

MOVING INDIVIDUAL DIFFERENCES IN FACE IDENTITY DISCRIMINATION FROM NOISE TO SIGNAL

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Présentée par
Lisa STACCHI
(Magliaso, Suisse)

Approuvée par la Faculté des lettres et des sciences humaines sur proposition des professeur-
e-s Prof. Dr. Roberto CALDARA (premier rapporteur), Prof. Dr. Bruno ROSSION
(deuxième rapporteur), Prof. Dr. Petra VETTER (troisième rapporteuse)

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Le Doyen Prof. Dr. Dominik SCHÖBI

This thesis was directed by Prof. Dr. Roberto CALDARA.

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Thesis examination committee:

Prof. Dr. Roberto **CALDARA**, University of Fribourg, thesis director, examiner

Prof. Dr. Bruno **ROSSION**, University of Lorraine, examiner

Prof. Dr. Petra **VETTER**, University of Fribourg, examiner

Prof. Dr. Nicolas **RUFFIEUX**, University of Fribourg, assessor

Prof. Dr. Michael **SCHMID**, University of Fribourg, other member of the committee

Prof. Dr. Björn **RASCH**, University of Fribourg, President of the examination committee

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Abstract

Determining the identity of other individuals is a key aspect of humans' everyday life and is mostly achieved by visually sampling the face of one's interlocutor. For decades, humans have been thought to use a universal strategy to extract facial identity information. However, in the last decade, this idea has been heavily challenged, and interest in individual differences in fixation patterns has grown considerably. This new line of work has highlighted that observers differ systematically in the way they direct their fixations towards facial regions during face identification. Strikingly, sampling strategies do not correlate with accuracy levels. On the contrary, forcing observers to fixate away from their preferred viewing position can weaken their performance. However, while evidence is accumulating in terms of (oculomotor) behavior, whether individual differences also extend to the neural level remains unaddressed. To fill this gap, we investigated whether and how preferences for fixations on certain viewing positions may also emerge in terms of neural activity.

In Study 1, we recorded implicit neural face discrimination using fast periodic visual stimulation paired with electroencephalographic recordings (FPVS-EEG). Responses were obtained while fixation was parametrically varied across 10 different viewing positions. From the same subjects, we also extracted their natural fixation pattern during a behavioral identity-related task. Our data highlight two main observations. First, we found that the pattern of neural responses across viewing positions varies across observers; that is, conditions triggering stronger or weaker responses varied across our participants. Second, these idiosyncrasies mimicked those observed at the oculo-motor behavioral level. In other words, we found that the more an individual naturally fixates on a facial information, the more likely that information is to trigger a strong neural face identity discrimination response. Altogether, these findings support the idea that individual differences in terms of viewing position preference are functionally meaningful.

In Study 2, we aimed to better understand these idiosyncrasies by assessing their reliability over time in terms of both response amplitude and response topography.

For this reason, we used a test-retest design with a six-month interval between the two sessions and the same FPVS-EEG paradigm and conditions tested in Study 1. Our data show that while overall FPVS-EEG provides a reliable measure of both the strength of neural face identity discrimination and the pattern of responses across viewing positions, participants differed in terms of their topographical reliability. Importantly, we found a positive and significant relationship between this parameter and the magnitude of the response itself: the stronger the response, the more defined and reliable its scalp distribution. These findings highlight the importance of considering the reliability of the response of interest, which cannot always be taken for granted. Nonetheless, the reliability of neural response patterns across viewing positions suggests that individual difference at this level reflects genuine variations across individuals.

Finally, in Study 3, we explored the hypothesis that the individual differences observed in Studies 1 and 2 could be reduced by modulating stimulus size. Specifically, we recorded neural face discrimination using FPVS-EEG while varying fixation across different viewing positions and parametrically rescaling stimuli across five sizes. Contrary to our expectations, individual differences persisted across all sizes. Nevertheless, our data also show that presenting stimuli at a 6.7° visual angle while enforcing fixation just below the nasion represents both the most optimal condition for most observers and the least optimal for a few.

Overall, the data presented in this thesis highlight the existence of individual differences in patterns of neural face identity discrimination responses across viewing positions and provide evidence supporting their functional meaning and reliability. While our results raise new, important questions regarding which factors drive these idiosyncrasies, they also highlight the need to reconceptualize individual differences as a unique and rich source of information rather than noise.

Résumé

Être capable de déterminer l'identité d'autrui est un aspect clef dans la vie quotidienne de chaque être humain et est réalisé principalement en échantillonnant visuellement le visage de son interlocutrice. Durant des décennies, on a pensé que les humains utilisaient une stratégie universelle pour extraire des informations sur l'identité d'une personne. Cependant, au cours de la dernière décennie, cette idée a été fortement remise en question, et l'intérêt pour les différences individuelles concernant les patterns de fixations s'est considérablement développé. Cette nouvelle branche de recherche a mis en évidence que les observateurs-trices diffèrent systématiquement dans leur façon de définir leurs points de fixation sur les différentes régions faciales lors de l'identification d'un visage. Étonnamment, les stratégies d'échantillonnage ne corrèlent pas avec les niveaux de performances. Au contraire, de forcer des observateurs-trices à s'éloigner de leur point de fixation de prédilection peut réduire leurs performances. Cependant, alors que des preuves s'accumulent en termes de comportement (oculomoteur), il n'a pas encore été déterminé si les différences individuelles s'observent également au niveau neuronal.

Afin de combler cette lacune, nous avons cherché à savoir si et comment des préférences pour certains points de fixation peuvent se manifester en termes d'activité neuronale.

Dans l'étude 1, nous avons enregistré la discrimination neuronale implicite de visages à l'aide d'une stimulation visuelle périodique rapide couplée à des enregistrements électroencéphalographiques (FPVS-EEG). Les réponses des participant-e-s ont été comparées pour 10 points de fixation différents. Pour ces mêmes participant-e-s, nous avons également analysé leur pattern de fixation naturel durant une tâche comportementale de reconnaissance de l'identité. Nos données mettent en évidence deux observations principales. Premièrement, nous avons découvert que le pattern de réponses neuronales en fonction des points de fixation variait selon les participant-e-s ; c'est-à-dire que les conditions déclenchant des réponses plus fortes ou plus faibles variaient d'un-e participant-e à l'autre. Deuxièmement, ces idiosyncrasies imitent celles observées au niveau comportemental oculomoteur. En d'autres termes, nous avons découvert que plus un individu se fixe naturellement sur une information faciale, plus cette information est susceptible de déclencher une forte réponse neuronale de discrimination d'identité faciale. Dans l'ensemble, ces résultats soutiennent l'idée que les différences individuelles en termes de préférences de zone d'observation sont fonctionnellement significatives.

Dans l'étude 2, nous avons cherché à mieux comprendre ces idiosyncrasies en évaluant leur fiabilité dans le temps en termes d'amplitude et de topographie de réponse.

Pour cette raison, nous avons utilisé un design expérimental de test-retest avec un intervalle de six mois entre les deux sessions, en utilisant le même paradigme FPVS-EEG ainsi que les mêmes conditions testées lors de la première expérience. Nos données montrent que, bien que le FPVS-EEG fournisse de façon globale une mesure fiable à la fois de la force de la discrimination neuronale de l'identité faciale et du pattern de réponses selon les points de fixation, les participant-e-s différaient en termes de fiabilité topographique. En particulier, nous avons trouvé une relation positive et significative entre ce paramètre et l'ampleur de la réponse elle-même : plus la réponse est forte, plus sa distribution topographique est définie et fiable. Ces résultats soulignent l'importance de considérer la fiabilité de la réponse d'intérêt qui ne peut pas toujours être considérée comme acquise. Néanmoins, la fiabilité des patterns de réponse neuronale en fonction des points de fixation suggère que la différence individuelle à ce niveau reflète de véritables variations entre les individus.

Enfin, dans l'Étude 3, nous avons exploré l'hypothèse selon laquelle les différences individuelles observées dans les Études 1 et 2 pourraient être réduites en modulant la taille du stimulus. Plus spécifiquement, nous avons enregistré la discrimination neuronale d'un visage à l'aide du FPVS-EEG tout en variant le point de fixation et en redimensionnant les stimuli selon cinq tailles. Contrairement à nos attentes, des différences individuelles ont persisté pour toutes les tailles. Néanmoins, nos données montrent également que de présenter des stimuli à un angle visuel de $6,7^\circ$ tout en imposant une fixation juste en dessous du nasion représente à la fois la condition la plus optimale pour la plupart des observateurs-trices, mais également la moins optimale pour une minorité d'entre eux-elles.

Dans l'ensemble, les données présentées dans cette thèse mettent en évidence l'existence de différences individuelles dans les patterns de réponses neuronales de discrimination d'identité faciale selon les points de fixation et fournissent des preuves soutenant leur signification fonctionnelle et leur fiabilité.

Alors que nos résultats soulèvent de nouvelles questions importantes concernant les facteurs à l'origine de ces idiosyncrasies, ils soulignent également la nécessité de reconceptualiser les différences individuelles comme une source d'informations unique et riche plutôt que comme du bruit.

*To my parents
Tiziana & Luca Stacchi*

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List of Acronyms

aSTS	Anterior superior temporal sulcus
ATL	Anterior temporal lobe face area
ASSR	Auditory steady state response
DTI	Diffusion tensor imaging
ECG	Electrooculography
ECoG	Electrocorticography
EEG	Electroencephalography
EPSP	Excitatory postsynaptic potential
ERP	Event-related potential
FFA	Fusiform face area
FFT	Fast Fourier transform
FID	Face identity discrimination
FIE	Face inversion effect
FPVS	Fast periodic visual stimulation
fMRI	Function magnetic resonance imaging
IFG	Inferior frontal gyrus
IPSP	Inhibitory post synaptic potential
MEG	Magnetoencephalography
OFA	Occipital face area
PET	Positron emission tomography
PSP	Postsynaptic potential
pSTS	Posterior superior temporal sulcus
ROI	Region of interest
SNR	Signal-to-noise ratio
STS	Superior temporal sulcus
TMS	Transcranial magnetic stimulation
VOTC	Ventral occipito-temporal cortex
VP	Viewing position

Introduction and thesis overview

“Individual differences have been an annoyance rather than a challenge to the experimenter. His goal is to control behavior, and variation within treatments is proof that he has not succeeded ... For reasons both statistical and philosophical, error variance is to be reduced by any possible device.”
(Cronbach, 1957, p. 674)

These words written more than five decades ago are more than ever at the center of an ongoing debate regarding explanations of the human mind. In cognitive neuroscience, it was widely accepted that one can understand how human cognition works by searching for commonalities across individuals. This approach makes sense because if something is systematically observed across many occasions, it is very unlikely to be a coincidence. However, attempting to find a common denominator may sometimes lead to unexpected and most importantly inaccurate outcomes. As Cronbach highlights, individual differences across people have often been considered an issue—a symptom of noisy measurements or human errors. However, as much as it is reasonable to assume that human cognition is governed by universal rules, it is also highly plausible that the innumerable and diverse experiences that each person undergoes lead to differences in how individuals process the world. These individual differences are therefore not deceiving noise but rather a signature of how human cognition is flexible and can be shaped by experience. Consequently, ignoring them might deprive researchers of a rich source of information and possibly lead to incomplete or even misleading conclusions about the very functioning of human cognition.

For instance, for decades, individuals have been thought to look at faces by using similar fixation patterns. However, more recent work has highlighted the existence of robust and reliable idiosyncratic visual sampling strategies. As such, the main goal of my thesis is to further investigate the presence of individual differences in face identity processing while providing a neural information-mapping

explanation. Specifically, this dissertation explores the possibility that individual differences in oculomotor behavior are mimicked by idiosyncratic neural response patterns across viewing positions (VPs; i.e., fixation locations). Therefore, we designed three experiments to attempt to answer the following questions:

1. Are there individual differences in neural face identity response patterns across VPs?
2. How do they relate to individual differences in sampling strategies?
3. Are these idiosyncratic neural responses reliable over time?
4. Is it possible to reduce the impact of VP on neural face identity responses?

In CHAPTER 1 of this thesis, I first introduce face processing in terms of where, when, and how it is achieved in the human brain. I then describe how individual differences in face identity processing have been addressed over the years. This short review highlights an imbalance in the literature: while oculomotor behavioral studies explore individual differences in sampling strategies, there is still a lack of information about whether neural face identity processing is differently influenced by VP across observers.

CHAPTER 2 introduces the experimental contributions of this thesis and how in each experiment we tried to contribute to filling the gap in the literature.

This is followed by a detailed description of the methodologies used across our experiments.

The following three chapters present the three experimental studies:

CHAPTER 3. In the first study of this dissertation, we explored the possibility that idiosyncratic sampling strategies relate to individual differences in neural biases for specific VPs.

CHAPTER 4. The second experiment assessed the reliability of idiosyncratic neural identity discrimination patterns across VPs. By testing our subjects twice over a period of six months, we explored the stability of neural responses across VPs in terms of amplitude and topography.

CHAPTER 5. The third and final study presented in this dissertation explores whether idiosyncratic neural face identity discrimination responses across VPs can be reduced by parametrically manipulating the size of the face input.

Finally, in CHAPTER 6, I discuss the major findings and implications of our studies as well as limitations and future directions.

CHAPTER 1

LITERATURE REVIEW

1.1. What Is So Special About Faces?

Human beings are highly social animals who rely on interpersonal relationships to grow and thrive from both a societal and a personal perspective. To be efficient in daily interactions, individuals must readily acquire and process a series of information about others. Impressively, humans can often gather most of this information from faces. One can infer at a glance the age, gender, ethnicity, mood, and demeanor of the person with whom one is interacting. Importantly, one can also quickly and efficiently make a series of judgments regarding their identity, such as detecting someone in a crowd, determining whether they are familiar, and in that case, retrieving their identity and biographical information from memory. Although all these tasks are seemingly effortless, they hide a unique complexity. More precisely, while it was suggested that faces evolved to specifically facilitate identification (Sheehan & Nachman, 2014), they represent a challenging object for the visual system because they are highly homogeneous with a constrained configuration: an oval head with two eyes above a nose above a mouth. As a result, rapidly extracting variant and invariant information from the innumerable highly similar exemplars one meets daily is computationally demanding for the brain. This ability is mainly observed for faces and more rarely for other visual categories, suggesting that face processing might be governed by a specific set of processes. As such, it is not surprising that many brain regions are dedicated to face processing, representing a complex neural network.

The hypothesis of face-specific processing is supported by studies reporting that compared to other visual categories, face stimuli are impacted differently by stimulus manipulation. A well-known example is the face inversion effect (FIE; Yin, 1969). The FIE refers to the phenomenon by which stimulus inversion is more detrimental to recognition of faces compared to other visual categories (e.g., houses or cars).

Arguably, this effect is rooted in the perceptual strategy triggered by faces compared to other stimuli. It was suggested that face stimuli are perceived more holistically than other objects; that is, they are processed as indivisible wholes rather than as sets of single elements (e.g., Tanaka & Farah, 1993). This concept of holistic perception and processing is closely related to the concept of gestalt, which is the

principle by which the whole does not equal the sum of its individual parts, and today it is still one of the core principles in face-processing research.

Historically, it was suggested that inverting faces disrupts holistic processing, which significantly increases the difficulty in recognizing exemplars. In contrast, objects do not rely as heavily on holistic processing; consequently, inverting them has relatively less impact on performance (Tanaka & Farah, 1993; Farah et al., 1995).

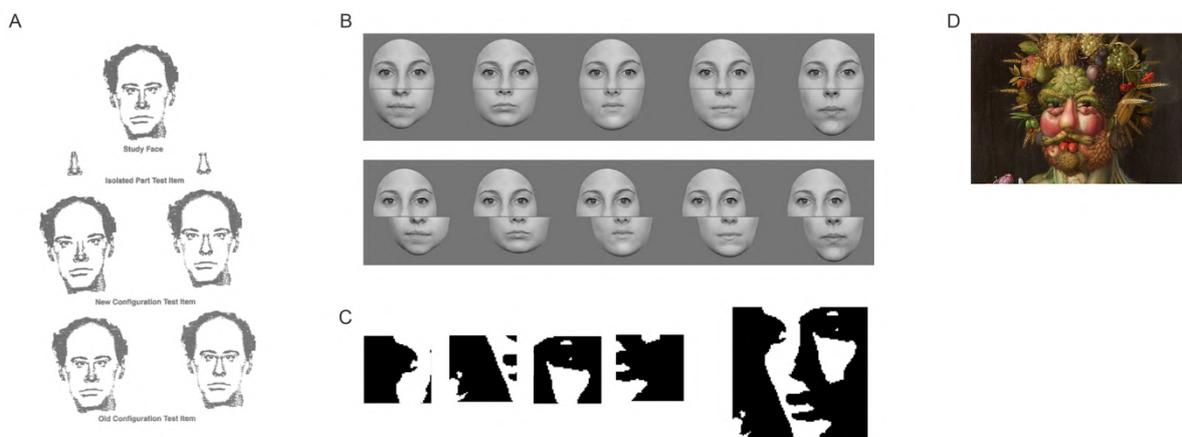
A vast number of studies have provided support for the existence of holistic processing for faces and argued in favor of the idea that it underlies the difference between face and nonface stimuli (Farah et al., 1998; Tanaka & Simonyi, 2016). For instance, studies have shown that recognition of face parts is more accurate when the items are presented within an upright face in its original configuration compared to either in isolation or within an upright face with a new configuration (i.e., the part-whole effect). Importantly, this part-whole effect was not observed for either inverted face or nonface objects, suggesting that these latter categories are more likely processed by parts (Tanaka & Sengco, 1997; Tanaka & Farah, 1993; Tanaka & Simonyi, 2016; Figure 1.1A).

Importantly, the holistic nature of face processing was argued not only to apply to stored representations (e.g., involved in recognition tasks) but also to online perception (e.g., involved in matching tasks). Concretely, this would result in phenomena such as the face composite illusion, which is characterized by significant difficulties in perceiving faces' top halves independently of their bottom halves. Initially introduced by Young et al. (1987) in the context of familiar face recognition and subsequently adapted by Hole (1994) to assess unfamiliar face matching, composite faces consist of whole faces whose top and bottom halves belong to two different identities (Figure 1.1B). In the context of (delayed) face matching, subjects are required to determine whether the top halves of two composite faces portray the same identity. Interestingly, when the bottom halves are different, subjects often need significantly more time to make a decision, and they often mistake two identical tops as being two different individuals. Importantly, the task difficulty decreases significantly when the two face halves are misaligned and/or when faces are inverted since this is thought to disrupt holistic processing and allow the observer to perceive individual parts more easily (Rossion, 2013).

Finally, behavioral studies have also shown evidence of holistic perception at the level of face detection. Specifically, studies using two-tone Mooney faces and Arcimboldo's painting (Figure 1.1C) have shown that when presented as wholes, although they do not contain face parts, these stimuli are effortlessly perceived as faces.

Figure 1.1.

Stimuli Used to Investigate Holistic Face Processing.



Note. A. A face is initially learned as a whole (top), and its components have to be recognized later as isolated parts (second row) or within a new (third row) or old (fourth row) configuration. From Tanaka and Sengco (1997). B. Example of composite faces. The top half of the face belongs to the same person while the bottom half portrays another identity. The identity of the bottom half influences the perceived identity of the top half, but only when images are intact. Adapted from Rossion (2013). C. Examples of two-tone Mooney faces. D. Arcimboldo's painting of a face. These images are composed of nonface parts. However, when these individual pieces are presented together, they are perceived as faces.

A Distinct Neural Pathway for Faces?

A dissociation between face and nonface stimuli extends beyond that documented by behavioral studies on neurotypical individuals. Specifically, case studies of patients with brain lesions have provided evidence of the possibility that faces and nonface objects rely on distinct and segregated neural pathways. Particularly relevant to this topic are the reports of individuals who exhibited a sudden incapacity to correctly process faces following brain injuries in the occipitotemporal cortex. Strikingly,

this impairment is highly selective and pertains only to the processing of facial information while leaving the visual processing of other categories relatively intact.

The first documented description of this cognitive disorder dates to the mid-19th century when Wigan reported on a man who could engage in long conversation with someone without being able to remember who that person was (Wigan, 1844; Finger, 2001). A few years later, Quaglino and Borelli (1867) provided a more detailed report (see Della Sala & Young, 2003 for an English translation). They described the case of a man who following a right hemisphere stroke could no longer recognize the faces of familiar people. Although this individual also exhibited an incapacity in recollecting the facades of houses he had previously known, Quaglino and Borelli proposed the crucial idea that the impairment was specific to faces. This cognitive disorder, which Bodamer later termed prosopagnosia in 1947 (Ellis & Florence, 1990), has since attracted the attention of thousands of researchers and has been at the center of innumerable scientific investigations. Along with other considerations, this observation suggests that the damaged brain regions in these patients were somehow essential to face processing but not object processing. The implications of this hypothesis are that face processing is likely to rely on a separate distinct neural network. The concept of functional independence, or at least partial segregation, between face and object processing found further support in reports of an individual showing the reversed pattern of behaviors, namely patient CK, who exhibited allegedly spared face recognition abilities but was severely impaired in recognizing previously known objects (Moscovitch et al., 1997). Additionally, when tested with Arcimboldo's faces, CK failed to detect the presence of nonface parts within the stimulus but showed no difficulties in quickly perceiving the whole as a face. Taken together, these early observations have led to one of the most influential theories in this domain, namely the face specificity hypothesis: the principle by which face processing is governed by distinct and specialized cognitive and neural mechanisms (however, see Gauthier et al. (1999) for an alternative hypothesis). The possibility of face-specific neural pathways has been investigated throughout the decades in monkeys and humans by means of increasingly sophisticated and precise techniques. In the next part, I describe how face specificity has been addressed in the brain and which regions have been systematically associated with it.

1.2. The Neural Face System

1.2.1. Early Evidence from Nonhuman Primates

The earliest neuroimaging evidence of the existence of face-specific neural regions come from studies on nonhuman primates. By means of single-cell recordings, this early body of work reported cells in the IT cortex responding more to complex, colored stimuli (e.g., faces and trees) (Gross et al., 1972) and to faces than to other complex objects (Desimone, Albright, Gross, & Bruce, 1984). Other face-selective clusters were found scattered across the temporal cortex (Bayli, Rolls, & Leonard, 1987), especially in the superior temporal sulcus (STS; Bruce et al., 1981). A number of studies trying to assess their response profiles reported that some of these clusters were insensitive to stimulus orientation, color, size, or distance (Perret et al., 1982), while others were described as view (Perret et al., 1992; Perret et al., 1985; Perret et al., 1982) and identity (Perret et al., 1984) sensitive. Additionally, presentation of masked faces and features in isolation revealed differential response across cells to different face parts (Perret et al., 1982).

The importance of this pioneering work is undeniable because it has provided crucial evidence of the existence and location of a face-sensitive neural network, which has guided numerous studies in human research (e.g., Rajimehr et al., 2009; Farzmahdi et al., 2016). However, although studies claim that nonhuman primates can serve as a model to approximate the human face neural networks (Passingham, 2009; Farzmahdi et al., 2016), the extent to which observations based on monkeys can transfer to humans remains an open debate (see Rossion & Taubert, 2019, for a critical discussion). Therefore, from this point forward, evidence and descriptions of the neural face network solely refer to human research.

1.2.2. The Human Neural Face System

1.2.2.1. Where: Localization of Face Areas

Around the late 1980s, neuroimaging techniques began to be increasingly used to assess the presence and possible location of activity in the human brain that was stronger for faces and face-related tasks

compared to other categories (Jeffreys, 1989; Bötzel & Grüsser, 1989; Haxby et al., 1991; Puce et al., 1996; Sergent et al., 1992). These early investigations suggested the temporal (Jeffreys, 1989; Bötzel & Grüsser, 1989) and occipitotemporal cortex (Haxby et al., 1991) as well as more specific regions including the fusiform gyrus (Sergent et al., 1992) and an area in the middle temporal gyrus (Puce et al., 1996) as source of face-preferential responses.

However, as Kanwisher et al. (1996) note, these early studies often suffered from important limitations such as uncontrolled stimuli and differences in tasks across visual categories or visual attention, which could have confounded their results. To overcome such methodological limitations, Kanwisher and colleagues designed a functional magnetic resonance imaging (fMRI) study where tasks matched, and face and object stimuli were both photographs. Across subjects and on the test-retest data of one subject, results showed a dissociation between the neural representations of objects and faces: while objects recruited bilateral medial areas to a larger degree, face processing involved more anterior areas of the right hemisphere (Kanwisher et al., 1996).

A more thorough assessment of face specificity was then provided in the famous 1997 paper by Kanwisher and colleagues. Crucially, in this paper, the authors proposed a new approach that would overcome the insidious process of assessing face specificity across the whole brain. Specifically, they divided their experiment into two main parts. The first part aimed to localize independently within each subject regions showing stronger response to faces compared to objects. These areas were then the subjects of the more detailed investigations conducted in the second part of the experiment. Following this protocol, Kanwisher and colleagues successfully replicated Sergent and colleagues' PET study results (1992) and reported that for the vast majority of subjects, there was one region that would systematically show greater response to faces than other objects: the right fusiform gyrus. Specifically, they reported that this "fusiform face area (area FF)" (Kanwisher et al., 1997) showed greater activity for passive viewing of intact two-tone faces compared to scrambled ones, front views of faces compared to houses, and side views of faces compared to hands.

Following this pioneering work, the fusiform face area (FFA) became the focus of a large number of studies, and its face specificity was tested under numerous conditions. Data showed greater activation

of the FFA when images of faces were presented compared to different types of objects, letter strings, textures, houses, flowers, or hands. Moreover, this region was reported to be responsive to a variety of face formats from photographs to cat faces to line drawings (Tong et al., 2000; Spiridon & Kanwisher, 2002).

Along with the FFA, early neuroimaging studies also identified several other face-selective regions. One of these is the occipital face area (OFA), which is considered to have a role in early face processing. A third main face-sensitive area revealed by the first reports was the posterior part of the superior temporal sulcus (pSTS). Allison et al. (2000) suggest that the pSTS is involved in the social aspect of face processing. Further investigation of the neural network implicated in face processing revealed several additional areas that showed significantly greater activity for faces than for other stimuli. These regions are found in the anterior temporal lobe face area (ATL-FA or ATL; Rajimehr et al., 2009; Collins & Olson, 2014), the anterior STS face area (aSTS-FA; Pinsk et al., 2009; Pitcher et al., 2011) and the inferior frontal gyrus face area (IFG-FA; Ishai et al., 2005; Fox, Iaria et al., 2009).

Importantly, besides these main regions, electrocorticography (ECoG) and fMRI studies have identified several more clusters of neurons selectively responding more to faces than to other visual objects (see Rossion, Hanseeuw et al., 2012 for whole-brain analysis and Jonas et al., 2016 for a detailed description of the ventral occipitotemporal cortex). Importantly, Rossion, Hanseeuw et al. (2012) have also noted that their number, size, and precise location vary across individuals.

Lateralization of Human Face Processing

While most neuroimaging studies report face-sensitive responses over both right and left hemispheres, there is a growing body of evidence indicating the existence of a right lateralization of face processing. fMRI as well as intracerebral recording studies investigating face specificity have systematically reported that the FFA, OFA, ATL, and more generally the ventral occipito-temporal cortex (VOTC) show larger responses in the right hemisphere compared to the left side (e.g., Rossion, Hanseeuw et al., 2012; Jonas et al., 2016; Hagen et al., 2020). Consistent with these reports, surface recordings of electroencephalography (EEG) have also reported that the early face-sensitive event-related potential

(ERP) component N170 (Box 1) emerges predominantly over the right hemisphere (Bentin et al., 1996; Rossion, Joyce et al., 2003). Additionally, studies deploying intracerebral electrical stimulation indicate that while stimulation of both hemispheres could trigger simple visual events, more complex face-related hallucinations occurred almost only during stimulation of contacts in the right hemisphere (Jonas et al., 2014; Rangarajan et al., 2014). Finally, in line with these observations, neuropsychological cases indicate that patients with acquired prosopagnosia share damage to the right hemisphere (Rossion, 2014) and that early visual deprivation to the right hemisphere can significantly impair later typical development of sensitivity to facial features spacing (Le Grand et al., 2003).

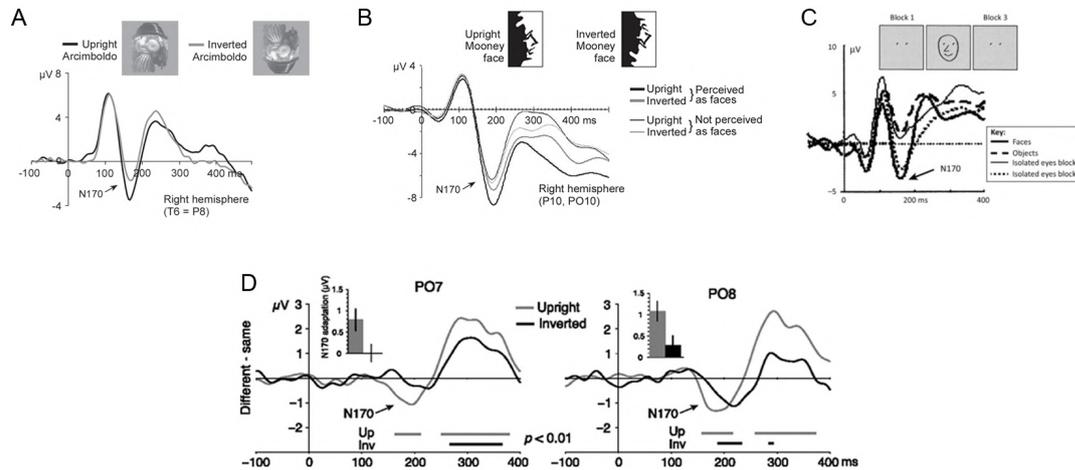
Box 1.1. The N170 Event-Related Potential Component

The N170 is considered the earliest and most robust event-related potential (ERP) to distinguish between face and nonface stimuli. It peaks between 130 and 200 ms after stimulus onset over occipitotemporal sites (Bötzel et al., 1994) with a right hemisphere dominance (Bentin et al., 1996). Since the mid-1990s, it has been extensively investigated by innumerable studies attempting to determine its neural generator, the nature of its face specificity, and its relationship with different cognitive processes (for an extensive review, see Rossion & Jacques, 2011).

Importantly, the N170 is not only elicited by faces per se but also by configurations or parts of them that are perceived by the observer as face-like. Examples of this are drawings, isolated face parts such as the eyes or faces without eyes (Eimer, 1998), and scrambled face parts (Rossion & Jacques, 2008). Another instance is configurations such as upright Arcimboldo paintings of faces and Mooney faces (Figure 1.2A, B). These stimuli are composed of nonface parts that are arranged into a face-like configuration. When they are presented upright and observers perceive them as faces, they elicit stronger N170 amplitude compared to when they are inverted and no longer interpretable as faces (Caharel et al., 2013; Rossion & Jacques, 2008). The role of subjective perception of a face has also been demonstrated by a study on priming. Data shows that geometric figures naturally not perceived as face-like (e.g., two dots) can trigger a face-like N170 if subjects are primed to interpret them as representations of face parts (Figure 1.2C; Bentin et al., 2002).

The N170 has also been shown to reflect identity processing (Jacques et al., 2007, but see Schweinberger & Neumann, 2016). Adaptation studies have reported that the repetition of the same identity leads to a decrease of the N170 amplitude for the second stimulus. The response magnitude is then restored to the original level when a new identity is presented (Jemel et al., 2005; Vizioli et al., 2010; Jacques & Rossion, 2006; Heisz et al., 2006; Jacques et al., 2007). This effect persists despite size changes between images and even if faces are turned by up to 30 degrees in viewpoint (Caharel et al., 2009). However, the effect is abolished for inverted faces. In this case, same- and different-identity conditions evoke comparable responses (Figure 1.2D).

Given the relatively low-spatial resolution of the EEG, source localization of the scalp N170 is not straightforward. Nonetheless, studies coupling scalp EEG with simultaneous intracranial recording or fMRI have suggested that two major contributors to this face-selective scalp response are the right fusiform gyrus (Sadeh et al., 2010) and the inferior occipital gyrus (Jacques et al., 2019).

Box 1.1. The N170 Event-Related Potential Component**Figure 1.2***Face- and Identity-Sensitive N170.*

Note. The N170 amplitude is larger for stimuli perceived as faces (A, B, from Rossion & Jacques, 2011) or face parts (C, from Rossion, 2014) even if they are made of nonface parts. D. When same-identity faces are repeated, the N170 shows reduced amplitude for the second image, suggesting that the neural population generating this ERP component adapts to identity. This effect is reduced and delayed for inverted faces. From Jacques et al. (2007).

In this section, I provided a description of regions that show face-sensitive neural responses and presented evidence for a right hemispheric dominance of face processing. In the next section, I will outline the most prominent models of face processing (past and present) to illustrate not only the role of the above-mentioned regions but also how they relate to one another and work together to allow complex face processing such as identity processing.

1.2.2.2. How: Models of Human Face Processing

Studies on clinical and neurotypical subjects provide not only information regarding which neural regions are face sensitive but also evidence concerning the functionality of each of these areas and how

they are connected and interdependent. While the involvement of specific neural regions finds significant consensus among researchers, the role played by each area sometimes remains uncertain. To piece together information often provided by independent groups, researchers have proposed various models of face cognition. Each framework integrates new evidence and attempts to explain and resolve apparent discrepancies. In the following section, I will briefly describe some of the most influential models, highlighting the gaps they attempted to fill.

Haxby and colleagues (2000) made one of the earliest attempts to bring neurofunctional findings on face processing together to create a cohesive and comprehensive view. This framework is based on neuroimaging findings but is also partly inspired by the cognitive model proposed by Bruce and Young in 1986. This earlier work proposed the crucial idea that different types of information are initially processed independently and are only later integrated within the cognitive system. Bruce and Young (1986) also suggested the concept of hierarchical processing, where one step can only build upon another. For instance, identity can only be retrieved once a face is recognized as familiar. These concepts, albeit in a revised form, shaped Haxby and colleagues' framework, which proposes that the face-processing network is a distributed and hierarchical system. It is a distributed system in that different neural substrates are dedicated to different aspects of face processing. It is hierarchical because it divides the face system into a core and an extended system. While the first is devoted to the visual analysis of faces, the latter is involved in further processing and integration of information.

Haxby and colleagues's model suggests that the core system is functionally divided into two pathways, each involved in the processing of different facial aspects (see Bruce and Young's 1986 cognitive model for an earlier version of this functional dissociation). While both pathways start in the OFA, the ventral stream continues in the FFA, where unchangeable aspects of faces (e.g., identity) are processed. Meanwhile, the dorsal stream continues in the pSTS and is responsible for the processing of changeable aspects of faces (e.g., expression). The core system then provides inputs to the extended system, comprising areas normally devoted to other cognitive functions, but that when "acting in concert" with the core system allowing recognition of face-related aspects. Specifically, the dorsal pathway extends

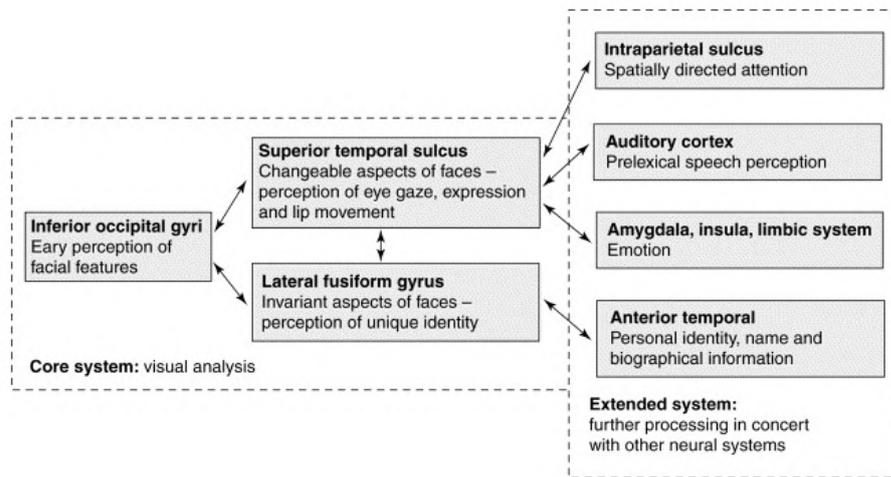
from the pSTS into three regions: the intraparietal sulcus involved in the process of spatial attention for analysis of individuals' attention direction based on their eye gaze and head orientation; the auditory cortex for the analysis of speech-related lips movements; and the amygdala, insula, and limbic system for the processing of emotions.

The ventral pathway extends from the FFA toward the anterior temporal regions, which intervene in the retrieval of semantic knowledge (e.g., name, identity, biographical information) when a perceived face is recognized as familiar (Figure 1.3).

The model suggested by Haxby and colleagues (2000) represents an important step forward in the conceptualization of the face-processing system. However, further methodological advances and new findings have provided evidence difficult to reconcile with this framework. At the center of the debate are three main aspects: the independence of the ventral and dorsal pathways, the idea of the OFA as the first and only entry point into the face system, and the hierarchical nature of the model (Atkinson & Adolph, 2011; Duchaine & Yovel, 2015; Bernstein & Yovel, 2015; Pitcher et al., 2014; Rossion, 2008). In the next section, I provide a description of findings challenging these concepts and of new models addressing these issues.

Figure 1.3

Haxby et al.'s (2000) Neuroanatomical Model of Face Processing.



Note. The model begins in the inferior occipital gyri (IOG or OFA). From here, processing of changeable and invariant aspects dissociates into two separate pathways. Processing proceeds predominantly in a hierarchical manner. From Haxby et al. (2000).

Independence of Dorsal and Ventral Pathways. Haxby's model suggests a neat separation between the processing of changeable (e.g., expression) and invariant (e.g., identity) aspects. However, studies have shown that regions processing one might also be involved in the processing of the other. For example, fMRI studies have found robust release from adaptation to expressions in the FFA (Xu & Biederman, 2010; Fox, Moon et al., 2009; Ganel et al., 2005), and a combination of fMRI and neural decoding revealed that facial expressions could be predicted by the pattern of activation in the FFA (Harry et al., 2013). On the other hand, studies have shown a release from adaption in the pSTS following a perceived change in identity (Fox, Moon et al., 2009). Another study indicates a region within the pSTS that is more responsive to facial expression when facial identity is held constant compared to when it varies. By measuring functional connectivity between pSTS and FFA, researchers have also shown increased connection between these two areas in response to same-identity compared to different-identity faces (Baseler et al., 2014).

Altogether, these results suggest that the dorsal and ventral streams can interact and both support processing of variant and invariant aspects (see O'Toole et al., 2002; Collins & Olson, 2014; Bernstein & Yovel, 2015 for models accounting for these results).

The Occipital Face Area as the Only Entry Point into the Face System? Another problematic aspect of Haxby et al.'s (2000) model is the idea that the OFA is the only entry into the visual face-processing system. However, this assumption is in contradiction with more recent findings. Specifically, if this was true, then disruption of the OFA should lead to a cascade of functional disruptions in all the remaining regions. Interestingly, this is not the case. For instance, using transcranial magnetic stimulation (TMS) to disrupt the activity in the right OFA during processing of static and dynamic faces leads to a reduction of activity for both stimuli in the right FFA, but only for static stimuli in the right pSTS, which continues exhibiting a normal response for dynamic stimuli (Pitcher et al., 2014).

Congruent results were reported by studies addressing anatomical white matter connectivity between neural face areas by means of diffusion tensor imaging (DTI). Studies have reported a strong connection between the OFA and the FFA (Gschwind et al., 2012; Pyles et al., 2013) and between both regions and early visual areas (Kim et al., 2006), although the projection with the FFA was weaker than that with the OFA (Gschwind et al., 2012). On the other hand, no connection was found between either the FFA or the OFA and the STS. Additionally, this latter region did not appear to be linked to either the occipital or the temporal cortex, which suggests that it might rely on input from motion-related areas and the nearby extrastriate cortex (Gschwind et al., 2012).

These observations of neurotypical individuals are supported by neuropsychological studies. Reports describe cases of patients with severe lesions to the right OFA and right FFA who nonetheless show normal face selectivity in the right pSTS (Dalrymple et al., 2011). Additionally, studies have described the cases of prosopagnosic patients DF and PS. Both show severe lesions to the right OFA and severe impairments in facial identity processing. Such behavioral difficulties are compatible with an absence of sensitivity to facial identity in the right FFA as indexed by a lack of release from adaptation when different identities are presented (Schiltz et al., 2006; Steeves et al., 2009). Importantly, due to the

damages, their right OFA no longer shows any face-selective activity. Despite this, both patients show typical face selectivity in their right FFA along with normal behavioral abilities to discriminate faces from objects (Atkinson & Adolph, 2011; Steeves et al., 2006; Milner et al., 1991). Additionally, PS also exhibits typical early neural markers of face sensitivity as recorded by both magnetoencephalography (MEG) and EEG (Alonso-Prieto et al., 2011). One explanation for this pattern of results could be that activity in the right FFA of these patients is driven by inputs from the contralateral intact OFA. However, this possibility is ruled out by the fact that unlike PS, patient DF also exhibits damages in the left OFA, which therefore cannot support activity in the right FFA. A final clinical case to further challenge Haxby's model is that of patient NS, who exhibits a damaged FFA but an anatomically intact OFA. If the OFA precedes the FFA, the former should not be impacted by lesions in the latter and therefore exhibit normal face-sensitive activity. However, this is not the case since neither the OFA nor the FFA show face-sensitive activity in patient NS (Delvenne et al., 2004).

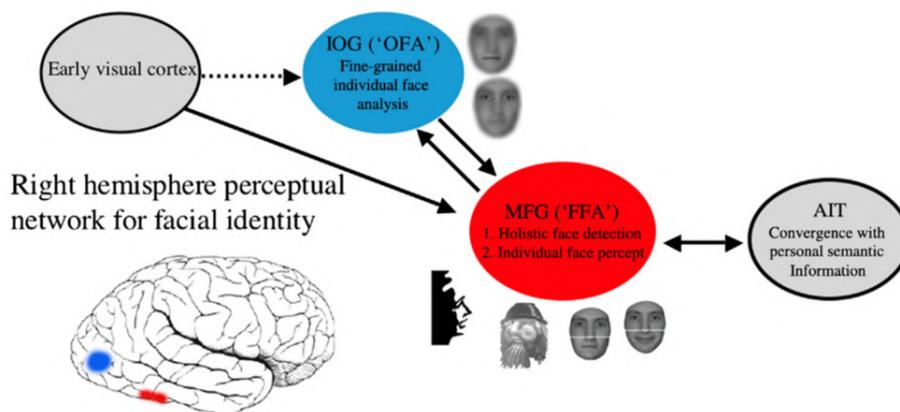
In order to appropriately account for the role of the OFA within the face system, Rossion (2008, see also Rossion et al., 2003) suggests a new model. In contrast with what had previously been proposed, Rossion suggests that the structure underlying the network is not merely feedforward but also involves a loop of reentrant information. Specifically, his model posits that the FFA would share direct connections with early visual areas and is responsible for forming an initial holistic percept of faces, which allows their discrimination from other visual categories (i.e., categorization). Face representations are then refined through reentrant connections with lower-order visual areas such as the OFA, which is responsible for the analysis of face parts (Figure 1.4). Finer processes such as facial identity discrimination are then possible through the integration of these different representations. This suggested dynamic between the OFA and FFA is supported by findings in neurotypical adults. When TMS is delivered to the rOFA, it leads to impairments in facial identity learning (Ambrus, Windel et al., 2017) and recognition, and it disrupts the ability to match face parts (Pitcher et al., 2007). Nonetheless, it does not affect face categorization (Solomon-Harris et al., 2013). Additionally, fMRI studies found stronger OFA activation for face parts over a combination of them (Arcurio et al., 2012;

Liu et al., 2010). Finally, Rossion and colleagues (2011) recorded neural activation of subjects viewing two-tone Mooney faces and Arcimboldo face-like paintings. These types of stimuli appear as faces only when they are perceived as a whole, while the illusion is disrupted when parts are considered individually. Rossion et al. (2011) found that presentation of these images led to an increased activation in both the FFA and pSTS but not in the OFA. Crucially, they also found that despite a lack of face sensitivity in her right OFA, prosopagnosic patient PS still succeeded in detecting faces from these stimuli.

Altogether, these reports challenge Haxby's model and converge toward the hypothesis that the OFA is unlikely the solely entry point into the face system. These reports also suggest that this area is highly involved in fine-grained analysis of face information that occurs after an initial holistic percept has been extracted from the FFA.

Figure 1.4

Neurofunctional Model of Face Identity Processing Proposed by Rossion (2008)



Note. Stimuli are first categorized as whole faces in the FFA, and then through the reentrant feedback loop between the FFA and the OFA, information undergoes a finer-grained analysis that allows integration of the identity-related information into the face representation. From Rossion (2008).

Temporal Characteristics of Face Processing

One further element of face processing that was lacking in Haxby et al.'s (2000) study was the temporal characteristics of the studied face areas. Specifically, in the 2000 model, hierarchy between different regions was inferred mainly based on neuropsychological studies. However, later neuroimaging investigations, especially those deploying TMS and combined fMRI and EEG, provided evidence suggesting a different organization. A series of TMS experiments showed that accuracy in face identity and facial expression discrimination decreased severely when pulses were delivered to the OFA at 60 and 100 ms after stimulus onset (Pitcher et al., 2007, 2008). Interestingly, temporary disruption of the OFA did not affect discrimination of face part spacing (Pitcher et al., 2007). A later TMS study compared temporary disruption of OFA and pSTS during a facial expression recognition task. Data showed that while pulses at the OFA impaired performance when delivered at 60 to 100 ms, stimulation of the pSTS had a negative consequence when conducted at 60 to 100 ms and at 100 to 140 ms (Pitcher, 2014). Together, these results led to the hypothesis that while both areas process facial expressions in parallel, they are functionally different due to the difference in processing duration.

Similar time characteristics of the OFA, FFA, and pSTS have also been reported using EEG paired with fMRI recordings. Sadeh et al. (2010) showed that activity in the FFA and pSTS strongly correlated with EEG responses indexing neural face selectivity at approximately 170 ms after stimulus onset. On the other hand, OFA activation was more strongly correlated with earlier EEG responses occurring at 110 ms following stimulus presentation (however, see Jacques et al., 2019 for evidence of later involvement of the OFA).

Duchaine and Yovel (2015)

In order to integrate these new findings regarding the temporal domain of face processing and earlier revisions of Haxby's model, Duchaine and Yovel (2015) proposed a new framework of face processing (Figure 1.5). Their model suggests that the organization of the face system is both hierarchical and

parallel and is divided into two main pathways: the dorsal stream, which is more sensitive to dynamic information and devoted to the analysis of changeable aspects, and the ventral stream, which is responsible for the processing of form information extracted from invariant aspects.

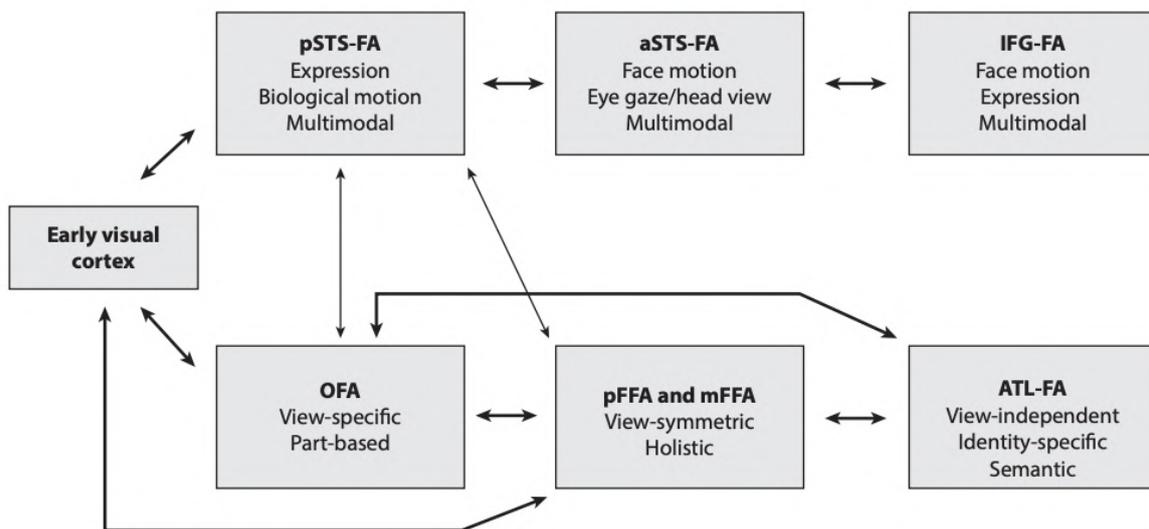
The Dorsal Stream. The dorsal stream is thought to be heavily involved with the representation of more changeable facial aspects such as expression, gaze, and mouth movements. Moreover, it is likely to be involved in the analysis of facial identity of dynamic familiar faces. This pathway starts in the STS. Activity in this region peaks at approximately 170 ms and is suggested to concern the processing of form and motion information that is received from early visual areas (MT/V5; see also Bernstein & Yovel, 2015). Additionally, the posterior portion of the STS is suggested to also be implicated in multimodal processing since it was shown to be responsive to both faces and voices (Watson et al., 2014). This region also shares a strong connection with the IFG, whose activity starts at 150 ms and peaks at approximately 250 ms.

The Ventral Stream. The ventral stream is involved in the processing of invariant aspects such as sex, age, and identity. It is proposed to start with parallel and reentrant information processing between the OFA and FFA. The OFA, which is characterized by cells with relatively small visual fields, is involved in processing face parts and representing them in a view-specific manner. It receives information from the early visual area, and its activation latency is estimated to be at 100 ms after stimulus presentation (but see Jonas et al., 2012, 2014, and Jacques et al., 2019 for evidence of involvement of the OFA in later face processing). The model also proposes a connection between the OFA and the dorsal stream, but its functional nature remains unclear. The ventral pathway continues in the more anterior FFA, which is connected to both the OFA and early visual areas. The activity in the FFA is timed to start shortly after the OFA at approximately 100 ms (Parvizi et al., 2012) and to peak at approximately 170 ms. It contains neurons with larger receptive fields, and it is involved in forming view-symmetric holistic representations and in the decoding of facial identity (Grill-Spector et al., 2004) and expressions (Xu & Biederman, 2010). Finally, the ventral stream ends in the ATL. This region communicates with both the OFA and FFA through reentrant connections (Rossion, 2008) and is involved in the processing and sharpening of image-invariant information (see Jonas & Rossion, 2021

for a description of a recently uncovered face-sensitive portion of the ATL). Duchaine and Yovel suggest that this area is most likely the locus of what Bruce and Young (1986) define as the face recognition unit and might be involved in the integration of semantic information (see also Volfart et al., 2020).

Figure 1.5

Duchaine and Yovel Framework of Face Processing



Note. Compared to Haxby's model, this framework no longer assumes that all information is first processed by the OFA. Interaction between the dorsal and ventral streams is possible, and the structure of the model no longer relies on strict hierarchy but allows for parallel processing. From Duchaine and Yovel (2015)

While this model provides a comprehensive view of the neural face network, it only partially accounts for findings in the literature. For instance, the dynamic between regions in the ventral stream is in contradiction with evidence from intracerebral investigations. Specifically, based on TMS and fMRI-EEG studies, the model suggests that the OFA activity latency is approximately 100 ms after stimulus onset. However, evidence exists suggesting the involvement of this area at later stages. Using

intracerebral electrodes, Jonas and colleagues (2012, 2014) recorded the N170 ERP component typically reported in scalp EEG studies in the OFA (see also Allison et al., 1999; Rosburg et al., 2010). More recently, Jacques et al., (2019) showed a clear correlation between the N170 ERP observed on the scalp at occipital temporal sites and the one recorded directly in the OFA using intracerebral electrodes. Furthermore, stimulation of this region through intracerebral electrodes induces high-level perceptual effects in participants, such as the inability to recognize familiar faces, discriminate unfamiliar ones, or perceive faces as a single unit. Altogether, these findings suggest that the OFA is heavily involved in identity processing (Jonas & Rossion, 2021; see also Rossion, 2008) and that restricting its contribution to the early stage of face processing might be inaccurate.

What Is Missing in Models of Face Processing?

This short review shows that there are clear, discordant hypotheses about the dynamics between areas involved in the processing of facial identity. However, what emerges across various models is the concept that facial identity processing is achieved not only through holistic face processing but also through a fine-grained analysis of facial information. The importance of facial elements that make it possible to distinguish between numerous exemplars raises an important question that is however not yet formally included in these frameworks, specifically whether all facial regions are equally important to discriminate identities and whether there are individual differences in what can be defined as diagnostic in a face. In the next section, I will review studies suggesting that different facial parts or facial features have different weights in facial identity processing. I will also describe the evidence suggesting the presence of individual differences in the way observers prefer to acquire facial information, and I will highlight the gaps that need to be addressed in order to better understand this issue.

1.3. The Role of Facial Information in Facial Identity Processing

In the previous section, I described the most influential models of face processing that try to explain how different subprocesses are achieved. As noted above, numerous studies as well as Rossion's 2008 model suggest that facial identity processing not only relies on holistic processing but also requires a finer processing of individual features, and it is impaired when areas involved in such processing are disrupted (temporarily or permanently).

The importance of face parts in identity processing raises another question: are all face parts equally relevant and important? In the next section, I will review studies attempting to determine whether some facial features are more important or diagnostic for face processing, especially identity processing, compared to others.

1.3.1. Behavioral Evidence

Originally, investigation of facial elements' diagnosticity was attempted by simply asking subjects to report which feature they used the most. Alternatively, a relatively more robust approach was to ask participants to describe several faces and report the number of instances of mention of each feature (see Davies et al., 1981 for a review).

Another approach consisted in selectively masking or manipulating face parts and assessing the impact on the observer's behavioral performance. For instance, by means of masking, Howells (1938) showed that different parts of the face are associated with different weights; hence, they are differently relevant to the observers. Howells (1983) showed that precluding access to information conveyed by the lower part of the face led to poorer performance than masking the upper part of faces did. However, other studies reported the opposite pattern, where better performance was associated with information conveyed by the upper part of faces (e.g., Goldstein & Mackenberg, 1966).

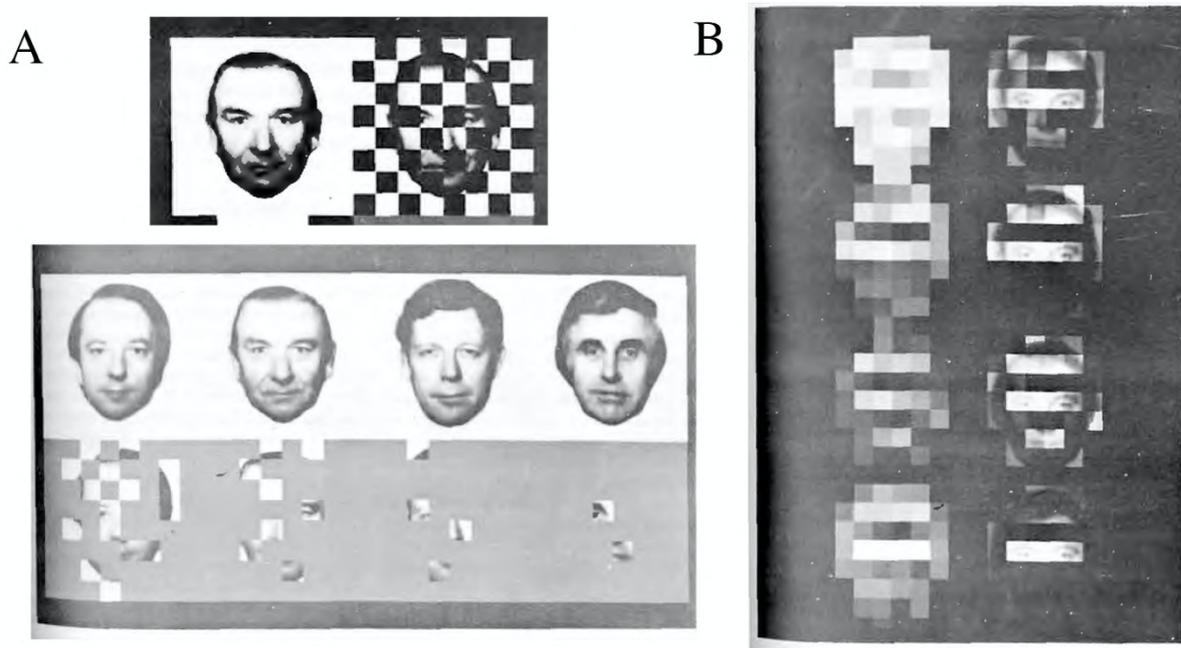
In 1979, Ellis and colleagues compared the role of internal (i.e., eyes, nose, mouth) and external (i.e., hair, ears) facial features, reporting that information carried by internal features was associated with better performance than external features were. When such comparison was performed between internal facial features, some studies suggested that occluding the mouth or eyes would lead to similar

performance levels (McKelvie, 1976). Similarly, it was also shown that when facial identity matching had to be performed between faces only differing in one feature, observers made a similar number of errors whether variance was in the eyes or the mouth region (Davies et al., 1977). However, other experimental reports indicated that among internal features, the eye region was the most important feature in facial identity-related tasks (e.g., Haig, 1986; Fraser, 1990).

The evolution of masking techniques led Haig to introduce a new, remarkable approach in 1985 that allowed determination of the diagnosticity of face parts. In its initial form, this approach consisted of creating masks the same size of face stimuli used in the experiment that were divided into 16 (8 x 8) squares or apertures. Once overlaid with face images, a random number of apertures in random locations were removed from the masks, resulting in only partially visible face stimuli (Figure 1.6A). Observers were then required to identify these images, and each aperture was scored in terms of the percentage of correct identification, which essentially revealed which facial information an observer likely used to correctly perform the task. Results were in line with previous observation and highlighted a strong use of eyes and eyebrows. Interestingly, although this work only tested six subjects, Haig indicates that due to a marked inter-individual variability, generalization across observers was not recommended (Figure 1.6B; Haig, 1985).

Figure 1.6

Early Version of the Image Categorization Technique and Results for Four Subjects.



Note. The top panel shows how face images were overlaid with a checkerboard-like mask that would make it possible to reveal only parts of the image behind the mask. The bottom panel shows original stimuli and their respective appearance after applying a given mask. B. Results for the four exemplar subjects. Squares are shade coded according to their relationship with behavior (the lighter the shade, the stronger the association with behavioral performance). From Haig (1985).

Through the advent of new technological tools and greater computational power, this technique was further developed and refined into what is now referred to as “bubbles” (Gosselin & Schyns, 2001). The new version allowed a dramatically large number of apertures or bubbles that could also vary in size, providing researchers with significantly greater flexibility. Through thousands of trials using bubbles varying in number and location, it is possible to extract a finer map of facial information and their diagnosticity for specific tasks. Earlier and later results highlight the relevance of the eye region during face identity-related tasks (Haig et al., 1985; Schyns et al., 2002; Sekuler et al., 2004). Additionally, a study tracking information use over time revealed that the left eye (from an observer’s perspective) becomes diagnostic for facial identity recognition a little under 50 ms before the right eye. As noted by the authors, this asymmetry in favor of the left side of the image is in line with observation

of a right-hemisphere advantage for face processing (Vinette et al., 2004). Importantly, this same work acknowledges the presence of individual difference in patterns of information use. Moreover, it suggests that due to great variance across observers, some regions on the face contour that reached statistical significance at the individual level were then lost by averaging across observers (Vinette et al., 2004). This resonates with what Haig already noted, reporting interindividual variance large enough to suggest that generalization across subjects was not necessarily appropriate (Haig, 1985).

1.3.2. Oculomotor Evidence

While image classification can directly link information use to performance, it also represents a rather unnatural setting since only pieces of faces are visible. This could in turn bias observers toward strategies more part based than those that would be deployed when considering whole face images (Goffaux & Rossion, 2006). To obviate to this issue and explore information sampling under natural viewing conditions, eye-tracking technologies can be used (see CHAPTER 2 for details on this technology) to monitor eye movements. Although they cannot provide certain evidence of information usage (see CHAPTER 6 for a discussion), it has been suggested that eye movements can be used as indications of overall attention allocation (Buswell, 1935; Henderson et al., 2003).

The first report on eye movements in relation to face stimuli was made in 1967 by Yarbus, who in his seminal work tracked the gaze of human observers while they were presented with different images. He first remarked that when viewing pictures of scenes, some elements received a high number of fixations while others fewer or none. This observation led Yarbus to question what makes observers fixate on some specific elements rather the others. After excluding a number of possible explanations (e.g., complexity, contrast, color), he hypothesized that the elements receiving a great number of fixations were those containing information relevant to the interpretation of the image (Yarbus, 1967).

He continued by noting that when observers viewed scenes containing humans faces, these were the elements most fixated on. Finally, he made an observation that has been at the center of research for decades. Like scene viewing, Yarbus noted that when an individual examined the image of a non-expressive face, not all the elements were equally fixated on. Specifically, observers moved their gaze

in a T-shaped pattern, looking predominantly at the eyes and making fewer additional fixations on the nose and mouth region (Figure 1.7).

Figure 1.7

Fixation Distribution of an Observer Visually Exploring Faces Under No Instruction.



Note. Lines trace the route of saccades. The exemplar observer reported here mostly sampled the eye region and to a smaller extent, the nose and mouth. Some saccades were also performed over the contour of the face. From Yarbus (1967).

This sampling pattern has also been found during identity-related tasks and has been replicated for years by independent research groups, which led to the assumption that it was universal (Luria & Strauss, 1977; Mertens et al., 1993; Williams & Henderson, 2007; Henderson et al., 2001).

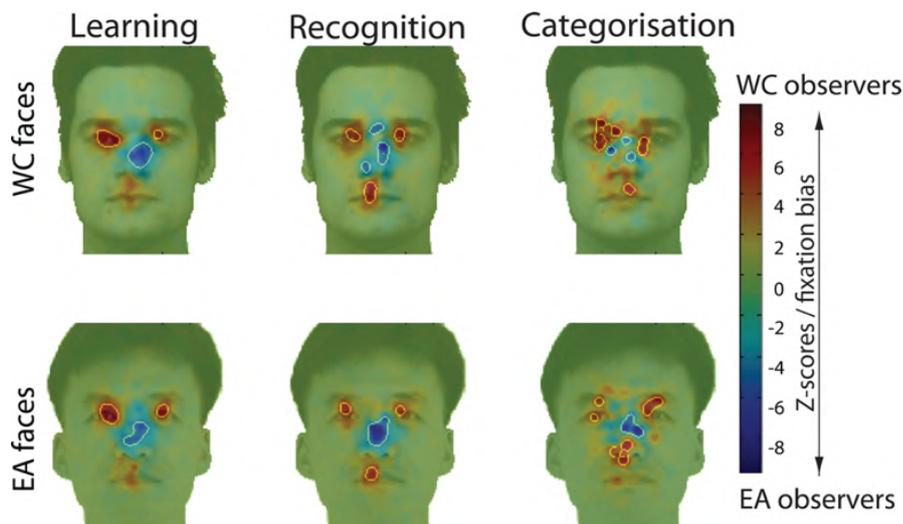
However, further investigations challenged this concept, suggesting that sampling strategies are not predefined but can change according to several factors. One of these is the location of diagnostic information. During a facial identity discrimination task, observers were presented with stimuli that only differed in the mouth. Under these circumstances, participants successfully discriminated between identities by redirecting their fixation away from the eye regions and toward the mouth region since it was the only diagnostic element (Peterson & Eckstein, 2014).

Importantly, these findings apply to a very specific group of individuals, namely Caucasians. A different set of results emerge when different populations are investigated because culture is another fundamental aspect that shapes sampling strategies.

The first strong evidence of cultural influence on fixation patterns was produced by a study by Blais et al. (2008). They tracked the eye movements of two populations—West Caucasians and East Asians—during a facial recognition task, revealing that despite achieving comparable recognition accuracy, the two groups exhibited significantly different visual scanning patterns. On the one hand, Caucasians showed the well-documented triangular pattern encompassing the eye, nose, and mouth regions. On the other hand, East Asians showed a significant deviation from this, directing the majority of their fixations toward the center of the face, a region considered to be optimal to integrate facial information globally (Figure 1.8).

Figure 1.8

Fixation Bias of West Caucasians (Red Areas) and East Asians (Blue Areas) for Learning and Recognition of Both West Caucasian and East Asian Faces.



Note. Compared to East Asians, West Caucasians fixated more on the eye and mouth regions, while East Asians fixated more on the center of the face. A similar bias for both race stimuli suggests that it is driven by the race of the observer, rather than the race of the face stimulus. From Blais et al. (2008).

These differences in sampling strategy have been replicated several times (e.g., Kelly et al., 2010; Miellet et al., 2012; but see Or et al., 2015), and they have been found for images of both Caucasian and Asian faces, for other tasks (e.g., categorization by race), for inverted faces (Rodger et al., 2010), and in children (Kelly et al., 2011; see Caldara, 2017 for a review).

However, as detailed in the next section, eye movement data show that even within the same culture and during the same task, it is still possible to find variations in sampling strategies due to individual differences.

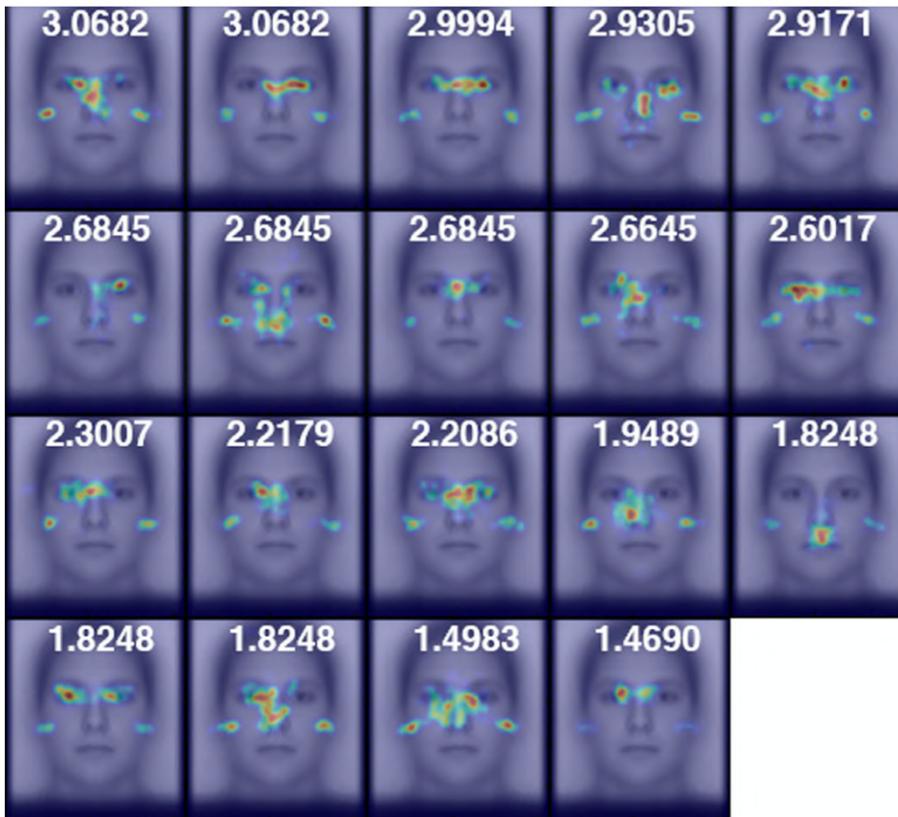
Idiosyncratic Sampling Strategies. Arguably, individual differences in sampling strategies were first documented by Walker-Smith and colleagues (1976), who recorded the eye movements of three observers during a face discrimination task and reported interindividual differences in scanning path and preferred facial features. For instance, they found that while the first subject fixated more on the right eye and the nose, the second observer focused more on the nose and mouth, while the third individual directed most of their fixation toward the eyes and nose.

However, subsequent studies not only did not focus on idiosyncrasies for almost four decades but mostly only reported group results obtained by averaging subjects together. Only recently has interest in idiosyncratic eye movements grown significantly. They have been documented in Caucasian observers across multiple studies. Specifically, it has been shown that contrary to earlier assumptions, both scanning patterns and the preferred VP (i.e., location of high-density fixations) are observer specific (Peterson & Eckstein, 2013; Arizpe et al., 2016; Kanan et al., 2015; Mehoudar et al., 2014; Figure 1.9). Additionally, although group studies suggest that the majority of Caucasians direct their first fixation just below the nasion (Hsiao & Cottrell, 2008; Peterson & Eckstein, 2012), single-subject analysis revealed the existence of variations for this metric as well (Peterson & Eckstein, 2013).

Crucially, these individual differences do not appear to correlate with behavioral performance: higher or lower scores in identity-related task were not related to specific patterns of oculomotor behavior (Mehoudar et al., 2014; Arizpe et al., 2016; but see Sekiguchi, 2011; Figure 1.9). This reinforces the idea that different sampling strategies can be equally efficient.

Figure 1.9

Examples of Individual Sampling Strategies and Their Respective Scores in Face Recognition.



Note. Heat maps clearly show how different subjects deploy different sampling paths. Importantly, higher or lower scores are not associated with a specific pattern. From Arizpe et al. (2016).

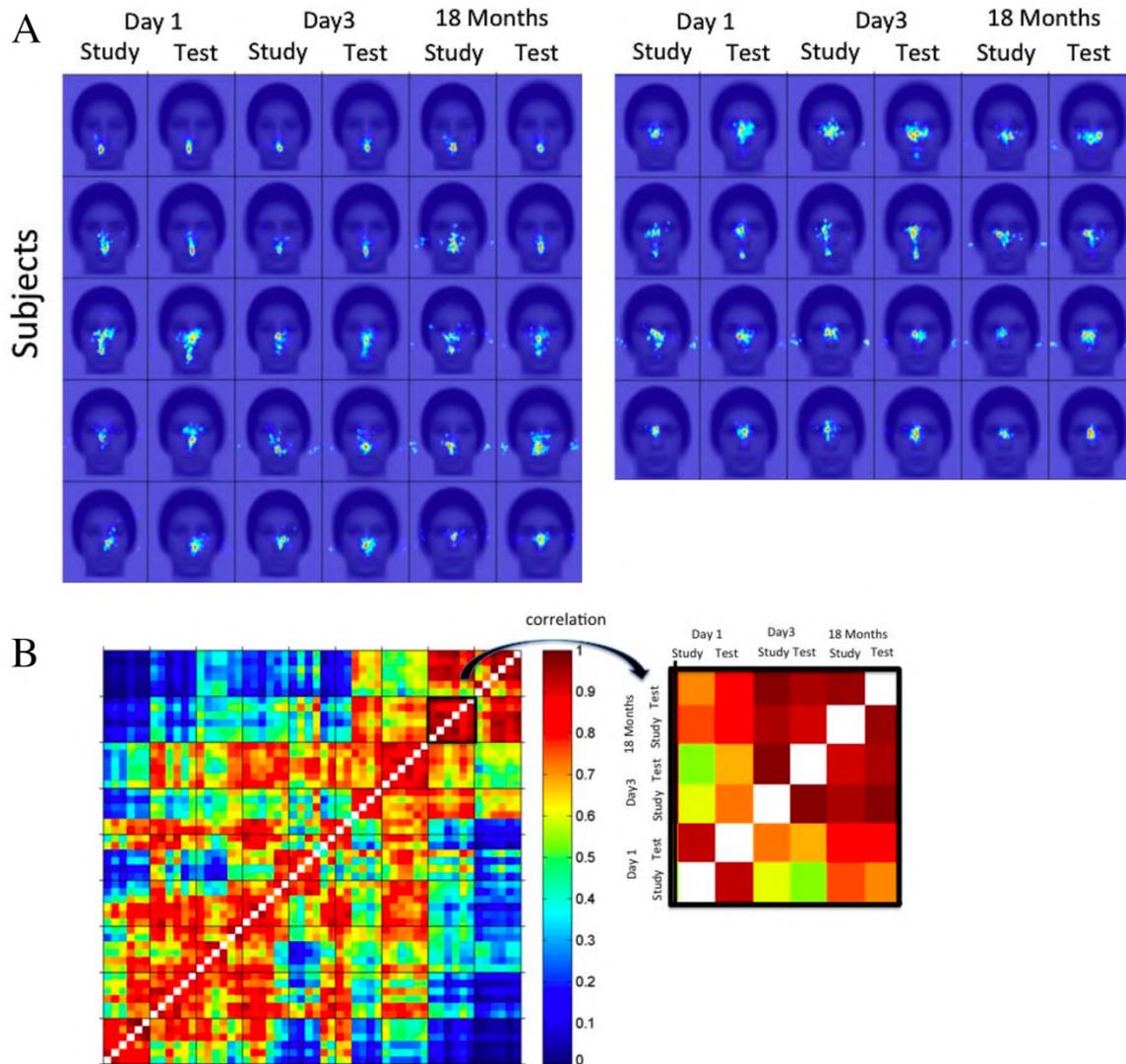
Further investigation of idiosyncratic sampling strategies suggests the existence of at least four different groups of observers who showed greater fixation on the left eye region (25% of the subjects), the right eye region (23%), the nasion region (23%), or the area encompassing the nose and upper lips (20%; Arizpe et al., 2016). Providing clear description of the degree of deviation from the canonical triangular fixation pattern, this study provides strong evidence of how group results can be misleading and result in a misrepresentation of a portion of the population. Importantly, evidence of individual difference in sampling strategies and landing position of the first fixation was also reported in Asian observers (Chuk et al., 2014).

One could argue that the observed individual differences are a simple byproduct of random noise and should therefore be reduced by averaging subjects together, for example. However, strong evidence indicates the existence of underlying genuine variations.

Reliable. First, it has been shown that idiosyncratic scanning patterns are stable over time. Studies applying a test-retest design showed that observers' sampling strategies are reliable over a period of time extending from a few days up to at least 18 months (Peterson & Eckstein, 2013; Mehoudar et al., 2014; Figure 1.10A). Specifically, data indicated that scanning pattern similarity across recording sessions was significantly greater within subject than between subjects (Figure 1.10B). Temporal reliability has also been addressed using classification algorithms trained on data from one session and tested on data from a different session. Results revealed above-chance accuracy of classifiers to match an observer with their eye movement strategies during an identification task (Peterson & Eckstein, 2013; see also Kanan et al., 2015 for similar findings during different face-related judgments).

Figure 1.10

Fixation Maps of Subjects Across Test Study and Test Phases over Different Recording Sessions (A) and the Similarity Matrix Obtained by Cross-Correlating These Maps (B).



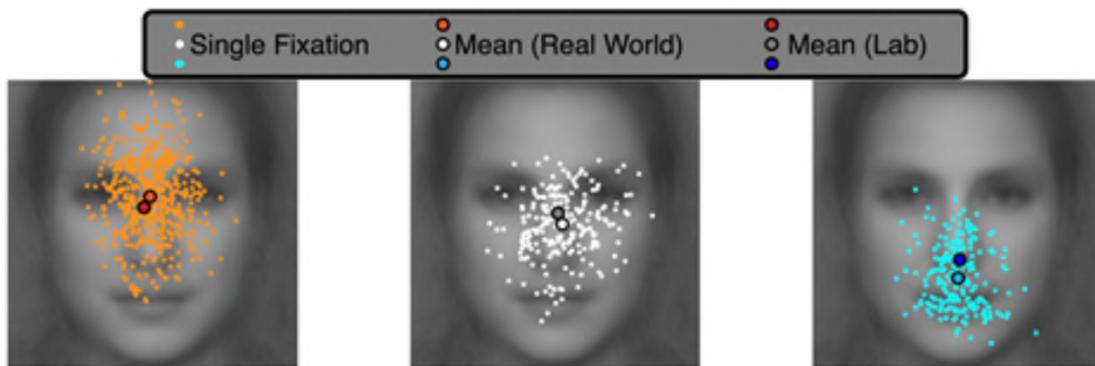
Note. Heat maps across sessions illustrate how the same subject reliably utilizes a similar scanning pattern. Likewise, the similarity matrix highlights greater similarity of fixation patterns within subject rather than between subjects. From Mehoudar et al. (2014).

Generalizable. Another crucial aspect supporting the idea of genuine variation across observers is provided by a study assessing the relationship between sampling strategies deployed within a lab setting and those used in the real world. Observers' eye movements were first recorded during an identity-related task in the lab and then tracked while participants walked around a university campus.

Correlation between these two measures showed that independent of the setting, the same observer consistently directed their fixations toward the same location (Figure 1.11). This finding is of crucial importance because it provides evidence that idiosyncratic sampling strategies are not biased by highly controlled and unrealistic lab settings. On the contrary, these data show that interindividual variations observed in the lab are a robust representation of sampling strategies deployed daily during real-world interactions (Peterson et al., 2016).

Figure 1.11

Fixations of Three Subjects Showing Mean Fixation Location for Real-World and Lab Settings.



Note. Despite the severe change in testing conditions, fixation biases are remarkably stable within subjects. From Peterson et al. (2016).

Functionally Relevant. Finally, it has been shown that idiosyncratic sampling strategies might play a role in optimizing facial identity processing. In their study, Peterson and Eckstein (2014) showed that forcing observers to perform a face identity task while fixating away from their naturally preferred VP caused a decline in performance. For instance, participants who normally direct their fixation toward the nose scored comparatively lower when fixation on the eyes was enforced. These results support the hypothesis that idiosyncratic sampling strategies do not simply reflect random routines but are functionally relevant.

Altogether, eye movement studies focusing on single-subject analysis provide strong evidence that different individuals prefer to sample faces from different locations. Since these variations cannot be accounted for by random factors such as noise, the question regarding the origin and extent of these idiosyncrasies arises. If fixations are drawn to a specific location because the sampling of facial information is more beneficial for facial identity processing, then it could be possible to also see this relationship at the neural level. Specifically, fixating on faces at a different VP might result in a modulation of responses indexing face identity processing.

1.3.3. Neuroimaging Evidence

Modulation of face processing by facial features has been also addressed at the neural level, especially by means of electrophysiological recordings. Unfortunately, as will become apparent, compared to eye movement research, neuroimaging studies have predominantly focused on group results and have mainly investigated face categorization or detection rather than identity processing. Nonetheless, neuroimaging studies provide an important starting point to understand how different facial features modulate neural face identity processing. In this context, studies have focused on responses to facial features in isolation or to fixations on specific regions of whole faces.

Masking and Local Manipulation. The first report on the relationship between N170 and face parts was made by Bentin and colleagues in their seminal work in 1996. Comparison of the component amplitude and latency in response to single facial features (i.e., eyes, nose, and lips) and whole faces revealed larger amplitude for eyes in isolation compared to whole faces, while isolated nose and lips led to a weaker and delayed N170. More recently, it has been shown that isolated eyes evoke a larger N170 compared to either eyeless or whole faces (Itier et al., 2007).

Additionally, the same ERP component was enhanced for inverted faces compared to either upright faces (Rossion et al., 2000; Itier et al., 2006) or inverted eyeless faces (Itier et al., 2007). To account for this pattern of results, Itier and colleagues (2007) suggest that the N170 reflects activation of two

distinct populations of neurons, one sensitive to faces and the other to the eyes, in the STS. Accordingly, in this model, activation of one or the other would depend on context. Specifically, when holistic processing is possible as it is for upright faces, face-sensitive neurons predominate and inhibit eye-sensitive neurons. However, disruption of holistic processing, as in the case of inverted faces, would cause a reduction in face-sensitive neurons' activity, which in turn would release eye-sensitive neurons from inhibition. This results in only face-sensitive neurons to be responsive for upright faces but both face- and eye-sensitive neurons to be recruited during inverted face processing. The same principle also applies to presentation of eyes in isolation, which also disrupts holistic processing, theoretically explaining why they elicit stronger N170 than whole faces do (Itier et al., 2006, 2007; Nemrodov & Itier, 2011; Itier & Preston, 2018; but see e.g., Sadeh & Yovel, 2010 for a different explanation of the N170 FIE).

To further investigate the contribution of different facial features to N170, ERP recordings have been paired with the bubbles image classification technique. Results indicate that the presence of the eye regions is positively correlated with the N170 amplitude (Schyns et al., 2003).

Neural responses across facial features have also been addressed by fMRI studies. One of these has reported that when presented in isolation, the nose, mouth, and left eye (from the observer perspective) resulted in a comparable level of activation in the OFA (Arcurio et al., 2012). On the other hand, investigations focusing on identity processing by measuring adaptation effect found a greater release of adaptation in both FFA and OFA for changes in the eyes compared to those in the nose and mouth (Lai et al., 2014; Harris & Aguirre, 2010).

Altogether, these studies suggest the eyes as the crucial region for face processing. However, it should be noted that as was the case for behavioral studies, these results relate to experimental conditions that are far from being ecological (e.g., isolated features, faces without features, or faces varying only locally). Therefore, they might not provide a full picture of how different features compare to one another in the context of whole and fully informative faces.

Enforced Fixation on Whole Faces. To address this missing information, a series of studies recorded electrophysiological neural responses while observers were requested to fixate on different facial features (i.e., VPs) within whole faces. Despite the significant methodological differences, once again, Bentin's (1996) initial observations were replicated since fixation of the eyes led to a larger N170 amplitude compared to other facial information (De Lissa et al., 2014; Nemrodov et al., 2014; Parkington & Itier, 2018).

Interestingly, a smaller number of studies have reported different results. Zerouali et al. (2013) showed that within their group of observers, fixation on the nasion led to a greater N170 amplitude than fixation on the eyes or mouth. Conversely, McPartland et al. (2010) showed that within their population sample, fixation on the eyes and the mouth led to comparable N170 amplitudes.

CHAPTER 2

THESIS RATIONALE AND METHODOLOGICAL INTRODUCTION

2.1. General Aim of the Thesis

The literature review presented in the previous chapter highlights two important facts. First, it provides evidence that different facial regions are differently relevant to facial identity processing as supported by studies using different techniques from image classification through eye movements to electrophysiology and functional imaging.

Second, the literature review exposes an imbalance between oculomotor behavioral and neuroimaging studies. While the former are increasingly becoming aware of and focused on individual differences and their functional meaning, the latter still mainly rely on group studies exploring general trends. Although group studies can be highly valuable tools, they can also lead to inaccurate assumptions. A clear example is the triangular fixation pattern for face stimuli that for decades was thought of as shared universally but was later revealed to be an artefact of averaging.

Moreover, as also emerges from the literature presented in the previous chapter, most of the research investigating VP-dependent neural responses has focused on either face categorization or detection or investigated identity processing by only modulating one feature at a time. However, in real life, faces change as wholes. Therefore, it remains unclear whether and how the VP could modulate neural identity processing when changes are not restricted to a single area. Prompted especially by findings in eye movements research, my thesis's main goal is to investigate individual differences in VP-dependent neural responses in the context of facial identity processing.

We investigated idiosyncrasies from various perspectives, not only looking for them but also evaluating their functional meaning (Study 1) and their temporal reliability (Study 2).

Moreover, in our research work, we discuss not only how idiosyncrasies can be useful but also how they can in some contexts represent an important limitation. Based on this, we also deemed it important to assess whether some experimental manipulations could help reduce variation across the neurotypical population (Study 3).

Study 1. The first study (CHAPTER 3) aimed to answer two related questions: “Does the VP modulate neural facial identity discrimination differently across individuals?” and “Is there a relationship between idiosyncratic sampling strategies and VP-dependent neural responses?”

To answer these questions, we separately recorded each participant’s neural activity and eye movements. Neural responses were obtained using EEG and fast periodic visual stimulation (EEG-FPVS; see the next section for details on this paradigm) while the participant fixated on one of ten VPs. This allowed us to extract an index of neural facial identity discrimination for each individual for each VP.

Eye movements were recorded using eye-tracker technology (see the next section for details) during a face identity-related task. Face stimuli used in the task were divided into 10 regions of interest, each one surrounding one of the VPs used during EEG-FPVS. We then computed the cumulative fixation duration for each VP and each observer.

A positive relationship between idiosyncratic eye movements and neural face discrimination responses would suggest a functional role of individual differences. That is, it would reflect a tuning between eye movements and neural responses that allows individual neural visual systems to be fed with the most appropriate and effective information.

Study 2. In the first study (CHAPTER 3) we found idiosyncratic VP-dependent neural facial identity discrimination responses. Additionally, individual differences were not only found in terms of VP-related patterns but also in relation to overall response amplitude and response topographical distribution. This motivated us to further explore the robustness of neural idiosyncrasies in the second study (CHAPTER 4).

The rationale was that a certain degree of fluctuations across individuals is to be expected due to some noise in measurement. Therefore, in order to make any further assumption based on these observations, one should first establish whether they are reliable and hence replicable. Therefore, we used a test-retest approach with an intersession interval of six months. If the idiosyncrasies observed were mainly due to genuine variations across individuals, then it should be possible to replicate them. If, on the other hand,

fluctuations were mainly driven by noisy measures, reliability should be low because noise is random in nature and changes over time, inducing different variations in the signal.

Study 3. The third study aimed to determine whether there are situations that induce a more homogeneous response across observers, de facto reducing individual differences. This question was driven by our previous studies, both of which suggested that individual differences in neural facial identity discrimination are not a fluke due to random noise but are likely meaningful variations. While this is extremely interesting and represents a rich source of information, one cannot ignore the fact that it could be problematic. If individual differences are meaningful and individuals have genuine different preferential responses, testing only one condition could misrepresent a portion of the sample. This could also represent an issue when the goal is to help identify, for example, impaired face cognition. If the baseline for comparison has a very wide range, detecting outliers becomes less accurate. However, testing many conditions is not always an option. For example, when investigating young children or special populations, long testing sessions can represent a serious challenge.

Therefore, we reasoned that one way to approach the problem would be instead of ignoring the presence of individual differences to find situations where they are naturally less prominent.

The individual differences observed in the first two studies are related to differential preferences across observers for given VPs. This might occur because different VPs result in different information available across the visual field. Therefore, a possible strategy to reduce individual differences would be to find a condition where varying VP has a smaller influence on the visual input. A way of achieving this is by reducing stimulus size. Therefore, in the third study (CHAPTER 5), we recorded EEG-FPVS responses while parametrically varying VPs' and stimuli's size. We hypothesized that as stimuli became smaller, differences in neural response across VPs would decrease and individual differences in response patterns would therefore become less apparent.

Before presenting these three studies and our findings, I will provide a detailed description of the above-mentioned measures of interest and the methods used to acquire them.

2.2. Methodological Approaches

2.2.1. Eye Movements and Eye-Tracker Technology

Eye movements can be conceptualized as an ensemble of saccades and fixations where saccades serve to redirect gaze from one point to another in the visual world. During fixations, the visual information perceived is projected onto the retina. Importantly, the spatial resolution is not uniform across the whole retina. The fovea constitutes its center, which extends for two degrees and is the locus of maximal visual acuity (Fairchild, 2005). Outside the fovea expanding for five degrees is the parafovea (Calvo & Lang, 2005), and beyond that is the portion of the visual field referred to as the periphery. Importantly, the further from the fovea, the lower the acuity of the visual field.

Eye tracking is a method used in a variety of fields to measure variables associated with oculomotor behavior. Currently, three approaches to eye movement measurements are used: scleral search coil, electrooculography (ECG), and video-based eye trackers. The scleral search coil technique has high spatial ($< 1^\circ$) and temporal resolution (< 1 ms) but is also extremely invasive. This approach has been used for decades and consists of subjects wearing contact lens in which a small coil is inserted.

The ECG consists of placing electrodes around the eyes and measuring the electrical activity generated by the muscles surrounding them. Finally, video-based eye trackers are less invasive and consist of projecting an infrared light onto the eye of the subject. This constant light generates a corneal reflection that is captured by a camera located near the infrared illuminator. The images are acquired at a high frequency (up to 2,000 Hz), and from these it is possible to determine two crucial pieces of information: the location of the corneal reflection and that of the pupil.

Unless one is using eye-tracking devices located on the subject (e.g., headset, glasses), the camera and the infrared illuminator locations are fixed. However, the head of the subject, even if resting on a chin and forehead rest, can shift slightly as the testing session progresses. Subjects' pupils on the images acquired by the camera can therefore change because the gaze shifts to a different location or because the head moves. On the other hand, the corneal reflection changes position on the images only when the head moves. Consequently, an image-processing algorithm can use the difference between the

location of these two elements to determine gaze location without being misled by a possible subject's head movements.

Because of its non-invasiveness and its precision, in the experimental work presented in Study 1, we recorded observers' oculo-motor behavior using SR Research Desktop-Mount EyeLink 2 K, a video-based eye-tracker with high resolution (0.01° of visual angle) and accuracy (down to 0.15° of visual angle) (see CHAPTER 3).

2.2.2. Electroencephalography

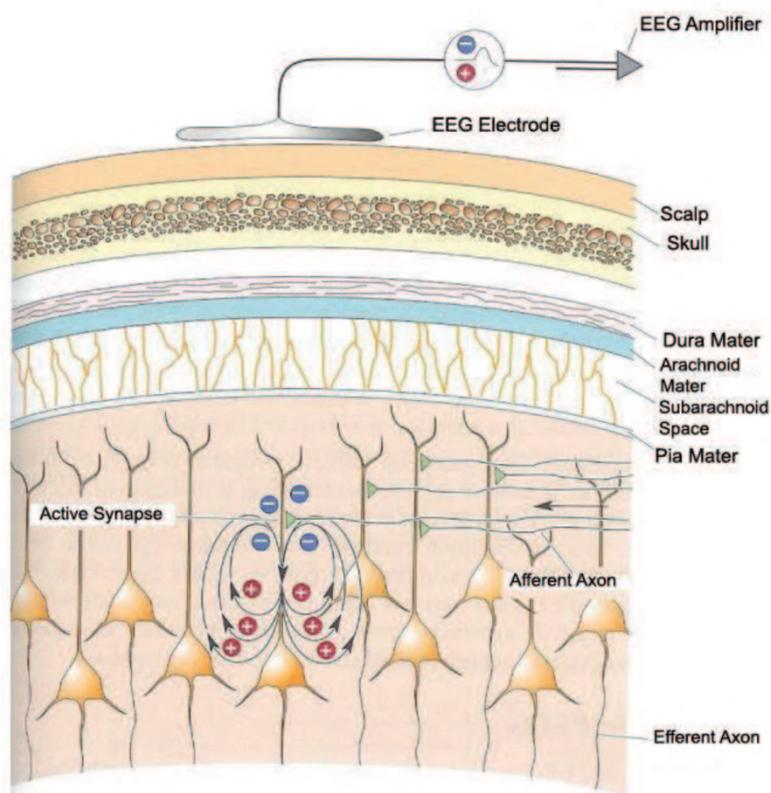
EEG is a technique used to record the electrical fluctuation in the brain that arises from cognitive, sensory, and motor processes. The first measurement of electrical brain activity is attributed to Hans Berger in 1924. Since then, due to its high temporal resolution, relatively low cost, and noninvasiveness, EEG has become a widely used brain-imaging technique utilized to investigate the time course of neural activity in both clinical (e.g., epilepsy diagnosis) and scientific settings.

Electrical changes in the brain are caused by neural communication. When a neuron is stimulated, its membrane changes in polarity, ultimately leading to a release of neurotransmitters. These chemicals exit from one neuron into the synaptic cleft and bind to the receptor of an adjacent neuron, causing a postsynaptic potential (PSP) that depolarizes the membrane. If the change in membrane potential is sufficiently large, this triggers an action potential that induces a new release of neurotransmitters. By continuing from one neuron to another, this loop allows information to travel. While the potential changes of action potential are very large intracellularly, what is measured extracellularly is very small. Moreover, action potentials are too short (1 ms) to sum up temporally, which increases the overall electrical change. On the other hand, PSP lasts longer, and because one neuron can receive from multiple neurons at the same time, a large number of PSPs can sum up together. Therefore, the electrical changes measured on the surface are most likely the result of the summation of many PSPs. Importantly, for these potentials to reach the surface and be recorded, they have to be triggered by neurons that are parallel to each other so as to not cancel out and need to be orthogonal to the recording electrode, hence

the cortex surface. Because of these criteria, the PSPs of pyramidal cells are thought to be the main generators of the voltage recorded by the EEG (Kirschstein & Kohling, 2009; Nunez & Srinivan, Figure 2.1). On the surface, the summed activity can be represented as positive and negative fluctuations (Box 2.1) whose absolute magnitude can be used as an index of changes in neural activity.

Figure 2.1

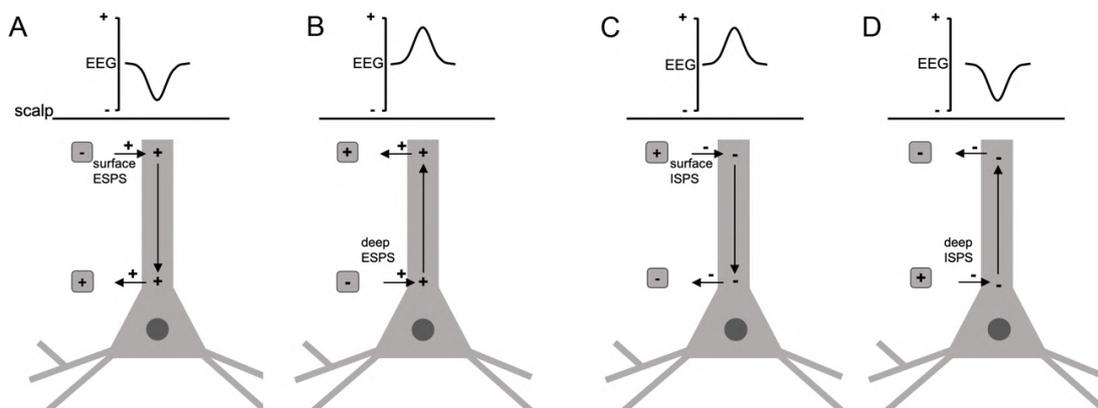
Schematic Representation of Neural Generator of the Signal Recorded by Scalp Electroencephalography



Note. Pyramidal neurons are aligned parallel to one another and perpendicular to the cortex surface. This allows multiple postsynaptic potentials to sum up together without cancelling each other out. This signal is then strong enough to travel to multiple layers and be detected by EEG electrodes.

Box 2.1. Generation of Positive and Negative Electroencephalography Fluctuations

During neural communication, different types of neurotransmitters are released. Inhibitory (e.g., GABA) and excitatory (e.g., glutamate) neurotransmitters trigger inhibitory and excitatory postsynaptic potentials (ISPS and ESPS) respectively. The induced flow of ions between intracellular and extracellular space generates sinks and sources. Specifically, in the case of an ESPS, positive ions flow into the neurons at sinks. This leaves the extracellular space relatively more negative. As positive ions travel through the neuron and exit it into the extracellular space at sources, they increase the positivity of extracellular space and leave intracellular space relatively more negative (Figure 2.1A, B). The reverse occurs for ISPS: negative ions flow into the neuron at sinks, leading to greater positivity in the extracellular space. When negative ions leave the cell at sources, they shift the polarity of the extracellular space, making it relatively more negative (Figure 2.1C, D). Simultaneous positive and negative spaces separated by a distance create dipoles. The signal recorded on the scalp corresponds to the extracellular polarity near the surface. Importantly, surface ESPS (Figure 2.1A) and deep ISPS (Figure 2.1D) both lead to a relatively more negative extracellular space near the surface and hence to a negative deflection. On the contrary, deep ESPS (Figure 2.1B) and surface ISPS (Figure 2.1C) both lead to a positive deflection. On the surface, these fluctuations can be recorded as a difference between the voltage recorded by electrodes at two separate locations (Kandel et al., 2000). However, while travelling from the neurons toward the surface, the signal must pass through several layers of tissue that can cause distortions in the signal's trajectory to the surface. Additionally, multiple neuron populations can be active simultaneously and might add together or cancel each other. The combination of all these factors results in severe difficulties in determining the origin of a signal from its scalp topography—the so-called inverse problem (Luck, 2014).

Figure 2.2*Origin of Positive and Negative Fluctuation on the Scalp*

Note. Excitatory postsynaptic potentials lead to a more positive extracellular space (A and B) and inhibitory postsynaptic potential to a more negative potential (C and D). Surface negative extracellular space leads to a positive deflection (A and D) on the scalp while surface positive extracellular space results in a negative deflection (B and C).

2.2.3. Event-Related Potentials

The EEG can be used to record various types of neural activity. While it can be deployed to track ongoing activity, for example, it can also be used to assess the relationship between specific stimulation and neural activity. This latter investigation can be performed through the recording of ERPs, which are voltage fluctuations evoked by and time locked to predefined sensory, motor, or cognitive events.

The most common approach to acquiring ERPs is through the iterative presentation of a discrete stimulus. The recorded neural responses are then averaged together. This process enhances responses that are directly related to the stimulus since any EEG background activity that is not time locked to the event is reduced. A crucial aspect of this approach is the relatively long interval inserted between stimuli. This allows for the neural systems that respond to a presented stimulus to return to a resting state or baseline before the onset of a new one. Due to the isolation of the neural response achieved by this approach, these ERPs are also termed transient. In contrast to discrete events, one can also record the EEG signal while presenting sequences of stimuli at a relatively high constant frequency rate. This results in an oscillatory periodic neural response synchronized to the stimulation frequency and called steady-state potential (SSP). SSP is the measure of interest in the scientific contributions of the present thesis. Therefore, in the next section, I describe SSP's characteristics, its potential neural generator, and how it can be used to investigate face processing. A discussion of its strengths also clarifies why it was preferred to traditional transient ERPs in this case.

2.2.4. Steady State Potential

Characteristics. One of the first reports of steady state potentials can be traced back to Adrian and Matthew's work in 1934 describing how neural activity appears to synchronize to a periodic visual stimulation: "At a signal the eyes are opened and the shutter lifted to turn on the flickering light. The result is a series of potential waves having the same frequency as that of the flicker" (p. 378).

The authors also reported that the waves generated by the stimulation could be highly stable for relatively long periods of time, which is why this response was later renamed steady state visual evoked potential (SSVEP; Regan, 1966).

Further studies focused on the frequency spectrum of this response and reported that stimulation at a given frequency F not only generates a neural response at this fundamental frequency but also at frequencies corresponding to multiple integers of the fundamental, namely its harmonics (i.e., $2F$, $3F$, ...). Ideally, when visual stimulation is conducted by means of a sinewave, the input signal should only contain one frequency. In real life, however, this is not necessarily true. A number of factors can contribute to harmonics in the visual presentation, which in turn could explain the presence of additional frequencies in the output response. However, this cannot be the sole driving factor since harmonics that were not found in the original stimulation have nonetheless been recorded in the neural response output (Teng et al., 2011, for sine waves; Roberts & Robinson, 2012, for square waves). Consequently, the presence of higher harmonics in the neural response following fast periodic visual stimulation (FPVS) is also thought to reflect the nonlinearity of the visual system (Labecki et al., 2016; Norcia et al., 2015; Rossion et al., 2020).

Neural Generator of the Steady State Visual Evoked Potential. The neural mechanisms underlying the SSVEP response are still under debate. In this respect, two main theories exist. On the one hand, the SSVEP response was suggested to be the byproduct of the superimposition of transient evoked potentials. On the other hand, it was proposed to be the result of phase resetting of ongoing neural oscillations.

The Superposition Hypothesis. Within the framework of ERPs, the SSVEP is explained by the superimposition hypothesis. In this context, an event-related response is a potential that develops independently of ongoing oscillation and that is added to on a single-trial basis. Consequently, the superposition hypothesis suggests that SSVEP and transient ERPs are generated by the same neural mechanisms. Specifically, it is proposed that the SSVEP is a combination of multiple discrete transient responses that are rapidly generated one after the other. If the temporal interval between stimuli onset

is shorter than the duration of the response elicited, then the $n^{\text{th}} + 1$ response begins while the n^{th} response is still unfolding and the two overlap. Consequently, if stimulation frequency is sufficiently high, the resulting SSVEP shape can approximate a sinusoidal wave. Within this framework, a lack of consensus exists regarding the linearity of this superposition.

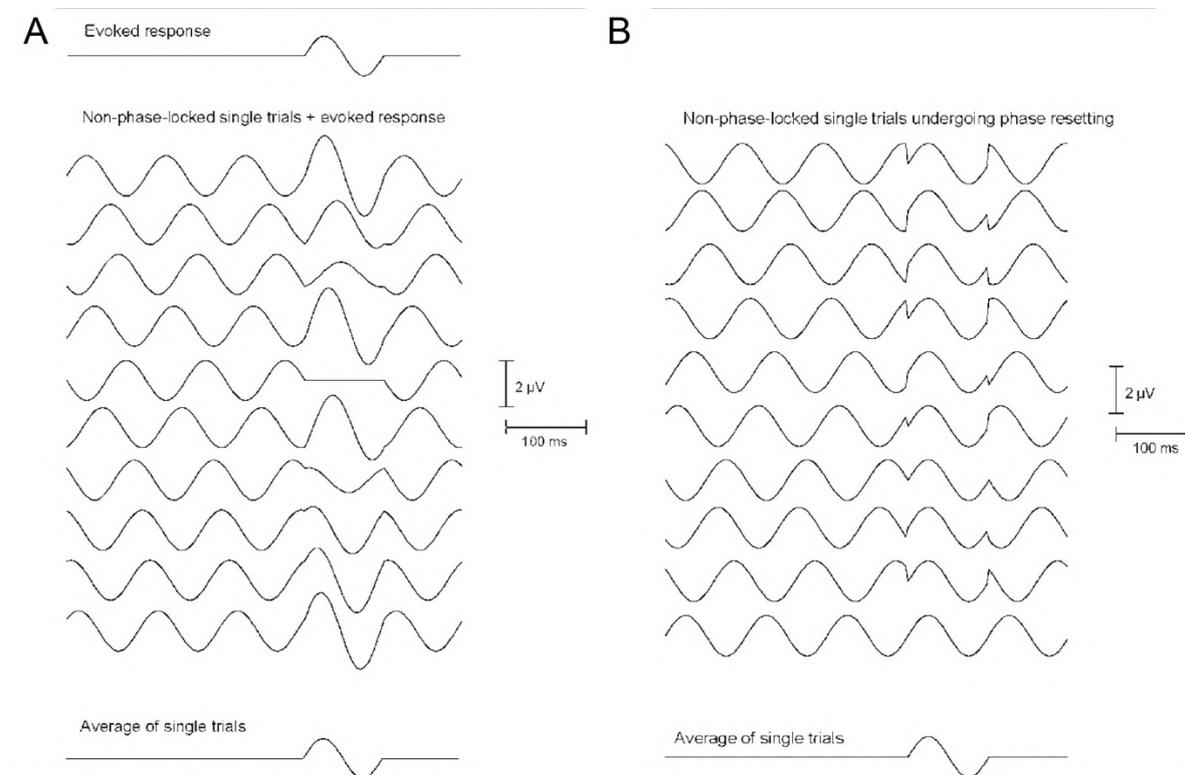
The superimposition hypothesis stems from a report in the auditory domain regarding a relationship between middle latency responses and the 40-Hz auditory steady-state responses (ASSRs; Galambos et al., 1981). Initial studies seemed to support this observation by showing that it was possible to accurately reconstruct responses at high frequencies by means of those elicited at lower frequencies. However, later work failed to replicate those findings and noted that the steady-state responses that were estimated through superposition were not a reliable reproduction of the observed ASSRs (e.g., artificial superposition led to steady state responses (SSRs) of greater amplitude compared to those recorded; e.g., Azzena et al., 1995; Santarelli et al., 1995). Moreover, it was reported that even if the accuracy of the simulation was acceptable at 40 Hz, it was not at higher or lower frequencies (Azzena et al., 1995). Researchers have tried to explain this inaccuracy by suggesting that synthesized SSR did not take into consideration natural processes such as neural adaptation (reduction in amplitude of the neural responses when quickly succeeding identical stimuli are presented; e.g., Azzena et al., 1995; Santarelli et al., 1995). By implementing this factor into their models, later studies succeeded in reliably recreating SSRs through the addition of transient evoked responses, both in the auditory domain (e.g., Bohórquez & Özdamar, 2008) and in the visual domain (Capilla et al., 2011). Additionally, Capilla and colleagues (2001) reported that implementing a nonlinear adaptation made it possible to uncover the presence of a linear relationship between SSVEP and ERPs. The authors argued that such linearity was evidence that the two evoked responses shared a common underlying neural mechanism.

The Phase-Reset Model. A different explanation is provided by the phase-reset models that explains ERPs (transient ERPs and SSVEPs) in terms of ongoing oscillations.

Arguably, the most common conceptualization of ERPs is that they are fixed-latency and fixed-polarity potentials that develop independently of background neural activity. In this context, the EEG signal contains evoked responses that are independent of but added to ongoing activity (Figure 2.3A). When

multiple trials are averaged together, background noise is drastically reduced, and only the evoked time-locked activity remains visible. However, this same result can also be explained by the phase-reset model. The principle of this model is that ERPs and ongoing oscillations are not two separate phenomena but that the former results from a phase resetting of the latter (Makeig et al., 2002; Fuentemilla et al., 2006; Figure 2.3B). Importantly, in this framework, an ERP can be generated without any amplitude change, which is not possible under the evoked model (Klimesh et al., 2004; Shah et al., 2004).

In the context of SSVEP, this hypothesis suggests that periodic responses reflect neural entrainment of ongoing oscillations. Specifically, the model proposes that the phase of ongoing oscillatory activity synchronizes with that of stimulation, inducing ongoing activity to oscillate at the same frequency of stimulation.

Figure 2.3*Schematic Illustration of Evoked and Phase Reset Models*

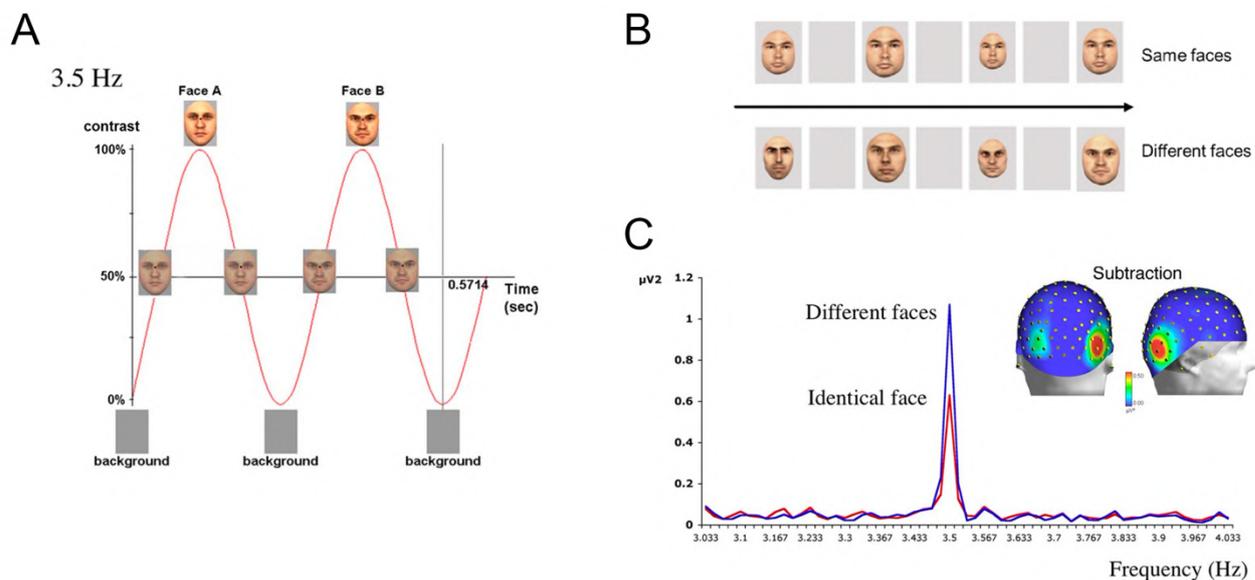
Note. A. An evoked response is added on a single-trial basis to an unrelated background EEG signal. B. The phase of ongoing oscillations resets with stimulus onset. In both cases, activity is time locked to stimulus onset and therefore remains in the signal after averaging. Adapted from Sauseng et al. (2007).

Dissociating elements of one model from those of the other is not trivial. For instance, the phase-resetting model predicts an increase of phase concentration after stimulus onset. However, if evoked responses that are time locked to stimulus onset are added to ongoing activity, this also results in an increase of phase concentration. Additionally, studies attempting to reconstruct ERPs under one model or the other have both succeeded. As a result, evidence is still inconclusive and does not allow rejection of either model, leaving this issue a subject of active debate (see Gruber et al., 2005; Klimesh et al., 2004; Jansen et al., 2003; David et al., 2005; and Makeig et al., 2002 for evidence in favor of the phase-reset model; see Rousselet et al., 2007; Shah et al., 2004; and Ahmadi et al., 2021, for evidence in favor of the evoked model; see Fuentemilla et al., 2006 and Fell et al., 2004 for evidence in favor of both models; and see Sauseng et al., 2007 for a discussion of the two models).

Fast Periodic Visual Stimulation in Face Research. In vision research, FPVS has been used for years to investigate different aspects such as selective attention (Morgan et al., 1996; Müller et al., 1998) figure/ground processing (Appelbaum et al., 2008), motion (Heinrich et al., 2003), and emotional arousal (Keil et al., 2003). However, it is only in the last decade that this stimulation has been heavily implemented in the study of facial identity processing (Rossion & Boremanse, 2011). In this context, the FPVS paradigm was initially designed to contrast two conditions: one where the dimension of interest varied and a control condition where such dimension was held constant (Figure 2.4A-B). To study facial identity discrimination, researchers compared neural responses elicited by sequences displaying faces of the same identity with those triggered by trials presenting faces of different identities (Rossion & Boremanse, 2011; Rossion, Alonso-Prieto et al., 2012; Nemrodov et al., 2015). Results indicate that both conditions elicited a periodic response clearly visible as an amplitude peak at the stimulation frequency and its harmonics. However, the comparison by subtraction of the two conditions revealed that different-identity conditions led to a significantly larger response than same-identity sequences over right occipitotemporal sites (Figure 2.4C).

Figure 2.4.

Schematic Representation of the First Version of the Fast Periodic Visual Stimulation Paradigm in the Context of Neural Face Discrimination



Note. A. Images are presented consecutively through sinusoidal contrast modulation, which gives the impression of images constantly present on screen. From Rossion and Boremanse (2011). B. Conditions are tested separately. One portrays only same-identity faces and the other only different identities. From Rossion and Boremanse, 2011. C. Comparison of the neural response to each condition. In both cases, a clear peak at the frequency of stimulation is visible. However, response to same-identity conditions is clearly reduced compared to different-identity conditions. Scalp maps illustrate the topographical distribution of the differential response (different identity – same identity). From Norcia et al. (2015).

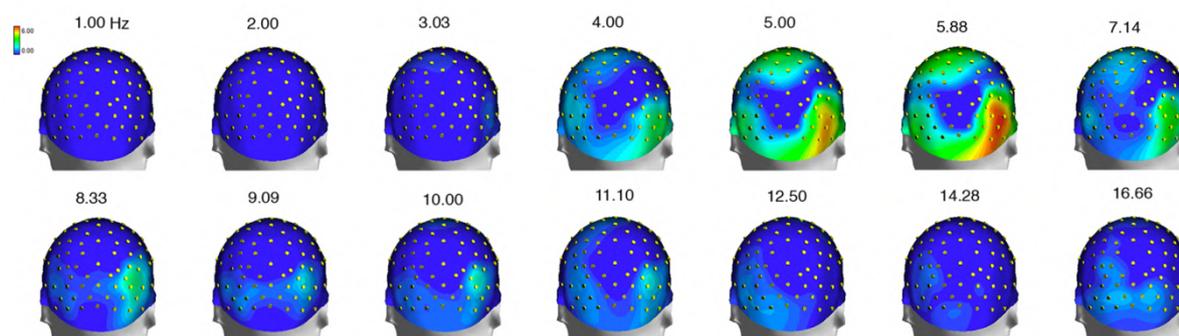
The neural mechanism underlying the difference observed in the context of facial identity discrimination is thought to relate to a stronger neural adaptation during same-identity sequences. Specifically, time-frequency analysis revealed that significant neural adaptation occurs suddenly within half of a second from the beginning of same-identity repetition (Nemrodov et al., 2015).

Importantly, differences between same- and different-identity conditions has been reported to be stronger when stimulation frequency is between 3 and 9 Hz and to peak at 5.88Hz (Figure 2.5; Alonso-Prieto et al., 2013). This specific tuning has been suggested to arise from the degree of neural dispersion or interference that is present at different frequencies. In other words, slower presentation rates allow for longer responses and hence a greater number of unrelated elements in the signal. In this case, the power in the frequency spectrum is distributed over broader bands. On the other hand, if stimulation

frequency is too fast, it is possible that presentation of one stimulus interferes with the processing of the previous one, not allowing for any major response to clearly unfold. Interestingly, when stimuli are presented at a frequency of 5.88 Hz, they remain on screen for 170 ms, allowing each neural response to develop without any interference for so long. Coincidentally, this is also the latency of the N170, the earliest face-sensitive ERP component, which is well known to show adaptation when the same identity is repeated (e.g., Jacques et al., 2007). In line with the superposition theory, this might suggest that the recorded face identity-sensitive FPVS response reflects the (non)linear combination of a series of this early component.

Figure 2.5

Topographical Distribution of the Difference Between Different- and Same-Identity Responses Elicited Through Fast Periodic Visual Stimulation at Different Frequencies.



Note. Identity discrimination responses are visible for frequencies between 4 and 8.33 HZ, peaking at 5.88Hz. Adapted from Alonso-Prieto et al. (2013).

An Oddball Paradigm. While the initial approach held several advantages over traditional ERP paradigms (see below), it still required post-hoc comparison between conditions. This procedure would assume a comparable level of attention from the subject and of noise in the signal, which is not always the case. To overcome this limitation, Liu-Shuang and colleagues (2014) implemented an oddball paradigm within the FPVS (oddball FPVS)¹, making it possible to present the two original conditions within one sequence. This paradigm has since become highly popular and has been deployed not only

¹ Note that within the experimental contributions of this thesis oddball FPVS will be referred to simply as fast periodic visual stimulation or FPVS.

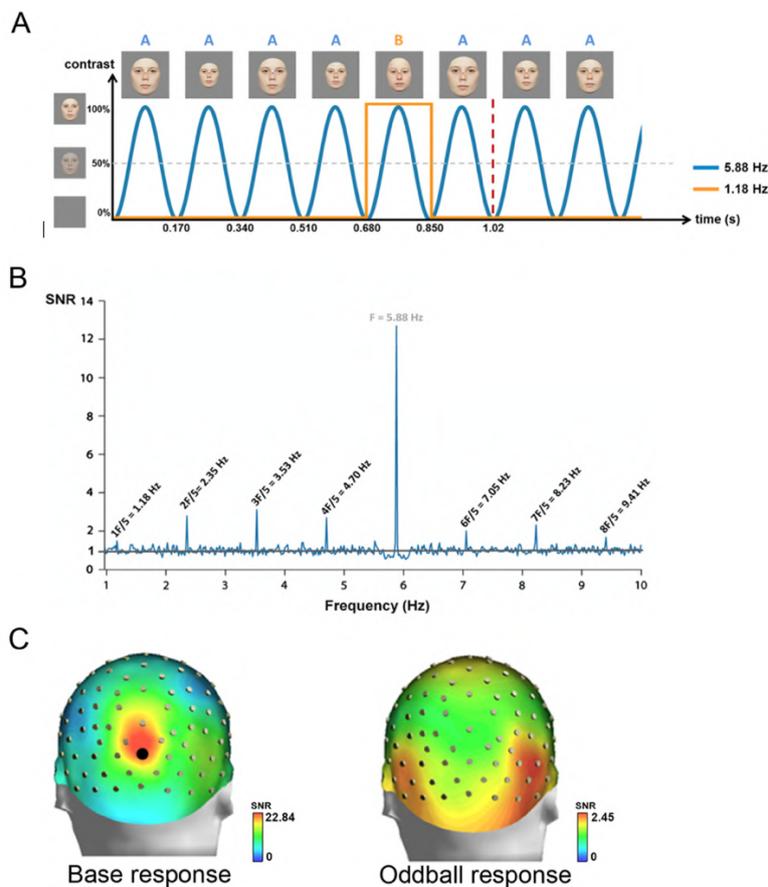
to study identity discrimination but also to face categorization, recognition, and facial expression discrimination (e.g., Retter & Rossion, 2016; Yan & Rossion, 2020; Poncet et al., 2019; Dzhelyova et al., 2017). However, the focus of the present thesis is facial identity discrimination; therefore, I detail the functioning of this version of FPVS only within this context.

Concretely, the oddball FPVS paradigm consists of presenting two types of stimuli: a base and an oddball. Within a given sequence, bases are images portraying the same facial identity (i.e., A) while oddball stimuli are images of different identities (i.e., B, C, D, E, ...). The design consists of a fixed number of repeated base images with an oddball stimulus inserted at a fixed periodic rate (e.g., AAAABAAAACAAAADAAA ...). Consequently, the stimulation contains two main frequencies: the base rate (i.e., F) corresponding to the frequency at which images are presented and the oddball rate, which corresponds to the frequency of identity change, or oddball presentation (F/n , where n is the fixed interval at which oddball images are inserted, e.g., if $F = 6$ Hz and $F/n = 6/5 = 1.2$ Hz, then oddball images will appear every fifth image; Figure 2.6A). As was the case for the earlier version of the paradigm, this rapid visual stimulation elicits a neural response at the same rate at which images are presented (i.e., the base response). However, because the stimulation now also contains another frequency the visual system can also synchronize to this second rate (i.e., the oddball response; Figure 2.6B, C). Importantly, a response to the oddball frequency is triggered only if oddball stimuli are processed differently than the base stimuli. When investigating facial identity discrimination, the oddball response is thought to be a consequence of the coupling between adaptation to the same-identity base stimuli and the subsequent release from it when a different oddball identity is introduced. Specifically, the response amplitude decreases as the system adapts, and it is restored to the original state when the system recovers from such adaptation. This introduces in the signal a second periodic response to the same rate of identity change. The implication of this dynamic is that if a system fails in discriminating identities, adaptation or release from it does not occur. Therefore, if different identities do not lead to a differential response, no oddball response emerges. Importantly, this logic does not apply in the opposite direction. The absence of an oddball response alone should be interpreted with caution and not as evidence of impaired identity discrimination. While it can reflect a genuine

impairment (as in the case of, e.g., prosopagnosic patients), the inability to record a response with scalp EEG could be attributable to several unrelated factors (e.g., cortical folding, skull thickness).

Figure 2.6

Schematic Representation of the Oddball Fast Periodic Visual Stimulation Paradigm and of the Neural Response That It Triggers



Note. A. Schematic representation of the oddball fast periodic visual stimulation paradigm. In contrast with the previous version, here same- and different-identity conditions are integrated within the same sequence. A base face (A) is presented at a fast periodic rate throughout the whole trial, and an oddball identity (B, C, D, E, ...) is inserted every n^{th} base image (in this case, every 5th image). This results in a sequence containing two frequencies: the base frequency and the oddball frequency (i.e., the frequency of identity change). B. Results of successful neural identity discrimination. A large peak is visible at the base frequency F indicating that the visual system successfully synchronized to the stimulation. Although of smaller amplitude, peaks are also visible at the oddball frequency ($F/5$) and its harmonics ($2F/5$, $3F/5$, ...), indicating that the visual system perceived and responded to the identity change, effectively discriminating across multiple identities. C. Topographical distribution of the base (left) and oddball (right) responses show how the two are spatially different. While the base is located over medial sites, discrimination response is bilateral with a stronger right lateralization. Adapted from Liu-Shuang et al., 2014.

A Measure of Neural Identity Discrimination

The assumption that the response recorded reflects high-level identity processing is ensured and supported by both methodological consideration and empirical observations. First, while the general response emerges at medial sites, oddball responses are localized over lateral occipitotemporal sites, predominantly over the right hemisphere. This suggests a spatial dissociation between the general response to flickering stimuli and that to identity changes. Additionally, image manipulation such as inversion and contrast reversal significantly diminish the response amplitude, suggesting that it is not image based. This is further supported by the fact that during each sequence, images vary in size at each cycle (1 cycle = 1 image), ensuring variations in pixel luminance and preventing the visual system from discriminating identities based on image matching. Dzhelyova and Rossion (2014b) suggest that this can be achieved by as little as a 20% size change across images.

Additionally, due to the design of the oddball FPVS paradigm, within one sequence, the visual system is confronted with multiple identities. A significant neural discrimination response emerges only if base and oddball stimuli are systematically discriminated over many different instances. Consequently, the response triggered by this stimulation cannot be driven by, for example, one distinctive exemplar face but requires a generalized ability to quickly differentiate among different identities.

Strengths and Advantages of the Oddball Fast Periodic Visual Stimulation Paradigm

As mentioned above, the oddball FPVS paradigm has multiple advantages over traditional ERPs, making it not only a valid approach to study face identity processing but also, depending on the context (e.g., process of interest, research goal), a more suitable tool.

First, the response triggered by this visual stimulation is an objective measure of neural facial identity discrimination. As already stated, the visual system synchronizes to the frequency of stimulation, meaning, ideally, the general and oddball rates. Through frequency decomposition techniques, it is possible to extract a high-resolution frequency spectrum of the recorded signal (e.g., Fast Fourier transform of a 60s sequence allows a resolution of 0.016 Hz). Because the response of interest is located at specific and predefined bins, it can be unambiguously quantified as the amplitude at base and oddball

rates (and their harmonics), while any other frequency bin can be considered unrelated background activity. This overcomes issues typical of transient ERP analysis related to arbitrary definitions of components and time windows of interest or decisions about how to quantify the amplitude of potentials (e.g., peak-to-peak vs. baseline-to-peak measures).

Another advantage of oddball FPVS response compared to transient ERP is its remarkably higher signal-to-noise ratio (SNR). This is partly due to the response being confined to narrow frequency bands and partly due to the fact that noise is spread over multiple frequency bins. Additionally, the experimenter can a priori avoid certain frequency ranges that might contaminate the response (e.g., the range of alpha waves) by accordingly choosing the stimulation rate.

A highly valuable consequence of a high SNR is that an oddball FPVS response can be estimated in a relatively short amount of time. Significant responses can be obtained with only four sequences generally lasting approximately 60 seconds each. This is especially relevant when targeting populations that would otherwise struggle to undergo long testing sessions (e.g., young children). The high SNR also makes the measure less susceptible to noise: an important aspect for investigating both the young population, which is likely to introduce movement-related artefacts, and individuals with brain lesions that might affect the propagation of the signal to the scalp (see Liu-Shuang et al., 2016 for a study on acquired prosopagnosia).

Altogether, these aspects of the oddball FPVS response are what motivated the methodological choice to use this paradigm to map individual differences in VP-dependent neural face identity discrimination.

CHAPTER 3

NEURAL REPRESENTATIONS OF FACES ARE TUNED TO EYE MOVEMENTS

Stacchi, L., Ramon, M., Lao, J., & Caldara, R. (2019). Neural representations of faces are tuned to eye movements. *Journal of Neuroscience*, 39(21), 4113-4123.

3.1. Abstract

Eye movements provide a functional signature of how human vision is achieved. Many recent studies have consistently reported robust idiosyncratic visual sampling strategies during face recognition. Whether these inter-individual differences are mirrored by idiosyncratic *neural* responses remains unknown. To this aim, we first tracked eye movements of male and female observers during face recognition. Additionally, for every observer we obtained an objective index of neural face discrimination through EEG that was recorded while they fixated different facial information. We found that facial features fixated longer during face recognition elicited stronger neural face discrimination responses across *all* observers when foveated. This relationship occurred independently of inter-individual differences in preferential facial information sampling (e.g., eye vs. mouth lookers), and started as early as the first fixation. Our data show that eye movements play a functional role during face processing by providing the neural system with the information that is diagnostic to a specific observer. The effective processing of identity involves idiosyncratic, rather than universal face representations.

3.2. Significance Statement

When engaging in face recognition, observers deploy idiosyncratic fixation patterns in order to sample facial information. Whether these individual differences concur with idiosyncratic faces-sensitive neural responses remains unclear. To address this issue, we recorded observers' fixation patterns, as well as their neural face discrimination responses elicited during fixation of ten different locations on the face, corresponding to different types of facial information. Our data reveal a clear interplay between individuals' face-sensitive neural responses and their idiosyncratic eye movement patterns during identity processing, which emerges as early as the first fixation. Collectively, our findings favor the existence of idiosyncratic, rather than universal face representations.

3.3. Introduction

The visual system continuously processes perceptual inputs to adapt to the world by selectively moving the eyes towards task-relevant, i.e. diagnostic information. As a consequence, eye movements do not unfold randomly, and during face processing humans deploy specific gaze strategies. For many years, face recognition was considered to elicit a T-shaped fixation pattern encompassing the eye and mouth regions, which was universally shared across all observers (Yarbus, 1967; Henderson et al., 2005). However, over the last decade, a growing body of work has challenged this view by revealing cross-cultural (e.g., Blais et al., 2008; Miellet et al., 2013), idiosyncratic (Mehouar et al., 2014), and within-observer (Miellet et al., 2011) differences during face recognition. For example, both Western and Eastern exhibit comparable face recognition proficiency while deploying respectively a T-shaped vs. more central fixation bias (for a review see Caldara, 2017). In addition, in line with early observations based on individual participants (Walker-Smith et al., 1977), recent studies demonstrate that observers deploy unique sampling strategies (Kanan et al., 2015; Arizpe et al., 2017), which are stable over time (Mehouar et al., 2014), and relevant to behavioral performance (Peterson and Eckstein, 2013). Specifically, individuals' sampling strategies deviate considerably from the well-established T-shaped pattern, which is merely the result of the group averaging of idiosyncratic visual sampling strategies of individual Western observers (Mehouar et al., 2014).

Despite the growing literature on the existence of idiosyncratic sampling strategies, their functional role and underlying neural mechanisms remain poorly understood. Some studies have investigated the impact of the fixated facial information input on neural responses, by recording the electroencephalographic (EEG) signals while observers fixated different facial information (i.e., viewing positions; VPs). This body of work has focused on the N170 face-sensitive ERP (Event Related Potential) component (Bentin et al., 1996), and has demonstrated that VPs differentially modulate the N170. The finding of the eye region eliciting larger amplitudes (de Lissa et al., 2014, Itier et al., 2006; Nemrodov et al., 2014; Rousselet et al., 2014) has been interpreted in terms of a universal *neural*

preference toward this facial information. However, these studies have mainly involved grand-average analyses, and did not control for *individual* fixation preferences. Consequently, it remains unclear whether idiosyncratic fixation biases concur with idiosyncratic neural responses.

A paradigm that has been increasingly used to examine different aspects of face processing, including e.g. face categorization, identity or facial expression discrimination (Liu-Shuang et al., 2014; Norcia et al., 2015; Rossion et al., 2015; Dzhelyova et al., 2016) involves fast-periodic visual stimulation (FPVS). Such FPVS paradigms involve stimulation with a series of stimuli that periodically differ with respect to a given dimension. Neural synchronization to the frequency of changes provides an implicit measure of the process of interest. Compared to traditional ERPs, the FPVS response is less susceptible to noise artefacts, and its remarkably high signal-to-noise ratio increases the likelihood of detecting subtle differences between experimental manipulations (Norcia et al., 2015). Such signal properties make the FPVS paradigm paired with EEG recordings ideal to investigate the relationship between VP-dependency of neural responses and idiosyncratic visual sampling strategies.

In the present study, we extracted observers' fixation patterns exhibited during an old/new face recognition task (Blais et al., 2008). Additionally, we recorded their neural face discrimination responses using a FPVS paradigm, in which same identity faces were presented at a constant frequency rate with periodically intervening oddball identities, while observers fixated one of ten VPs. We then applied a robust data-driven statistical approach to relate the idiosyncratic sampling strategies to the electrophysiological responses across all electrodes independently. As early as the first fixation, we find a strong positive relationship between idiosyncratic sampling strategies and neural face discrimination responses recorded across different VPs, which can be observed across all observers. In particular, independently of the sampling strategy, the longer a VP was fixated under natural viewing conditions, the stronger the neural face discrimination response during its enforced fixation.

3.4. Methods

3.4.1. Participants

The sample size opted for was motivated by studies using the same FPVS paradigm to index neural face discrimination that were published up to data acquisition (Dzhelyova and Rossion, 2014a, 2014b, Liu-Shuang et al., 2014, 2016; sample size range: 8-12). In Dzhelyova and Rossion's (2014b) study using a within subject design, the observed minimal effect size resulting from a repeated ANOVA was .2 (partial-eta). As the effect size estimation is often overly optimistic in the literature, we planned our experiment based on an effect size of .1 and an estimated sample size of 15 participant which results in a power of .95 to detect an effect. Based on prior experience and the requirement of high-quality data from independent methods, we chose to test a total number of 20 participants. Our cohort comprised 20 Western Caucasian observers (11 females, two left-handed, mean age: 25±3 years) with normal or corrected-to-normal vision and no history of psychiatric or neurological disorders. Three observers were excluded due to poor quality of the eye movement data. All participants provided written informed consent and received financial compensation for participation; all procedures were approved by the local ethics committee. Finally, all observers performed the eye-tracking and the EEG experiment during the same testing session and systematically in this order. It is worth noting, that the stimuli used across those sessions are different and cannot account for an order effect. In addition, none of the observers were aware of their fixation biases.

3.4.2. Procedures

3.4.2.1. Eye-tracking

Experimental design

Stimuli consisted of 56 Western Caucasian (i.e. WC) and 56 East Asian (i.e. EA) identities respectively obtained from the KDEF (Lundqvist et al., 1998) and the AFID (Bang et al., 2001). Faces were presented at a viewing distance of 75 cm and subtended 12.56° (height from chin to hairline) x 9.72° (width) of visual angle on a VIEWPIX/3D monitor (1920 x 1080 pixel resolution, 120 Hz refresh rate).

Observers completed two learning and recognition blocks per stimulus race. In each block, observers were instructed to learn 14 face identities (7 females) randomly displaying either neutral, happy or disgust expressions. After a 30 second pause, a series of 28 faces (14 old faces) were presented and observers were instructed to indicate as quickly and as accurately as possible whether each face was familiar or not by key-press. To prevent image matching strategies, learned identities displayed different facial expression in the recognition blocks. Each trial involved presentation of a central fixation dot (which also served as an automatic drift correction), followed by a face presented pseudorandomly in one of four quadrants of the computer screen, to avoid potential anticipatory fixation strategies. During the learning phase, stimuli were presented for five seconds; during the recognition phase presentation was terminated upon participants' responses. Eye movements were recorded during both the learning and recognition phases.

Data acquisition and processing

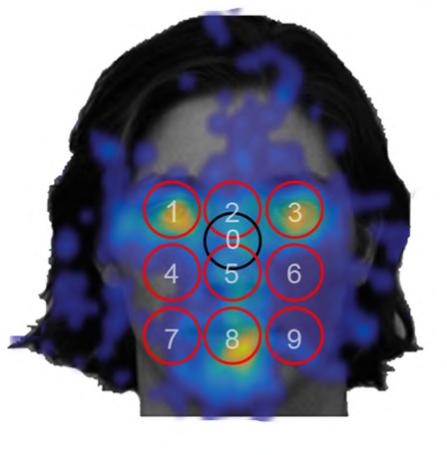
The oculomotor behavior was recorded for each participant using an EyeLink 1000 Desktop Mount with a temporal resolution of 1000 Hz. The raw data are available in the public domain (Stacchi et al., 2018). Data were registered by using the Psychophysics (Brainard, 1997) and the EyeLink (Cornelissen et al., 2002) Toolbox running in a MatlabR2013b environment. Calibrations and validations were performed at the beginning of the experiment using a nine-point fixation procedure. Additionally, before each trial a fixation cross appeared in the center of the screen and participants were instructed to fixate on it until a new stimulus appeared to ensure that eye movements were correctly tracked. A new calibration was performed at this stage if the eye drift exceeded 1° of visual angle.

After removing eye blinks and saccades using the algorithm developed by Nystrom et al. (Nyström and Holmqvist, 2010), observers' eye movement data from the Old-New task were processed to create individual fixation maps, independently for learning and recognition phase. For both phases we removed noisy trials suffering from loss of data and/or precision and for the recognition session we only considered trials where subjects provided a correct response. Previous studies have shown that

with this paradigm there are no differences in the sampling strategies used to sample WC or EA faces (Blais et al., 2008; Caldara, 2017). Therefore, in order to increase the signal-to-noise ratio, fixation maps were extracted independently of the stimulus race. After pre-processing the eye movement data, fixation maps were computed independently for each subject based on 54 and 60 trials for the learning and recognition phase respectively. These were the minimum number of trials available for all subjects. Individuals' fixation intensities (based on the cumulative fixation duration) were derived using these fixation maps and pre-defined circular regions of interest (ROIs; see Figure 3.1). The ROIs covered 1.8° of visual angle and were centered on the ten viewing positions fixated during the FPVS experiment.

Figure 3.1

Illustration of the regions of interest (ROI) surrounding the 10 viewing positions (VPs).



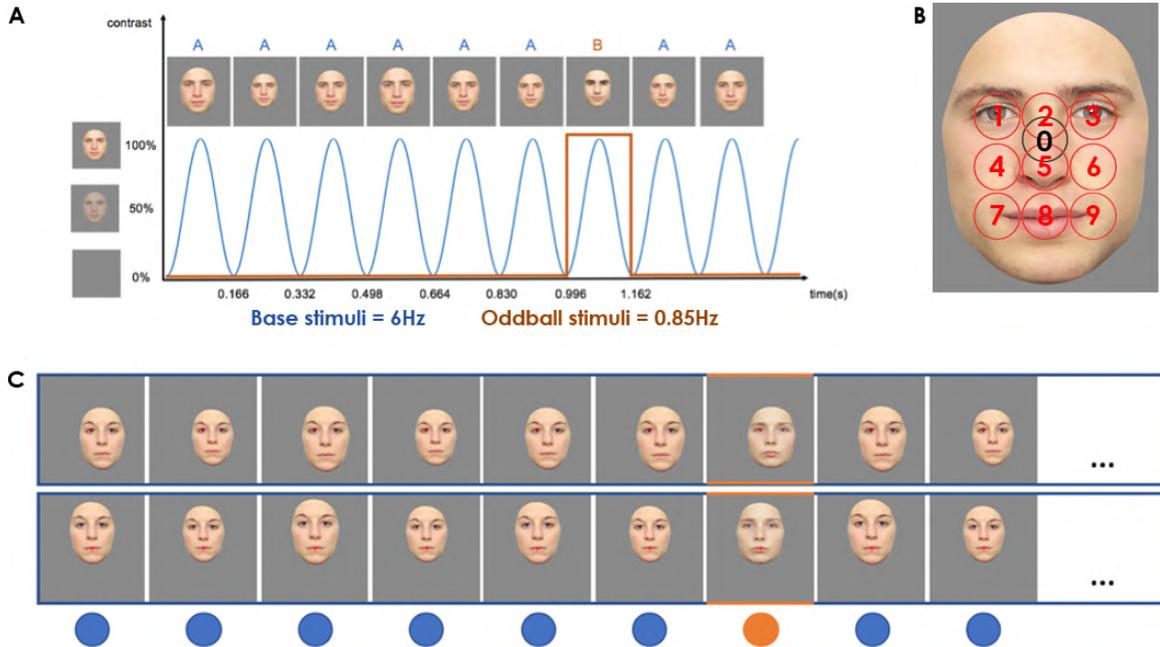
Note. Observers' fixation maps were overlaid onto a ROI mask to compute the fixation intensity per ROI. The ROI were covering 1.8° of visual angle and were centered on 9 equidistant viewing positions (red circles) and on an additional VP corresponding to the center of the stimulus (black circle).

3.4.2.2. EEG

Experimental design

We used full-front, color images of 50 identities (25 female) from the same set described previously (Liu-Shuang et al., 2014). All faces conveyed a neutral expression, were cropped to exclude external facial features, and were presented against a grey background. Each original stimulus subtended 11.02° (height) x 8.81° (width) of visual angle at a viewing distance of 70 cm.

Face-stimuli were displayed through the fast periodic visual stimulation (i.e., FPVS) paradigm at a constant frequency rate of 6 Hz. Each trial lasted 62s and consisted in presenting a series of same-identity faces (i.e., base), with intervening oddball identities every 7th base, hence at a frequency of 0.857 Hz (Figure 3.2A, C). The experiment comprised a total of 20 trials: ten conditions (the viewing positions participants were required to fixate on; Figure 3.2B, C), with two trials per condition (trials differed with respect to the gender of the face stimuli). To prevent eye-movements, participants were instructed to maintain fixation on a central cross. The position of face stimuli was manipulated to vary, across trials, the fixated viewing position, hence the facial information. Faces were presented through sinusoidal contrast modulation (see Figure 3.2A). Additionally, two seconds of gradual fade in and fade out were added at the beginning and end of each trial. To maintain subjects' attention, the fixation cross briefly (200ms) changed color (red to blue) randomly between seven and eight times within each trial; participants were instructed to report the color change by button press. Subjects were also monitored through a camera placed in front of them communicating the experimenter computer. No additional eye-tracking was performed during EEG acquisition, as these measures were considered as sufficient for the intended purposes. Finally, to avoid pixel-wise overlap, stimulus size varied randomly from 80% to 120% of the original size (visual angle ranged from 8.82 - 13.22° (height) to 7.05 - 10.57° (width)).

Figure 3.2*FPVS paradigm and viewing positions.*

Note. (A) Faces were presented at a frequency rate of 6Hz through sinusoidal contrast modulation. Base stimuli consisted of images of the same facial identity; interleaved oddball stimuli conveying different identities were presented every 7th base stimulus. (B) Illustration of the 10 viewing positions (VPs) fixated by participants. (C) Examples of two trials displaying fixation on the left eye (VP1, top row), or mouth (VP8, bottom row).

Data acquisition and processing

Electrophysiological responses were recorded with Biosemi Active-Two amplifier system (Biosemi, Amsterdam, Netherlands) with 128 Ag/AgCl active electrodes and a sampling rate of 1024Hz. Electrodes were relabeled according to the more conventional 10-20 system notation following the guidelines by Liu-Shuang et al. (2015). Additional electrodes placed at the outer canthi and below both eyes registered eye movements and blinks; the magnitude of the offset of all electrodes was reduced and maintained below $\pm 25\text{mV}$. The recorded EEG was analyzed using Letswave 5

(<https://github.com/NOCIONS/Letswave5>); (Mouraux and Iannetti, 2008)). The raw data are available in the public domain (Stacchi et al., 2018). Preprocessing consisted in high- and low-pass filtering the signal (with a 0.1Hz and 100Hz Butterworth band-pass filter (4th order)). Data were subsequently downsampled to 256Hz and segmented according to condition resulting in 20 66-second epochs, which included two seconds before and after stimulation. Independent component analysis was performed on each participant's data to remove contamination due to eye-movements and blinks.

Noisy electrodes were interpolated using the three nearest spatially neighboring channels; this process was applied to no more than 5% of all scalp electrodes. Segments were then re-referenced to a common average reference and cropped to an integer number of oddball cycles, excluding two seconds after stimulus onset and two seconds before stimulus offset (~58-second epochs; 14932 bins). Epochs were then averaged separately for each subject per condition.

Frequency domain

Fast Fourier Transform (FFT) was applied to the averaged segments and amplitude was extracted. The data were baseline corrected by subtracting from each frequency's amplitude the average of its surrounding 20 bins excluding the two neighboring ones. Finally, for each subject and condition, the summed baseline-corrected amplitude of the oddball frequency and its significant harmonics provided the index of neural face discrimination. Following previous procedures (Dzhelyova et al., 2016), harmonics were considered significant until the mean z-score across all conditions was no longer above 1.64 ($p < .05$). Based on this criterion we considered the first 11 harmonics excluding the 7th harmonic, which is confounded with the base stimulation frequency rate.

3.4.3. Statistical analyses

Using the iMAP4 toolbox (Lao et al., 2017) we computed a linear regression to explore the relationship between the fixation bias (the z-scored fixation duration) displayed during the recognition phase and neural face discrimination (i.e., the FPVS response amplitude). To this aim we performed a linear mixed-effects model with random effect for intercept and *Fixation duration* grouped by subject. To

avoid a-priori assumptions regarding topography of the effect, we regressed the two variables at all scalp electrodes independently and results were Bonferroni-corrected.

$$FPVS_amplitude \sim 1 + Fixation_duration + (1 + Fixation_duration / Subjects) \quad (1)$$

This computation will determine whether, VP-dependent fixation duration are associated with the amplitude of the neural face discrimination response elicited by each VP. Importantly, because the analysis takes into consideration idiosyncrasies, there is no a priori expectation on how VPs are ranked. We opted for this approach in light of individual differences in fixation patterns reported previously (Mehouard et al., 2014; Arizpe et al., 2016; Kanan et al., 2015), and similar idiosyncrasies assumed to exist for neural face discrimination responses across VPs. Therefore, the model used here allows each subject to have his/her specific VP-pattern and a relationship emerges if the fixation pattern is predictive of the neural response pattern of the same subject. Finally, as the current work does only focus on individual subjects, we did not perform any analysis involving average fixation maps and average EEG responses.

To determine whether fixation maps would show a stronger correlation with EEG responses of the same subject, we randomly sampled the fixation maps of our subjects in order to correlate eye movement from one observer with EEG response of another observer. On these new data we performed the same regression described above. This process was repeated a thousand times, and within each iteration we summed the significant F-values ($p < 0.5/128$). We then ranked the one thousand summed significant F-values and selected the 95th percentile as the threshold to assess statistical significance. Only if the summed significant F-values from the original analysis were above this simulated threshold, results were retained as being significant.

Additionally, although the main focus of this work was to isolate the relationship between eye movements during correct recognition of faces and neural face discrimination responses, in order to provide a comprehensive view of our data we also investigated whether such relationship would occur when considering fixation biases based on the (i) first or (ii) second face fixations in each trial.

Moreover, we also performed the same analysis by considering the eye movements of the learning phase. We thus investigated the potential existence of such relationship between eye movements and neural face discrimination for (i) all fixations, (ii) the first or (iii) the second only for the learning and recognition phases.

3.5. Results

3.5.1. Behavior

As expected, subjects' recognition performance in the Old-New task, as indexed by d' , was significantly better for Western Caucasian ($M=1.62$, $SD=.64$) than East Asian faces ($M=0.97$, $SD=.60$), $t(16)=5.72$, $p<.01$. Subjects' performance was nearly at ceiling for the FPVS orthogonal task ($M=.91$, $SD=.18$). Note that a color change was considered as detected if observers reported it within 700ms from its onset. Due to technical issues, one subject's behavioral responses were not recorded.

3.5.2. Eye-movements and FPVS response

Description of fixation and neural biases at the group and individual level

Table 3.1 summarizes the number of fixations and the similarity between fixation maps during learning and recognition sessions (indexed by the cosine distance, with a distance of zero indicating identical fixation maps). The average fixation map (computed for descriptive purposes and shown in Figure 3.3A) demonstrates that, *as a group*, observers preferentially sampled facial information encompassing the eyes, nasion, nose and mouth. However, because the focus of this work was to investigate the relationship between fixation patterns and neural responses at the individual level, group data were not subject to any further analysis.

Table 3.1*Number of fixations and fixation maps' similarity between learning and recognition session.*

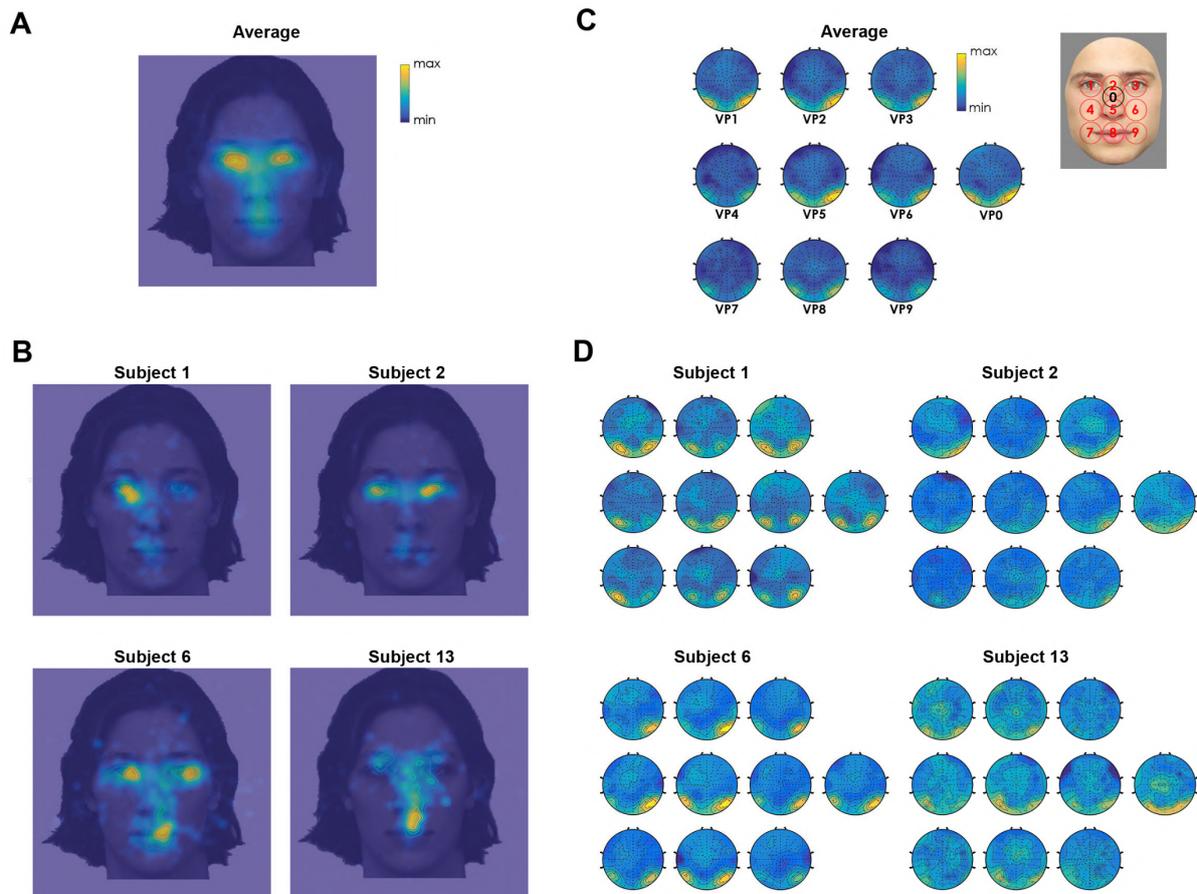
	Average number of fixations (SD)		Cosine distance between learning and recognition fixation maps		
	Learning	Recognition	All fixations	1st fixation	2nd fixation
S1	13.0 (3.6)	3.4 (1.2)	.19	.12	.11
S2	15.6 (2.0)	5.2 (2.0)	.22	.08	.07
S3	15.4 (3.6)	4.5 (2.7)	.28	.09	.07
S4	10.0 (2.7)	5.7 (3.2)	.23	.07	.21
S5	13.9 (2.2)	6.8 (3.8)	.14	.09	.08
S6	17.7 (1.4)	8.4 (4.4)	.22	.05	.06
S7	11.2 (1.9)	3.6 (2.3)	.16	.20	.14
S8	16.1 (1.6)	4.8 (3.1)	.09	.10	.10
S9	13.9 (3.0)	2.2 (0.9)	.62	.09	.08
S10	14.6 (2.6)	3.4 (1.9)	.32	.16	.18
S11	17.0 (1.8)	6.4 (3.0)	.16	.06	.12
S12	16.8 (1.6)	6.8 (4.7)	.18	.03	.13
S13	13.1 (4.0)	3.0 (0.9)	.32	.11	.15
S14	13.9 (4.1)	2.7 (1.6)	.28	.05	.27
S15	11.7 (2.0)	4.0 (1.7)	.06	.03	.14
S16	10.9 (2.7)	4.7 (2.3)	.23	.08	.17
S17	16.0 (3.0)	7.4 (4.5)	.33	.04	.04

At the individual level, the majority of individual observers' fixation maps did not *perfectly* conform to the grand average fixation pattern (Figure 3.3A, B; Figure 3.4), clearly demonstrating the existence of idiosyncratic visual sampling strategies. Mirroring these results, the grand average neural face discrimination response amplitudes varied as a function of VPs, with the greatest amplitudes for

the central position (Figure 3.3C). However, the neural responses amplitudes also markedly differed across individuals (Figure 3.3D; Figure 3.4).

Figure 3.3

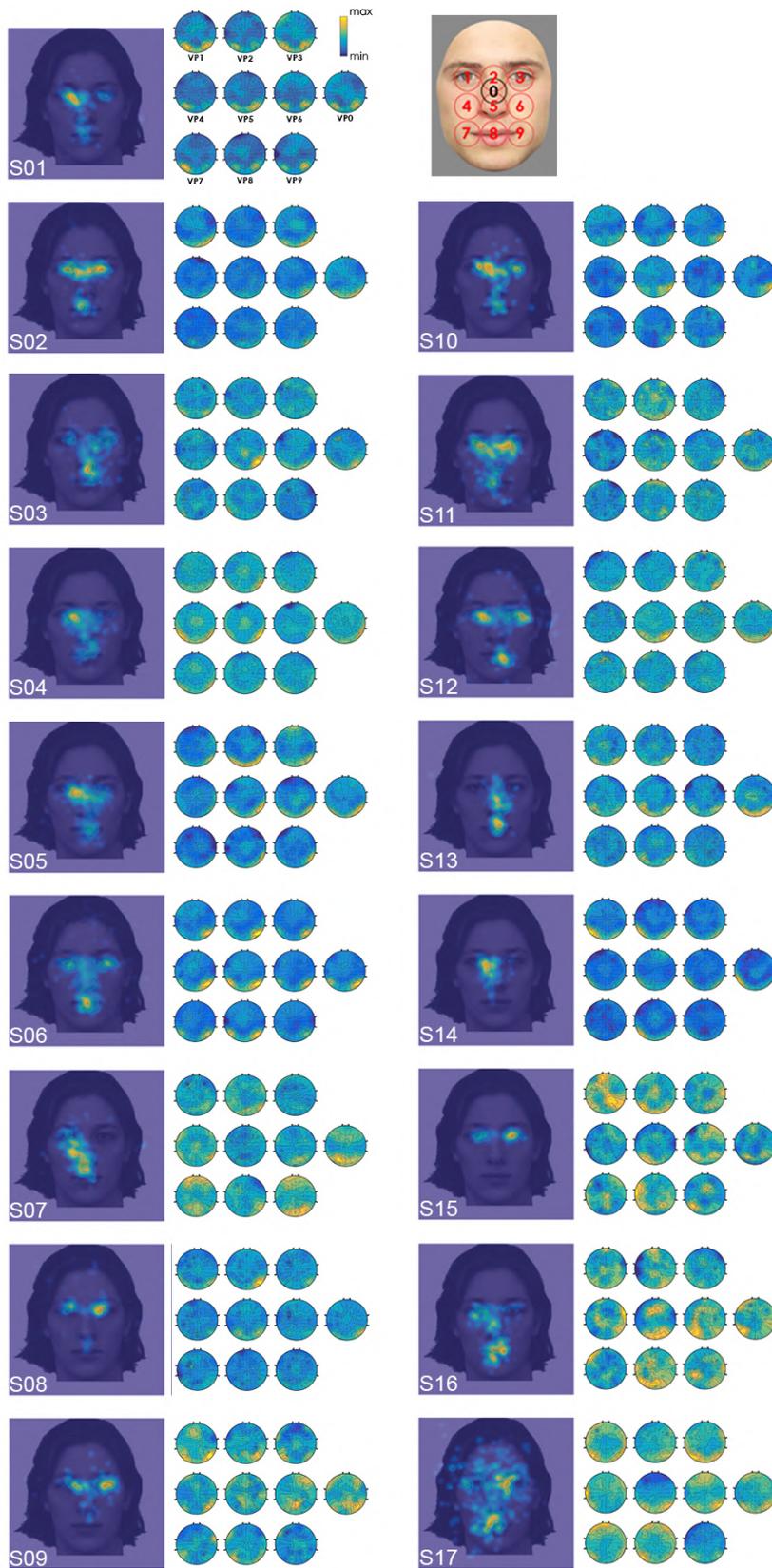
Fixation maps and oddball responses.



Note. A and C show the grand-average fixation map and FPVS responses respectively, while B and D show the two measures for the same subjects. For illustration, only four subjects are reported.

Figure 3.4

Fixation maps for the recognition session and neural face discrimination responses



Regression analysis: Assessing the relationship between fixation and neural biases

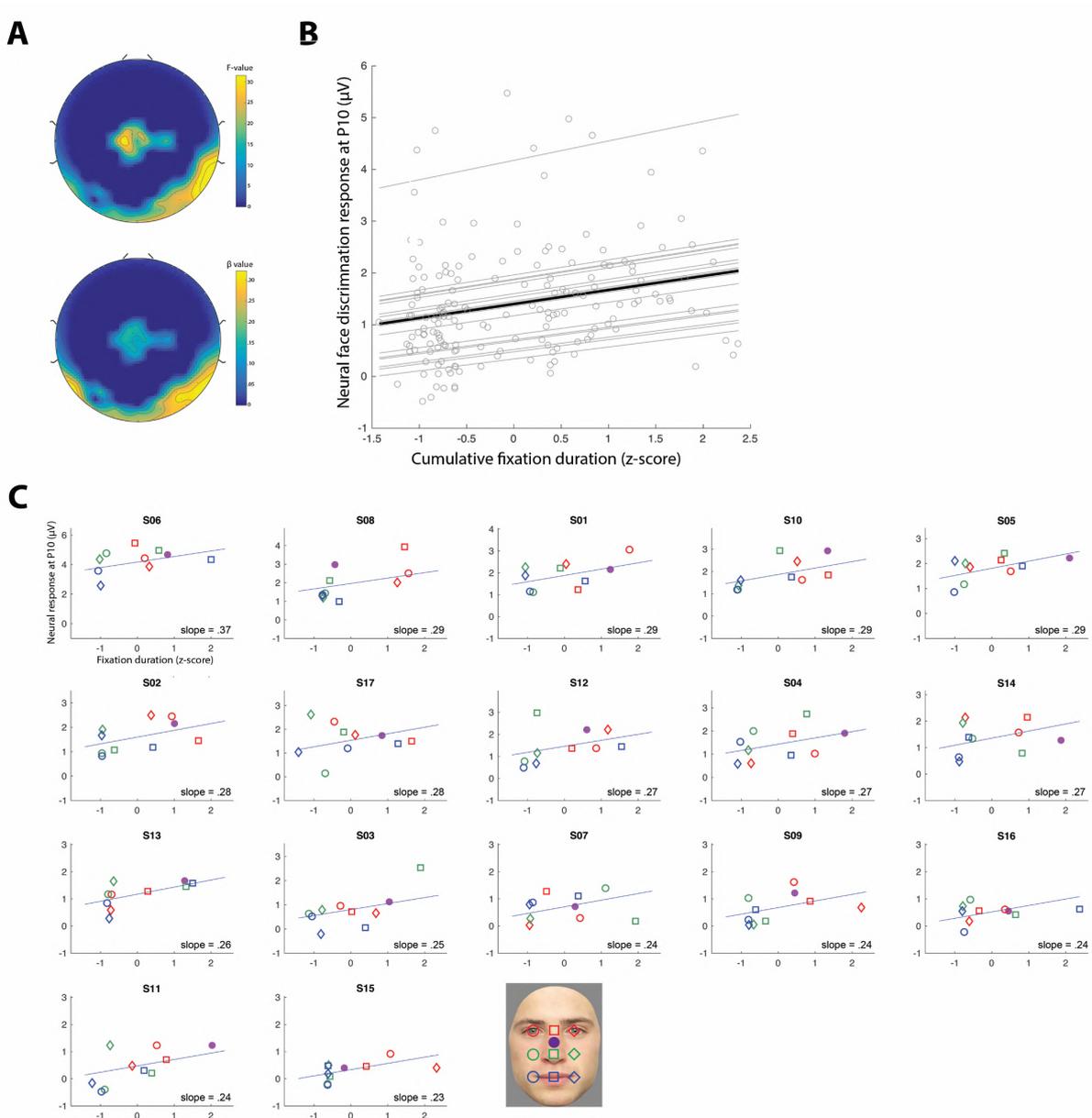
The data-driven regression between individuals' fixation durations and FPVS responses across VPs computed independently on all electrodes revealed a positive relationship at right occipito-temporal and central-parietal clusters (see Figure 3.5A).

The occipito-temporal cluster includes 12 significant electrodes with the strongest effect at P10 ($F(1,169)=32.91$, $\beta=.27$ [.17 .36], $p=4.40e-08$) and the smallest at P9 ($F(1,169)=13.26$ $\beta=.20$ [.09 .31], $p=3.61e-04$) (Table 3.2). Despite inter-individual variations in the neural face discrimination response amplitude and fixation durations, we observed a positive relationship for *all* observers (Figure 3.5B, C).

An effect was also found on the central-parietal cluster comprising 13 electrodes, with C1 showing the strongest effect ($F(1,169)=33.05$ $\beta=.14$ [.09 .19], $p=4.14e-08$) and FCz exhibiting the smallest effect ($F(1,169)=15.41$ $\beta=.12$ [.06 .18], $p=1.26e-4$) (Figure 3.5A; Table 3.2).

Figure 3.5

The relationship between fixation duration and neural face discrimination responses across VPs observed across all subjects considered individually.



Note. (A) Regression F-values (left) and beta maps (right) are shown only for electrodes exhibiting a significant effect ($p < 3.91e-04$) (B) Scatterplot illustrates individual subjects' (light grey lines) as well as the group (black line) effect at electrode P10. (C) Zoom in into B. Each subject is plotted along with their individual correlation (blue line). VPs are color- and shape-coded as indicated in the legend. The subjects are ordered as a function of their relationship magnitude (slope). Although observers exhibited idiosyncratic VP-dependent fixation durations (see also individuals' fixation maps in the following Figure 3.7), all showed a positive relationship, with facial features fixated longer (i.e., VPs) eliciting stronger neural responses. Note that here the neural face discrimination response magnitude is displayed at the occipito-temporal electrode showing the largest effect (i.e., P10).

Table 3.2.*Results for fixation-dependent regression analyses (for the recognition session).*

all fixations			1st fixation			2nd fixation		
	F values	β -values		F values	β -values		F values	β -values
Occipito-temporal cluster			Occipito-temporal cluster			Occipito-temporal cluster		
P10	32.91	.27	P10	33.21	.27	P10	24.48	.24
PO10	28.54	.29	I2	28.90	.26	PO10	23.15	.27
I2	27.82	.25	PO12	25.92	.27	Iz	22.43	.21
PO8	24.99	.26	PO10	25.76	.28	I2	20.05	.22
Iz	24.71	.22	POI2	24.43	.22	I1	17.78	.20
O2	24.23	.21	Iz	23.79	.21	PO8	17.17	.22
PO12	23.90	.26	I1	22.45	.22	PO11	17.08	.20
TP8	21.95	.12	PO11	17.92	.23	PO12	16.82	.22
POI2	20.15	.21	O2	17.32	.18	O2	16.16	.18
I1	19.60	.21	POI1	16.70	.18	POI2	16.02	.19
P8	18.05	.17	Oiz	15.87	.18	POI1	15.94	.17
POI1	17.57	.19	PO8	14.08	.23	P9	13.99	.20
PO11	14.75	.20	P8	13.60	.19	Oiz	13.32	.16
Oiz	14.04	.17	PPO6	13.31	.15			
PO7	13.99	.17						
PPO6	13.75	.14						
P9	13.26	.20						

all fixations			1st fixation			2nd fixation		
Centro-parietal cluster			Centro-parietal cluster			Centro-parietal cluster		
	F values	β -values		F values	β -values		F values	β -values
C1	33.05	0.14	C1	22.49	0.11	FCC2h	25.49	0.13
C1h	29.70	0.14	FCC1	18.12	0.11	C1	23.89	0.13
FCC2h	26.15	0.13	FCC1h	17.86	0.12	C1h	22.12	0.12
FCC1	24.92	0.14	C1h	16.93	0.10	FCC1	21.69	0.13
FCC1h	23.35	0.14	FCC2h	16.60	0.10	FCC1h	19.77	0.13
C2h	23.12	0.13	CCP1h	15.74	0.10	C2h	19.66	0.12
CCP1h	23.07	0.11	CPz	15.43	0.11	FCz	17.47	0.13
CCPz	19.44	0.13	C2h	15.29	0.10	C4h	16.59	0.09
Cz	17.44	0.12	CCPz	14.39	0.10	CCPz	15.49	0.11
C4	17.00	0.10	FC5h	14.16	0.10	Cz	15.46	0.11
C4h	16.87	0.09	FFC3h	13.80	0.11	FCC2	14.21	0.10
C3h	16.57	0.09				CPz	13.86	0.10
CPz	15.64	0.11				C2	13.85	0.10
FCz	15.42	0.12				CCP1h	13.48	0.08
C2	14.97	0.10				FCC2h	13.37	0.09
Pvalue range: 4.1e-08-3.6e-04			Pvalue range: 3.9e-08-3.5e-04			Pvalue range: 1.1e-06 – 3.5e-04		
Summed F-values		670.9	Summed F-values		474.07	Summed F-values		500.79
Simulated threshold		536.32	Simulated threshold		345.67	Simulated threshold		310.82

Note. Reported here are significant (Bonferroni corrected) electrodes for each fixation-dependent analysis (ranked by F-values). For each analysis we report summed F-values and the simulated threshold determined through the random iterations (see Analysis).

Finally, in order to determine whether fixation maps would correlate better with EEG responses of the same subject, we run simulations of the same analyses when EEG responses were correlated with fixation maps of different observers. In each iteration we summed the significant F-value and the 95th percentile of this distribution constituted our simulated threshold (see Data analyses). The sum of significant F-values (670.89) obtained using the original data exceeded the simulated threshold determined (536.32), and was therefore significant (Table 3.2). Significant results were also obtained for analyses carried out on the *first* (summed F-values = 474.07, simulated threshold = 345.67) and the *second* fixation (summed F-values = 500.79, simulated threshold = 310.82) (Figure 3.6B; Table 3.2). The results of the same analyses performed on data acquired during the learning session were significant only for the first fixation (summed F-values = 447.33, simulated threshold = 315.06) (Figure 3.6A; Table 3.3).

Table 3.3

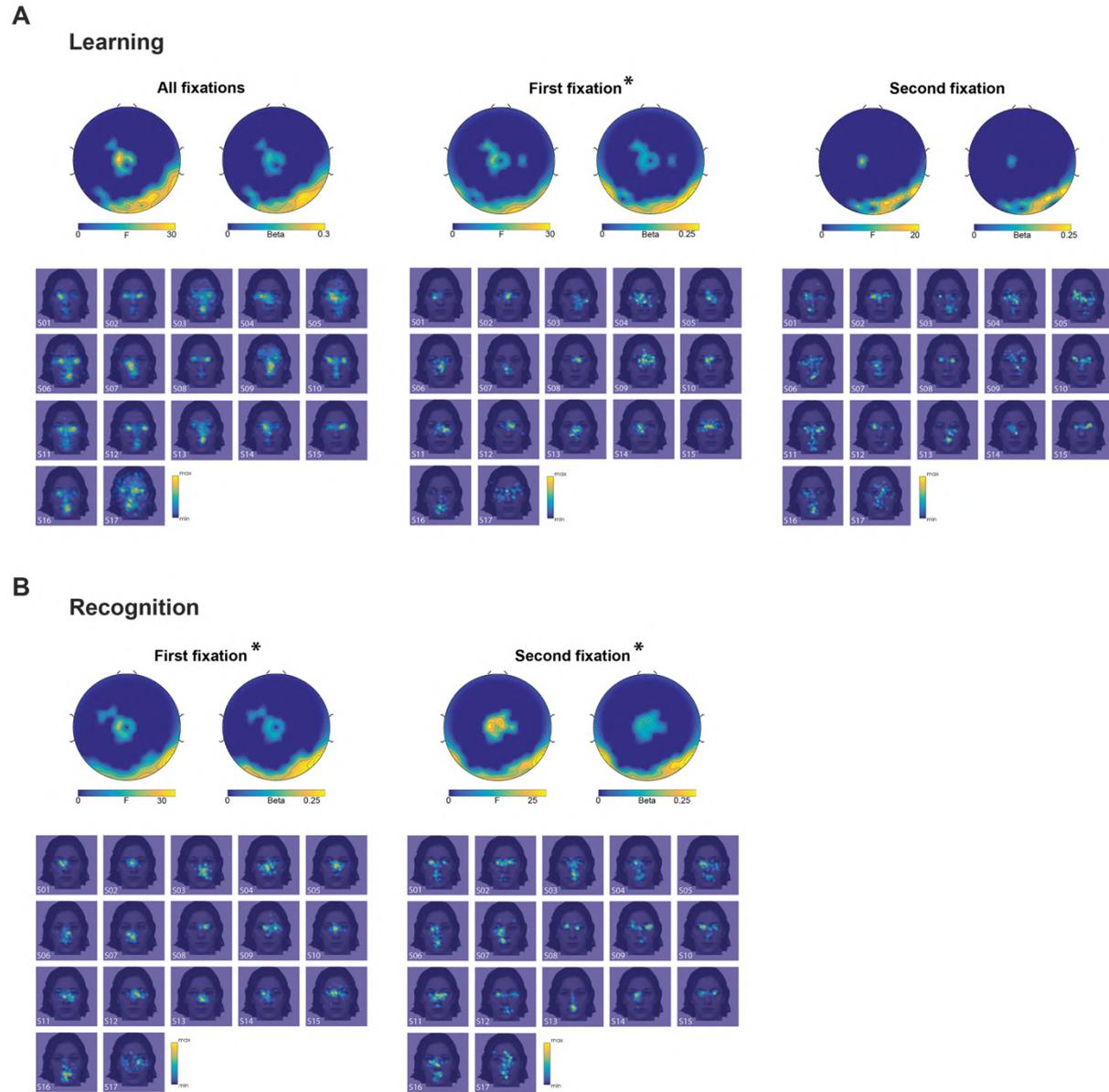
Results for fixation-dependent regression analyses (for the learning session).

all fixations			1st fixation			2nd fixation		
	F values	β -values		F values	β -values		F values	β -values
Occipito-temporal cluster			Occipito-temporal cluster			Occipito-temporal cluster		
O2	29.65	0.22	I2	31.97	0.27	O2	20.00	0.19
I2	29.41	0.26	POI2	24.44	0.22	PO10	17.79	0.24
PO8	28.32	0.28	Iz	24.13	0.21	O1	17.69	0.19
PO10	27.82	0.29	PO12	22.02	0.25	P10	17.57	0.22
Iz	26.91	0.22	I1	20.55	0.21	I2	17.23	0.21
P10	23.25	0.23	PO10	18.55	0.26	Oz	17.13	0.15
Oz	22.00	0.18	POI1	18.03	0.19	POI2	15.51	0.19
POI1	21.38	0.20	Oiz	17.85	0.18	PO8	14.60	0.21
PO12	21.37	0.25	PO11	17.32	0.22	POI1	14.22	0.17
POI2	19.82	0.21	P10	16.41	0.23			
P9	18.22	0.10	O2	16.21	0.17			
Oiz	17.77	0.18	Oz	15.17	0.16			
I1	17.02	0.20	PO7	13.92	0.16			
TP8	15.78	0.10	P9	13.80	0.20			
P8	15.33	0.16						
PPO6	15.16	0.15						
PO7	13.36	0.16						
Centro-parietal cluster			Centro-parietal cluster			Centro-parietal cluster		
C1	26.53	0.13	C1	20.22	0.11	C1	18.01	0.11
FCC1	23.18	0.13	FFC3h	19.63	0.13			
FCC5h	22.21	0.12	FCC1h	18.24	0.12			
FCC1h	20.12	0.13	FCC1	17.06	0.11			
C2h	19.25	0.12	CCP1h	15.72	0.09			
FCC2h	17.69	0.11	C2h	15.03	0.10			
CPz	14.85	0.11	FCC2h	14.90	0.10			
Cz	14.30	0.11	CCPz	14.21	0.10			
FFC3h	13.67	0.11	C1h	14.17	0.10			
			FFC1	14.01	0.10			
			C4	13.77	0.08			
Pvalue range: 1.8e-07 - 3.4e-04			Pvalue range: 6.6e-08 - 2.8e-04			Pvalue range: 1.4e-05 - 2.2e-04		
Summed F-values		534.39	Summed F-values		447.33	Summed F-values		169.73
Simulated threshold		534.96	Simulated threshold		315.06	Simulated threshold		447.35

Note. Reported here are significant (Bonferroni corrected) electrodes for each fixation-dependent analysis (ranked by F-values). For each analysis we report summed F-values and the simulated threshold determined through the random iterations (see Analysis).

Figure 3.6

Results of the analyses performed using the fixation bias computed based on the learning (A) or recognition (B) data.



Note. For the learning session, analyses are reported for all, only the first or second fixation. For the recognition session, analyses are reported for only the first or second fixation. F- and beta-values are reported only electrodes showing a significant ($p < 7.81e-05$) are shown. Below each topography of the effect are the fixation maps of all observers.

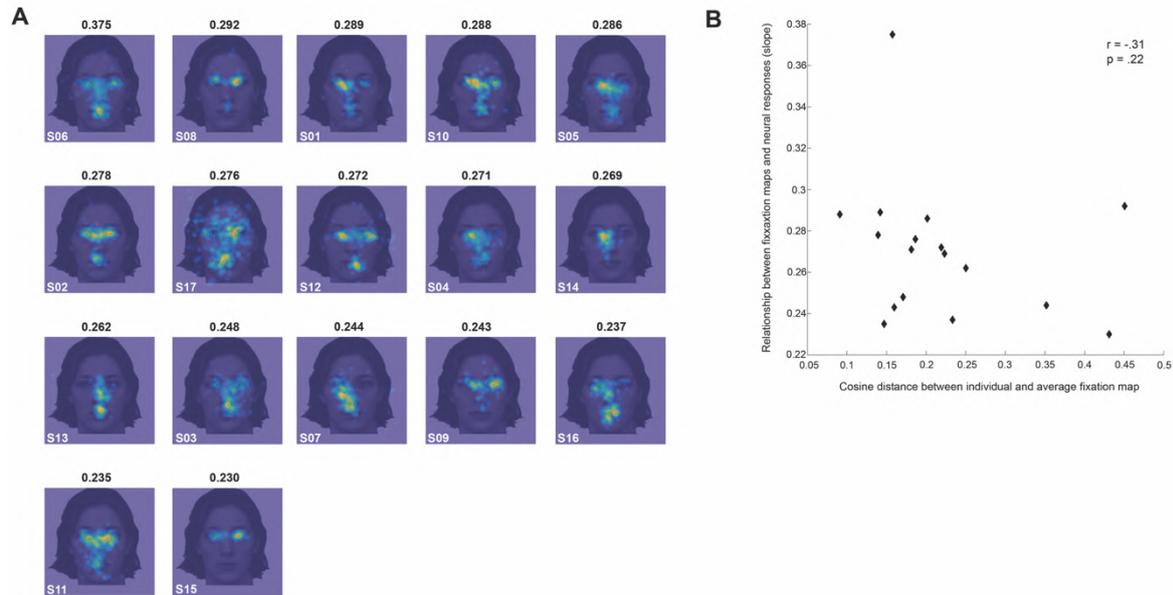
* indicates which effect was significant at the simulated threshold.

Can Specific Fixation Biases Account For The Observed Relationship?

To explore whether subjects exhibiting a particular fixation bias during recognition (e.g., for the eyes) would show a stronger relationship between fixation and neural biases, we first ranked observers' fixation maps based on the magnitude of their individual relationship. As shown in Figure 3.7A, subjects showing similar fixation patterns could exhibit relationships of slightly different magnitude (e.g., nasion: S04 and S05), while observers exhibiting different fixation maps could rank closely in terms of relationship strengths (e.g., S11 and S16). Additionally, we computed the distance of each observer's fixation map from the average fixation pattern. In this case, each map is treated as a vector and the measure of interest is the cosine distance between each observers' map and the average one (a distance of zero indicates identical fixation maps). This produces a value ranging between 0 and 1 for each subject. The higher the distance the more dissimilar that given subject's pattern is from the average. Finally, we performed a Spearman correlation between this distance and the strength of the relationship between fixation and neural bias, which resulted to be non-significant ($r=-.31$, $p=.22$) (Figure 3.7B).

Figure 3.7

Fixation maps and strength of the fixation-neural-bias relationship.



Note. (A) Observers' fixation maps sorted as a function of the slope of observers' relationship between fixation bias and neural face discrimination response amplitude. The slope is reported for the occipito-temporal electrode showing the strongest effect (i.e., P10). (B) The scatterplot illustrates the lack of correlation between: the cosine distance of individuals' fixation maps from the average fixation map (y-axis) and strength of the relationship between fixation and neural bias (x-axis). Data show there was not a particular fixation bias more likely to correlate with the neural bias. Note that a cosine distance of 0 indicates identical fixation maps.

3.6. Discussion

This study investigated the relationship between *idiosyncratic* visual sampling strategies for faces and the magnitude of neural face discrimination responses during fixation on different facial locations. Our data show that visual information sampling is distinct across observers, and these differences are positively correlated with *idiosyncratic* neural responses predominantly at occipito-temporal electrodes. Specifically, the Viewing Positions (VPs) that elicited stronger neural face discrimination responses coincided with the VPs that were more fixated under free-viewing conditions. Altogether, our data show that face processing involves idiosyncratic coupling of *distinct* information sampling strategies and *unique* neural responses to the preferentially sampled facial information.

For many years, the accepted notion in vision research was that face processing elicits a unique and universal cascade of perceptual and cognitive events to process facial identity, with particular importance ascribed to information conveyed by the eye region. For instance, eye movement studies have revealed a bias towards sampling of the eye region (Blais et al., 2008), the diagnosticity of which has been further documented by psychophysical approaches (e.g., Bubbles) (Gosselin and Schyns, 2001). Electrophysiological studies have also reported increased N170 magnitude during fixation on the eyes, compared to other information (de Lissa et al., 2014; Nemrodov et al., 2014). Collectively, these independent findings were taken to support the existence of a fixation and neural preference for the eye-region that is shared across *all* observers.

However, this idea has recently been challenged. For example, findings from eye movement studies emphasize idiosyncrasies in sampling preferences that are highly distinct from the group-average T-shaped pattern (Mehouard et al., 2014; Arizpe et al., 2017), or by the existence of cultural differences (Blais et al., 2008; Caldara, 2017). These individual differences are not systematically associated with performance, as “mouth lookers” (i.e., observers showing preferential fixation on the mouth) could perform similarly to “eyes lookers”. Equally, two “eyes lookers” could exhibit very different performance (Peterson and Eckstein, 2013). Nonetheless, each observer’s adopted sampling strategy is

optimal in the sense that performance is maximal when fixation is enforced on preferably sampled information, and decreases during fixation of other information (Peterson and Eckstein, 2013). These results suggest that individual differences do not reflect random inter-subject variation, but rather subtend functional idiosyncrasies in face processing.

Our results replicate and extend these previous findings, by showing that idiosyncratic visual sampling strategies strikingly mirror individuals' patterns of neural face discrimination responses across VPs. Specifically, the facial regions preferentially sampled during natural viewing were those eliciting stronger neural face discrimination responses when fixated. This pattern was present in all observers, with even some of them showing a perfect match between the most fixated facial feature and the one eliciting the strongest neural response at the electrode showing the strongest statistical relationship.

Interestingly, such relationship emerged also when fixation bias was computed only based on the first or the second fixation. This observation suggests that from very early information intake fixations are directed towards observer-specific preferred face information. Moreover, it also indicates that idiosyncratic fixation strategies emerge as early as the first fixation on faces.

When considering single fixations performed during face learning, a significant relationship emerged only on the first one. The reduced sensitivity of the learning phase compared to the recognition phase, might be due to the imposed time duration (i.e., 5 seconds) to process faces during this part of the experiment. This long time period introduces an inherent variability in information sampling. In the recognition session, however, observers are required to recognize faces as quickly and as accurately as possible, eliciting a restricted number of diagnostic fixations (Table 3.1) during a short period of time (i.e., $M = 1457.3$, $SD = 421.3$). However, it is worth noting that overall observers deployed similar fixations across both sessions (Table 3.1), a result that reinforces the idea of a reliable occurrence of idiosyncratic eye movement strategies over (a long period of) time (Mehouard et al., 2014) for the face recognition task.

The effect we find could be partially related to an overall preference toward facial features, such as the eyes and mouth or the center of the face (i.e., T-shaped pattern). However, significantly weaker effects are observed when correlating fixation maps and neural response derived from different individuals. These observations clearly demonstrate the existence of a tight coupling between idiosyncratic fixation biases and neural responses, instead of a general tuning for facial features per se.

The strong and striking relationship between information sampling and neural idiosyncrasies suggests a functionally relevant process. Eye movements feed the neural face system with the diagnostic information in order to optimize information processing. The eyes constantly move to center elements of interest in the fovea, where visual acuity is greatest. This critical functional role, coupled with the relationship reported here between idiosyncratic sampling strategies and the neural face discrimination response pattern thus leads to two main considerations. First, our data show that face identity processing involves a fine-tuned interplay between oculomotor mechanisms and face-sensitive neural network. Second, the diagnosticity associated with different facial information varies across observers. For a long time, researchers have debated on the nature of face representations, mainly opposing the idea of faces being represented as indivisible wholes (holistic or configural), as opposed to a collection of multiple, distinctively perceivable features (featural). This ongoing debate cannot be settled based on our finding of visual and neural idiosyncrasies. These idiosyncrasies do, however, refute the concept of a *single* face representation format shared across observers.

Our observations raise further important methodological and theoretical questions. The first concerns the traditional approach of standardizing the visual input to allow comparability across observers. The idiosyncratic differences in facial location tuning call into question the appropriateness of using a single visual stimulation location. Specifically, the conventional central presentation used in the majority of face processing studies might inherently create a perceptual bias that favors some but not all observers, which exhibit differential neural responses for this fixation location (and others). Additional open questions concern for instance (a) the extent to which the relationship between the visual sampling strategies and neural response patterns is *task-* and *category-*specific, and (b) the direction of this

relationship. Future studies are required to accurately determine the neural structures underlying the observed relationship (for example, by means of fMRI). Finally, our approach may offer a promising novel route in clinical settings, if disorders comprising face processing impairments (i.e., prosopagnosia, autism, schizophrenia, etc.) involved an abnormal relationship between fixation patterns and neural responses to faces.

CHAPTER 4

RELIABILITY OF INDIVIDUAL DIFFERENCES IN NEURAL FACE IDENTITY DISCRIMINATION

Stacchi, L., Liu-Shuang, J., Ramon, M., & Caldara, R. (2019). Reliability of individual differences in neural face identity discrimination. *NeuroImage*, *189*, 468-475

4.1. Abstract

Over the past years, much interest has been devoted to understanding how individuals differ in their ability to process face identity. Fast periodic visual stimulation (FPVS) is a promising technique to obtain objective and highly sensitive neural correlates of face processing across various populations, from infants to neuropsychological patients. Here we use FPVS to investigate how neural face identity discrimination varies in amplitude and topography across observers. To ascertain more detailed inter-individual differences, we parametrically manipulated the visual input fixated by observers across ten viewing positions (VPs). Specifically, we determined the *inter-session reliability* of VP-dependent neural face discrimination responses both across and *within* observers (6-month inter-session interval). All observers exhibited idiosyncratic VP-dependent neural response patterns, with reliable individual differences in terms of response amplitude for the majority of VPs. Importantly, the topographical reliability varied across VPs and observers, the majority of which exhibited reliable responses only for specific VPs. Crucially, this topographical reliability was positively correlated with the response magnitude over occipito-temporal regions: observers with stronger responses also displayed more reliable response topographies. Our data extend previous findings of idiosyncrasies in visuo-perceptual processing. They highlight the need to consider intra-individual neural response reliability, in order to better understand the functional role(s) and underlying basis of such inter-individual differences.

Keywords: Individual differences, face discrimination, reliability, viewing positions, FPVS-EEG

4.2. Introduction

Faces convey an abundance of information and our ability to process them efficiently is crucial for social interactions. This continues to motivate a large and growing area of research dedicated to unraveling the principles governing human face cognition. The majority of studies have sought to identify *commonalities* across neurotypical observers. Consequently, individual differences have long been considered as noise, the influence of which should be minimized by averaging. Studies employing such group statistics across a range of methodologies have identified the eye region as a highly diagnostic source of information during processing of facial identity: it receives the most fixations (Yarbus, 1967; Henderson et al., 2005) in Western observers (e.g., Blais et al, 2008; for a review see Caldara, 2017), is behaviorally relevant (Schyns et al., 2002), and elicits stronger neural face-sensitive responses (Nemrodov et al., 2014; de Lissa et al., 2014).

However, an increasing number of studies indicates that group-average results are not necessarily representative of the population (Arizpe et al., 2017). Adding to inter-individual variability on the behavioral level (e.g., Wilhelm et al., 2010; Herzmann et al., 2010; Kaltwasser et al., 2014), recent findings emphasize the importance of idiosyncratic visual sampling strategies. Specifically, fixation patterns exhibited by individual observers suggest reliable preferences in sampling different facial information (Mehoudar et al., 2014; Kanan et al., 2015; Peterson & Eckstein, 2013; see also Walker-Smith et al., 1977).

Efforts have also been made to characterize the neural correlates of individual differences in perceptual abilities. For instance, these studies have shown that subjects' electrophysiological face-sensitive event-related potentials (ERPs) differ in terms of both amplitude and latency (Gaspar et al., 2011; Herzmann et al., 2010; Kaltwasser et al., 2014; Das et al., 2010; see also Turano et al., 2016 for sub-group analyses). Inter-individual variation has also been reported for neural face discrimination responses obtained using a different approach: fast periodic visual stimulation (FPVS). FPVS relies on the brain's tendency to synchronize to the frequency of external stimulation. This is exploited to derive

a neural measure of a process of interest, such as face discrimination. Face discrimination has been successfully measured with FPVS in an oddball paradigm, where a sequence of same-identity base stimuli are presented at a constant high frequency rate, with periodically intervening oddball stimuli conveying different identities (e.g., A-A-A-A-A-A-B-A-A-A-A-A-A-C-...). Neural synchronization to the oddball frequency (the frequency of identity change) provides an implicit, objective and highly sensitive measure of neural face discrimination that has been used in healthy and neuropsychological cohorts (Liu-Shuang et al., 2016; Liu-Shuang et al., 2014; Norcia et al., 2015).

Using this paradigm Xu et al. (2017) was the first to report pronounced individual differences in terms of both the amplitude and topography of this neural face discrimination response. Beyond this, the authors reported small but significant correlations with behavioral performance, suggesting that the magnitude of this neural response is at least partially driven by face identity processing abilities. Although their findings further emphasize the functional importance of neural idiosyncrasies, two important questions remain unanswered.

The first question concerns the impact of facial information fixated. Normally, in the context of neuroimaging studies observers are required to fixate a point on or near the center of the face (Liu-Shuang et al., 2014, Xu et al., 2017). Standardizing the visual input is a commonplace procedure in pursuit of comparable stimulus-related responses. The aforementioned functional individual differences in visual sampling strategies, however, suggest that the *diagnosticity* of visual information differs across observers. If such observer-dependent preferences for specific facial information or viewing positions (VPs) also existed on the neural level, standardizing the input through enforced fixation on one only VP would be problematic. Specifically, recording the response during fixation of a central VP (e.g., the nose) might accurately represent observers who prefer encoding face-stimuli at this VP, but may misrepresent those who prefer other facial information (e.g., the left eye). To clarify this issue, in our FPVS paradigm we presented whole-face stimuli under enforced fixation to ten different VPs.

Such potential individual differences in VP-preference are directly related to the second open question: To which degree do idiosyncratic FPVS face identity discrimination responses reflect genuine, intrinsic inter-individual differences, as opposed to situational noise. One way to assess this is to determine whether the idiosyncratic face discrimination responses reoccur systematically over time. Noise is a random factor, which therefore impacts a measure of interest differently across recordings. Conversely, intrinsic characteristics of a given subject are more stable (Seghier & Price, 2018). As a consequence, their influence on a given response should systematically reoccur over time. Thus, quantifying test-retest reliability across a range of VPs provides a detailed mean to estimate the impact of nuisance factors on the signal(s) of interest.

To this date, the reliability of face discrimination responses obtained by FPVS has only been investigated across trials acquired within the same testing session and a single VP (Xu et al., 2017). The authors reported the inter-trial stability of the group amplitude obtained by averaging multiple bilateral electrodes. However, their report provided no information regarding the topographical reliability. Additionally, the investigated within-session reliability of trials spaced in the scale of minutes does not address the issue of reliability across longer temporal intervals.

In the present study, we sought to determine the reliability of the face discrimination responses (as measured with the FPVS paradigm) across two acquisition sessions separated by a 6-month inter-session interval. Aiming for a comprehensive understanding of individual differences in the face discrimination response, we computed reliability on three different aspects of the response. First, we addressed the reliability of the neural information-dependent response patterns observed across VPs. Second, we determined the reliability of the response amplitude independently for each VP, to assess the consistency of the response strength of individual observers. Third and finally, we computed each observer's VP-specific topographical reliability.

Collectively, our analyses aim to provide a comprehensive characterization of individual differences in neural face discrimination measured with the FPVS paradigm. We believe that this is a

crucial prerequisite for studies aiming to deploy this paradigm for empirical and clinical purposes, and to establish its functional significance in both healthy and impaired populations (Liu-Shuang et al., 2016; Xu et al., 2017).

4.3. Methods

4.3.1. Participants

We tested fourteen adults (seven females, one left-handed; mean age: 24.5 ± 3.8 years) with normal or corrected-to-normal vision and no history of psychiatric or neurological disorders. Participants were either undergraduate students from the University of Fribourg, or acquaintances of the experimenters. All subjects provided written informed consent and received financial compensation for participation. The experiment was approved by the local ethics committee.

4.3.2. Procedure

Stimuli and procedure

Stimulus material and procedures were identical to those previously reported (Liu-Shuang et al., 2014; Stacchi et al., 2019a²). Stimuli comprised full-front, colored images of 50 face identities (25 females) displaying neutral expressions. Images were cropped to exclude external facial features and were embedded in a grey background. Stimuli were presented on a VIEWPixx/3D monitor (1920x1080 pixel resolution, 120Hz refresh rate) and subtended an average of 11.02° (height) x 8.81° (width) of visual angle at a viewing distance of 70cm. In each 62s trial, face images were shown through sinusoidal contrast modulation at a frequency of 6 Hz, with image size varying randomly between 80-120% at each cycle to minimize pixel overlap (visual angle ranged between 8.82 - 13.22° (height) and 7.05 - 10.57° (width)). A randomly selected face identity (base stimulus) was repeated throughout the sequence, with different face identities (oddball stimuli) interleaved every 7th face (i.e., $6 \text{ Hz}/7 = 0.85 \text{ Hz}$; Figure 4.1A). Each trial began and ended with 2s during which maximal image contrast progressively ramped up (fade

² This citation refers to CHAPTER 3 of this thesis.

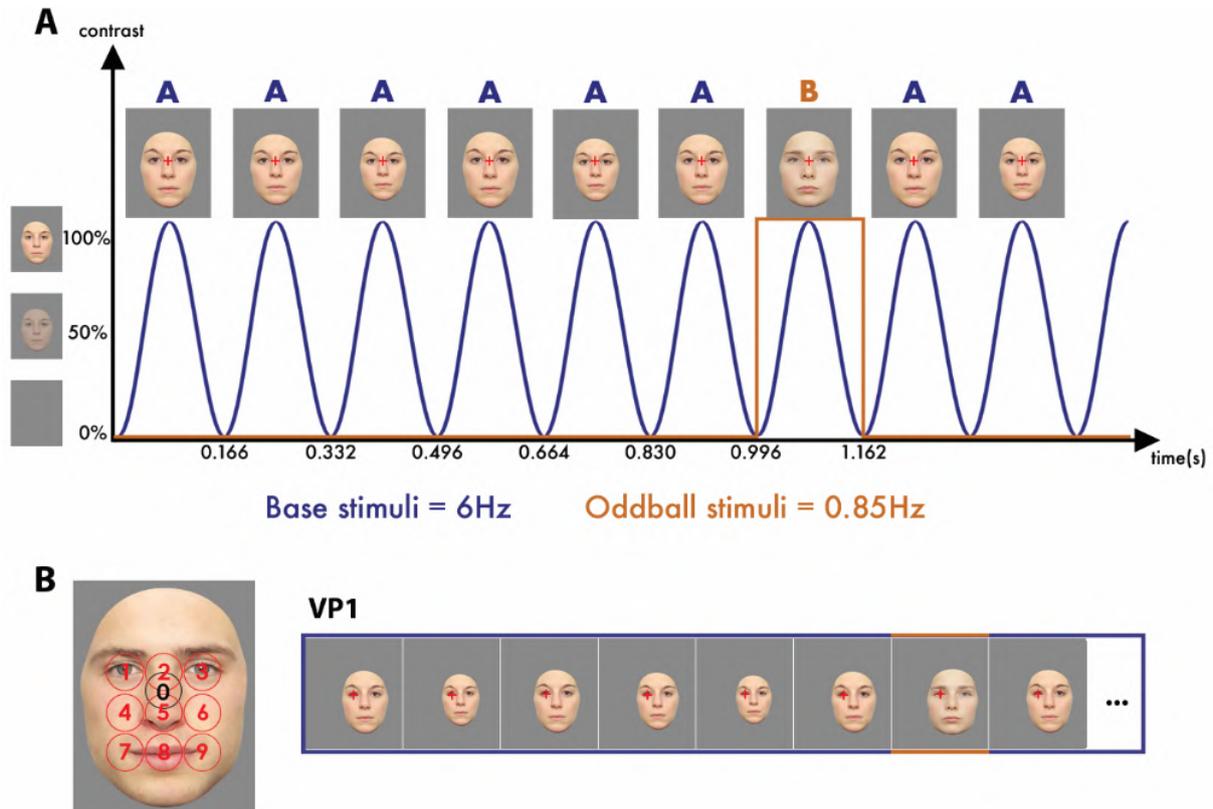
in) and down (fade out), respectively. Observers were instructed to fixate a cross in the center of the screen while responding via button press to a brief (200ms) change in the color of the fixation cross, which occurred randomly eight times within each trial. This served to ensure maintenance of fixation, and a constant level of attention. Subjects were accurate at this task (0.93 ± 0.1). Performance of one subject (S14) could not be computed during the first session due to technical issues.

We manipulated the viewing position (VP) by spatially arranging the stimuli in order to have one of ten facial regions behind the central fixation cross (Figure 4.1B). Thus, these ten conditions differed in terms of the information being fixated by the observers throughout a trial. Note that VP0 was located slightly below the nasion, at what has been reported to be the “optimal” fixation position for face identity processing at the group level (Hsaio & Cottrell, 2008). Each observer completed 20 trials (two repetitions per VP condition) during an initial acquisition session, and 20 trials during a second acquisition session 6-months later. Generally, each session comprised two runs of ten trials each. However, subjects were allowed to ask for breaks whenever they felt the need.

The same settings and procedure were used during these two sessions, stimuli were taken from the same database and subjects' behavior was monitored through a webcam located inside the booth. In total, we obtained 40 trials (4 repetitions x 10 conditions) for each observer.

Figure 4.1

Schematic illustration of the FPVS paradigm and the experimental conditions.



Note. (A) Faces were presented through sinusoidal contrast modulation. Base stimuli displayed the same facial identity and appeared at a frequency of 6Hz. Different identity (oddball) faces were interleaved every 7th stimulus. Displayed here are stimuli presented at VP2. (B) In each condition faces were aligned in order to have one of the ten viewing positions (VPs) in the center of the screen and fixated by the subject (see right for an example).

EEG acquisition

Electrophysiological data were acquired through the Biosemi ActiView software with a Biosemi Active-Two amplifier system recording from 128 Ag/AgCl active electrodes at a sampling rate of 1024Hz. Four electrodes located at the outer canthi and below the eyes were placed for blink monitoring. In this active electrode system, the quality of electrode contact with the skin was evaluated by the offset relative to the magnitude of the feedback loop formed by the CMS-DRL electrodes, which was held

below ± 25 mV throughout the recording. During data acquisition a 0.16-100Hz filter was applied to remove any slow drifting over time. Digital triggers were sent at the start and end of each stimulation sequence by the VIEWPixx screen to the acquisition computer.

4.3.3. Analysis

Preprocessing. EEG data were processed with Letswave 5 (Mouraux & Iannetti, 2008). Continuous data were first digitally bandpass filtered to exclude frequency below 0.1Hz and above 100Hz (4th order Butterworth filter). The signal was then downsampled to 256Hz and segmented relative to each condition. For each observer, we extracted 20 x 66s epochs, which included 2 extra seconds pre- and post-stimulation. An independent component analysis using a square mixing matrix algorithm was computed to filter our noise related to blinks expressed by each subject (one single component was selected based on its topography and the correspondence between its temporal waveform and that of the ocular channels). Data were then visually inspected for interpolation of noisy electrodes (max. 5% of all scalp electrodes per observer were replaced through linear interpolation of the 3 surrounding electrodes). Data were then re-referenced to a common average reference and cropped to an integer number of oddball's cycles starting 2 seconds after stimulation onset and ending 2 seconds before stimulation offset (= 14932 bins).

Frequency domain analysis. The amplitude of EEG responses in the frequency-domain was extracted using the Matlab's built-in Fast Fourier Transform (FFT) function. Baseline-correction was applied to all of the resulting amplitude spectra by subtracting from each frequency bin the average of its surrounding 20 bins excluding the 2 immediately neighboring bins. For visualization purposes, we also converted the raw amplitude values into signal-to-noise ratio (SNR) by dividing each frequency bin by the average of its surrounding 20 bins excluding the 2 immediately neighboring bins. We average the resulting signal over 24 occipito-temporal electrodes (A9-A16, A22-A29, B6-B11, D31-D32; cf., Figure 4.2A) to include channels sensitive to both the general and the face discrimination response. Since the periodic neural response to our stimulation is spread over multiple harmonics (Figure 4.2) (i.e., integers

multiples of the stimulation frequency), we first determined the relevant range of frequency harmonics to take into account, independently for base and oddball frequencies. To this end, we z-scored the signal after averaging across conditions, subjects, and electrodes (Z-scores were computed following the same logic as the baseline-correction). Harmonics were considered as significant until the z-scores of two consecutive harmonics failed to exceed 1.64 ($p < .05$, one-tailed). Significant responses at the oddball frequency (0.85 Hz) and its harmonics reflect face identity discrimination, while responses at the base frequency (6 Hz) represent a combination of face-related processing and general visual responses to the stimulus presentation. Based on this threshold the oddball response, which indexes implicit neural face discrimination, was quantified by summing the first nine oddball harmonics (i.e., 0.85 to 7.71 Hz), excluding the 7th harmonic since it is confounded with the base stimulation frequency rate. The base response was significant until the ninth harmonic (i.e., 6 to 54 Hz). However, since we were mainly interested in the face identity processing and not in the general visual response, we only considered the fundamental base frequency (i.e., 6 Hz) and our analysis aimed to be a sanity-check for our experimental manipulation of fixated visual input.

Statistical analysis

Reliability of individual differences in VP-dependent patterns of response amplitude at the oddball frequencies. To assess whether the patterns of response amplitude across VPs were stable across the two sessions, we carried out a regression between the two measures. We averaged trials from the same session and then regressed the face discrimination responses of session one (*AmplitudeSession1*) onto those of session two (*AmplitudeSession2*), using *Subject* as a random effect to account for individual differences (1). To avoid any a priori assumption regarding the topography of the effect, we performed

the analysis for each scalp electrode independently and applied and Holm-Bonferroni-correction to account for multiple-comparisons.

$$AmplitudeSession1 \sim AmplitudeSession2 + (1|Subject) \quad (1)$$

Reliability of inter-individual differences in face discrimination response amplitudes. To investigate whether inter-individual variations in response amplitude were stable over time, we computed their reliability using Chronbach's alpha coefficient. This measure, which has been used previously in a similar context (Xu et al., 2017), evaluates the similarity of responses across measurements. We computed Chronbach's alpha across four trials, for each VP and electrode independently. High reliability indicates that observers, who exhibit strong responses at one time point are more consistent across different trials and sessions. Conforming with standard practice, we chose a coefficient threshold of .8, which indicates that responses are biased by 20% by noise, while the remaining 80% represents the measure of interest (Nunnally, 1973). In addition to single-electrode analyses, to account for the variability across observers in the oddball response topography, we pooled 12 bilateral occipito-temporal electrodes and recomputed the reliability at each VP.

Reliability of individual face discrimination response topographies. To determine the stability of the scalp distribution of the response over time, topographical reliability was computed by means of Chronbach's alpha for each observer, at each VP independently. Signals that were subject to analysis were taken from posterior electrodes (cf., Figure 4.6A), which included typically responsive channel in the context of neural face discrimination. Compared to amplitude computation, here we opted to consider a larger ROI in order to determine whether initially responsive clusters would be stable or change (expand, shift, or decrease) over time. High reliability of this posterior ROI would indicate that the electrodes showing stronger responses and forming responsive clusters, are the same across time. Conversely, low reliability would suggest that the response predominantly emerges at different electrodes at different time-points. This would finally lead to different responsive clusters over time.

Face discrimination response amplitude and topographical reliability. We investigated the relationship between the topographical reliability (across 44 individual channels) and magnitude (average of a 12-channel ROI) of the face discrimination response using Holm-Bonferroni corrected Spearman correlations for each VP independently.

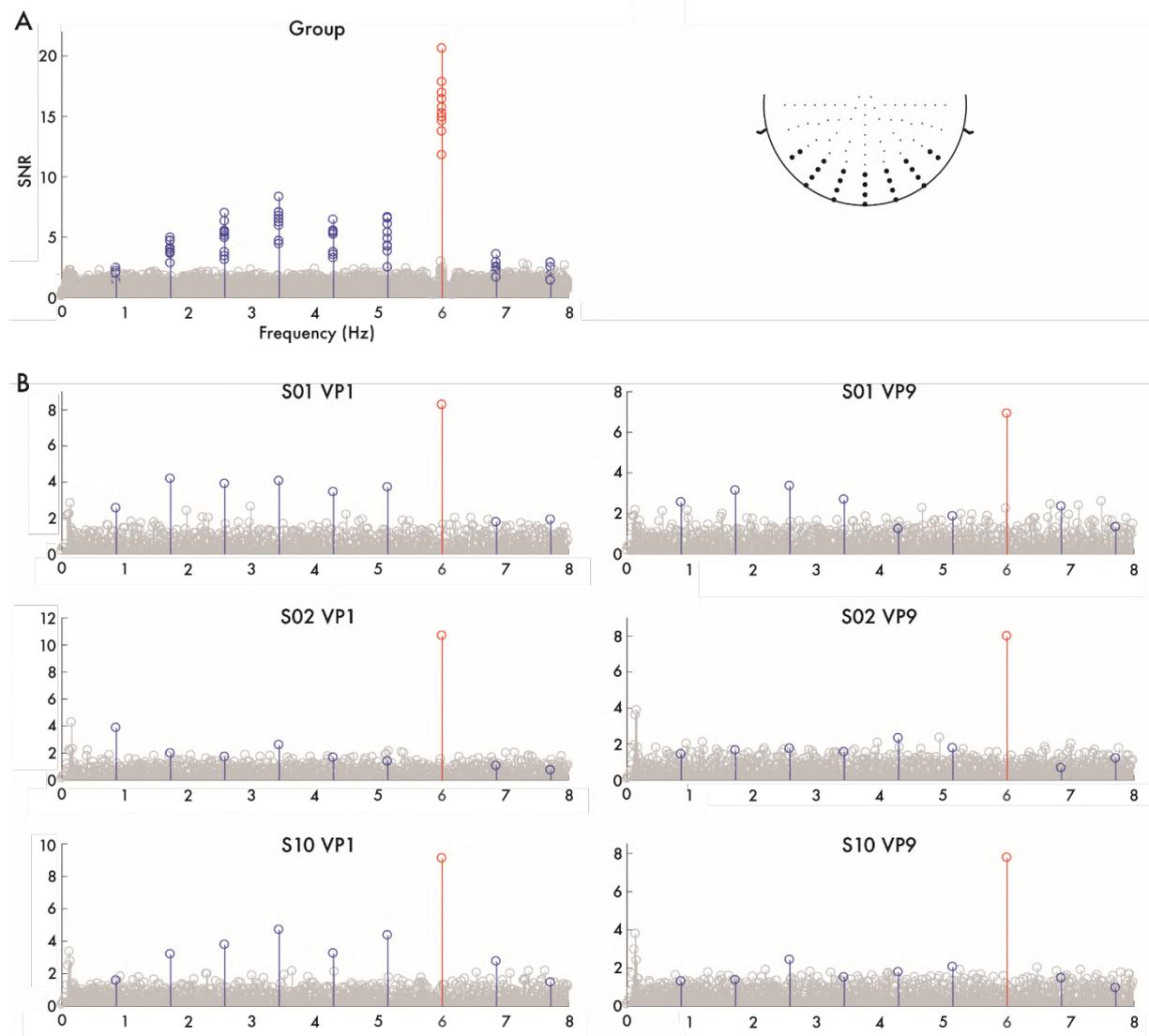
4.4. Results

Base frequency: General visual response

A response at the base frequency (6 Hz) indicates successful synchronization of the visual system to the contrast between background and face-stimuli (Dzhelyova et al., 2017; see Figure 4.2). At the group level this general visual response was expressed predominantly at occipito-temporal electrodes (Figure 4.3). Conditions involving fixations on the left or right side of the face led to the majority of facial information being represented on the opposite visual field, and a shift of the response to the contralateral hemisphere. For example, fixation on the left eye (Figure 4.3; VP1) led to most facial information being presented in the right visual field, which elicited strongest responses in the left hemisphere. Overall, averaging across 15 occipito-temporal electrodes (A10-A15, A23-A28, B7-B9) led to strongest general visual responses for VP2 (i.e., nasion VP; 1.05 μ V), followed by VP0 (i.e., “optimal”, 1.04 μ V). Given this study’s focus on the FPVS face *discrimination identity* response, the general visual responses expressed at the base frequency are not considered for further analyses.

Figure 4.2

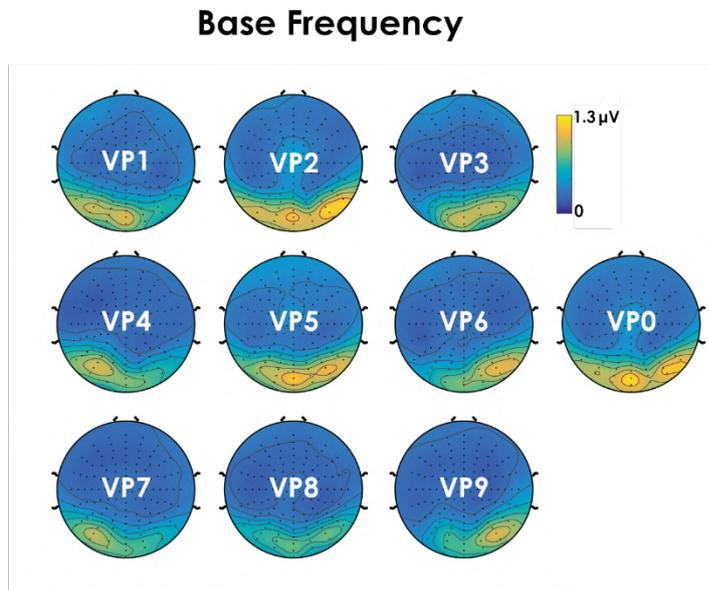
Frequency spectra.



Note. (A) SNR spectrum averaged across 24 posterior electrodes (right) and all subjects, with all VP conditions overlapping (each dot represents the response magnitude for a VP condition). Orange peaks indicate the general visual response while blue peaks index the face identity discrimination response. (B) SNR spectrum averaged across the same 24 electrodes in three exemplary subjects for two VPs. Note that an SNR of 1 represents noise level.

Figure 4.3

Response topography for the neural response at the base frequency.



Oddball frequency: Face discrimination response

Significant responses at the oddball frequency (i.e. 0.85 Hz = rate of face identity change) and its harmonics at occipito-temporal electrodes were found in all participants, and indicate successful neural face discrimination (Figure 4.2B for three exemplary subjects) (Liu-Shuang et al., 2014). Here, we manipulated facial information fixated to determine the effect on subjects' neural face discrimination response, both in terms of amplitude and topography, and compare the inter-, and intra-individual differences across a time-interval of 6 months to estimate their reliability.

VP-modulation of the face discrimination response. We averaged the baseline-corrected signal from 4 trials to assess the effect of VP on the amplitude of the face discrimination response. In line with previous work (Liu-Shuang et al., 2016; Xu et al., 2017), this response was generally expressed at occipito-temporal electrodes (Figure 4.4; Supplementary Figure 4.8). Therefore, we quantified the neural face discrimination responses within a single bilateral occipito-temporal region-of-interest (ROI) comprising

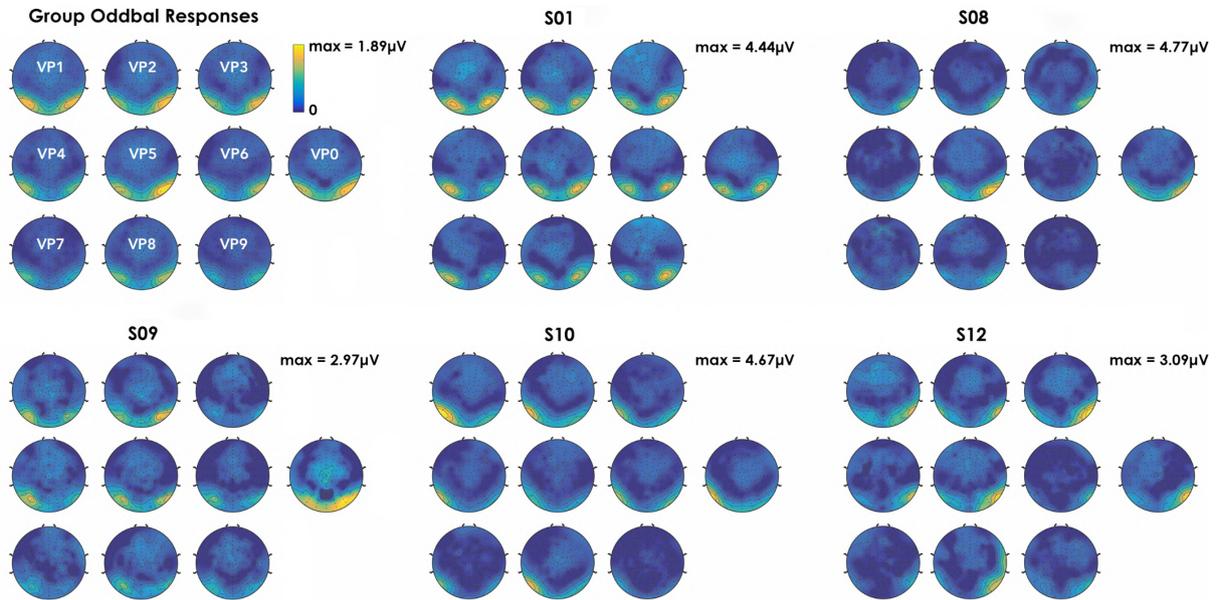
12 electrodes (D31, D32, A9-A12, B6-B11) across which responses were averaged. This was done both at the group level (on the grand-average signal) and at the individual level.

At the group level, the face discrimination response amplitude was strongest for fixation at VP5 (i.e., nose; $1.33\mu\text{V}$), followed by VP1 (i.e., left eye; $1.32\mu\text{V}$) and VP0 (i.e., nasion; $1.25\mu\text{V}$) (Figure 4.4; for group and individual subject values see Supplementary Table 4.1). However, at the individual level, we observed strong inter-individual differences in the observer-specific response patterns, which deviated from the group level observation (Figure 4.4; Supplementary Figure 4.8). Contrarily to the group, VP1 elicited the overall strongest response across observers (i.e., left eye, 4 subjects), followed by VP5 (i.e., nose, 3 subjects) (cf. Supplementary Table 4.1 for all values).

Mirroring these observations, individual observers' response topographies differed from the group topography. On average the response was right-lateralized for the majority of the VPs. At the individual level, however, patterns were more heterogeneous and oddball responses could be located at right-, left-, or bilateral occipito-temporal electrodes (Figure 4.4).

Figure 4.4

Neural face discrimination responses.

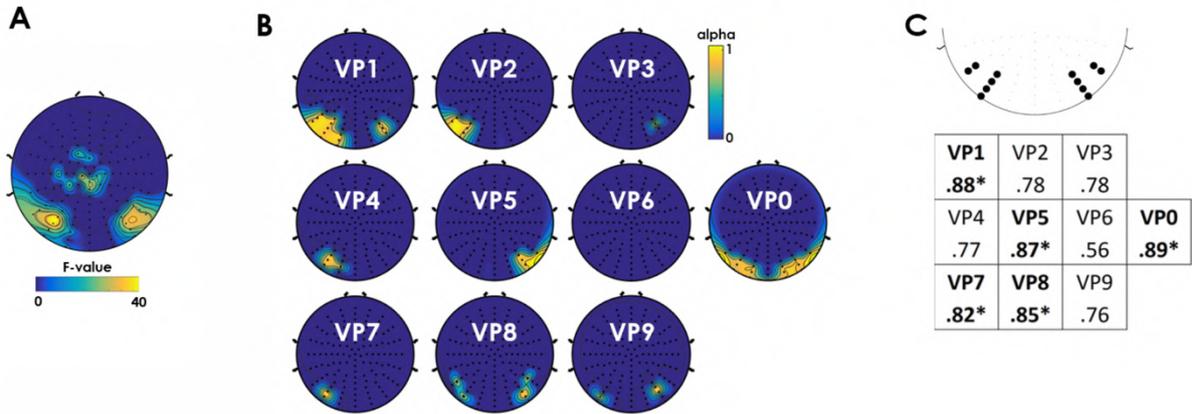


Note. Face discrimination responses (quantified as the summed baseline-corrected amplitudes at oddball frequencies) are shown at the group-level and for five example subjects across the ten VP conditions. Though globally responses occur consistently over occipito-temporal channels, variation in response amplitude and topography are visible between and within subjects.

Reliability of individual differences in VP-dependent patterns of response amplitude at the oddball frequencies. To determine whether patterns of response amplitude across VPs observed at the first session would be predictive of those recorded 6 months later we computed a linear regression between the two measures at each electrode independently. This analysis revealed a positive relationship at bilateral occipito-temporal clusters (Figure 4.5A). The effect ranged between .39 (A10; $p < .001$) and .52 (A28; $p < .001$).

Figure 4.5

Reliability of the VP-patterns and FPVS response amplitude.



Note. (A) Data-driven regression results. F-values of non-significant electrodes were set to 0. VP-patterns were most stable at occipito-temporal electrodes. (B) Reliability of response amplitude across subjects is shown for each condition and each electrode respectively. Alpha values below the .8 threshold were set to 0 for visualization purposes. (C) Reliability of response amplitude computed across 12 occipito-temporal electrodes (top) for each VP.

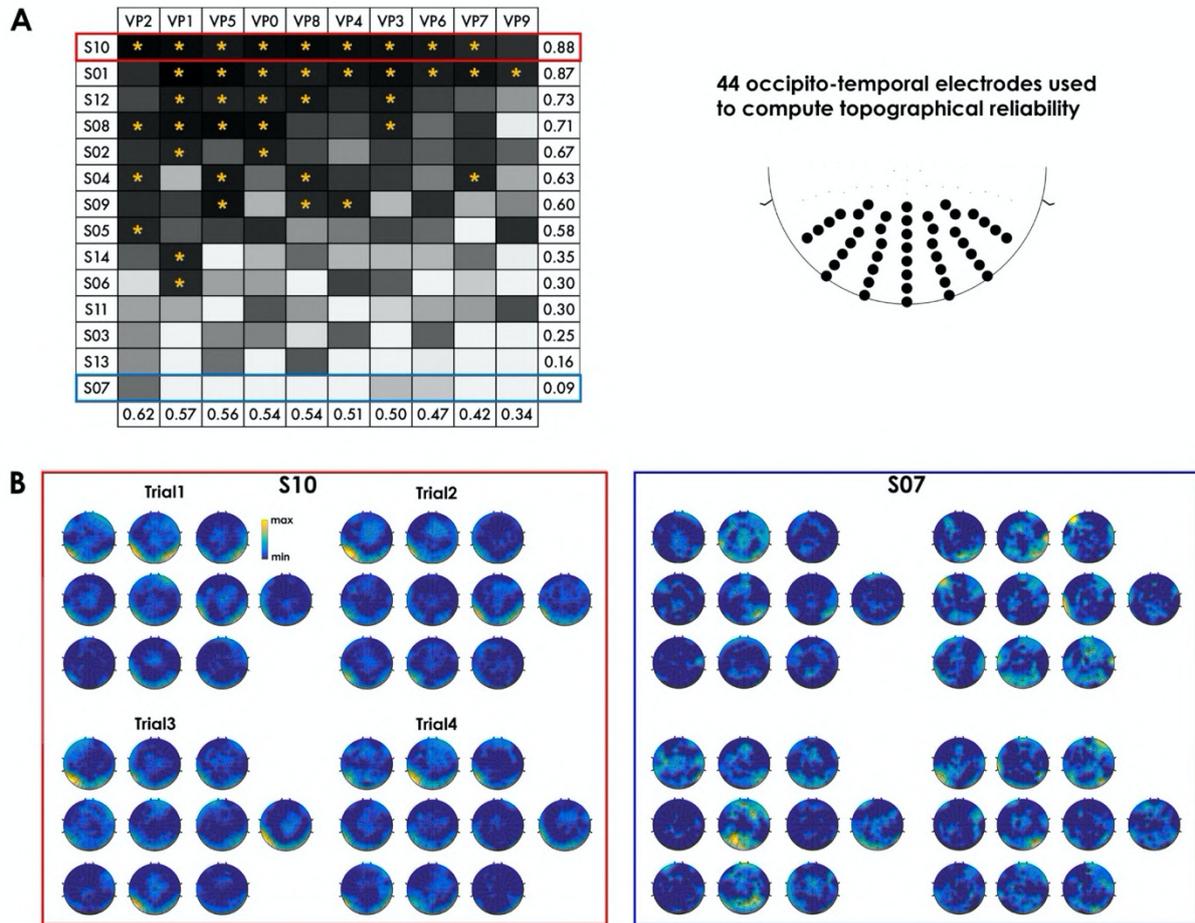
Reliability of inter-individual differences in face discrimination response amplitudes. Cronbach's alpha was computed across four trials for each VP and electrode independently to assess the reliability of inter-individual differences in amplitude. The results show that most reliable responses were located at occipito-temporal electrodes. All VPs, with the exception of VP6 (right cheek), elicited reliable responses at at least one channel (Figure 4.5B). Overall, VP0 was the condition with the largest cluster of reliable electrodes. When averaging 12 bilateral occipito-temporal electrodes, reliability ranged between .89 (VP0) and .56 (VP6) (Figure 4.5C). Contrarily to analysis on single electrodes, here only five VP out of the 10 elicited reliable responses in the selected ROI. Interestingly, these five VPs all involved fixating the midline or the left side of the face.

Reliability of individual face discrimination response topographies. We have shown that the response patterns across VPs and the response amplitude within each VP were both reliable over a 6-month interval at the group level for our observers. To better understand potential individual differences in response reliability (i.e., are all observers equally reliable in their response topography? Is each subject equally reliable across different VPs?), we computed topographical reliability within each observer and for each VP independently.

Response consistency varied across VPs and observers. Across VPs, the average reliability pooled across all observers ranged between .62 (VP2; i.e., nasion) and .34 (VP9; i.e., right corner of the mouth). Across observers, the averaged alpha values from all VPs ranged between .88 (S10) and .09 (S07) (Figure 4.6A). Across VPs and the entire cohort, the majority of observers (10/14) showed a reliable response topography for at least one VP. Two observers showed high topographical reliability for nearly all VPs (9/10 VPs), while eight exhibited reliable response topographies for only certain VPs (cf., S10 and S09, see Figure 4.6). The remaining observers did not show any reliable responses between sessions (e.g., S07, see Figure 4.6A).

Figure 4.6

Topographical reliability of the FPVS response.



Note. (A) Individual topographical reliability computed across 44 occipito-temporal electrodes for each subject and VP. The color scale ranged between $\alpha = 0$ (white) and 1 (black). Asterisks indicate $\alpha \geq 0.8$. (B) VP-dependent FPVS responses for the most (left) and least (right) reliable subject across all four trials.

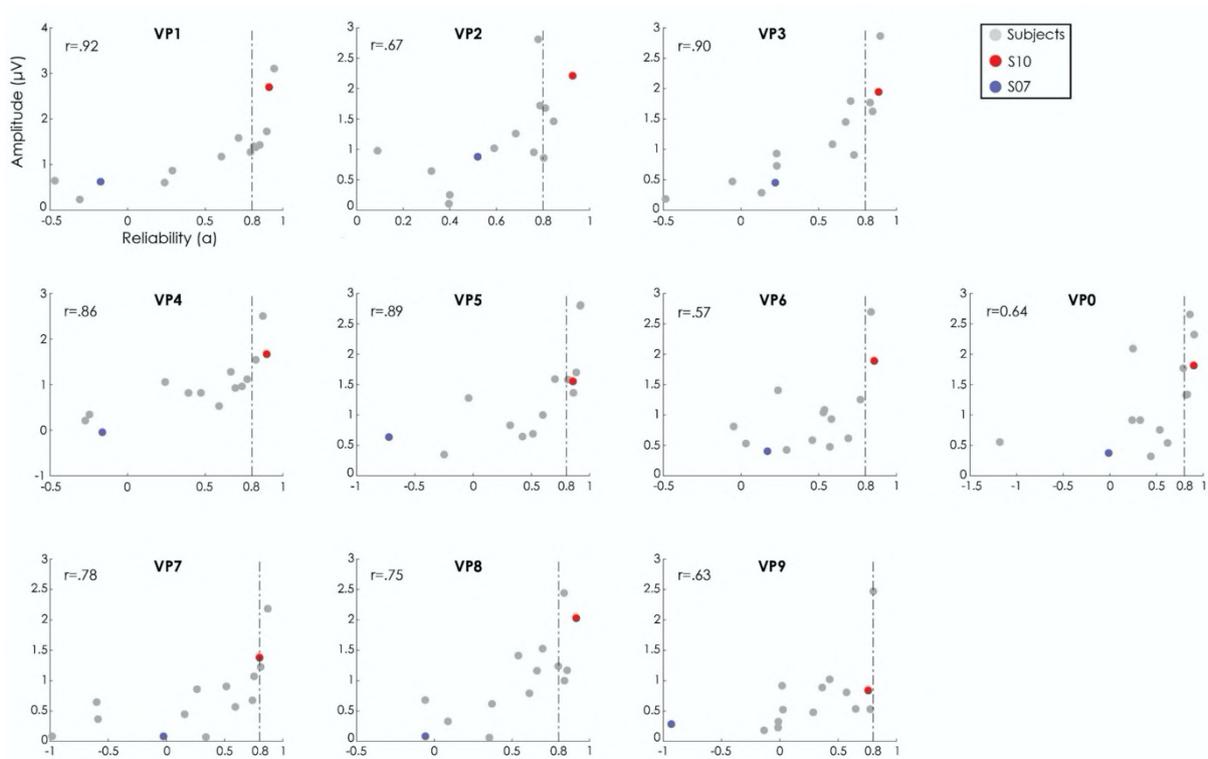
Relationship between FPVS response amplitude and topographical reliability. Visual exploration of our data suggested that subjects with more reliable topographies also exhibited stronger and more typical neural face discrimination response distributions over bilateral occipito-temporal clusters of electrodes. As illustrated in Figure 4.7, correlation analyses showed significant positive relationships between the response amplitude pooled within this region and the topographical reliability at each VP. The highest

4. RELIABILITY OF INDIVIDUAL DIFFERENCES IN NEURAL FACE IDENTITY DISCRIMINATION

and lowest correlations were found for VP1 (left eye; $r=.92$, $p<.001$) and VP6 (right cheek; $r=.57$, $p=.03$), respectively.

Figure 4.7.

Scatter plots demonstrating the relationship between individual observers' response amplitude and response reliability.



Note. For each VP, the average amplitude across trials over occipito-temporal channels is plotted against the reliability score across individual trials for all subjects. Stronger face discrimination responses were more reliable. The dotted line marks the threshold for a response to be considered reliable ($\alpha=0.8$).

4.5. Discussion

The present study aimed to provide novel insights into individual differences in FPVS face identity discrimination recorded by EEG. We explored inter-individual variability by considering the influence of the facial information being fixated (viewing position; VP) and the consistency of face discrimination responses over time. Our data underline the effect of VP on responses not only at the group level, but especially at the level of individual observers, who exhibited idiosyncratic patterns of responses across VPs. Specifically, for any given VP, we observed individual differences – both in terms of response amplitude, as well as its topography. Our reliability analysis showed that the VP-patterns recorded at the first session were largely predictive of those observed at the second session, i.e., 6 months later. Additionally, individual differences in the stability of response amplitude systematically occurred across trials and sessions for the majority of the VPs at occipito-temporal electrodes. Concerning topographical reliability, we report a considerable degree of variation of the scalp distribution of the neural face discrimination responses across observers. Finally, we observed a positive relationship between the topographical reliability of individual observers' responses, and the response amplitude over occipito-temporal electrodes.

Recently, Xu et al. (2017) reported individual differences in the amplitude EEG face discrimination responses indexed by fast periodic visual stimulation (FPVS). Similar to numerous neuroimaging (and behavioral) studies, the authors standardized the visual input by instructing their subjects to fixate on one predefined VP (VP0, i.e., the center of the face). In the present study we observed that subjects exhibited idiosyncratic patterns of responses across VPs: while some subjects show stronger responses when fixating central VPs, others exhibit higher responses to facial information in other regions (e.g., VP1, left eye). Our findings indicate that observations made based on a single location (i.e., standardized input) may lead to a misrepresentation of a large proportion of subjects. The importance of these idiosyncrasies is further highlighted by the fact that the patterns observed at one session could predict those exhibited 6 months later. This suggests that the robust “neural preference” for some VPs over others is unlikely to be noise-related. Instead, the observed reliable VP-dependent responses at

occipito-temporal sites are likely to reflect intrinsic characteristics of each individual's face-sensitive neural networks.

Together, these observations may reconcile previous seemingly inconsistent findings regarding the facial features eliciting the strongest face-sensitive neural response. The majority of studies addressing this question reported that fixation on the eyes leads to stronger responses compared to other features (e.g., Nemrodov et al., 2015; de Lissa et al., 2014). However, other studies suggest that fixation on other facial regions evokes comparable or stronger responses (e.g., Zerouali et al., 2013; McPartland et al., 2010). Importantly, these different findings were made in the context of group studies, which stressed commonalities in neural responses (at the expense of individual differences) in neural responses. Here, adopting an individual observer approach, we observed that while many subjects exhibited stronger responses for the eye-region, others exhibited “neural preferences” for VPs closer to the center of the face (i.e., VP2 / nasion, VP0 / center, VP5 / nose). This variation in the population questions the existence of a *per se* optimal position for face processing (see Caldara, 2017) and could account for discrepant findings reported in the context of earlier group-studies.

Our data also show that individual differences modulate a given measure – here the FPVS face discrimination response – on different levels. In the present context, individual differences could be expressed in terms of the neural response amplitude, scalp distribution, or response reliability. This last parameter is crucial to determine whether an observation carries potentially meaningful information, as opposed to reflecting random noise. Altogether, our results lead to two main considerations.

First, although individual difference can provide a unique source of information, not all should be considered equally meaningful. Disregarding whether an individual exhibits reliable responses over time can mask effects in a similar vein as does averaging across observers. In order to identify *genuine* variations of interest, reliable responses have to be separated from unreliable ones, which inherently carry more noise. This is important in studies investigating the relationship between multiple responses. Those obtained from unreliable observers are less likely to correlate across measures and will therefore

introduce noise, potentially masking otherwise stronger relationships. Similarly, quantifying individuals' reliability would also facilitate determining commonalities across subjects.

Second, individual differences in reliability also indicate that this parameter should ideally be assessed for any tested cohort. More concretely, an estimate of good internal consistency reported for a measure within one group of observers cannot be expected to exist in the context of other independent observers. Individual subjects' reliability is an additional parameter that could be reported along with a given finding to help its interpretation and assess the extent to which it can be generalized. We suggest that – at least in the context of face discrimination measured with FPVS – response amplitude over occipito-temporal regions can provide an initial estimate of its stability over time.

The relationship we report here suggests that precise and stable topographies may relate to better neural responses. This hypothesis is in line with recent findings reporting that the magnitude of face sensitive neural responses were associated with behavioral face recognition (Xu et al., 2017; Elbich & Scherf, 2017). Therefore, functionally meaningful topographical reliability may represent an additional promising parameter to track e.g., development changes in face processing, or effects of interventions in clinical populations. A covariance between neural response reliability and amplitude at the individual level could also be exploited as an objective index to track potential improvements or impairments in face processing. Further research is required to understand the cause(s) of differential neural response reliability – functional or anatomical – as well as the directionality of the observed relationship between reliability and response magnitude.

4.6. Acknowledgements

This work was supported in part by an FSR-FNRS postdoctoral grant awarded to JLS [grant no: FC 91608].

4.7. Supplementary Material

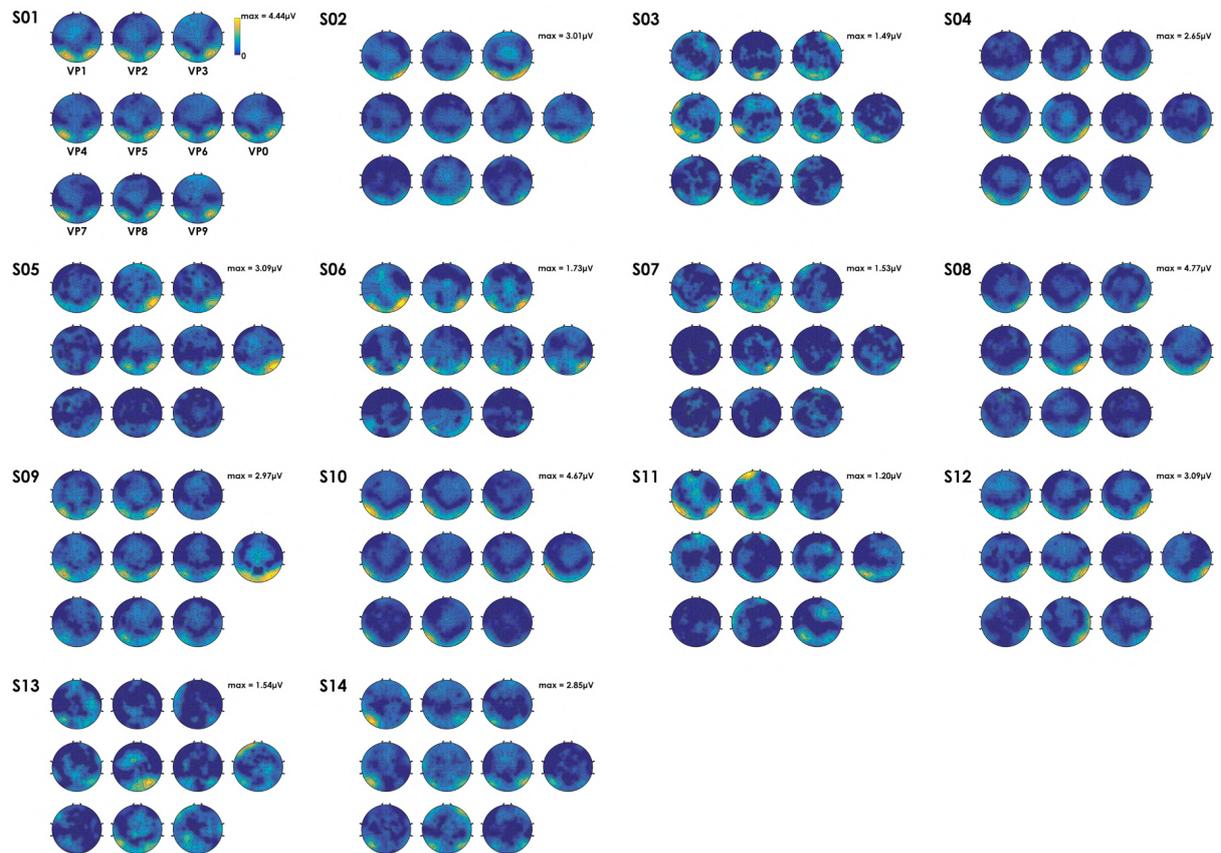
Table 4.1. Amplitude of the neural face discrimination response (μV).

	VP0	VP1	VP2	VP3	VP4	VP5	VP6	VP7	VP8	VP9
Group	1.255	1.328	1.193	1.169	.968	1.335	1.001	.745	1.029	.706
S01	2.645	3.093	2.802	2.856	2.493	2.799	2.686	2.173	2.431	2.460
S02	1.328	1.391	.943	1.785	.805	.991	.923	.668	1.153	.797
S03	.311	.223	.243	.464	.517	.635	.467	.356	.320	.172
S04	.746	.593	.850	.900	.950	1.355	.576	1.216	.989	.469
S05	1.760	1.163	1.670	1.442	.806	1.582	1.074	.636	.607	.520
S06	.906	1.263	.968	1.075	.913	.822	.802	.437	.671	.218
S07	.366	.612	.870	.444	-.058	.627	.395	.074	.075	.275
S08	2.313	1.716	1.451	1.761	1.268	2.787	1.031	1.061	1.516	.513
S09	2.084	1.573	1.711	.720	1.532	1.691	1.244	.849	1.228	1.011
S10	1.803	2.684	2.201	1.935	1.654	1.543	1.879	1.368	2.017	.826
S11	.531	.856	.634	.278	.198	.340	.416	.062	.054	.525
S12	1.320	1.418	1.251	1.616	1.106	1.572	.607	.558	1.160	.877
S13	.546	.634	.097	.175	.331	.681	.521	.076	.782	.316
S14	.907	1.368	1.009	.921	1.044	1.270	1.397	.895	1.403	.907

Note. Values represent responses pooled across 12 bilateral occipito-temporal electrodes at the group and individual level across 10 VPs.

Figure 4.8.

Face discrimination response.



Note. Summed baseline-corrected amplitudes at oddball frequencies averaged across four trials for each subject and each condition.

CHAPTER 5

STIMULUS SIZE MODULATES IDIOSYNCRATIC NEURAL FACE IDENTITY DISCRIMINATION

Stacchi, L, Caldara, R. (submitted). Stimulus size modulates idiosyncratic neural face identity discrimination.

5.1. Abstract

Human observers show reliable individual differences in neural facial identity discrimination across viewing positions. When faces cover the visual angle typical of natural social interactions (80-100cm - $\sim 12^\circ$ - 14°), neural face discrimination responses strongly vary across observers as a function of the fixated face area. Critically, these neural responses directly relate to the unique idiosyncratic preferences in facial information sampling of the observers (e.g., the eyes for some, the mouth for others). This functional signature in facial identity processing might relate to observer-specific diagnostic information processing. Although these individual differences are a valuable source of information for interpreting the data, they can also be difficult to isolate when it is not possible to test a high number of conditions. To address this potential issue, we explored whether reducing stimulus size would help decrease these inter-individual variations in neural identity discrimination responses. We parametrically manipulated the size of face stimuli (covering 3° , 5° , 6.7° , 8.5° and 12° of visual angle), as well as the fixation location (left eye, right eye, just below the nasion, nose and mouth), while recording electrophysiological responses. Same identity faces were presented with a base frequency of 6Hz. These images were periodically interleaved with different face identities to trigger an objective and implicit index of neural face identity discrimination (FID). Our data show robust and consistent individual differences in neural face identity discrimination across viewing positions for all face sizes. Nevertheless, FID was optimal for a larger number of observers when both faces subtended 6.7° of visual angle and the fixation was just below the nasion. This condition is the most suited to reduce the natural variations in neural FID patterns observed across observers, defining an important benchmark to measure neural FID where it is not possible to assess and control for the idiosyncrasies of each observer.

Keywords: Idiosyncrasies, face discrimination, stimulus size, viewing positions, FPVS-EEG

5.2. Introduction

An increasingly large body of work is providing evidence of functionally meaningful individual differences in face processing. Eye movement studies have reported significant differences across cultures during face recognition (e.g., Western Caucasians vs. East Asians; e.g., Blais et al., 2008; Kelly et al., 2010; Miellet et al., 2012; for a review see Caldara, 2017). Notably, variations have also been reported between individuals from the same cultural background during face identification, suggesting that observers have idiosyncratic visual sampling strategies which are not well represented by group-averages (Walker-Smith et al., 1977; Mehoudar et al., 2014). These idiosyncrasies have been shown to be reliable over a period of 18 months (Mehoudar et al., 2014), across settings (i.e., lab vs. real world; Peterson et al., 2016), and to be sufficiently distinct to allow algorithms to identify an observer from their scanning paths (Kanan et al., 2015). Crucially, such individual differences in sampling strategies do not appear to correlate with behavioral performance in identity-related tests. That is, individuals exhibiting different fixation biases can attain similar performance levels (Arizpe et al., 2016, Blais et al., 2008). However, forcing observers to fixate away from their naturally preferred viewing position (VP) is detrimental to their face identification performance (Peterson & Eckstein, 2013), suggesting that these idiosyncrasies are functionally meaningful.

Recently, individual differences in face discrimination have also been documented at the neural level by means of the fast periodic visual stimulation (FPVS) electrophysiological approach (Stacchi et al., 2019a). FPVS consists in presenting faces of varying identities embedded at periodic intervals in a stream of same-identity faces displayed at a particular base frequency (e.g., AAAAAABAAAAACAAAAAD...). A neural response at the same frequency of identity changes provides an index of the ability of the neural system to discriminate between identities (Liu-Shuang et al., 2014; Rossion et al., 2020). Importantly, studies have shown that the amplitude of the response triggered by FPVS is positively correlated with behavioral performance for face recognition tests (Cambridge Face Memory Test, Xu et al., 2019; Benton Face Facial Recognition Test, Dzhelyova et al., 2020), and a FPVS-like identity discrimination task (Retter et al., 2021). Recent findings also show

that presenting faces at diverse facial viewing positions (e.g., left eye, right eye, etc.) leads to significant variations across participants in terms of neural amplitude patterns and topographies (Stacchi et al., 2019a; see Xu et al., 2019 for similar individual differences during fixation of a central viewing position (VP) just below the nasion). VP-dependent neural responses differed across individuals, with some participants exhibiting larger responses while fixating the left eye and others during fixation of the nose (Stacchi et al., 2019a³; 2019b⁴). Interestingly, the more a face region was fixated by an observer during natural viewing, the more likely this region was to trigger a strong neural FID response in the EEG-FPVS. Furthermore, these robust idiosyncrasies across VPs were reliable over a period of 6 months (Stacchi et al., 2019b; see Dzhelyova et al., 2019 for two-months reliability of the FPVS response at the central VP). Altogether, these findings suggest that individual differences recorded through EEG-FPVS can reflect genuine and functionally meaningful variations in face discrimination.

While individual differences can be a unique source of information to understand their underlying relationship with neural processes, they also have manifold methodological implications that should be carefully considered. If not appropriately accounted for, idiosyncrasies could contribute to misleading conclusions and the misrepresentation of single subjects. For example, assessing neural FID at only one viewing position would intrinsically result in participants having rather weak responses due to their idiosyncratic preference for another VP. One VP could be sub-optimal for one participant and optimal for another one, generating noise in the interpretation of the data. As such, these individual differences in VPs would ideally require experimenters to assess participants across numerous conditions, effectively increasing testing duration. This is not always a realistic goal, neither with traditional ERPs nor with the FPVS paradigm, which requires significantly less time than the former to extract high signal-to-noise ratio (SNR) responses. For instance, young or clinical populations might be unable to undergo long testing sessions. Additionally, the need to test multiple viewing positions would result in less time available to test other experimental manipulations. Ideally, researchers would also be required

³ This citation refers to CHAPTER 3 of this thesis

⁴ This citation refers to CHAPTER 4 of this thesis

to first record the oculo-motor behavior of observers to establish their preferred viewing position and only subsequently proceed to the EEG recording. However, this approach would require at least two sessions and two different techniques, engendering heavy experimental constraints.

To overcome these issues, the current study aimed to determine if it is possible to reduce the extent of individual differences across VPs as expressed during neural face identity discrimination. Essentially, altering the viewing position of a face induces a change in the information input to the visual system. More specifically, in terms of information intake, the face region which is fixated is sampled at high resolution as the fovea is the portion of the retina with maximal visual acuity, while the facial information surrounding the point of foveation is sampled at a lower resolution. This is highly relevant when stimuli are relatively large and only a small portion of a face can be sampled within the fovea and a single fixation. In our previous studies we used relatively large face stimuli covering the visual angle typical of natural social interactions (80-100cm - $\sim 12^\circ$ - 14° ; Stacchi et al., 2019a; 2019b). We thus expect that when stimuli are smaller and most of the facial features can be sampled within one fixation, the viewing position will play a minor role in information gathering. If this prediction is correct, then adjusting stimulus size could help to reduce individual differences in neural responses for FID across VPs, and therefore make participants more comparable within the group.

To this aim, we thus recorded EEG signals of observers while face images were presented through fast periodic visual stimulation to trigger neural FID. Experimental conditions varied along two dimensions, each with five levels: viewing position (left-, right-eye, nose, mouth and just below the nasion) and size (3° , 5° , 6.7° , 8.5° , 12° of visual angle). We expect stimulus size to impact both the response amplitude, independently of VPs, and response patterns across VPs. Firstly, it is reasonable to foresee that when stimuli are too small, it might become more difficult to rapidly extract the fine-grained information necessary to successfully discriminate between face identities. This should lead to decreased and non-significant FID responses. To probe this hypothesis, our analysis will first focus on determining the minimum size at which we can reliably obtain valid responses. Only once those conditions are identified will we assess the impact of VP on response patterns.

Then, for the significant neural FID responses, we hypothesize that for smaller face sizes the point of fixation will no longer be relevant because almost all of the information could be sampled by fixating any facial region. This would result in participants no longer showing preferences for specific VPs. Therefore, in this scenario, the arbitrary choice of a fixed VP when measuring neural FID would not be problematic. Alternatively, it is possible that as stimuli become smaller, observers' VP-related biases will not necessarily be reduced but will nonetheless converge towards the same region. When the whole face can be sampled through one fixation only, observers could benefit more from a central viewing position (i.e., just below the nasion – see Blais et al., 2008; Mielle et al., 2013), which allows equal and simultaneous sampling of all face features (i.e., the nose or the viewing position located just below the nasion).

Regardless of these hypotheses, identifying an experimental condition that systematically triggers significant neural FID and simultaneously reduces individual variations in response patterns across VPs would represent a significant methodological advance. It would also increase the already impressive efficiency of the FPVS technique in establishing a representative index of neural FID in only a few minutes.

5.3. Methods

5.3.1. Participants

We tested a sample of thirty-five young Caucasian adults, mainly undergraduate students at the university of Fribourg (7 males, 2 left-handed, M mean age: 22.4 ± 2.5 , range: 18-30). Participants had normal or corrected-to-normal vision, and none had reported to have a history of psychiatric or neurological disorders. They all provided written consent prior to the experiment. The study was approved by the local ethics committee.

5.3.2. Procedure

Stimuli and procedure

Stimuli consisted in images of 50 face identities (25 females), all displaying a neutral expression. Faces were all full-front, colored, cropped to remove external facial features and embedded in a grey background. Stimuli were presented on a VIEWPixx/3D monitor (1920 x 1080 pixels resolution, 120Hz refresh rate) by means of Matlab2016b (PsychToolbox and a custom graphics toolbox). Within each 62s trial, a stream of faces was presented through sinusoidal contrast modulation at a base frequency of 6Hz, hence each stimulus lasted 0.166ms.

Each sequence consisted in one randomly selected base face which was repeated throughout the whole trial, and different randomly selected oddball identities (different from the base identity) interleaved periodically every 7th base face (i.e., $6\text{Hz}/7 = 0.85716\text{Hz}$) (Figure 5.1A). Within each trial, faces size randomly varied between 90 and 110% in order to minimize pixel overlap. This 20% variation has been shown to be sufficient to reduce low-level adaptation (Dzhelyova et al., 2014).

In order to maintain attention and fixation, participants were instructed to monitor a fixation cross presented in the middle of the screen and overlapping the images stream. The cross changed color randomly 8 to 10 times each trial and subjects had to report by button press the occurrence of such change. At this task participants performed nearly at ceiling ($M = 0.92$, $SD = 0.12$).

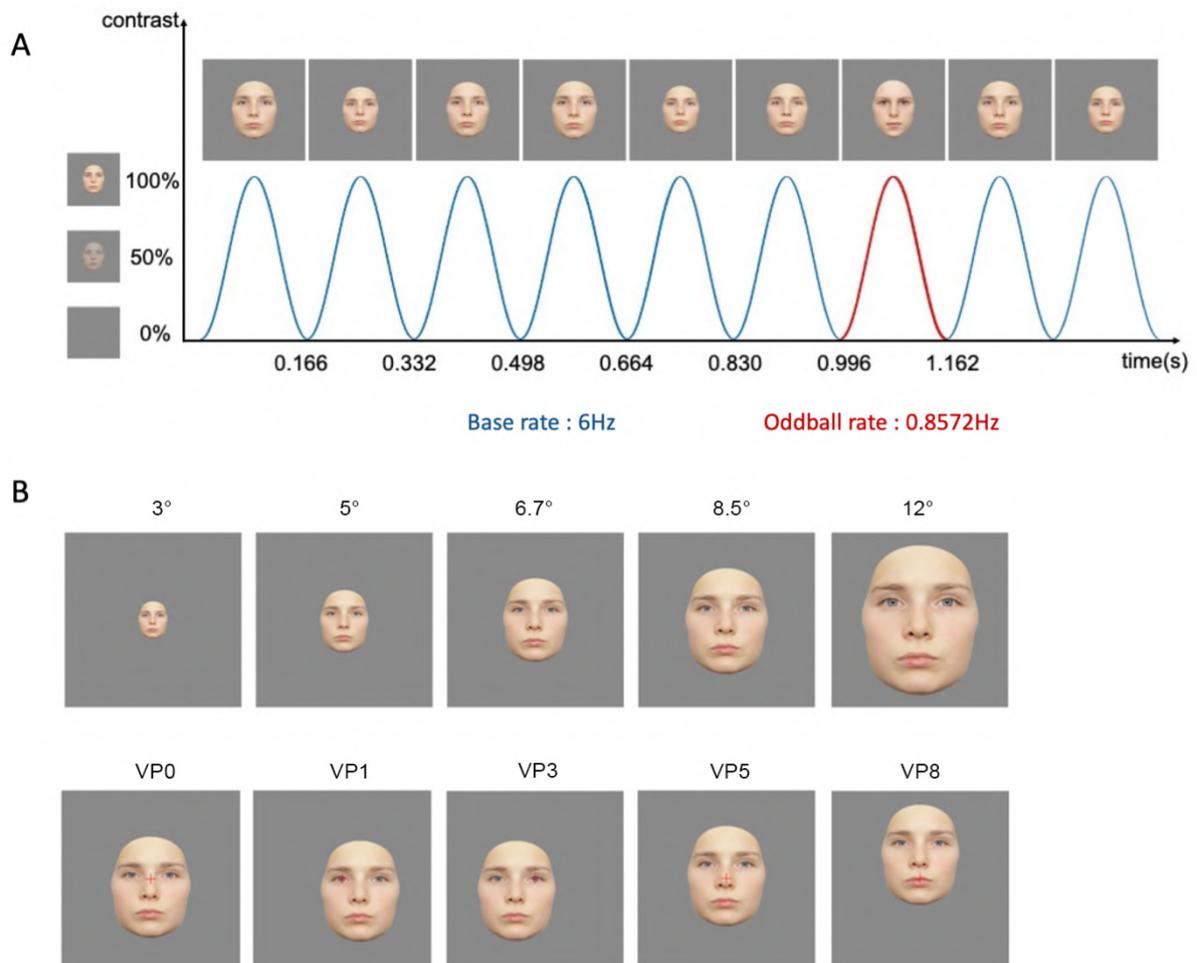
Trials varied along two dimensions: stimuli's size and viewing position (VP). Size was parametrically modulated across 5 steps. These sizes were chosen in order to not overlap despite the within trial 20% variation. We varied VP by arranging faces so that one out of five facial regions were aligned with the center of the screen, hence the fixation cross. VP consisted of left and right eye, nose, mouth and a region slightly below the nasion (Figure 5.1B; Figure 5.2). The last VP was selected to include the fixation location typically tested with this paradigm while the remaining VPs were selected so to induce fixation on the main facial features.

Each combination of size and VP was presented twice, once with male faces and once with female faces, resulting in a total of 50 trials (5 sizes x 5 VPs x 2 repetitions). Trials with evident motion-related

noise contamination were repeated at the end of the experiment ($M = 3$). Including numerous breaks taken to ensure subjects' attentive state, testing lasted approximately one hour and a half.

Figure 5.1

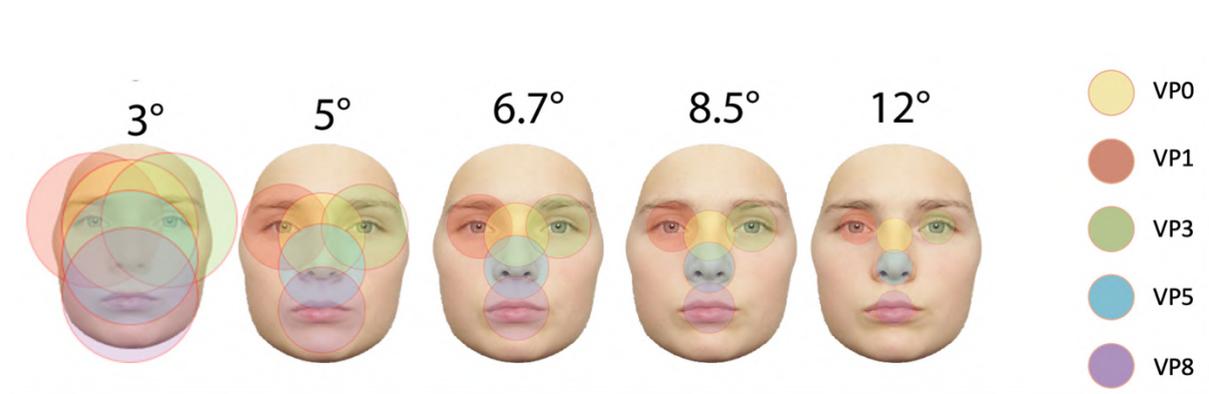
Schematic illustration of the paradigm and the experimental conditions.



Note. A. Faces were presented using fast periodic visual stimulation and a sinusoidal contrast. B. Conditions varied in terms of stimulus size (top row) and viewing position (bottom row).

Figure 5.2.

Schematic illustration of a 2° foveal visual field depending on stimulus' size and VP.



Note. To allow for an easier comparison of the foveal coverage across conditions, the foveal visual field was resized accordingly.

EEG acquisition

EEG was acquired by means of Biosemi ActiView software with a Biosemi Active-Two amplifier system and 128 Ag-AgCl Active electrodes. Offset was lowered and maintained below 25mV relative to the common mode sense (CMS) and driven right leg (DLR) by slightly abrasive the scalp and adding saline solution. The signal was digitalized at a sampling rate of 1024Hz and online bandpass filtered between 0.1 and 100Hz to remove slow drifts over time.

Digital triggers were sent by means of VIEWPixx screen.

5.3.3. EEG preprocessing and statistical analysis

Preprocessing

Preprocessing was carried out in Letswave 5, an open-source toolbox running in Matlab 2016b.

First, the EEG signal was filtered with a bandpass fourth-order zero-phase Butterworth filter between 0.1 and 100Hz and downsampled to 256Hz. Subsequently, data were segmented in epochs starting 2s before stimulation onset until 2s after stimulation offset. Independent component analysis was computed using a square mixing matrix algorithm and the component that more strongly related to eye-blinks was removed in each subject (components were identified through its topography and the correspondence between its time-course and that of frontal electrodes located above the eyes). Data were then visually inspected and cleaned using trial substitution and channel interpolation. First, bad trials flagged during data acquisition and therefore repeated at the end of the experiment were compared with their repetition and the one containing more noise (larger fluctuation or noise over a larger number of channel) was removed. Subsequently, noisy channels were visually identified and replaced through linear interpolation of their 3 closest neighboring electrodes (max. 5% of all scalp electrodes were interpolated per observer). Data were then re-referenced to the average of all electrodes and additionally cropped between 2 seconds after and before stimulation onset and offset respectively. This resulted in segments of approximately 58.33 seconds (= 14933 bins). This specific length was selected as it corresponds to an integer number of oddball cycle, which will allow for precise extraction of frequencies of interest. Finally, epochs were averaged together within condition for each subject separately.

Frequency domain analysis

Frequency spectrum was extracted from averaged epochs by mean of Fast Fourier Transform (FFT) Matlab's built-in function.

Significant harmonics

In order to assess the number of base and oddball harmonics to include in the response quantification, data were averaged across subjects and 26 occipital temporal electrodes (selected based on previous studies and visualization of the current dataset through conditions and subjects; A9-A16, A22-A29, B6-B12, D30-D32). The grand-average signal was z-scored (20 surrounding frequencies (excluding immediately adjacent and 2 most extreme bins (minimum and maximum))) and responses to base and oddball fundamentals and harmonics were isolated. Harmonics were retained for further analysis if their z-score exceeded the 1.64 ($p < 0.05$, one tailed) threshold for more than half of the conditions. This led to 4 significant harmonics for the base frequency (from 6Hz up to 24Hz) and 10 harmonics for the oddball frequency (from 0.8572Hz to 8.572Hz), excluding the 7th as it corresponds to the fundamental of the base. However, as the 10th harmonic frequency falls within the alpha range, we only retained harmonics up to, and including, the 9th (i.e., 7.715Hz).

Response quantification

In order to quantify base and oddball responses, FFT signals were first baseline-corrected by subtracting from each frequency the average of 20 surrounding frequencies (excluding immediately adjacent and 2 most extreme bins (minimum and maximum)). Subsequently, baseline-subtracted harmonics were summed together.

Relationship between base and oddball responses

Visual inspection of the data suggested that both the base and the oddball response amplitude increased at larger sizes. We performed within subject Spearman correlation to explore whether the two responses co-varied. We applied Holm-Bonferroni correction to control for multiple comparisons.

Effect of stimulus size on response amplitude

To evaluate the impact of stimulus size on both the base and oddball responses amplitude, 26 occipito-temporal electrodes were pooled together (i.e., A9-A16, A22-A29, B6-B12, D30-D32). Subsequently, size effect was evaluated for each VP separately using a linear mixed model. To account for inter-individual variations, the variable subject was added to the model, which can be summarized as follows:

$$Amplitude \sim Size + (1/Subjects) \quad (1)$$

Post-hoc contrasts between each size were corrected for multiple comparisons using Tukey's HSD test.

Significance and outliers detection

The impact of size and viewing position variation was evaluated based on two criteria. The first is response significance. The main goal was to determine whether a response can be reliably obtained from a large portion of the subjects independently of condition, or on the contrary, some parameters are sub-optimal for such purpose.

Second, we aimed to determine the extent and homogeneity of VP-dependent preference across Sizes. Specifically, our goal was to assess whether at some sizes the neural bias would either decrease or it would converge across subjects towards the same VP.

Response significance detection

We first determined response significance at the individual level. We reasoned that if a Size would systematically fail to elicit a significant response it could be excluded from further statistical analysis on VP related preference, hence reducing data dimension and number of comparisons.

Therefore, for each type of response (base and oddball), each subject and each condition independently, FFT epochs were cropped into segments composed of group-significant harmonics (1st-4th for base response and 1st-9th harmonics, excluding the 7th for the oddball) and 24 surrounding bins. These smaller

epochs were then summed together before pooling 26 occipital temporal electrodes together. Finally, the z-score of the frequency of interest was computed by means of the same parameters used at the group level.

Responses above 1.64 ($p < 0.05$) were considered as significant. In order to later compute proportions, responses were then relabeled as 1 if they were significant and as 0 otherwise. However, the focus of subsequent analyses was more on the *absence* of a significant response. Therefore, to facilitate visualization, proportion and proportion difference estimation of non-significant responses, binomial values were switched, with 1 indexing a non-significant response and 0 a significant one.

Outlier detection

Within this paper we defined a preferential response as a significantly stronger, or outlier, response for a VP compared to responses to other VPs. Therefore, outlier detection was performed on each subject and Size independently by estimating the deviation of each VP-related response through the median absolute deviation (i.e., MAD). Therefore, each response was converted into its deviation (MAD_{score}) as it follows:

$$MAD_{score} = (x_i - M_j)/MAD \quad (2)$$

$$where \text{MAD} = c * \text{median}(|x_i - M_j|);$$

where x_i is the i^{th} item of the data series, M_j is the median of the data series, $c = 1/0.75$ quantile of the data series.

Any response with a deviation exceeding 2.5 was considered an outlier (Leys et al., 2013). As for significance detection, responses' deviation score was relabeled as 1 if the response was considered an outlier and 0 otherwise. Importantly, subjects might exhibit more than one outlier response. To avoid considering each subject multiple times, for statistical comparison of the total number of subjects exhibiting outlier responses, each participant was counted not more than once.

Complete information regarding the number of subjects showing outlier or non-significant responses across VPs and size were then summarized separately.

Changes in proportion in terms of non-significant or outlier responses were evaluated by means of McNemar mid-p test, which is well suited to compare dependent samples of medium or small sizes (Fagerland et al., 2013). Multiple comparisons were controlled using Holm-Bonferroni correction. Moreover, 95% confidence intervals of proportions and proportion differences were estimated by means of 5000 bootstrap samples.

Finally, once identified the condition(s) most optimal in terms of significant responses and outlier convergence, we explored the impact of these conditions on subjects for whom it did not trigger extremely large responses. Our aim was to not only identify the condition most optimal for the majority of subjects but also the one that was the least sub-optimal (i.e., triggering weaker within subject responses compared to other conditions). To do this, for each size of interest, we explored the response triggered by the “optimal” VP in terms of significance and how it ranked with respect to responses evoked by other viewing positions.

5.4. Results

Base response

The neural response at the general frequency was computed to ensure the proper synchronization of the visual system to the visual stimulation.

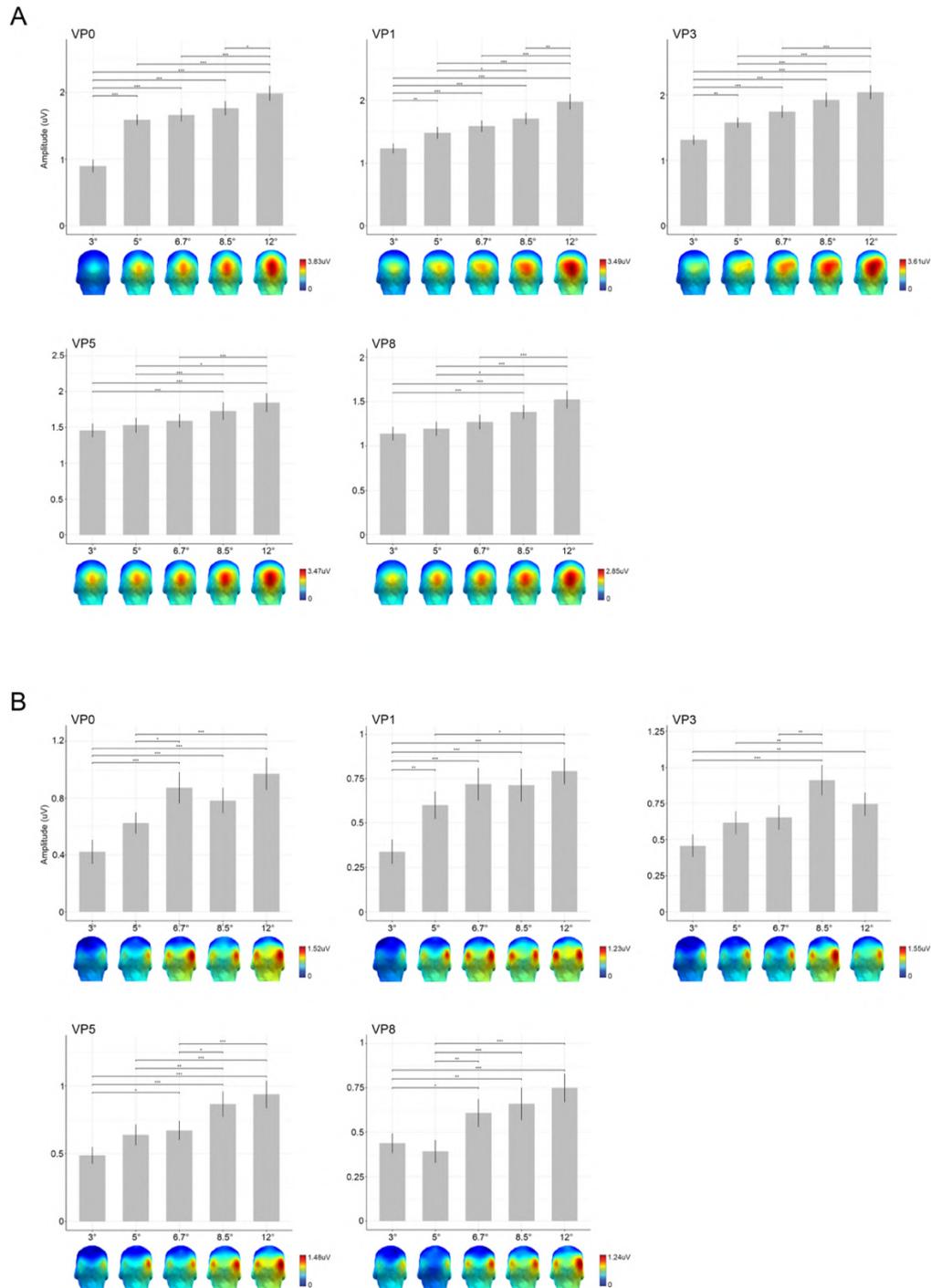
The results of the linear mixed model evaluating the effect of size on the response amplitude shows that size has a significant effect on response amplitude at all VPs [VP0, $F(4, 136) = 56.33$, $p < 0.0001$; VP1, $F(4, 136) = 30.11$, $p < 0.0001$; VP3, $F(4, 136) = 33.84$, $p < 0.0001$; VP5, $F(4, 136) = 9.96$, $p < 0.0001$; VP8, $F(4, 136) = 13.42$, $p < 0.0001$]. Post-hoc comparisons showed that the base response grows significantly as stimuli's size increments (Figure 5.3A). Topography shows a medial-occipital distribution for conditions where fixations were directed towards the center of the face. When fixations

were enforced on the left and right eye we found an additional activity in ipsilateral occipital regions, which increases with stimuli's size (Figure 5.3A).

At the individual level, the base response was significantly stronger than surrounding noise in all 25 conditions for all 35 subjects except for one condition (i.e., 3°-VP0) for S16.

Figure 5.3

Grand-average base and oddball responses for all sizes and viewing positions.



Note. Responses at the base (A) and oddball (B) frequencies are visualized as the average across subjects and as the average over occipito-temporal electrodes (bars) or at each electrode (topographies). Error bars represent the standard error.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Oddball response

Group level

The oddball response was used as an index of neural FID. The results from the linear mixed model revealed a main effect of stimulus size on response amplitude, independently of the VP considered [VP0, $F(4,136) = 14.21, p < 0.0001$; VP1, $F(4,136) = 13.77, p < 0.0001$; VP3, $F(4,136) = 9.40, p < 0.0001$; VP5, $F(4,136) = 14.83, p < 0.0001$; VP8, $F(4,136) = 11.64, p < 0.0001$]. Post-hoc contrast between sizes showed that response amplitude increases significantly with stimuli's size.

However, it plateaus at size 6.7° or 8.5° depending on the VP considered, in which case a further size increment does not lead to a significantly larger response. Figure 5.3B summarizes the group responses as well as the results of the contrasts extracted from the linear mixed model.

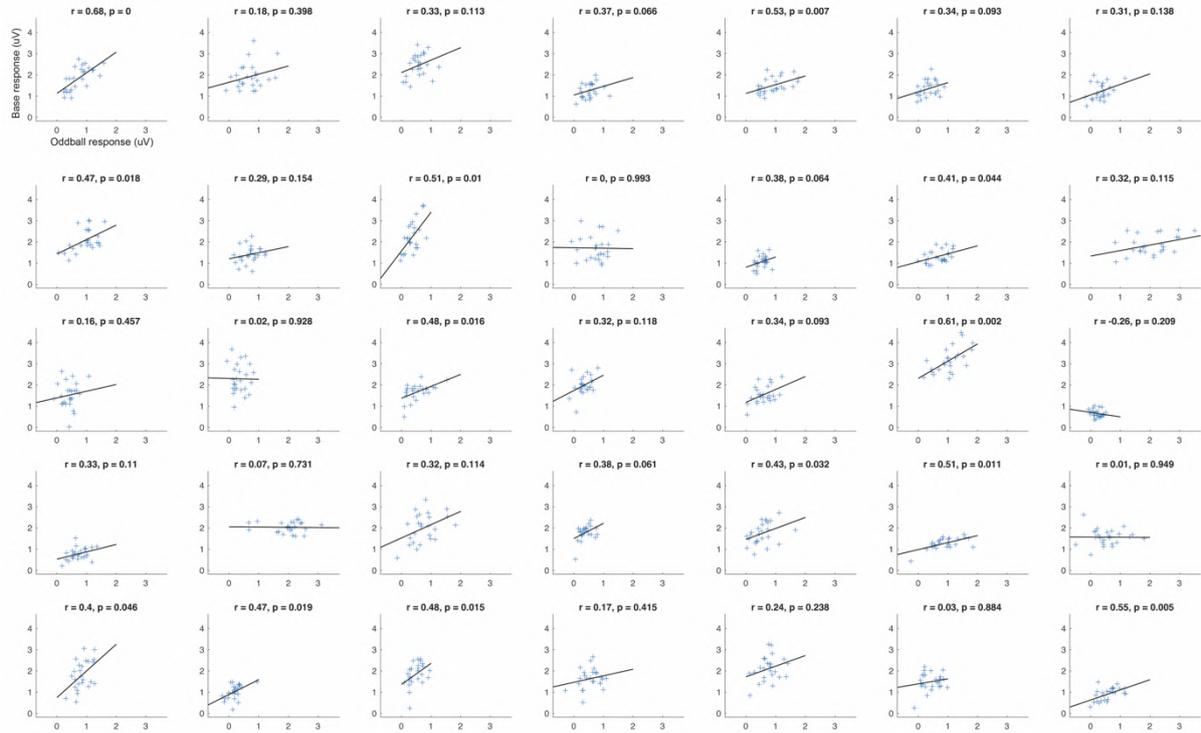
Individual level

Base and oddball relationship

Holm-Bonferroni corrected Spearman correlations between oddball and base response resulted in only one subject showing a significant relationship between responses at the base and oddball frequencies (S1, $r = .68, p < 0.001$, see Figure 5.4 for all subjects).

Figure 5.4

Relationship between base and oddball responses.



Note. Scatterplot of the base (y-axis) and oddball (x-axis) responses for all condition for each subject separately. Correlation coefficient and p-value is reported for every participant.

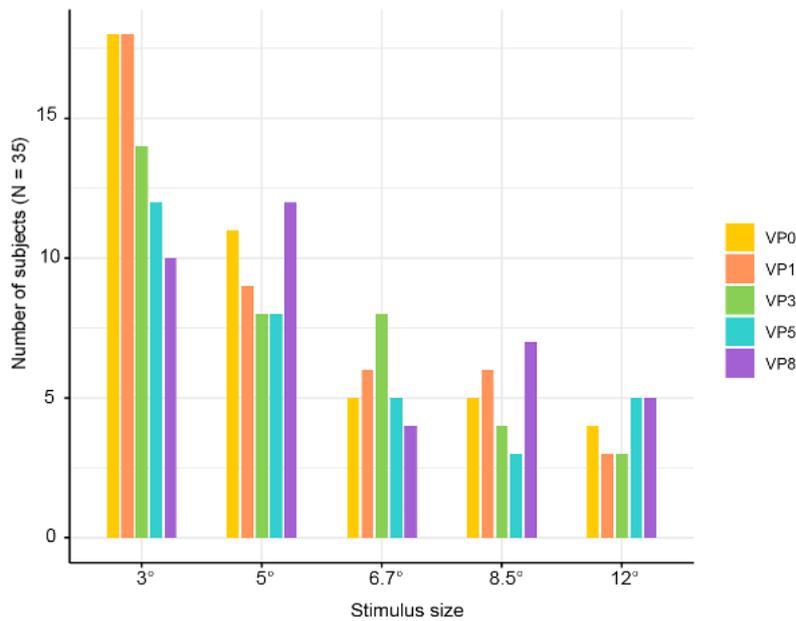
Response significance

The significance of the response was severely modulated by the stimulus's size. Figures 5.5 and 8 highlight the number of subjects who failed to show a significant response according to Size and VP. As it becomes apparent, the smallest size that was tested was associated with the largest number of non-significant (NS) responses. Importantly, most subjects (i.e., 27/35) exhibited non-significant responses for some viewing positions, but significant neural FID for other VPs (Figure 5.6 and 5.8). To ensure that significance of those responses was not due to a subtle difference, significant responses were also evaluated against a more severe threshold of $p = 0.01$. This showed that a pattern of significant (at $p < 0.01$) and non-significant (at $p < 0.05$) responses persisted in 25 subjects (Supplementary Table 5.1 for z-score of all subjects in all conditions).

Collapsing all VPs together within each size shows that at the smallest stimulus size (3°), 85.7% (95% CI 74.4, 97.1) of subjects exhibited at least one non-significant response. When considering the next size (5°), the total number of NS subject decreased by 9 (25.7%, CI 9,42.5, mid p = 0.0032) leaving only 60% (95% CI 43.4, 76.6) of subjects with at least one non-significant responses. A similar significant decrease (8 subjects, 22.9% CI 8.7, 37.1, mid p = 0.0018) is observed between sizes 5° and 6.7°, where less than half of the subjects (37.1%, CI 20.8, 53.5) exhibit now a non-significant response (Table 5.1, Figure 5.5 and 5.8). As the size keeps increasing the number of non-significant subject stabilizes and the remaining differences are no longer significant (see Figure 5.6 for all differences).

Figure 5.5

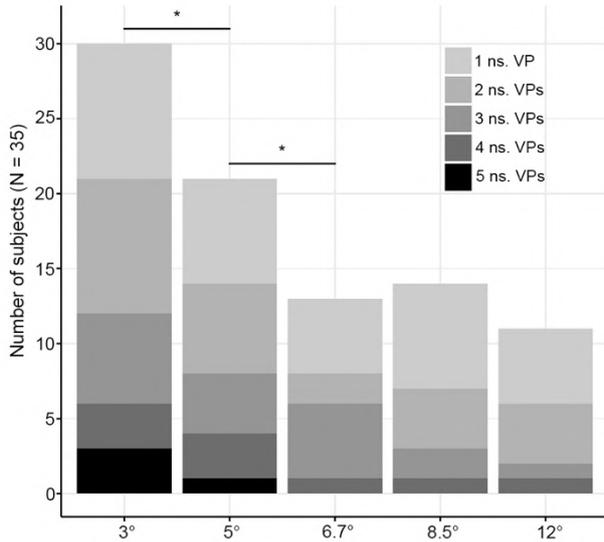
Distribution of non-significant responses across size and VP in terms of number of subjects.



Note. The same subject could have more than one NS condition and therefore the cumulative some within one Size or VP can exceed the total number of subject (N = 35).

Figure 5.6

Number of subjects showing a non-significant according to only stimulus's size.



Note. The stack bars illustrate the exact number of VPs that were NS for each subject. For example, green bars represent the number of subjects with three non-significant responses in each Size.

* indicates significant differences between the number of subjects at mid $p < 0.05$.

Table 5.1

Proportion and proportion difference across conditions of number of subjects exhibiting a non-significant neural FID response.

Proportion (%)				
3°	5°	6.7°	8.5°	12°
85.7 (74.4, 97.1)	60.0 (43.4, 76.6)	37.1 (20.8, 53.5)	40.0 (23.7, 56.3)	31.4 (16.1, 46.8)
Proportion difference between groups (%)				
3°-5°	5°-6.7°	6.7°-8.5°	8.5°-12°	
25.7 (9.0, 42.5)	22.9 (8.7, 37.1)	2.9 (-5.6, 11.6)	8.6 (-2.8, 19.9)	

Note. Number in parentheses are 95% confidence interval estimated as ± 2 standard errors.

Outlier VP-dependent responses

Because the two smallest sizes (i.e., 3° and 5°) triggered a non-significant response in more than half of the subjects, we decided to not investigate these conditions beyond descriptive statistics and to mainly focus on the remaining sizes.

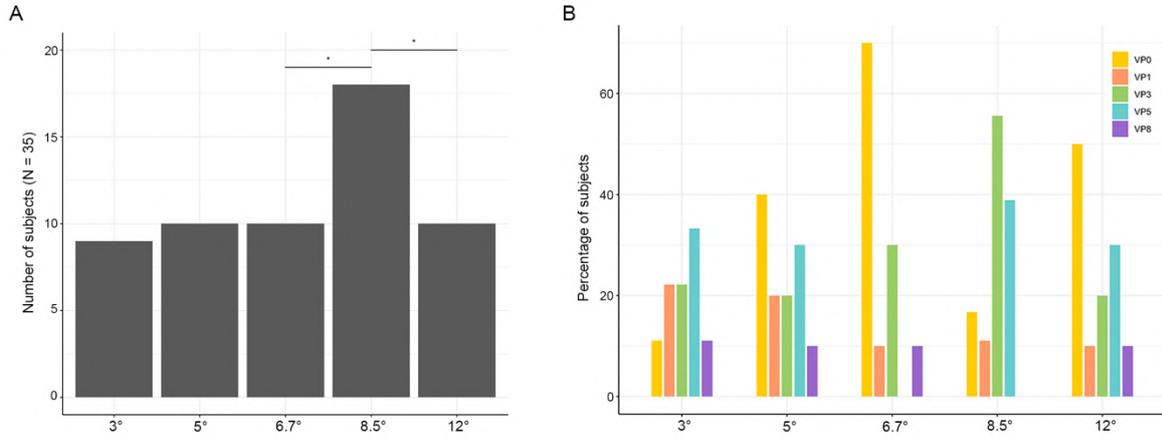
As shown in Figure 5.7A, size 8.7° leads to more than half of subjects to show at least one outlier response (51.4%, CI 33.5, 69.3), while in Size 6.7° and 12° this occurs in less than a third of the participants (Table 5.2). Additionally, the paired difference of 8 subjects (22.9%, CI, -1.6, 47.3) between Size 8.5° and 12° is significant (mid $p = 0.039$) as well as the paired difference of 8 subjects (22.9%, CI 2.7, 43.1) between Size 6.7° and 8.5° (mid $p = 0.0245$) (Table 5.2).

The outlier distribution across VPs shows that VP0 led to a larger number of outliers in Size 6.7° and 12°, while this was obtained by VP3 in Size 8.5°. Importantly, VP0 in Size 6.7° is the outlier response for 70% of the subjects showing an extreme response. On the other hand, VP0 includes only 50% of subjects in Size 12°, and VP3 55.6% of subjects in Size 8.5° (Figure 5.7B).

Finally, at Size 6.7°, 8.5° and 12°, fixation on VP0, VP3 and VP0 respectively, led to a non-significant response in five, four and four subjects (Figure 5.5). Excluding those, the same viewing positions also triggered a response amplitude below-the-median (i.e., $MAD_{score} < 0$; with respect to other viewing positions within the same size) in five, five and six additional subjects (Table 5.3, Figure 5.8).

Figure 5.7

Distribution of outlier responses.



Note. A. Number of subjects showing at least one outlier response.

* indicates significant difference in total number of subjects at mid $p < 0.05$.

B. Distribution of subjects exhibiting outlier responses across VPs and sizes. The y-axis represents the number of subjects showing an outlier response for a given VP over the absolute number of subjects showing at least one outlier response at a given size. Please, note that a subject could exhibit more than one outlier response per size and as such numbers do not perfectly add up with figure A and could lead to percentages more than 100%.

Table 5.2.

Proportion and proportion differences between conditions of number of subjects exhibiting outlier responses.

Proportion (%)				
3°	5°	6.7°	8.5°	12°
25.7 (10.9, 40.5)	28.6 (13.1, 44.0)	28.6 (13.5, 43.6)	51.4 (33.5, 69.3)	28.6 (13.6, 43.5)
Proportion difference between groups (%)				
3°-5°	5°-6.7°	6.7°-8.5°	8.5°-12°	
2.9 (-17.0, 22.7)	0 (-19.4, 19.4)	-22.9(-2.7, -43.1)	22.9 (-1.6, 47.3)	

Note. Numbers in parentheses are 95% confidence interval estimated as ± 2 standard errors.

Table 5.3.

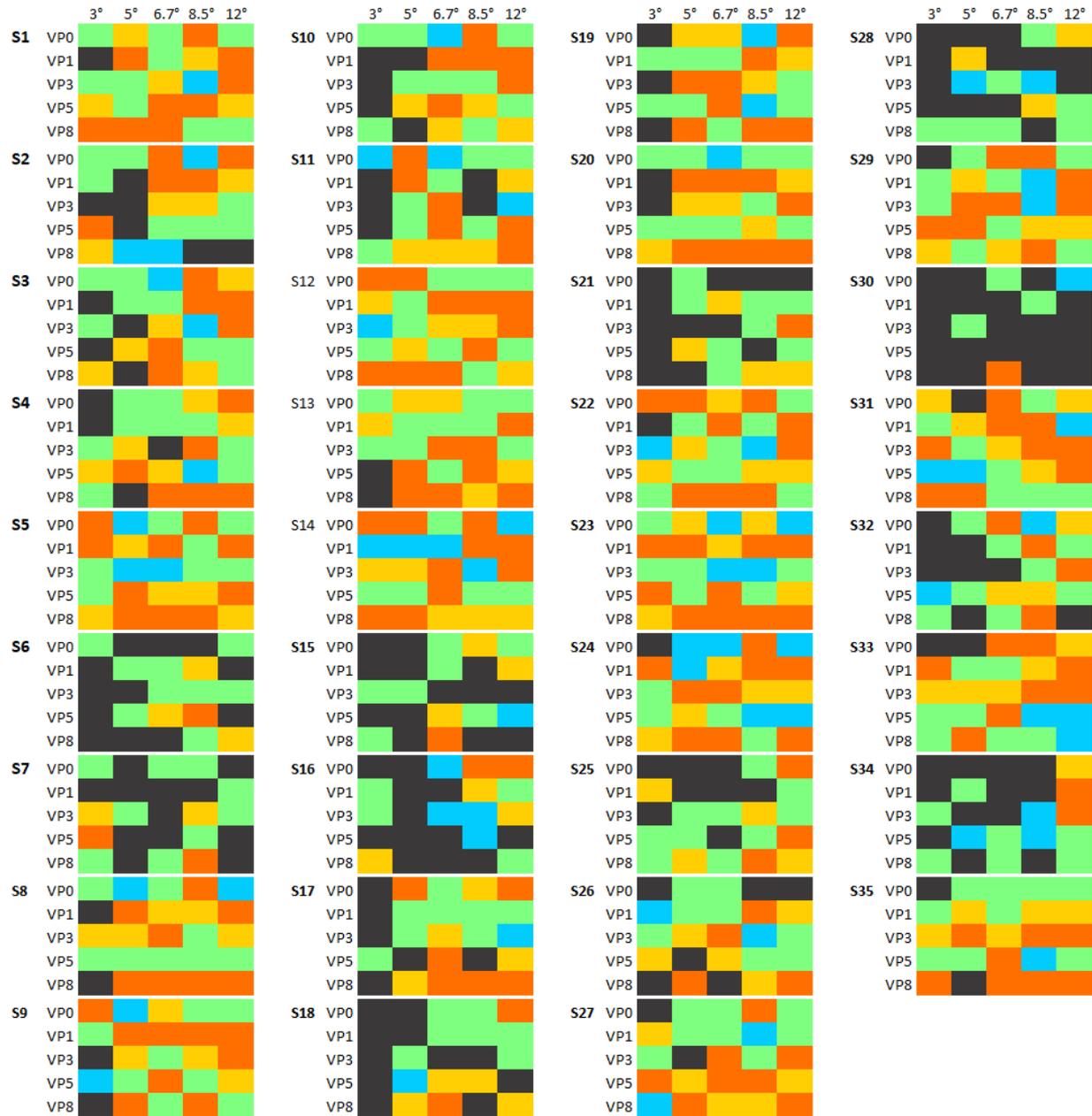
Number of subjects exhibiting a MAD score above, equal to, or below different thresholds for each VPs and Sizes.

	MAD>2.5	MAD>0	MAD=0	MAD < 0
<hr/>				
3°				
VP0	1	10	1	5
VP1	2	7	4	4
VP3	2	13	5	1
VP5	3	11	4	5
VP8	1	11	8	5
<hr/>				
5°				
VP0	4	11	4	5
VP1	2	13	5	6
VP3	2	13	8	4
VP5	3	14	6	4
VP8	1	2	4	16
<hr/>				
6.7°				
VP0	7	14	4	5
VP1	1	16	4	8
VP3	3	6	9	9
VP5	0	11	7	12
VP8	1	10	5	15
<hr/>				
8.5°				
VP0	3	11	4	12
VP1	2	8	6	13
VP3	10	9	7	5
VP5	7	11	9	5
VP8	0	7	7	14
<hr/>				
12°				
VP0	5	14	6	6
VP1	1	8	8	15
VP3	2	11	3	16
VP5	3	15	8	4
VP8	1	9	8	12

Note. Subjects were included in these categories only if they exhibited a significant neural FID.

Figure 5.8

Summary of each subject MAD score and response significance.



Note. If a response z-score was below 1.64 ($p < 0.05$) it is color coded as dark grey. Significant responses are color coded according to their MAD score. Orange indicates a MAD score < 0 , yellow indicates MAD score $= 0$, light green indicates MAD score > 0 and light blue indicates a MAD score > 2.5 (outlier).

5.5. Discussion

This study aimed to assess the impact of stimulus size on rapid neural face identity discrimination response as a function of the face region (viewing position) fixated. We tested participants with fast periodic visual stimulation where a stream of same-identity faces was presented at a general frequency of 6Hz with different-identity faces periodically interleaved every 7th image (i.e., 0.85Hz). Across conditions, stimuli varied in their size and in the viewing position that participants were required to fixate.

The impact of size variation on neural face discrimination response

Our data show that stimulus size modulates the amplitude of neural FID: the smaller the stimuli the weaker the response. Interestingly, while amplitude appears to linearly increase across stimulus sizes at the base response, the oddball response seems to benefit from stimulus size increments only until 6.7°-8.5° of visual angle but does not show significant amplitude increases for 12°. This observation could be explained by the modulations of the visual processes involved in the extraction of information used during FID. Specifically, identity processing involves both a holistic coarse percept of faces and a finer-grained analysis of information that are idiosyncratic to each face (e.g., Rossion, 2008; Rossion et al., 2011). At small sizes (e.g., 3° of visual angle), the extraction of detailed idiosyncratic information is more difficult, especially given that stimuli remained on screen for only 166ms, allowing for only one fixation at a pre-determined location. As stimulus size grows this fine-grained analysis, and therefore identity discrimination, becomes easier. However, when size increases above a certain threshold, holistic processing might then become impaired, as holistic processing starts to worsen when stimuli are larger than 6° of visual angle (McKone, 2009). Therefore, it is possible that performance for face identity processing is better for mid-range face sizes, as both fine-grained and holistic mechanisms can be used to attain optimal neural FID. When stimuli are either too large or too small, they favor one or the other perceptual strategy. However, our data do not show a weakening of neural FID for larger faces, but, nonetheless, they also do not show any further significant improvement for stimuli larger

than 6.7°-8-5° of visual angle (depending on the viewing position considered). Further studies would be required to explore whether, after the plateau observed here, neural FID decreases for stimuli larger than 12°.

The impact of size variation on VP-dependent neural FID

The main goal of the current study was to determine whether reducing face size would reduce neural response variation across viewing positions and/or across observers. We addressed these hypotheses in two steps. First, we assessed the significance of neural responses, so as to exclude from further analysis conditions that were less likely to trigger significant neural FID responses. At the individual level, we observed a greater number of non-significant responses for smaller sizes compared to larger stimuli. Additionally, analysis revealed that the number of subjects showing non-significant FID responses significantly decreased between 3° to 6.7° of visual angle but did not change substantially between the three largest sizes. Based on these results, we did not further investigate 3° and 5° sizes, as they failed to trigger a systematic neural FID.

Analysis of the data from the three remaining sizes (6.7°, 8.5° and 12° of visual angle) revealed that the 8.5° size triggered extremely high responses (outlier responses/visual sampling preference) in more subjects than for the sizes of 6.7° and 12° of visual angle respectively. Importantly, compared to size 12°, size 6.7° led to a greater agreement between observers. Specifically, at size 6.7° more than half of those exhibiting an outlier response did so when fixating the central viewing position (VP0), and in general this viewing position triggered an above-the-median response in 21 out of 35 participants, and a non-significant response in only five of them. Finally, fixation below the nasion still triggered an above-the-median response in two out of three observers when considering only subjects showing a strong positive bias for a different viewing position.

Altogether, these observations indicate that the 6.7° size, which is the smallest among those systematically leading to significant neural FID (i.e., 6.7°, 8.5° and 12°), reduced individual differences in neural bias the most overall. In fact, a large portion of subjects showed a convergence on VP0 in

terms of either outlier responses or above-the-median response. This finding is in line with our expectation that although VP-dependent biases do not appear to decrease with increasingly smaller stimulus sizes, they appear to converge towards the same central viewing position (VP0). At this size, it is likely that both holistic as well as fine-grained mechanisms can be used to process information gathered from a single fixation in order to reach optimal neural FID. Therefore, fixating just below the nasion represents a strategic location to perceive faces as a unit and at the same time sample facial regions such as the eyes with relatively high resolution (fixation on VP0 at 3° of visual angle places the eyes just outside foveal vision, Figure 5.2).

Individual differences at small scales

In order to identify an experimental condition that reduces the influence of viewing position on neural FID we applied different criteria. The first aimed to filter the conditions in terms of robustness of the evoked FID neural responses. Consequently, we discarded the two smallest sizes (3° and 5°), as they led to many non-significant responses across conditions. Importantly, while these two conditions were no longer interesting with respect to our original goal, the pattern of responses recorded in these two cases become relevant from a theoretical perspective and is worth discussing. We found that even at the smallest visual angle (3°), most of our observers still exhibited responses indicative of both optimal and suboptimal viewing conditions. In other words, more than three quarters of our participants exhibited non-significant responses for some VPs, but at the same time highly significant responses when fixation was constrained to other VPs. These observations might indicate that fixation of specific viewing positions can provide an advantage for FID even under challenging conditions, such as when fine-grained information is more difficult to extract. However, future studies are necessary to clarify what drives these individual differences. For example, a question that cannot be addressed within our current methodology is the contribution of different facial information to the recorded neural response. Although fixation was constrained to a specific viewing position, observers still had access through parafoveal and peripheral vision to information from the whole face that could be used to achieve FID.

There is not a straightforward relationship between the information fixated and its use in natural vision (e.g., Caldara et al., 2010), as such this question remains open.

5.6. Conclusions

Our data show that FID neural responses increase with stimulus size, reaching a plateau from 6.7°-8.5° of visual angle onwards. Individual differences across VPs were present for *all stimulus* sizes, even for the smallest. However, importantly, when faces are centered below the nasion and subtend 6.7° of visual angle these individual differences across VPs are significantly reduced. This stimulus size should be used conventionally to reduce the impact of potential individual differences in neural FID response patterns, as it decreases the likelihood of obtaining and interpreting non-representative measures at the single-subject level. Altogether, these findings highlight the need to rigorously control for face stimulus size and viewing position, while positing a benchmark to reduce FID idiosyncratic responses. Overall, they prompt the necessity for further studies to elucidate the mechanisms at the root of individual differences during face processing.

5.7. Acknowledgments

LS was partly supported by a Swiss National Science Foundation grant awarded to RC (10001C_201145).

5.8. Supplementary Material

Table 5.4.

The neural FID response in terms of z-score for each participant in each conditions.

		3°	5°	6.7°	8.5°	12°
S1	VP0	2.03	3.06	4.73	4.74	10.32
	VP1	1.14	2.70	7.14	5.25	7.22
	VP3	3.16	4.66	3.22	9.12	5.36
	VP5	1.95	2.94	2.04	5.25	8.24
	VP8	2.08	2.35	2.40	5.35	7.65
S2	VP0	3.61	3.63	4.93	7.98	4.15
	VP1	4.17	1.62	3.96	2.37	4.66
	VP3	0.15	0.94	4.35	4.21	8.77
	VP5	2.65	1.41	4.57	4.42	5.81
	VP8	2.94	4.38	4.63	-0.66	1.60
S3	VP0	6.54	5.26	7.88	3.62	3.31
	VP1	0.21	3.31	5.06	3.37	3.67
	VP3	3.64	1.60	3.01	8.25	1.91
	VP5	0.53	4.76	2.68	2.84	3.87
	VP8	2.29	0.96	2.51	3.79	5.41
S4	VP0	0.22	3.97	3.86	4.45	4.24
	VP1	1.44	3.47	6.66	5.13	4.84
	VP3	3.53	3.18	1.39	2.88	5.43
	VP5	2.50	2.17	4.34	7.50	4.30
	VP8	5.35	1.58	1.71	2.57	2.25
S5	VP0	2.11	4.09	6.64	3.24	5.10
	VP1	2.35	2.61	5.69	6.23	2.61
	VP3	2.13	3.46	9.17	6.17	4.05
	VP5	4.34	1.87	4.96	6.16	2.72
	VP8	1.64	1.71	2.99	2.77	3.70
S6	VP0	3.66	1.55	-0.22	1.09	5.53
	VP1	0.32	4.67	5.49	3.16	0.85
	VP3	-0.64	1.12	3.28	4.99	3.19
	VP5	0.31	3.50	1.79	2.50	0.17
	VP8	1.61	-0.30	-0.09	3.41	1.86
S7	VP0	1.99	0.90	2.24	2.78	0.19
	VP1	0.17	0.09	-1.66	1.06	5.50
	VP3	1.68	3.16	1.51	1.67	2.29
	VP5	2.30	1.13	-0.15	3.26	1.47
	VP8	2.28	-0.69	1.80	2.15	0.56
S8	VP0	7.75	7.90	10.73	5.73	8.72
	VP1	1.15	6.58	6.37	5.54	5.21
	VP3	5.72	6.15	5.20	5.50	9.49
	VP5	5.96	7.76	11.39	7.31	5.69
	VP8	0.33	3.24	3.53	2.75	3.42

5. STIMULUS SIZE MODULATES IDIOSYNCRATIC NEURAL FACE IDENTITY
DISCRIMINATION

		3°	5°	6.7°	8.5°	12°
S9	VP0	2.16	6.60	3.71	5.52	4.77
	VP1	2.90	2.86	2.44	4.28	3.93
	VP3	0.83	4.92	5.09	7.12	2.87
	VP5	7.16	7.73	3.90	6.26	5.90
	VP8	1.54	3.23	4.80	4.32	6.17
S10	VP0	1.99	3.51	6.66	1.66	6.56
	VP1	-0.22	0.66	2.34	1.67	2.53
	VP3	-0.43	3.39	2.91	5.03	2.29
	VP5	0.70	1.85	1.68	3.96	6.26
	VP8	3.37	0.32	2.11	6.72	5.28
S11	VP0	4.84	1.73	6.79	5.10	6.93
	VP1	0.40	2.93	4.58	1.12	4.41
	VP3	-0.74	3.30	4.56	1.14	11.07
	VP5	0.25	6.94	4.48	6.13	4.23
	VP8	2.85	6.93	4.00	6.60	3.34
S12	VP0	4.01	3.48	7.25	7.60	7.21
	VP1	3.29	6.32	3.47	5.07	3.74
	VP3	8.31	7.41	4.75	6.20	7.01
	VP5	7.54	5.72	6.83	3.97	5.84
	VP8	2.90	3.35	4.05	9.61	9.43
S13	VP0	4.99	4.04	7.52	10.47	6.80
	VP1	2.66	5.62	5.62	10.42	3.72
	VP3	3.08	2.34	4.46	6.42	5.98
	VP5	1.51	1.96	8.00	6.64	6.32
	VP8	-0.29	2.05	1.94	8.91	3.95
S14	VP0	9.86	4.47	18.37	13.69	21.74
	VP1	14.93	13.72	16.53	8.72	9.27
	VP3	5.34	10.70	11.43	10.77	4.17
	VP5	10.12	7.58	8.21	22.91	13.70
	VP8	4.14	6.86	14.57	17.60	10.52
S15	VP0	1.52	1.38	3.20	3.04	2.84
	VP1	0.60	-0.65	2.71	-0.11	1.79
	VP3	2.19	1.98	0.86	1.03	0.47
	VP5	1.01	0.70	2.22	4.98	4.04
	VP8	2.40	0.37	2.08	1.55	1.63
S16	VP0	0.51	1.35	4.63	1.97	0.47
	VP1	2.93	0.95	1.18	2.28	1.74
	VP3	5.55	0.95	4.13	5.17	1.82
	VP5	1.01	0.84	1.33	3.28	-0.55
	VP8	3.06	0.80	0.54	1.49	4.93
S17	VP0	0.34	1.87	11.05	6.26	4.39
	VP1	1.05	2.14	5.83	5.87	5.62
	VP3	0.92	2.03	6.19	8.70	8.15
	VP5	3.55	1.15	4.90	0.73	4.70
	VP8	0.42	1.79	2.81	3.17	2.64
S18	VP0	0.34	1.17	4.82	2.93	1.92
	VP1	1.19	1.42	5.02	3.15	6.06
	VP3	-0.88	1.94	1.32	1.46	3.53
	VP5	1.35	2.49	3.21	2.32	-0.65
	VP8	0.08	1.71	2.68	0.95	2.42

5. STIMULUS SIZE MODULATES IDIOSYNCRATIC NEURAL FACE IDENTITY
DISCRIMINATION

		3°	5°	6.7°	8.5°	12°
S19	VP0	0.15	5.31	3.43	4.05	6.04
	VP1	3.26	7.09	7.51	2.52	5.39
	VP3	1.23	3.95	2.98	3.38	9.08
	VP5	3.11	7.13	2.69	8.28	8.39
	VP8	0.20	3.89	6.45	2.09	3.46
S20	VP0	6.19	6.48	7.91	9.63	14.34
	VP1	1.48	6.73	6.09	4.54	8.14
	VP3	0.96	4.74	6.00	8.06	4.46
	VP5	4.97	5.42	8.52	9.19	7.40
	VP8	2.04	2.26	2.00	3.54	7.15
S21	VP0	1.19	6.02	-0.87	0.44	1.40
	VP1	0.90	3.04	1.84	2.88	4.91
	VP3	0.87	-0.23	0.73	4.18	1.87
	VP5	0.34	2.39	5.33	-0.62	4.04
	VP8	1.06	1.08	3.75	1.65	2.20
S22	VP0	2.97	4.05	4.87	6.27	8.32
	VP1	0.73	6.39	2.92	9.97	4.19
	VP3	8.05	6.67	10.38	10.10	4.75
	VP5	4.70	7.18	5.45	7.47	9.95
	VP8	4.74	2.19	3.72	6.05	9.99
S23	VP0	10.17	14.33	12.85	11.54	8.25
	VP1	2.68	4.44	12.67	8.85	15.52
	VP3	7.09	13.87	9.26	9.08	13.01
	VP5	2.53	12.04	7.77	10.69	8.53
	VP8	7.23	9.00	8.95	9.22	6.16
S24	VP0	-1.38	10.00	13.04	4.51	10.83
	VP1	2.37	6.66	7.94	4.34	6.02
	VP3	4.70	2.29	1.76	3.02	9.25
	VP5	6.79	3.70	7.68	8.66	12.20
	VP8	3.27	2.88	6.29	5.67	4.36
S25	VP0	0.22	1.36	1.48	5.46	1.85
	VP1	1.94	1.40	0.99	1.52	3.43
	VP3	0.65	4.75	3.30	4.31	2.88
	VP5	1.88	5.82	1.25	5.22	1.67
	VP8	2.90	1.67	2.01	3.28	2.87
S26	VP0	0.71	4.58	4.49	0.78	0.73
	VP1	3.40	3.77	3.90	2.75	2.66
	VP3	1.83	3.13	2.46	9.48	7.94
	VP5	1.69	0.03	6.57	4.28	8.71
	VP8	0.00	1.86	0.33	3.61	2.71
S27	VP0	-1.37	7.64	9.38	4.67	6.14
	VP1	1.87	5.97	9.00	8.94	13.73
	VP3	2.27	1.61	3.00	7.96	3.93
	VP5	2.38	2.50	5.33	4.04	8.44
	VP8	6.75	3.59	5.91	6.21	4.75
S28	VP0	-0.08	0.69	1.51	1.76	2.93
	VP1	-1.77	2.26	1.52	1.23	0.65
	VP3	0.39	6.31	2.18	4.11	-0.84
	VP5	0.27	0.77	0.96	2.44	6.12
	VP8	1.84	4.00	2.51	1.38	3.92

5. STIMULUS SIZE MODULATES IDIOSYNCRATIC NEURAL FACE IDENTITY
DISCRIMINATION

		3°	5°	6.7°	8.5°	12°
S29	VP0	1.19	7.55	3.81	2.96	8.94
	VP1	3.64	4.59	5.30	5.64	3.72
	VP3	5.29	4.93	2.21	6.84	3.05
	VP5	2.32	3.08	4.56	3.06	5.31
	VP8	3.67	5.50	4.08	3.82	4.57
S30	VP0	0.32	1.26	1.67	-0.06	5.79
	VP1	-1.49	-0.77	-0.18	2.95	0.63
	VP3	0.56	2.25	0.66	0.55	1.44
	VP5	1.42	1.07	0.98	1.03	0.13
	VP8	1.51	-0.15	-1.10	0.79	0.74
S31	VP0	1.87	0.54	2.96	3.83	3.35
	VP1	2.66	2.53	1.97	2.72	8.16
	VP3	2.08	2.37	3.87	2.43	4.59
	VP5	6.14	6.33	5.32	4.02	5.82
	VP8	1.65	1.98	4.62	9.94	4.74
S32	VP0	0.96	2.17	2.11	3.49	4.53
	VP1	0.56	1.25	3.55	2.19	7.25
	VP3	0.99	1.58	1.12	2.85	2.55
	VP5	3.91	3.43	2.70	2.43	3.23
	VP8	3.16	-1.59	4.66	1.74	1.38
S33	VP0	0.58	0.64	4.17	4.48	5.18
	VP1	3.72	7.07	5.02	4.33	7.22
	VP3	4.56	4.48	3.53	3.94	4.82
	VP5	5.97	5.83	3.42	8.69	12.68
	VP8	5.11	2.18	6.89	8.52	7.14
S34	VP0	-0.99	1.18	0.82	0.76	3.84
	VP1	1.59	1.99	0.29	0.36	5.22
	VP3	4.79	0.70	1.02	6.17	3.42
	VP5	0.36	5.92	4.91	4.03	4.67
	VP8	2.32	1.04	4.30	0.72	3.97
S35	VP0	-0.25	8.38	9.41	5.95	10.76
	VP1	3.58	5.61	6.37	4.84	7.92
	VP3	1.86	3.81	5.64	6.63	3.35
	VP5	2.63	7.84	5.28	11.99	10.00
	VP8	1.66	0.66	2.73	2.14	5.56

Note. For comparison: z-score > 1.64, $p < .05$; z-score > 2.32, $p < .01$; z-score > 3.1, $p < .001$

CHAPTER 6

GENERAL DISCUSSION AND CONCLUSIONS

6.1. General Discussion

This thesis addressed the question of how individual differences in viewing-position might shape rapid neural face discrimination. Variations between individuals are to be expected independently of the measure used or the process recorded. They appear in recording due to a number of factors (e.g., noisy data, morphological differences), but they do not necessarily reflect genuine differences. However, in face processing, a growing body of literature is documenting the existence of reliable and functionally meaningful variation in terms of, for example, sampling strategies, namely the way individuals gather visual information. Prompted by these observations, we aimed to address the following questions:

- 1) Do individuals exhibit differences in neural bias across VPs?
- 2) Do these idiosyncratic neural biases relate to those exhibited in sampling strategies?
- 3) Are individual neural differences reliable over time?
- 4) Is it possible to reduce individual differences in neural bias through experimental manipulation?

To address these questions, we used an FPVS paradigm to trigger a robust and objective neural index of rapid face discrimination. Among many others, one of the advantages of using this paradigm was the possibility to obtain a high SNR neural response within a few minutes. In the context of our research questions, this was especially important because it allowed us to test multiple conditions, namely enforced fixation at different VPs. Thanks to the high SNR of the response evoked by FPVS, we were able to test between 10 (Study 1 and 2) and 25 (Study 3) conditions, each time using a full within-subject design and within a reasonable amount of time. This allowed us to track the response profile of each individual across VPs and compare it to their specific eye movements in Study 1, through two sessions in Study 2, and across variations of a second dimension in Study 3.

In the following section, I will summarize the main findings of these investigations.

6.1.1. Main Findings

Study 1. Our first study had two main goals: to determine whether individual difference in neural bias for different VPs exists both in terms of eye movements and neural responses and to assess the relationship between these two measures. Our results confirm the presence of idiosyncrasies at both levels. Specifically, we replicated previous findings of individual variations in both scanning path and location of the first fixations. Similarly, we also observed that the strength of neural face discrimination responses was modulated by the location of fixation differently across subjects; that is, while some subjects showed a neural bias indexed as stronger responses for some VPs, other participants exhibited such a bias when fixation was enforced on different locations. Crucially, we also demonstrated the presence of a robust relationship between sampling strategies and neural bias. Specifically, the more a facial region was fixated under natural viewing conditions, the more likely this was to trigger a stronger neural face discrimination response compared to other VPs. Altogether, these findings suggest the existence of a tuning between eye movement and neural biases during facial identity-related processing. Additionally, this observation provides the first empirical evidence in favor of functionally meaningful idiosyncratic VP-dependent neural face discrimination.

Study 2. Motivated by findings from our first study, our second work aimed to more precisely assess the nature of idiosyncratic neural preference during face discrimination. Specifically, we assessed the reliability of these individual differences over a period of six months. We reasoned that if idiosyncrasies were driven by noise, these would not be consistent over different sessions. In fact, noise is unstable and constantly changing; therefore, if it was the main contributor to the observed individual differences, it would lead to a systematic within-subject fluctuation across recordings.

Our results show that patterns of neural bias across observers were overall reliable. Data also show that between-subjects ranking in terms of response strength is consistent over time: individuals who responded strongly or weakly did so consistently over both testing sessions. Additionally, we found that the reliability of topographical distribution of the neural response varied across subjects but could be

predicted by the strength of the response itself. More precisely, subjects showing stronger neural face discrimination responses were also those who exhibited a reliable topography over time.

These observations suggest that individual differences in rapid neural face discrimination mainly reflect genuine variations.

Study 3. Results from Studies 1 and 2 reinforce the need to consider individual differences in neural responses to avoid relying on average data that do not constitute a satisfying representation of actual subjects. However, we also reasoned that investigating multiple conditions requires testing sessions of considerable duration. This might not be an issue with healthy young adults but might represent an issue when testing clinical or very young populations. Additionally, testing multiple VPs when there are other parameters of interest becomes potentially difficult and highly time and energy consuming even for neurotypical adults. Because of this, in our third study, we aimed to determine whether there was an experimental condition that would reduce idiosyncratic VP-dependent neural face discrimination. We hypothesized that by reducing the variation in visual input provided by foveation across VPs, we would reduce the response difference across them. With this aim, we assessed individual differences in VP-related neural patterns across five stimulus sizes, expecting smaller scales to lead to less within-subject variation. Contrary to our hypothesis, variation across VPs was not reduced at smaller sizes. However, we found that among the tested conditions, fixation on the center of the face (just below the nasion) of stimuli subtending 6.7° of visual angle led to the most homogenous set of responses. Specifically, at this size, this VP was the preferred one for most of the subjects, who showed a clear bias. Additionally, compared to the others, this VP was the less detrimental for the majority of subjects either not exhibiting strong preferences or preferring other VPs. Altogether, this study suggests that it is possible to reduce the risk of misrepresenting participants while testing only one VP. Nonetheless, we also show that individual differences in VP-dependent neural patterns persist at all sizes. This reinforces the need to carefully evaluate variations across participants and their impact on the data and the conclusions drawn from them. Importantly, variations at very small sizes also raise questions about what triggers them because differences in visual input do not appear to be a sufficient explanation.

In the next section, I will discuss implications of our observations as well as questions that I believe should be addressed by future studies in order to better understand individual differences.

6.1.2. Discussion

Individual Differences to Account for Seemingly Discordant Results

The three studies included in this dissertation argue in favor of individual differences as a unique source of information. Variations across individuals have long been regarded as nuisance in the data that could be attenuated if not eliminated by averaging across participants. In the context of face processing, disregarding individual differences has resulted in misleading assumptions about, for example, the universality of sampling strategies. Some studies over the years have tried to raise awareness of the risks of collapsing data across subjects and have warned that it might result in a misrepresentation of single individuals. However, this argument had few adherents until more recently. In the past decade, studies have begun to focus on individual differences, evaluating their reliability and functional meaning. Still, some research fields have considerably more information than others. In the face-processing literature, evidence is accumulating regarding idiosyncratic sampling strategies. However, very little is known about how different neural visual systems respond to different facial information. At the group level, multiple reports have provided evidence of eye sensitivity in the context of face categorization or detection. Interestingly, even at the group level, there are some incongruencies across studies. While the majority agree that fixation on the eyes enhances the face-sensitive N170 component (e.g., De Lissa et al., 2014; Nemrodov et al., 2014), a few other reports outline discrepant findings (e.g., Zerouali et al. 2013; McPartland et al., 2010).

Although relating to a different subprocess, namely face identity processing, results presented in our three studies suggest an explanation of discordant results across reports. As we show in our third experiment, while some sizes are more likely to trigger a more homogenous set of neural biases, this does not necessarily mean that everyone conforms to the same pattern. Concretely, this means that in the majority of cases, random sampling from the population results in most of the subjects exhibiting a

set of responses matching the typical one but also in some other individuals not conforming to it. When averaging across participants, commonalities among “typical” subjects prevail over differences between “nontypical” subjects. Importantly, in rarer occasions, population sampling might include a larger number of subjects showing a different pattern of responses, which would lead to seemingly different results at the group level.

Interestingly, this idea was first proposed five decades ago. Walker-Smith and colleagues (1977) report individual differences, albeit while only testing three subjects, and suggest that contradicting evidence in the existing literature at the time might have been due to the practice of favoring group analysis at the expense of single-subject analysis.

Optimizing Neural Face Processing in Correlational Studies

Individual differences in neural response patterns across VPs are extremely relevant when one wishes to correlate behavioral and neural measures.

Most behavioral tasks assessing face processing do not enforce fixation on a specific VP. Observers are free to explore a face using their preferred sampling strategy. This allows each individual to showcase their natural abilities without being biased toward specific face regions. The only constraint imposed is the time they are allowed to view a face, which can be used to isolate early face processing from other mechanisms such as self-doubt. However, free visual inspection is usually not allowed in EEG testing, where fixation is generally enforced somewhere toward the middle of the face. This choice comes from the sensitivity of EEG recording to muscle activity. Participants constantly moving their eyes contaminates the signal, making it potentially unusable or at least notably reducing its SNR (but see e.g., De Lissa et al., 2020, for coregistration of EEG and eye movements). The choice of enforcing fixation toward the center of the face is often motivated by results of eye movement studies reporting that this is the landing position of the first fixations under natural viewing conditions and that they are sufficient for face identity processing (e.g., Hsiao & Cottrell, 2008). However, research focusing on single-subject analysis revealed the presence of individual differences already at the first and second fixation. Crucially, the preferred VP of a subject relates to the location that allows for better face identity

processing. Forcing an observer to fixate at a different location deteriorates their performance. In line with these observations, we showed that enforcing fixation on face regions that are naturally fixated less is more likely to trigger a weaker neural face discrimination compared to VPs that are naturally sampled more. Importantly, we showed that this relationship emerges when considering the first or second fixation but persists when considering all fixations performed under natural viewing conditions. Therefore, while the methodological choice of enforcing fixation in one location is extremely beneficial for EEG data quality, the arbitrary choice of such a location might introduce a bias that is not present in behavioral tasks. This might result in correlating one measure acquired at one level of difficulty with a neural measure acquired at a different level. Studies have shown that this does not prevent correlations from emerging. For example, Xu and colleagues (2019) found a significant positive correlation between a neural index of face identity discrimination acquired at a predetermined fixed VP and a behavioral measure of face identity recognition obtained under free viewing conditions. However, whether this approach provides the most comprehensive description of the relationship of interest remains an open question.

Individual Differences when Screening for Impaired Face Cognition

Individual differences not only have an impact when investigating the normal population; they are also an important factor to consider when assessing participants who are expected to be different from the normal population. This is especially important for studies aiming to use a given measure as a tool to guide identification of low-performing individuals.

In our studies, especially in the third one, we showed how the same subject can exhibit weak or even nonsignificant responses when fixating on some VPs but stronger responses when fixation was enforced on a different VP. This observation is very important because it means that the same individual might be inaccurately categorized as belonging to the bottom part of a continuum simply because of a suboptimal VP.

On the one hand, this highlights the need to rely on multiple measures to assess face cognition skills. On the other hand, it also suggests that assessing neural responses across multiple VPs or guided by eye movement data (e.g., preferred VPs) might be a better and more informative approach.

Reliability as a Potential Additional Measure

When attempting to measure one's skill, the tendency is often to assess how well one performs or how strong the response is. However, we show that for neural face processing, the magnitude of a participant's response is tidily linked to the reliability of its topographical distribution. Specifically, individuals who exhibited stronger responses shared a more focal and stable distribution than participants with weaker responses. Nonetheless, while our data reveal the existence of a relationship between these two elements, they provide no information concerning causality or whether one aspect might emerge before the other. To address this issue, future studies should track neural face discrimination response in populations likely to undergo changes in the face network such as developmental populations and should observe the evolution of response magnitude and topographical distribution.

Recent studies have shown that the amplitude of neural face discrimination responses correlates with behavioral performance in both face memory and rapid facial identity discrimination tests (Xu et al., 2019; Retter et al., 2021). The stronger an observer's responses, the higher their behavioral score. These data provide empirical evidence that the magnitude of the neural response recorded through FPVS can reflect the efficiency of the face system. In the same vein, the relationship between strong, focal, and reliable responses indexes a more optimal processing than weaker and scattered responses. It might be possible that a less efficient face network deploys more distributed resources to perform identity discrimination, for example. On the other hand, as a region becomes more proficient and specialized, it is also engaged more systematically and hence more reliably. However, given the low spatial resolution of EEG (Box2), future studies on this topic should also use neuroimaging techniques allowing a more detailed investigation of the neural structures leading to (un)reliable topographies.

Clarifying the relationship between response amplitude and topographical reliability could introduce a new tool to track changes in the face network. Specifically, topographical reliability could be used as an early marker to detect either an improvement or decline of face cognition. This could not only be important in developmental studies but also in assessments of interventions (e.g., congenital prosopagnosia).

6.1.3. General Limitations

Mismatch Between Eye Tracking and Fast Periodic Visual Stimulation Electroencephalography Setting

In Study 1, we compared natural fixation patterns with neural response patterns across VPs. However, during eye movement recording, subjects were required to perform an old-new task, which means learning and subsequently recognizing previously seen faces. In contrast, with FPVS-EEG, we assessed face identity discrimination. This difference in targeted process is not ideal because it is possible observers based their judgment on different information. Additionally, the stimuli used during the eye movement experiment included external features such as hairs and ears, which were cropped out of the face images used during FPVS-EEG.

While we still successfully found a relationship between eye movement and neural responses, more comparable settings might have revealed a clearer pattern of results.

Low Spatial Resolution of electroencephalogram

In our studies, we assessed neural face discrimination using EEG recordings. While this technique has its advantages, it also suffers from the inverse problem and therefore from low spatial resolution. Consequently, the source of individual differences in terms of amplitude as well as topography and reliability could not be determined.

For example, we reported that neural face discrimination could be either right or left lateralized or bilateral (see also results from Xu et al., 2019; Retter et al., 2021; Dzhelyova et al., 2019). However,

studies using fMRI as well as intracranial stimulation consistently report the presence of a right-hemispheric dominance for face processing (Rossion, 2014; Jonas et al., 2014; Rangarajan et al., 2014). Comparing within-subject EEG findings with recordings from techniques with higher spatial resolution might provide guidelines on how to interpret topographical variations recorded on the scalp. Additionally, as already mentioned above, high spatial resolution imaging would also help clarify the source of (un)reliable topographies like those reported in Study 2.

Small Number of Trials

Typically, FPVS responses are extracted from at least four trials (Liu-Shuang et al., 2014; Dzhelyova et al., 2019). However, in our studies, we consistently administered only two 62-second trials per condition to all our subjects. This choice was due to our interest in testing a relatively large number of conditions (ranging from 10 to 25). On the one hand, obtaining clear and significant neural face discrimination under these circumstances is proof of the strength of the FPVS-EEG technique and highlights the high SNR of the response elicited. On the other hand, we must acknowledge the fact that this practice was suboptimal. It is likely that increasing the number of trials would have also increased the SNR of the recorded response revealing significant responses in subjects that failed to show one in the current setting. Future studies should attempt to better balance the number of trials and conditions. Nevertheless, we do not expect that a relatively lower SNR is at the root of the observed individual differences since they are in line with results from independent groups (see Xu et al., 2019; Retter et al., 2021; and Dzhelyova et al., 2019 for individual differences in neural face discrimination responses elicited using FPVS).

Small Sample Sizes

The sample sizes used in the studies reported in this thesis were relatively small. This consideration is important in terms of the generalizability of our findings to the population. Specifically, because we were interested in exploring individual differences, testing a larger number of individuals would have allowed us to investigate the presence of patterns and their frequency more carefully. While we report

individual differences, we also note that some preferences are more likely to occur than others (e.g., a bias for the central VP). However, because of small samples, it is difficult to hypothesize about the prevalence of less frequent biases or patterns. Additionally, a larger number of observers belonging to the same category would have allowed us to explore in Study 2, for example, an association with response reliability. Finally, with a larger number of subjects, we might have included more individuals exhibiting rarer patterns or extreme biases. A more heterogenous set of responses might have revealed clearer or even additional relationships between measures of interest.

Arbitrary Choice of Viewing Positions

Another limitation relates to the choice of VPs. To determine them, we arbitrarily located nine equidistant points forming a rectangle whose top angle had to be centered on the eyes and the bottom middle point on the mouth. The 10th point corresponded to a location just below the eyes.

We chose this arrangement to target the main facial features. The 10th point was added to ensure comparability with previous work using FPVS to investigate neural face discrimination.

Using the same location of VPs across all subjects is both advantageous and disadvantageous. On the one hand, it allowed us to compare the response elicited by the same fixation across subjects. On the other hand, we might have approximated the preferred VP of some subjects. A better and more accurate approach would have been to base the choice of VP location on each observer's fixation map. This would have also made it possible to precisely target the most and least fixated facial regions and therefore decrease the number of tested conditions.

6.1.4. Future Directions

The work presented in this thesis provides empirical evidence of individual differences in information sampling preferences at both the oculomotor behavioral and neural levels. Our findings feed into the growing literature supporting the concept that idiosyncrasies can be a valuable source of information rather than a problematic noise to reduce. Nonetheless, I believe that individual differences may remain

a topic of active debate until we better comprehend them. Specifically, since their existence is becoming increasingly obvious, it is now time to better understand their origin as well as how deep they extend into the neural face network. Therefore, future studies should attempt to clarify both aspects.

Understanding the Source of Individual Differences

The data presented in this dissertation not only show the existence of individual differences in sampling strategies and in VP-dependent neural face discrimination but also clearly hint at an intricate combination of factors that might underly them. For example, in Study 3, we modulated the size of the stimuli, expecting VP dependency to be reduced at small scales. This hypothesis was motivated by the rationale that presenting small faces should have decreased the difference in visual input across VPs. Consequently, fixating below the eyes, for example, should have allowed sampling similar information than fixation on the nose. Nonetheless, we still observed within-subject variations across VPs and between-subject differences in sub(optimal) points of fixation. The persistence of these differences raises a crucial question: What drives individual differences in patterns of neural face discrimination across VPs?

Different elements might be at play and to different degrees account for the pattern of data observed.

Contribution of Fixated Versus Surrounding Information

The first major aspect that should be addressed is also one of the major limitations of this thesis, namely controlling for the contribution of foveal and parafoveal information to rapid neural face discrimination. In our experiments, all the facial information was always fully available to subjects, even during EEG when fixation was enforced on one location. This means that observers could have used both local and more global information to achieve face identity processing. While the choice of not constraining the amount of information available increases the ecological value of our experiments, it also represents an important limit to the interpretation of our results since the diagnostic value of the fixated information remains to be proven. In other words, stronger neural responses to specific VPs cannot be explained as a bias for a given local information but only as a preference for a sampling location.

Additionally, because we could not establish which information was used, we cannot infer which strategy (local vs. global) was deployed by subjects and whether this varied across VPs or stimulus size. This is particularly important to note because it has been shown that the same subject under specific experimental conditions can alternate between local and global sampling strategies (Miellet et al., 2011).

Prompted by our finding of idiosyncratic oculomotor and neural preferences, future studies should aim to clarify whether they are driven by fixated or surrounding information or both. To disentangle these different contributions, it would be interesting to use a gaze-contingent paradigm like Spotlight, which Papinutto and colleagues (2017) implemented to study the amount of facial information acquired within one fixation. This technique, originally introduced by Caldara and colleagues (2010) to study information use across cultures, consists of combining face stimuli with apertures centered on the point of fixation. These apertures, which can vary in diameter, are the only region containing diagnostic information to the task. In contrast with the first version, the Spotlight used by Papinutto and colleagues (2017) does not replace regions outside the apertures with a black mask; rather, it substitutes them with a noninformative average of multiple faces. This procedure allows the presentation of facial regions within the context of a whole face while at the same time controlling for the amount of information observers used. By comparing neural face discrimination recorded across various aperture sizes with that obtained without any contingency, it would be possible to determine the nature and reliability of information use during enforced fixation under an FPVS paradigm. By assessing which information drives the neural response, we would come closer to understanding the reasons beyond individual differences: do observers prefer different information, different strategies, or both?

Once the answer to this question is better understood, it would then be possible to focus on a second aspect that might shed further light on what drives neural preferences for specific VPs, namely properties of the visual field.

Contribution of Visual Field Properties

A crucial element that might play a role in identity processing across VPs is the properties of the visual field. Although visual acuity decreases the further from the fovea, it does so in a nonhomogeneous way. Studies have shown that face processing is better and faster when stimuli are presented in the upper versus lower (Quek & Finkbeiner, 2014) and left versus right visual field (e.g., Yovel et al., 2003). However, if individual differences existed in these asymmetries (e.g., more or less pronounced or not conforming to the average), it might be possible that sampling strategies as well as VP dependency in neural face discrimination reflect an attempt by the visual system to optimize perception and hence processing.

For instance, Peterson and Eckstein (2013) suggested that an individual with better upper than lower visual field vision might prefer to fixate on the mouth to sample with high acuity the lower part of the face but still manage to gather high-quality information from the upper regions.

To address this possible explanation of individual differences, future studies should evaluate VP-dependent neural face discrimination responses in relation to the physical properties of each participant's visual field. Specifically, if asymmetries in the visual field play a role in determining observers' preferences for specific VPs, then we would observe neural preferences for VPs that align the majority of the stimulus within the advantageous hemifield. Importantly, this aspect might also relate to the use of parafoveal and peripheral information when fixation is forced on certain VPs. It is plausible that when a given fixation locates the majority of the stimulus within the suboptimal hemifield (in terms of peripheral vision), observers might rely more on information acquired from central vision than from the periphery.

I believe that investigating these elements together and establishing how they interact might provide unique insight and a far more comprehensive view of individual differences.

Importantly, this should be complemented by investigating how a certain visual input triggers a cascade of process within face-sensitive areas that eventually results in successful identity discrimination. This

can only be achieved by complementing EEG data with those from neuroimaging techniques with better spatial resolution.

Understanding the Extent of Individual Differences Within the Neural Face Network

Our studies clearly show that the neural face discrimination response is idiosyncratically modulated by the VP fixated across subjects. Future studies should now assess how deep these individual differences run. In other words, are they simple differences in information preference, or do these different biases shape how identity processing is achieved by identity-sensitive cortical regions?

It is possible that depending on the information systematically fed to the neural face network, identity processing might rely to a greater extent on a specific region.

An interesting comparison could be that between observers deploying a global versus local sampling strategy. Cross-cultural studies have shown that these two types of observers rely on different spatial frequencies to process identity. At the group level, Caucasians sample faces more locally, extracting more high spatial frequencies compared to Asians, who deploy more global strategies using low spatial frequencies to a greater extent (Tardif et al., 2016; Estéphan et al., 2018).

Interestingly, sensitivity to high and low spatial frequencies might also differ between two cortical regions crucial for identity processing, namely the OFA and FFA. On the one hand, the OFA has been associated with a fine-grained analysis and more sensitive to high spatial frequencies. On the other hand, the FFA appears to be involved in extracting a holistic percept and might rely more (at least in early stages of processing) on low spatial frequencies (Goffaux et al., 2011; Rotshtein et al., 2007).

Therefore, future studies should attempt to determine whether observers systematically using global strategies to extract identity-related information might also show greater FFA activation compared to individuals relying more on local strategies, who might in turn engage the OFA to a greater extent. Additionally, exploring more precisely the underlying neural mechanisms associated with individual differences would also benefit the formalization of future neurofunctional models of face processing. By accounting for the existence of idiosyncrasies, new frameworks might provide a more accurate representation of human face cognition.

6.2. Conclusions

Taken together, the data described in the three experimental contributions presented in this thesis highlight the presence of individual differences in the strategy used by observers to sample facial information and in the pattern of neural face discrimination responses triggered by fixation on different facial regions (VPs). Crucially, this work provides evidence that these individual differences are functionally meaningful and reliable. This is in stark contrast with the idea that variations across individuals are due to noise. The fact that the roots of individual differences might not be crystal clear should not discourage but rather motivate further investigations. The closer we can get to understanding what shapes the visual system, the closer we will get to seeing the full picture. Ultimately, I believe that the only approach that will bring concrete results is one that integrates multiple measures and considers individual differences from multiple perspectives. Understanding what makes people different might in the end be what will allow understanding of something as complex and flexible as human face cognition.

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Lisa Stacchi
Via A. Fordele 3
6702 Claro, Switzerland

PERSONAL INFORMATION

Affiliation	University of Fribourg (Switzerland)
Email Address	lisa.stacchi@unifr.ch
Date of Birth	14.11.1992
Gender	Female
Nationality	Swiss
Country of Residence	Switzerland
Cell	0041 79 396 62 92

EDUCATION

2011-2014	Bachelor in Science in Psychology University of Fribourg
2014-2016	Master of Science in Psychology Option: Cognitive Neuroscience Supervisor: Prof Roberto Caldara University of Fribourg (Switzerland)

2016- Present **PhD student in Science in Psychology**
Cognitive and Visual Neuroscience
Supervisor: Prof Roberto Caldara
University of Fribourg (Switzerland)

WORK EXPERIENCE

July - Internship at the prison **LaStampa** in Lugano
August 2013 (Switzerland)

Conducted counseling sessions with inmates

September - Internship at the **Institute of Neuroscience**
October 2015 **and Psychology**

University of Glasgow
Supervisor: Dr. Guillaume Rousselet
Assisted lab's ongoing EEG projects

November 2015 - **E-Prime tutor** for Bachelor students
February 2016 (University of Fribourg)

March - Internship at **LCNS research group**
April 2016 University of Fribourg

Supervisor: Dr. Lucas Spierer
Assisted with neuroimaging projects (MRI,
TMS and EEG) involving non-/human primates

October 2016 - Present	University graduate assistant University of Fribourg I supervise Bachelor and Master students for their thesis
November 2016 - February 2017	I was a tutor for the E-Prime course for Bachelor students
Fall semester 2019 and 2020	I gave the first part of the "Sleep and Visual Neuroscience" course (i.e., Visual part) in English to Master Students

PERSONAL SKILLS

Language

Italian: Native speaker
English: IELTS score 8 (C1)
French: Fluent
German: Basic communication knowledge

Digital skills

Office softwares
Matlab: EEGLab, Letswave, Psychtoolbox, Fieldtrip
Python
R
SPSS
E-Prime
PsychoPy

Data analysis

EEG (ERP, steady-state evoked response)
Oculomotor behavior

Laboratory skills

Data acquisition: EEG (BioSemi)
Eye-movements (EyeLink)

PUBLICATIONS

Ruffieux*, N., Ramon*, M., Lao*, J., Colombo, F., Stacchi, L., Bourrat, X., Accolla, E., Annoni, J.-M. & Caldara, R. (2016). Residual Perception of Biological Motion in Cortical Blindness. *Neuropsychologia*, 93, 301-311. (* equal contribution)

Stacchi, L., Liu-Shuang, J., Ramon, M., & Caldara, R. (2019). Reliability of individual differences in neural face identity discrimination. *NeuroImage*.

Stacchi, L., Ramon, M., Lao, J., & Caldara, R. (2019). Neural representations of faces are tuned to eye movements. *Journal of Neuroscience*, 39(21), 4113-4123.

Stacchi, L., Huguenin-Elie, E., Caldara, R., & Ramon, M. (2020). Normative data for two challenging tests of face matching under ecological conditions. *Cognitive Research: Principles and Implications*, 5(1), 1-17.

Fysh, M. C., Stacchi, L., & Ramon, M. (2020). Differences between and within individuals, and subprocesses of face cognition: implications for theory, research and personnel selection. *Royal Society open science*, 7(9), 200-233.

Stacchi, L., & Caldara, R., (In preparation). Reducing individual differences in neural face identity discrimination.

TALKS

Let's Face It: Idiosyncratic Neural Signatures of Face Discrimination. Alpine Brain Imaging Meeting, 2017, Champéry, Switzerland.

Idiosyncratic Neural Signatures of Face Discrimination - A Fast Periodic Oddball Stimulation Study. Vision Science Society, VSS 2017, St. Pete Beach, Florida.

Unravelling the neural coding of idiosyncratic fixation strategies for faces. 40th European Conference of Visual Perception, 2017, Berlin, Germany.

Idiosyncratic neural signatures of face discrimination. Swiss Psychological Society, 2017, Lausanne, Switzerland.

Assessing the reliability of neural face identity discrimination with FPVS. 42nd European Conference on Visual Perception, 2019, Leuven, Belgium.

Neural face representations are tuned to eye movements. Swiss Psychological Society, 2019, Bern, Switzerland.

POSTERS

Mapping the neural correlates of idiosyncratic fixation strategies for faces. 3rd Symposium on cutting-edge methods for EEG research, 2017, Glasgow, United Kingdom.

Assessing the reliability of neural face discrimination with fast periodic visual stimulation. Vision Science Society, VSS 2018, St. Pete Beach, Florida.

Normative data for two ecologically valid tests of face identity matching. Vision Science Society, VSS 2019, St. Pete Beach, Florida.

PUBLICATION LIST

Experimental research paper presented in this thesis:

Stacchi, L., Ramon, M., Lao, J., & Caldara, R. (2019). Neural representations of faces are tuned to eye movements. *Journal of Neuroscience*, 39(21), 4113-4123.

Stacchi, L., Liu-Shuang, J., Ramon*, M., & Caldara*, R. (2019). Reliability of individual differences in neural face identity discrimination. *NeuroImage*. (*equal contribution)

Stacchi, L., & Caldara, R., (submitted). Stimulus size modulates idiosyncratic neural face identity discrimination.

Other publications

Ruffieux*, N., Ramon*, M., Lao*, J., Colombo, F., Stacchi, L., Bourrat, X., Accolla, E., Annoni, J.-M. & Caldara, R. (2016). Residual Perception of Biological Motion in Cortical Blindness. *Neuropsychologia*, 93, 301-311. (* equal contribution)

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Déclaration sur l'honneur

Par ma signature, j'atteste avoir rédigé personnellement cette thèse sans aide extérieure non autorisée, n'avoir utilisé que les sources et moyens autorisés, et mentionné comme telles les citations et paraphrases. Cette thèse n'a pas déjà été présentée devant une autre faculté.

J'ai pris connaissance que le comportement scientifique délictueux selon les directives de l'Université de Fribourg* est sanctionné.

Nom(s) : STACCHI

Prénom(s) : LISA

Lieu et date : 03.12.2021

Signature manuscrite : 

Références bases légales

- Règlement du 11 décembre 2014 pour l'obtention du doctorat à la Faculté des lettres de l'Université de Fribourg
- Règlement du 18 décembre 1990 (Etat le 22 janvier 2004) de doctorat de la Faculté des lettres de l'Université de Fribourg

* Directives du 13 mai 2008 concernant la procédure de prononcé des sanctions disciplinaires selon l'art. 101 des Statuts du 31 mars 2000 de l'Université de Fribourg dans les cas de violation des règles de l'intégrité scientifique lors de la rédaction de travaux pendant la durée de la formation

