment 1, the significant interaction between orientation and size revealed that size had a stronger effect on upright face recognition than on inverted face recognition. For upright faces, accuracy was dependent on face size, with performance following a parabola shaped curve with size 3 and size 4 eliciting the best accuracies. Evidence for this comes from the significant quadratic models found with the curve fit analysis. These results are in line with those found in McKone et al. (2009) demonstrating that at extremely large and extremely small face sizes, holistic processing and therefore recognition ability, is disrupted. Further evidence for this can be found in the analysis of the experiments without size 1. Without Size 1 the interaction effects between Orientation and Size and Task and Size disappear, but the main effect of size remains significant. On the other hand, the direction of the data for both experiments suggests that at even larger face sizes (the other end of the size spectrum), we may find an interaction effect similar to the one found with the inclusion of size 1, as very large faces may be too large to fully process all the features. If the features of the face cannot be observed within the given time frame, as with large faces, they cannot be holistically processed into a single percept, thus leading to a deficit in recognition akin to viewing an inverted face. Studies using blurred faces of celebrities found that large faces were more difficult to recognize possibly due to difficulty examining all the details of the face whereas in smaller faces all the features are closer together making processing the obstructed stimuli easier (Mousavi and Oruc 2020). In contrast, accuracy for inverted faces was much lower across all sizes, however, a similar parabola shaped effect of size existed here as well. Similarly to upright faces, this effect seems driven by the extreme face size as removing size 1 eliminated the interaction effect. This finding aligns with the idea that holistic processing is more disrupted by smaller sizes for upright faces, while feature-based processing—which is primarily used for inverted faces—is less affected by size variations (Yang et al., 2014; Oruc and Barton 2010).

Further examination of these results showed that all upright faces were recognized above chance level which highlights the ability of humans to recognize faces even at the smallest face size. Inverted faces were also recognized above chance at all face sizes except the smallest face size, suggesting that at extreme face sizes, when holistic processing was disrupted, recognition was severely limited. These results demonstrate that the effect of size on face judgment accuracy is driven by the extremely small face size (and the parabola shape suggests that it might be the case at extremely large face size as well). It is also important to note that the effect of size is much smaller than the effect of task and orientation.

While orientation did not significantly impact reaction time, size had a notable effect, with size 1 (0.9° horizontal x 1.4° vertical) yielding the fastest reaction times. The significant interaction between orientation and size on reaction time suggests that integrating features in larger faces is influenced by whether the face is upright or inverted. This may be attributed to the increased difficulty in processing larger faces which require more time for the larger amount of visual information to be integrated, thereby slowing down the recognition process. It is possible that because the entirety of the smaller sized faces is within the fovea, it takes less time to process these faces. It is also important to note that while RTs were faster for smaller faces, accuracy for size 1 was significantly lower than for other sizes, with many participants scoring near or below 50% accuracy, particularly for inverted faces. For upright size 1 faces, 33 participants scored at or below 50% accuracy (i.e. chance level) while 46 did so for inverted size 1 faces. The lack of a significant FIE on RT contrasts with previous research that has often demonstrated a delayed response for inverted faces compared to upright faces (Jiang et al. 2011; Mundy and Sadusky 2014). This suggests that participants may have been responding quickly, but inaccurately, potentially clicking through smaller face trials without fully processing the stimuli. As such it is crucial that the results for RT be interpreted in a different way than previous research as it does not necessarily reflect actual participant reaction speed, but how confident participants are in their responses to a given

face size. In difficult conditions (i.e. smaller faces) they may simply choose a response at random as quickly as possible given the instructions on speed prioritization.

The significant interaction effect between task and size on accuracy, coupled with the significant interaction on reaction time, underscores the differential processing demands of the two tasks. Gender identification, which has been suggested to predominantly engage in feature-based processing, appears to be influenced by face size, however it seems to be less sensitive to size variations in terms of RT, yet benefits from optimal sizes in terms of accuracy. In contrast, face recognition, which relies more on holistic processing, shows a more uniform sensitivity to size variations across both accuracy and reaction time. This distinction highlights the importance of considering task-specific processing mechanisms when examining the effects of face size. Additionally, the significant interaction between task and size on reaction time further suggests that while both tasks benefit from an optimal size, the extent of this benefit varies, with gender identification showing a small advantage over face recognition. Again, these differences could also be a result of the experimental paradigm which presented the faces for the same amount of time for the test phase in both gender and recognition tasks. Regardless, these results demonstrate that size has a significant role to play across face judgment tasks.

3.4.2 Limitations

While these experiments provide valuable insights, they are not without limitations. One of the most important limitations comes from the different ways studies report the size of the stimuli. Many studies have only provided one dimension (vertical or horizontal visual angle) or use measures such as simulated distance that do not seem to correspond to the mathematical calculation of visual angle (Table 3-3). To further emphasize this aspect, we measured several faces and input these values into the visual angle formula to accurately measure the distance these faces would represent. In many of these instances the simulated distance was a little bit larger than the mathematical formula showed. Similarly, there is a limitation with the size of the screens that are used which can limit the resolution and image

size. There is a possibility that at larger face sizes there are unique effects that cannot be captured with common computer monitors. Perhaps viewing larger face sizes results in increasingly less accurate responses as the current data trends suggest and previous research has reported, or perhaps they increase accuracy (McKone et al, 2009, Yang, 2014). Regardless, all of these studies suffer from ecological validity as size on a computer screen cannot be properly equated to real world distances where monitor compression to pixels is less defined than real 3D images would be.

Another limitation is the exclusive use of Caucasian faces which limits the generalizability of the findings to other ethnic groups. Future research should include a more diverse set of stimuli to explore potential cultural and ethnic differences in face processing. It is important to note that a majority of the participants in both experiments were not Caucasian and could be subject to other race effects despite our attempts to ensure familiarity with Caucasian faces by living in Canada for a minimum of 5 years (Lindsay et al. 1991; Michel et al. 2006). A between subjects' analysis was conducted between white and non-white self-identifying participants, but no significance difference within each experiment was found.⁶ Regardless, it would also be interesting to examine the difference across tasks and orientations with more context cues and a more diverse sample in the stimuli (hair, glasses, facial hair, surrounding environment/scene, etc.). Additionally, the controlled laboratory setting may not fully capture the complexities of real-world face processing, where factors such as movement, lighting, and emotional expressions can influence performance. Essentially, future studies should aim to replicate these findings in more ecologically valid settings.

⁶Experiment 1: Accuracy= ($F(1, 104) = 0.657, p = .419, \eta_p^2 = 0.006$; $d' = (F(1, 104) = 0.229, p = .633, \eta_p^2 = 0.002$; RT= ($F(1, 104) = 0.348, p < .557, \eta_p^2 = 0.003$)
Experiment 2: Accuracy= ($F(1, 105) = 0.651, p = .422, \eta_p^2 = 0.006$; RT= ($F(1, 105) = 0.619, p = .433, \eta_p^2 = 0.002$)

Table 3-3 Basic literature review.

A basic literature review showing the variability between face size studies in terms of sample size, trial numbers, and way of reporting face size.

Study	Vertical VA	Horizontal VA	Distances	Sample, trials per cond.
Current experiment	0.9°-22.3°	0.7°-15.3	0.6m-13.7m	N=106 & 107, 40 trials
Van Belle et al. 2010	7.5° & 15°	5° & 10°	~1-3m	N=9, 81 trials
Mckone et al. 2009	0.275°-89.86°	N/A	0.11m-34.7m	N=11&10, 12&50 trials
Yang et al. 2014	N/A	1°-10°	~1.3m-13m	N=8, 40 trials
Jefferys et al. 1992	1°-8°	N/A	~1.65m-13m	N=3, 2 trials
Ross & Gauthier 2015	N/A	0.35°-4.14°	~0.1m-14m	N=101, 160 trials
Stacchi & Caldara, 2022	3°-12°	N/A	~4.2m-1.1m	N=30, 50 trials

3.4.3 Conclusion

In conclusion, this research provides evidence that face size significantly impacts gender identification and face recognition tasks, with distinct effects on accuracy and reaction time. While there is a statistical effect of size it does appear to be small in comparison to other factors like orientation and task, which show much larger effects across all sizes. The differential effects of size across orientation and task were also very small and driven by the smallest face size. These findings highlight the interplay between holistic and feature-based processing mechanisms and underscore the importance of considering task-specific demands in face processing research across several measures. The results for the upright recognition task across both studies were statistically similar, suggesting a stable effect despite the difference in task during the encoding phase. Future studies should continue to explore these dynamics across different populations and real-world contexts to further enhance our understanding of face perception. Larger, more diverse samples and stimuli (e.g. Adolescence, seniors, cross-cultures, etc.) should be incorporated along with different face judgment tasks (e.g. emotion identification) to examine how consistent and generalizable these results are. These findings have practical implications, particularly in areas such as face recognition technology, security, and surveillance. Understanding the optimal size range for different face processing tasks can inform the design of more effective facial recognition systems. For instance, ensuring that faces are presented within the optimal size range

identified in this experiment could enhance the accuracy and speed of automated face recognition systems. Similarly, it could be used as evidence in court to demonstrate the abilities of humans to accurately recognize faces even at great distances and when distracted with other tasks.

General Discussion

The results across the three chapters of this thesis provide new insights into the flexibility of holistic processing. This research demonstrates that both behavioral and neural responses to faces are sensitive to Orientation, Fixation Location, and Size, advancing our understanding of the cognitive and neural mechanisms underlying holistic face and house perception.

The Neural Inversion Effect

The inversion effect for faces, mostly captured by the N170 ERP component, is a well-documented phenomenon where the inversion of a face disrupts holistic processing, leading to increased N170 amplitude and delayed latency. The findings in Chapters 1 and 2 reinforce this perspective, but with the added value of using MUA (mass univariate analysis), which provided a more detailed temporal analysis of the neural response. Unlike traditional ERP peak analysis, MUA captured the entire epoch, offering a more comprehensive understanding of how inversion impacts the neural dynamics of face processing temporally.

Both chapter 1 and 2 consistently found that inversion of faces increased N170 amplitude, but the use of MUA revealed that the most substantial differences were not confined to the N170 peak itself but extended into the P1-N170 and N170-P2 transition intervals. The earlier differences found around the P1 have been ignored in the past, in favour of the large differences seen around the N170 peak amplitudes, however, this appears to be where the earliest statistical difference between upright and inverted faces occurs. Importantly, this temporal extension shows that face inversion disrupts processing beyond early holistic integration, implicating additional neural mechanisms.

This disruption by inversion extends to house processing which also demonstrated an inversion effect as early as the P1 and as late as the P2. Differences between faces and houses were also found at these early timepoints. These differences have been mostly dismissed in the literature on the account of contrast and luminance differences between the two

categories, however, the current stimuli were equalized across contrast and luminance. This suggests that while the perception of objects such as houses is influenced by inversion, there is still a difference between how and when humans process face inversion (Itier and Taylor 2004). The consistency of findings across both chapters strengthens the reliability of the observed effects, especially considering the larger sample size and trial numbers used in Chapter 2. The key novelty is that MUA allows for a deeper exploration of the entire epoch, across the scalp, uncovering statistical differences that conventional ERP analyses may overlook.

In contrast to previous ERP literature, which reported no or minimal inversion effects for non-face objects (Rossion et al. 2000; Itier and Taylor 2004; Itier et al. 2006; Kloth et al. 2013; De Lissa et al. 2014), Chapters 1 and 2 provided strong evidence for a house inversion effect (HIE) using MUA. This finding challenges the traditional view that non-face objects are processed featurally rather than holistically. The inversion of houses elicited increased N170 amplitude and delayed latency, similar to faces, but the timing, strength, and topographical distribution of these effects differed significantly. This is a novel finding that has not been reported before and it demonstrates a significant departure from what previous work has suggested possible for holistic processing. Specifically, this suggests that holistic processing is more malleable than previously theorized with objects being processed holistically as well. Without holistic processing being the distinguishing factor between face and object processing, researchers must look for alternative ways of explaining their differences.

These findings contribute to ongoing debates regarding the qualitative versus quantitative nature of the face inversion effect (Sekuler et al. 2004; Rossion 2008; Matsuyoshi et al. 2015). While the FIE has traditionally been viewed as a qualitative shift in processing strategy, the presence of a strong HIE for houses suggests that similar mechanisms may operate for non-face objects, albeit in a delayed fashion with fewer peak differences. These differences could reflect differences in experience and familiarity with faces versus houses, as faces are more homogenous and experienced more frequently than

houses. There is some research that has suggested that the difference between stimuli based on the amount of experience and biological relevancy does not dramatically influence behavioural responses such as recognition (Oruc and Barton 2010), however the neural effects may be more sensitive to these types of differences. The quantitative differences observed in MUA support the notion that face and house inversion may be more similar at the neural level than previously believed but driven by distinct neural mechanisms. Such a discovery would not have been possible without MUA that enabled us to examine every timepoint and electrode being recorded. Specifically, some quantitative differences appear in the significant effects for faces observed in earlier components such as the P1, indicating that holistic processing might begin earlier than previously thought. The inversion effect for houses was strongest around the N170-P2 interval, but with differences in timing, amplitude, and topography compared to the FIE, suggesting that while both faces and houses engage holistic processes, the neural underpinnings and time course of these effects may differ. This finding provides further evidence that holistic processing is not as face specific as previously thought and may extend to other categories. Similarly, there are some qualitative differences in how long inversion influences face processing compared to house processing. For instance, there are several more peak differences seen at earlier time points for faces compared to houses. Inversion appears to have less of a dramatic influence on house than face processing in terms of latency and amplitude. This distinction highlights the broader implication of the findings for the object recognition literature, suggesting that holistic processing is not exclusive to faces.

Moreover, the HIE was observed to be stronger and more sustained in Chapter 2, likely due to the larger sample size and higher statistical power. In Chapter 1, similar effects were present but did not reach statistical significance after correction. The differences in timing and location of peak effects between FIE and HIE still suggest distinct neural generators for face and house processing, reinforcing the idea that the two categories engage different neural mechanisms. Chapter 2 provided an opportunity to directly compare the inversion effects for faces and houses within the same participants, unlike Chapter 1, where

the comparisons were made across independent samples. The analysis revealed that, while both faces and houses exhibit inversion effects, the temporal, spatial, and quantitative aspects of these effects differ. Specifically, the statistical peak of the FIE occurs earlier (~170ms) with a bilateral posterior distribution, while the HIE peaks later (~200ms) at medial occipital sites. This suggests that while both stimuli may rely on holistic processing, the nature and origin of their processing differ.

Despite the findings above, it is important to note that the neural origins of the Inversion effect are still unknown. The reframing of the timing for both face and house processing provided by MUA does not provide information on why amplitudes and latencies differ between these stimuli or what neural mechanisms are involved. It is not possible to determine if the amplitude differences are due to more neural activity in the same areas or different neurons with different activity. More research using MUA across additional cognitive measures (e.g. MEG, FMRI, etc.) needs to be conducted in order to better understand the inversion effect and its neural origins.

Fixation Location Effects

Both chapters examined the role of fixation location on face processing and found strong and consistent effects, further supported by the use of MUA. The fixation location influenced the N170 amplitude, with stronger responses for fixations on the eyes. This result is consistent with previous studies showing that eye fixations elicit larger N170 responses than fixations on other facial regions, such as the nose or mouth. This observation supports the idea that holistic face processing is malleable and influenced by the specific area of focus. Chapters 1 and 2 reported a significant interaction between fixation location and orientation for faces, where the inversion effects varied depending on the fixation position. For example, inverted faces elicited the strongest N170 responses for eye fixations, whereas upright faces showed a gradient of responses, with the strongest activations for nasion and eye fixations. MUA revealed that these effects extended beyond the N170, impacting the retinotopic

component known as C2 (~125ms) and the later N170-P2 interval. The use of a within-subject design in Chapter 2 allowed for a more robust assessment of these effects, offering a comprehensive view of how gaze position modulates neural responses to upright and inverted faces.

A novel contribution of this thesis is the demonstration that fixation location also affects house processing, a finding that was not statistically significant in Chapter 1 but was clearly observed in Chapter 2. The larger sample size and increased trial count in Chapter 2 allowed for greater statistical power, resulting in the observation of a significant main effect of fixation location for houses. While the effect was smaller than what was observed for faces, there was indeed a fixation location effect for houses. This finding is novel as no prior study has reported any fixation location effect for non-face objects. Similar to faces, fixation on different parts of a house (e.g., Left window, Door, etc.) led to significant changes in the amplitude and timing of the ERPs. Unlike faces, the strongest fixation effects for houses were seen at occipital sites rather than posterior lateral electrodes. Additionally, the interaction between fixation location and orientation was evident, with certain fixation locations amplifying the inversion effect, especially during the P1-N170 transition. This retinotopic C2 component seen for objects confirms that where someone looks on houses influences their perception. This reinforces the idea that even objects with variable structures, like houses, are subject to some form of holistic or configural processing.

The fixation location effects for faces and houses revealed important distinctions and similarities. For faces, fixation effects were observed earlier (~55-226ms) and were stronger at posterior lateral sites. In contrast, the effects for houses emerged later (~113 ms) and were stronger at medial occipital sites. These differences reflect the inherent structural differences between the two categories that have been reported in previous work. The early onset of fixation effects for faces could be due to the ever-changing nature of faces that are biologically relevant stimuli. This could also help explain why inversion influences house processing later in time as non-animate objects are stable stimuli that do not require constant immediate updating to be processed successfully. The presence of this fixation effect for

houses challenges prior assumptions that these effects were exclusive to faces. While faces display significant gaze-dependent modulations of the N170, houses demonstrate a similar effect in timing with a smaller statistical difference. The fixation effect for houses appeared to be dependent on differences observed at the beside the door fixation location while there is a larger diversity of responses for each face fixation location. This is a critical finding, as it suggests that gaze location influences the early neural encoding of both face and at least some object categories even earlier than previously thought. Moreover, while faces exhibited a clear gradient of effects based on fixation location, the effects for houses were more evenly distributed, with subtle but significant differences depending on where the gaze was focused. These findings highlight the broader role of spatial attention in shaping neural responses to visual stimuli, regardless of whether the stimuli are faces or houses.

Size effects on face recognition

The two size experiments presented in Chapter 3 highlight the critical influence of stimulus size on face processing. Across both experiments, face size was shown to significantly modulate recognition accuracy and gender classification, with medium-sized faces yielding the best performance. This supports the idea that holistic face processing operates most effectively when faces are presented at sizes that mimic typical viewing conditions (interaction distance) in everyday life.

The findings suggest that extremely small or large face sizes disrupt optimal holistic processing, potentially due to differences in visual detail availability and perceptual scaling. Importantly, upright faces showed greater sensitivity to size changes compared to inverted faces, underscoring the role of holistic processing in upright face perception. The consistent effects across both experiments provide evidence for the notion that size influences the efficiency of holistic processing. While size does statistically influence holistic processing, the actual changes in accuracy and reaction times across the sizes are minimal, especially at social distances. Face size does play a role in holistic processing, however the degree to

which it has an impact is limited when examining face sizes at social interaction distances. These results add to the growing body of literature demonstrating that face processing is not uniform across different visual scales. By showing that face size modulates behavioral responses, the study highlights an essential boundary condition for models of holistic processing.

The significant interaction between task and size as well as size and orientation in terms of accuracy suggests that face size influences processing across both tasks and orientations differently. The reaction time data indicated that task-specific demands interact with face size in complex ways that do not always match what was found in previous studies. This was likely due to the different paradigm of the current study that limited the face presentation time during the test phase. Regardless, it seems that these interaction effects for both experiments were mainly driven by the smallest face size as the interaction was no longer significant when the smallest size was removed from the analysis. This indicates that holistic processing remains uninfluenced by face size across a wide range, spanning from size 2 ($2.0^\circ \times 3.1^\circ$; equivalent to $\sim 4.3\text{m}$) to size 5 ($15.3^\circ \times 22.3^\circ$; $\sim 0.6\text{m}$), which fits within the framework of previous research that has also found an ideal size range for holistic processing (McKone 2009). While only the smallest size drove the interaction, the trends of the data for both experiments appear to suggest the same would be true at even larger face sizes than the largest one tested. Regardless, these experiments provide a great insight into how the understudied variable of size influences holistic face processing. Another interpretation is that size is not vital for holistic face processing as there is no interaction effect when size 1 is removed. Since accuracy for inverted faces at size 1 did not significantly differ from chance it is possible that participants were guessing at this size and their scores do not reflect their actual ability. The results with size 1 could be biased and therefore it may be prudent to examine the results without size 1 with more weight. Taken together, these results suggest that face size may only matter at extreme sizes, however, for research design purposes there appears to be a large range at which face size has little influence on holistic processing, accuracy, and reaction time.

Limitations and future directions

This body of work is not without its limitations. One notable limitation is the lack of ecological validity of the stimuli used in each experiment. These stimuli were highly controlled, consisting only of Caucasian faces, edited to be greyscale, with just the outline of the face visible. This limits the conclusions of the findings to the visual processing of Caucasian faces. Additionally, the stimuli were presented for less than a second, which does not reflect real-world scenarios where participants would have more time to process visual information. Moreover, these experiments were conducted in highly controlled environments, with participants using chinrests and viewing stimuli on computer screens in sound- and light-attenuated rooms. Such settings further restrict the applicability of these results to real-world contexts. Future studies should compare these tightly controlled experimental conditions with more ecologically valid settings (e.g., observing full, non-white faces in naturalistic environments with colour) to understand how these controls influence visual processing.

Beyond the overarching limitations, specific criticisms are noted within individual chapters. For instance, chapters 1 and 2 relied on the MUA toolbox LIMO, a relatively new tool still under development. During the course of analyzing these datasets, several updates and changes to the toolbox drastically altered the results it produced. Some differences are linked to the way electrodes are correlated across the scalp (a researcher-directed process), while others stem from updates to statistical corrections, such as shifts from Ordinary Least Squares to Weighted Least Squares at the individual participant level or from Cluster Mass to TFCE at the group level. The effects of some factors remain unclear, such as the influence of the baseline or baseline length on these analyses, which is not yet fully understood. Furthermore, the multivariate nature of MUA in EEG data complicates the calculation of statistical measures like effect size. While LIMO developers currently recommend using Mahalanobis distance to calculate effect size, this approach is novel and lacks interpretative precedence for MUA with EEG data. Similarly, there are no established guidelines for

selecting the most appropriate correction technique for different analyses or understanding their respective costs and benefits. In this thesis, a Bonferroni-adjusted α was used to mitigate Type I errors from multiple statistical tests when doing follow-up analyses (Ranganathan et al., 2016). Future research should explore these factors to clarify their impact, and it is crucial to acknowledge that MUA and the LIMO toolbox are still evolving. Comprehensive analyses using various MUA toolboxes (e.g., FMUT) and additional correction techniques will be essential for deepening our understanding of these methods (Fields and Kuperberg 2020; Durston and Itier 2021). Another important critique of this work, and EEG research in general, is the lack of standardization in data-cleaning practices. Studies employ widely varying methods for removing trials with artifacts and filtering the raw EEG data, ranging from automated to manual visual inspections, both of which are prone to subjectivity and the risk of either over- or under-zealous rejection of data. Some researchers have even suggested that raw, unfiltered data might be the most reliable choice for these reasons (Delorme 2023).

For the behavioral studies in chapter 3, one specific limitation involves the restricted range of stimuli sizes. Future studies should consider using larger computer screens to examine the effects of larger face sizes. Additionally, it would be valuable to investigate other real-world face judgment tasks, such as emotion identification, to determine whether the findings are consistent across different tasks.

Future directions for chapters 1 and 2 should include additional object categories as well as participants with expertise with specific objects (e.g. architects with houses). It is entirely possible that other objects may not share the same neural response and inversion effect as houses do especially in participants with different experiences/expertise with these objects. There is some evidence to suggest expertise such as with dogs or cars, can influence the neural and behavioural response to inversion (Diamond and Carey 1986; Arata 1991; Rossion and Curran 2010). It is possible that there are expertise differences for stimuli size and fixation location as well. For instance, Greebles, a completely artificially designed object category, have been shown to elicit different behavioural and neural responses than other

objects especially after training (Gauthier and Tarr 1997, 2002; Gauthier et al. 1998, 2004; Rossion et al. 2000). It is additionally important to examine other objects that have been used in past research to show there is no inversion effect for objects (e.g. Wrist watches, ball, etc.). It would also be interesting to examine the influence of objects that appear like faces. Pareidolia, or the tendency to perceive a face within a non-animate object, is a common experience in everyday life and it would be interesting to see if these face-like objects are perceived in the same way as faces at the neural level. This could help us determine if the fixation location and inversion effects found in this thesis are due to the face-likeness of the stimuli used or if it is consistent across object stimuli. Additionally, at the behavioural level, it would be interesting to examine the effect of face size across different face judgment tasks (i.e. emotion identification, visual search tasks, etc.) with varying degrees of difficulty to determine if there are other tasks that influence face processing. It is possible that the effect of face size would be more pronounced with more difficult tasks or perhaps disappears entirely for a specific task.

Conclusion

In conclusion, this thesis advances the field of cognitive neuroscience by demonstrating that holistic face processing is influenced by orientation, fixation location, and size. These findings have important theoretical implications for models of face perception, as they challenge the view that holistic processing is a fixed and uniform process or a uniquely face-specific process. Instead, this research suggests that holistic processing is dynamic and malleable, shaped by a complex interplay of factors, and can be seen in non-face objects such as houses. The inversion effect for houses is a novel finding that supports this view, however other object categories need to be examined to uncover the effects generalizability. Methodologically, the use of advanced statistical techniques such as MUA provides a more comprehensive understanding of the temporal dynamics of face processing, offering new insights into the underlying neural responses.

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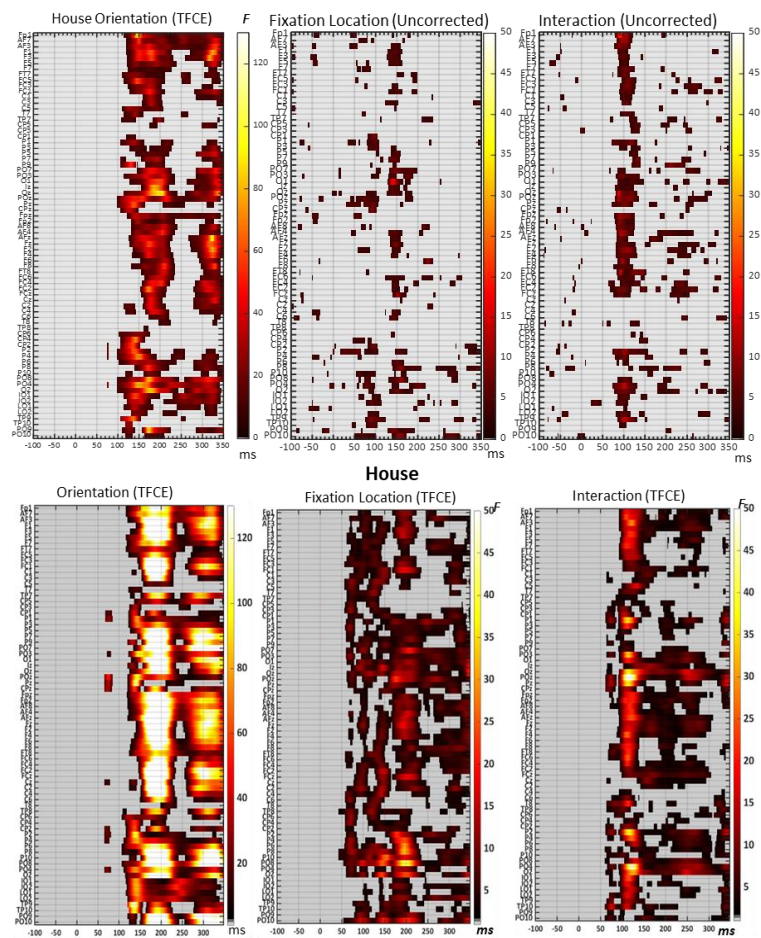
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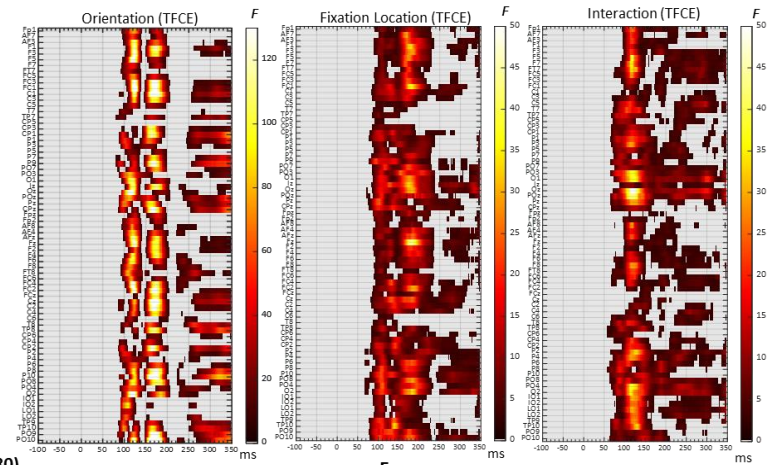
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Appendix

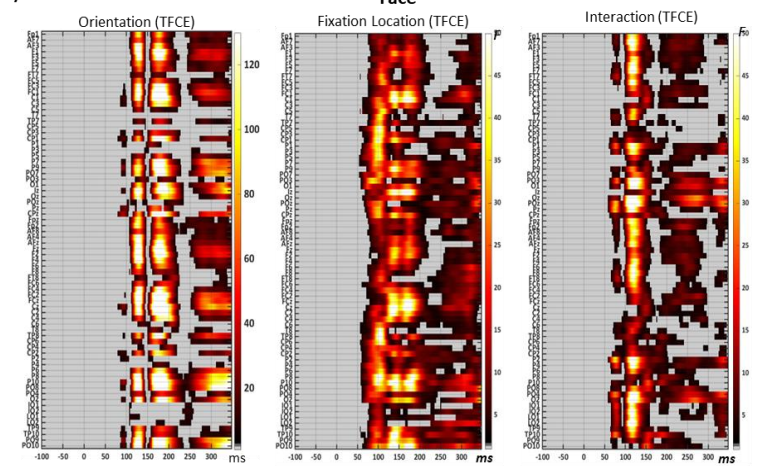


Appendix Figure 1 –

Chapter 1



Chapter 2 (n=80)



Appendix Table 1 Average trials per condition Chapter 1

Orientation	Fixation location	Data Set 1: Houses (n=20)		Fixation location	Data Set 2: Faces (n=20)		Data Set 3: Faces (n=32)		Combined Data Set 2 & 3 (n=52)	
		Mean	SD		Mean	SD	Mean	SD	Mean	SD
Upright	Above Window	51.53	9.38	Forehead	57.96	13.48	57.45	9.97	57.70	12.15
	Below Window	52.26	8.97	Nasion	63.12	9.93	63.4	7.94	63.26	9.13
	Center	52.95	10.01	Nose	62.31	10.86	62.1	8.97	62.20	10.05
	Beside Door	53.21	8.18	Mouth	60.28	12.49	58	10.93	59.14	11.90
	Left Window	44.89	7.72	Left Eye	59.43	14.05	59.65	10.14	59.54	11.22
	Right Window	46.95	7.4	Right Eye	60.09	12.12	59.7	9.64	59.9	9.77
Inverted	Above Window	52.26	7.01	Forehead	56.40	13.02	56.3	11.58	56.35	12.37
	Below Window	54	7.98	Nasion	61.37	10.18	60.25	8.66	60.81	9.56
	Center	53.11	9.36	Nose	63	9.48	61.15	8.74	62.07	9.17
	Beside Door	54.42	9.06	Mouth	62.46	9.37	59.35	9.82	60.90	9.58
	Left Window	44.68	10.17	Left Eye	62.34	10.24	60.5	8.35	61.42	9.522
	Right Window	43.05	7.29	Right Eye	57.90	13.23	59.25	10.96	58.57	12.31
upright	Door	45.79	8.39							
inverted	Door	46.79	9.31							

Appendix Table 2 Average trial numbers per condition Chapter 2 N=80

Orientation	Fixation location	Houses		Fixation location	Faces	
		Mean	SD		Mean	SD
Upright	Between Windows	72.86	11.17	Nasion	70.95	12.61
	Center	72.95	11.96	Nose	71.19	12.47
	Beside Door	71.44	12.00	Mouth	63.8	14.68
	Left Window	71.26	12.31	Left Eye	67.91	12.25
	Right Window	70.51	13.78	Right Eye	69.08	13.65
Inverted	Between Windows	73.63	11.46	Nasion	71.26	11.59
	Center	74.05	11.53	Nose	72.03	11.82
	Beside Door	72.99	11.89	Mouth	70.28	13.24
	Left Window	71.66	11.83	Left Eye	69.65	12.67
	Right Window	72.41	12.11	Right Eye	70.6	11.89

Appendix Table 3

average hit rate and false alarm rate

Size/orientation	Hit rate avg	False Alarms rate avg
UP S1 (H0.7° x V0.9°, $\cong$ 13.7m)	0.44	0.38
UP S2 (H2° x V3.1°, $\cong$ 4.3m)	0.49	0.31
UP S3 (H5.5° x V8.3°, $\cong$ 1.58m)	0.5	0.29
UP S4 (H8.7° x V12.3°, $\cong$ 1m)	0.54	0.3
UP S5 (H15.3° x V22.3°, $\cong$ 0.6m)	0.53	0.33
INV S1 (H0.7° x V0.9°, $\cong$ 13.7m)	0.45	0.43
INV S2 (H2° x V3.1°, $\cong$ 4.3m)	0.49	0.41
INV S3 (H5.5° x V8.3°, $\cong$ 1.58m)	0.5	0.42
INV S4 (H8.7° x V12.3°, $\cong$ 1m)	0.52	0.41
INV S5 (H15.3° x V22.3°, $\cong$ 0.6m)	0.51	0.44