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Clarifying the Neurophysiological Basis of the Other-Race Effect

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Summary

The other race effect (ORE) is a well-known phenomenon whereby individuals tend to identify more accurately faces from their same-race (SR) as opposed to faces from the other-race (OR). First reported by Feingold (1914), almost a hundred years ago, since then the ORE has found consistent support at the behavioural level. In spite of a general consensus regarding the robustness of this effect, theoretical accounts have thus far failed to reach an agreement concerning the causes underlying this phenomenon. Two main strands exist within the academic literature, differing on the alleged roots of the ORE. One regards this phenomenon as stemming from different levels of expertise individuals hold with SR and OR face (i.e. the expertise based accounts); the other advocates the importance of social cognitive factor (i.e. the social cognitive accounts). Neuroimaging data can provide important insights in understanding the basis of the ORE. These studies though have thus far failed to reach a degree of consistency. EEG data for example are highly contradictory. A number of studies report no race sensitivity on the N170 face preferential component, while others show that this component is in fact modulated by race. However, discrepancy is found even amongst the study reporting N170 modulation to race, with some showing larger N170 to SR faces, while others revealing the opposite pattern. Similarly, fMRI data show the same degree of inconsistency, especially with regards to the role played by the fusiform face area (FFA). The aim of this thesis is to clarify the neurphysiolological basis of the ORE in order to gain further insights into its origins. To this end three studies (two employing EEG and one fMRI) were designed to answer three main questions related to the ORE: when, how and where in the brain does this phenomenon occur.

The first study investigates the conjoint effects of race and the face inversion effect (FIE - regarded as a marker of configural face processing) on the N170. Interestingly, no race modulations on this ERP component were observed for upright faces. Race however impacted upon the magnitude of the electrophysiological FIE, with SR faces leading to greater recognition impairment and eliciting larger N170 amplitudes compared to inverted OR faces. These results indicate that race impacts upon early perceptual stages of face processing and that SR and OR faces are processed in a qualitatively different manner.

The second study exploites the advantages conferred by adaptation paradigm to test neural coding efficiency for faces of different races. An unbiased spatiotemporal data-driven analysis on the newly developed single-trial repetition suppression (srRS) index, which fully accounts for the paired nature of the design, revealed differential amounts of repetition suppression across races on the N170 time window. These data suggest the SR faces are coded more efficiently than OR faces and, in line with the previous results, that race is processed at early perceptual stages.

The final study investigates whether and where in the brain faces are coded according to the laws predicted by valentine's norm based multidimensional face space model. Representational Dissimilarity Matrices (RDM) showed that faces are coded as a function of experience within the dominant FFA according to the laws of valentine's theoretical framework

Importantly in all experiments I tested both Western Caucasian (WC) and East Asian (EA) observers viewing WC and EA faces. A crossover interaction between the race of the observers and that of the face stimuli is in fact crucial to genuinely relate any observed effect to race, and exclude potential low level confounds that may be intrinsic in the stimulus set.

These data, taken together indicate that the ORE is an expertise based phenomenon and that it takes place at early perceptual level of face processing.

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1. Introduction

It was July when in 1984, in her own house, Jennifer Thompson, a Caucasian woman, was assaulted and raped by an African American man. The victim later identified Ronald Cotton as her assailant both in photo-spreads as well as in a live line-up. The woman seemed extremely confident in her choice, and the idea that the convicted man was risking a life sentence did not affect her decision making process. Jennifer claimed that her assailant had a very distinctive nose, just like the one of the identified criminal. Cotton was thus convicted. The years passed and Cotton was serving his sentence in prison. In 1987, however, one of Cotton's fellow inmates confessed that it had been him three years earlier to have committed rape on Jennifer Thompson. The confession was not enough for Cotton's release, in light of the weight placed on the eyewitness identification. It was only years later, in 1995 that unequivocal DNA evidenced proved Cotton's innocence. The man, after unjustly serving 11 years in prison for a crime he did not commit, was released. Upon his release, Cotton was offered $5000 compensation, which he refused. How could such a fatal case of misidentification have occurred? How can an individual, like Jennifer Thompson, commit such an error in recognizing a face? Are human beings not supposed to be expert and thus extremely proficient at face recognition? While compelling evidence indeed demonstrated humans' outstanding ability in face recognition, the ease with which it occurs leads us sometimes to forget the highly complex neural and computational mechanism underlying face processing. It is only when these mechanisms come to fail that we begin to ponder about their intricacy. One such case is the recognition of other-race faces. People are consistently more accurate at recognizing faces from their same race as opposed to other race. This well documented phenomenon is known as the Other Race Effect (ORE – Feingold, 1914). In a recent survey, 80% of experts agreed that the ORE is reliable enough to be presented in court (Kassin, Tubb et al. 2001). These data do not signify that this phenomenon always occurs, or that is equally displayed by all individuals, but they suggest that it has potentially devastating consequence in daily life (as it was the case for Ronald Cotton). Importantly, there is no generally agreed upon reason for why or how it occurs. The purpose of this thesis is to investigate the neural basis of the ORE for faces. In doing so I will attempt to answer three specific questions: when, how and where in the human brain the ORE occurs. Shedding light on the neuphysiological basis of this phenomenon will provide an unbiased way to understand its origin and frame it within a precise theoretical account.

Given the nature of the ORE, and the fact that it is a phenomenon occurring with faces, the opening pages of this thesis will focus on the general realm of face processing. The very first paragraphs will describe and evaluate one of the most influential accounts of face processing: the Bruce and Young model (1986). A review of the behavioural and neuroimaging data for and against the view that faces are special will follow. Before looking at the neurophysiological work carried out on the ORE, I will provide an account of the main theoretical hypothesis regarding the origin of this phenomenon. A brief section on the methods employed throughout this work (i.e. elctro-encephalogram and functional magnetic resonance imaging) will precede the original empirical studies included in this thesis.

1.1 Bruce and Young Model of Face Processing

Preamble

The scope of these first paragraphs is to provide an understanding of one of the main models of face processing that has dominated the face literature within the last 20 years: Bruce and Young (1986) model. In doing so, an attempt will be made to make the reader aware of some of the main interrogatives in the field of face processing; moreover I aim to provide a framework that will allow the reader to begin to grasp the complexity underlying the neural and computational mechanism underlying face processing. In evaluating the evidence for and against this model, this chapter will also introduce a neuropsychological condition which has been crucial to our understanding of face processing and that will be referred to several times throughout this thesis: prosopagnosia.

One of the first and most influential models of face recognition is the one put forward by Bruce and Young (BY - 1986) (Figure 1). Based on observations gathered from both patients and normals, the authors argued that discrete stages of face processing can be isolated in brain damaged patients or through experimental manipulations, thus concluding that face recognition occurs in a *modular* fashion (Rakover and Cahlon 2001). Each stage (or module) plays a specific cognitive and/or functional role in processing and storing facial codes. The model, often referred to as the "box and arrows model" (Rakover and Cahlon 2001) is depicted in Figure 1, with the boxes representing the modular units, and the arrows the direction of information flow. Facial information is accessed sequentially (Bruce and Young 1986) by each unit, which feeds on information transformed and outputted by the preceding module.

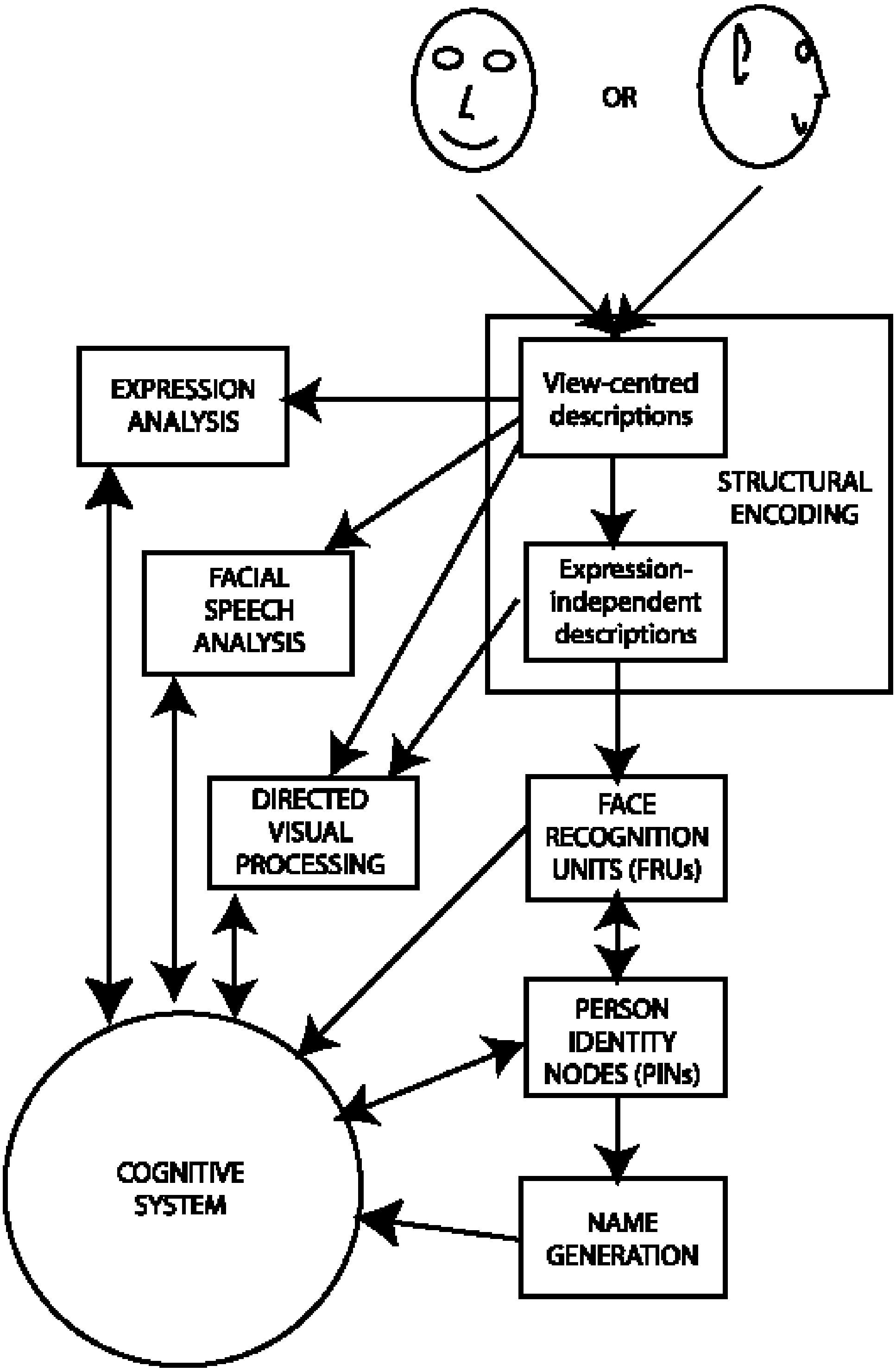

Figure 1 – the Bruce and Young model

Like all model of face recognition, Bruce and Young's account has to deal with a multitude of extremely complex issues. For example, from the very moment in which a face enters the visual field and has to be categorised as a human face, one of the first challenges encountered is forming a percept comprehensible at the cerebral level. Initially, in fact, such a representation has to be based on mere projections of light reflection from the surface of the object at hand (e.g. a face) to the back of the retina.

However, a substantial number of three-dimensional shapes can have an extremely similar two-dimensional projection. This problematic multidimensional reconstruction, deeply rooted dimension reductionality theory, represents one of the major challenge scientists must face when investigating neural and psychological mechanisms underlying efficient and successful processing of highly unspecific retinal projections.

In the attempt to resolve this issue, Bruce and Young referred to the work of Marr (1978; Marr 1982), which directly tackles the manner in which a structural representation of an object is constructed.

According to Marr (1978; Marr 1982) there are three stages beyond retinal representation. In the first stage, the *primal sketch,* light intensity changes from the image projected on the retina are grouped into distinct structures. This process allows the detection of the object from the background and leads to the creation of *the viewer centred representation,* which represent the second stage of the Marr's model. The latter, also referred to as *2½D sketch*, contains surface layout information from the observer's perspective. Finally an *object centred representation* (i.e. 3D model), allowing recognition of the object from any viewpoint, is computed. This last stage relies on both *bottom-up* processes, induced by the object, as well as *top-down* processes stemming from the subject's experience.

While Marr's model offers invaluable contribution towards the understanding of how structural representations are construed, it still fails to provide a satisfactory answer to a crucial question within the realm of face recognition: what are the *invariant* properties of a face required to form a structural representation that allows distinguishing across exemplars/recognition. This question is at the core of Bruce and Young's work and it encompasses the initial stages of their theory.

The process of "Structural encoding", representing the first unit of the model, comprises two discrete modules: the "view-centred" and the "expression-independent" descriptions, both dealing with the extraction of visual-structural information needed to differentiate across identities.

Within the first of these 2 stages (i.e. the "view-centred" module), low level visual information, such as luminance and contrast, is extracted from the target face to form what Bruce and Young define *pictorial code*. This representation is thus influenced by orientation, size and colour of the target stimulus (Rakover and Cahlon 2001). The second set of codes computed within the structural encoding stage – namely the "expression-independent" descriptions – can be quantified as a representation of the target face emerging from different view-points, combined with the visual information provided by the "view-centred" module. This representation, referred to as *structural code,* is independent of facial expression and appearance and embodies the abstract portrayal of the configuration of the face as a whole, including the individual facial features required for face recognition as well as their spatial relation. The representation of a face is built upon information gathered within both stages. However, factors such as experience or familiarity determine the relative weights of the contribution of facial codes from different units. Unfamiliar face representations rely mainly on "view-centred" information. Accordingly, empirical data suggest that a change in low level visual information – for example, caused by a change in viewing angle – significantly diminishes recognition performance for un-familiar, but not for familiar faces (Megreya and Burton 2006). Yet, more recent evidence calls for a re-evaluation of this aspect of the model. Russell (2007) show a greater impact of surface reflectance compared to shape in the recognition of familiar faces, indicating the importance of low level visual properties to the recognition of this sub-category.

Indeed "expression-independent" information is widely used in everyday life. For example, we have no troubles identifying the face of a familiar individual regardless of changes in external features, such as hair style. It has been shown that external facial features impact differentially upon recognition performance of familiar and unfamiliar faces (Ellis, Shepherd et al. 1979; Young 1984; Young, Hay et al. 1985). Ellis (1979) showed that while individuals relied equally on internal as well as external features in recognizing unfamiliar faces, internal features are more diagnostic for familiar face recognition. A large number of studies have highlighted the differential importance of several internal features to identification (Davies, Ellis et al. 1981; Sadr, Jarudi et al. 2003 300; Vinette, Gosselin et al. 2004; Avidan, Hasson et al. 2005). What seems to be even more important in identifying a face though is the relation amongst these features, rather than the features in isolation (for a review Maurer, Grand et al. 2002).

Several lines of research show that amongst the internal features the eyes are most diagnostic (e.g. Young, Hay et al. 1985; Vinette, Gosselin et al. 2004) followed by the mouth and the nose (Caldara, Zhou et al. 2010).

Controversially, however, it still remains to be clarified whether the diagnosticity of internal traits is invariant to factors such as expertise (however see Caldara, Zhou et al. 2010). It has been argued, for example, that *race* shapes the choice of salient information individuals choose to fixate upon when scanning a face (Fu, Hu et al. 2012). Fu (2012) found that Chinese participants spent significantly more time fixating the nose and mouth of same race (SR) compared to other race (OR) Caucasian faces during an old/new recognition task. The reverse pattern (i.e. more time on the eyes for OR compared to SR faces) was observed when the same group of participants were fixating OR faces. Somewhat contrasting are the data put forward by Blais (2008). The authors showed that regardless of the task (i.e. learning, old/new, categorization) and the race of the face stimuli, western Caucasian (WC) participants tend to fixate more on the eyes and mouth, while Eastern Aasin (EA) participants more on the nose. Moreover, a follow up study from the same lab, further showed by means of gaze contingent paradigm that, although the fixation strategies were different across WC and EA observers, the most diagnostic information required to recognize a face were contained within the same region, with both groups mostly relying on the eyes (Caldara, Zhou et al. 2010). While several factors could be held accountable for these apparently divergent results (e.g. methodological differences), it is worth noting that Fu et al. only tested Chinese participants, while Blais and her collaborators looked at both WC and EA observers. This point is crucial in that, firstly a full crossover interaction is required to determine whether the observed results can be genuinely related to the race of the observers; and secondly Blais (2008) explain that the observed differences emerge when comparing fixation patterns across groups (i.e. WC minus EA fixation maps).

While the above results are somewhat diverging, they can both be accounted for within BY's framework. As explained earlier, the model predicts that, as a function of expertise, face representations will be construed with differential contribution of diverse types of information. Having different information available in the stored face percept could result in fixating different areas of a face in the attempt to best match the available information profile (i.e. SR and OR faces, as shown by Fu, Hu et al. 2012). Alternatively the same facial regions might be fixated (as shown by Blais, Jack et al. 2008), more or less efficiently. The only unavoidable outcome predicted by BYs model is that expertise will impact upon recognition performance, which is what both studies report (higher accuracy for SR compared to OR faces).

We have seen so far how, in the first stages of BY model, the representation of a target face is formed through a combination of lower (e.g. light reflectance projections on the retina) and higher (e.g. the expression independent representation) level visual input.

This newly formed face percept has to now be compared against stored information about known faces. Such information is stored within the "face recognition units" (FRUs). Within the "cognitive system" – depicted in the bottom right of Figure 1 as a cloud – the codes generated within the "expression-independent description" and those stored within the FRUs are compared, and the similarities between the two are assessed. If the two representations are deemed similar enough, the target face is recognised. It is so that identity-specific semantic information about the person is accessed. These are held within the "person identity nodes" (PINs), and can be accessed only after recognition. Empirical evidence supports this claim, showing that it is not possible to access identity-specific information without having first identified the face (e.g. Young, Hay et al. 1985; Schweich, Van der Linden et al. 1992). According to Bruce and Young, "there is only one person identity node for each person known" (p.312, 1986), and a limited amount of representations can be stored and retained within memory. Only when PINs are successfully activated, we know that we have correctly identified our target. Finally, after effective retrieval of semantic information, which is itself dependent on successful recognition, the relevant name is accessed through the "name generation" unit. In support of this sequential hierarchy, several lines of research have shown for example that the name of a person is recovered significantly after the information related to the person in question (Sergent 1985; Young, McWeeny et al. 1986; Young, McWeeny et al. 1986).

It is important to understand that, according to Bruce and Young (1986), the FRUs and the PINs carry out distinct functional role. The former contains only to the visual information of the identity of a face, which are exemplified as abstract long term memory representations; the latter, instead stores codes about the person's face, voice, name or distinctive semantic information, such as a particular piece of clothing (Ganel and Goshen-Gottstein 2002). It is this specific response profile that allows identifying a person through alternative routes. The information stored within the PINs can be accessed through associative memories formed in the "cognitive system". As shown in Figure 1 the "view centred descriptions" unit is directly linked to the "expression analysis" and "facial speech units", which, through the cognitive system are linked to the PINs, bypassing the “expression independent” modules. To this end it is important to clarify that PINs lead to the recognition of a person as opposed to the recognition of a face. The view of the existence of an alternative *parallel* route leading to face recognition is still nowadays strongly debated (e.g. Calder and Young 2005).

Supporting the parallel route hypothesis is the evidence gathered by patients’ studies, specifically prosopagnosic individual, which fit well also within the broader BY’s framework. Before reviewing the evidence for and against the parallel route hypothesis, it would seem appropriate to provide an understanding of the main concepts and debates reigning in the academic literature around prosopagnosia. In this next session therefore the focus of this chapter will monetarily shift away from the BY’s model of face processing to be centred on prosopagnosia, which will be often referred to throughout this thesis.

Prosopagnosia - The term prosopagnosia comes from the ancient Greek language: *prospon*, meaning face, the prefix *privative a* (alpha), which added to words negates their meaning, and *gnosia*, translated as knowledge. As the word itself suggests, prosopagnosia is a disorder characterised by a deficit in face recognition abilities, often in the absence of impairments in low level visual abilities (Bentin, Deouell et al. 1999; de Gelder and Rouw 2000; Nunn, Postma et al. 2001). In individuals affected by this condition, face recognition is dramatically impaired, yet a person’s recognition can be attained through alternative means. To achieve identification in facts prosopanosic patients strongly rely on the voice of an individual, or on characteristic external features, such as specific hairdo or eccentric clothes. The extent to which prosopagnosia is a deficit solely related to face processing however is still matter of debate (Behrmann and Avidan 2005). A number of neuropsychological studies on prosopagnosic patients suggest a dissociation between recognition of faces and objects (McNeil and Warrington 1993; Moscovitch, Winocur et al. 1997) with the processing of the latter being intact. Moreover, data from ERP (Bentin, Allison et al. 1996), fMRI (Kanwisher, McDermott et al. 1997) and non-humans primate electrophysiology (Perrett, Rolls et al. 1979; Rolls 1984) indicate the existence of a specialized cortical face network[1] (Kanwisher 2000), which is damaged – either

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[1] More details on the existence of a dedicated cortical face network on paragraph 1.2

functionally or structurally – in prosopagnosic individuals. These data would thus seem to suggest that prosopagnosia is indeed a deficit specific to faces.

On the other hand however it has been argued that both faces and objects processing are sub-served by the same neural mechanisms (Tarr and Cheng 2003); and that the observed dissociation amongst the two categories is a mere consequence of the strenuous demands placed on the system by faces (Tarr and Cheng 2003). Faces are in fact the only stimulus category for which humans hold an astonishing expertise. As a consequence, whereas other objects are usually categorised at a basic level (for example, as a chair or apple or house), face processing classically entails within category identification, based fine-grained discrimination of perceptually similar exemplars. A number of studies have attempted to shed light onto whether face impairment in prosopagnosic individuals can be exhaustively accounted for in terms of a general deficit in within category discrimination. Supporting this stand, a number of data have reported difficulties for within-class categorization of objects sharing the same complex configuration (Damasio, Damasio et al. 1982; De Haan and Campbell 1991; Etcoff and Freeman 1991; Gauthier, Behrmann et al. 1999). A different strand of research though showed no differences between normals and patients in within category objects discrimination (De Renzi, Faglioni et al. 1991; Sergent and Signoret 1992; Farah, Wilson et al. 1995; Duchaine, Dingle et al. 2004), leaving the debate of whether prosopagnosia is a domain specific condition widely open (Kanwisher 2000; Tarr and Gauthier 2000; Haxby, Gobbini et al. 2001; Maurer, Grand et al. 2002; Grill-Spector 2003; Tarr and Cheng 2003).

Different types of prosopagnosia – Within the academic literature prosopagnosic patients are classified in three sub-categories. These are:

1) Acquired prosopagnosia
2) Congenital prosopagnosia
3) Developmental prosopagnosia

As the name itself suggest, the first type of prosopagnosia – namely *acquired prosopagnosia* –refers to that category of patients that have acquired the deficit at some stage during their life span, usually as a consequence of structural or functional brain damages (e.g. Behrmann and Moscovitch 2001). C*ongenital prosopagnosics* instead are born with the deficit and they do not display any structural brain damage (for a review see Behrmann and Avidan 2005). Finally, *developmental prosopagnosia* is a lifelong variant of the disorder, which develops in childhood. It can include both cases of acquired prosopagnosia – at the condition that the acquisition of the disorder occurred before birth or in childhood (de Gelder and Rouw 2000; Farah, Rabinowitz et al. 2000; Barton, Cherkasova et al. 2003; Duchaine and Nakayama 2004) – and congenital prosopagnosia.

A further distinction amongst prosopagnosic patients often occurs on the basis of the different forms of deficit displayed. The two main types reported in the academic literature are those of *apperceptive* and *associative* prosopagnosia (Lissauer 1890). In individual affected by the former face recognition brake-down occurs at the very initial stages of face processing and it is epitomised by the inability to form an intact face percept (Lissauer 1890). Consequently, apperceptive prosopagnosic patients for example find it difficult to perform same-different judgement on pictures of different faces; and they are unable to assess age, gender or race from a face stimulus alone. These individuals in facts strongly rely on external cues (such as voice and clothing) in order to identify a person (Barton, Cherkasova et al. 2004). Within BY's model, such a deficit would take place at early structural stages of face processing, specifically within the expression independent unit. Associative prosopagnosic patients instead, in spite of a relatively intact computation of a face percept fail to achieve identification due to impairments to the links between early face perception and the semantic information held in memory (Lissauer 1890). Individuals affected by this facet of the condition may perform better on same-different judgments of two face stimuli, and are significantly better at deriving age and gender information from a face (Gainotti and Marra 2011). However, they struggle when asked to identify the person or provide such information as the target's occupation or name (Gainotti and Marra 2011). Associative prosopagnosic patients may also be able to recognize information that is external to the face, such as hair or voice; and they are likely to report that faces are not distinctive (Gainotti and Marra 2011).

Interestingly though, a number of authors have challenged the existence of pure associative prosopagnosia (e.g. Davidoff and Landis 1990; Farah 1990). The claim stands that, when assessed extensively, all visual agnosic patients – including prosopagnosics – display perceptual deficits (e.g. Joubert, Felician et al. 2003; Bukach, Bub et al. 2006). For example, although it has been reported that some prosopagnosic patients' performance on unfamiliar face matching task (i.e. judging whether the pictures of two faces belong to the same identity) falls within the normal range in terms of accuracy, while their reaction times are well above the norm (e.g. Davidoff and Landis 1990; Delvenne, Seron et al. 2004; Bukach, Bub et al. 2006). It has to be noted however that prosopagnosic patients display consistent variability in terms of the level of perceptual deficit displayed (e.g. Sergent and Signoret 1992; Schweich and Bruyer 1993; Barton, Cherkasova et al. 2004). This observation has led a number of researchers to assert that the distinction between associative and apperceptive prosopagnosia should be based on the degree of perceptual impairment, rather that the type (Mayer and Rossion 2007). Finally, recent studies have suggested that the shortcomings possessed by prosopagnosic patients stem from the extraction of configural information, such as the metric relationship amongst internal features (eyes, nose, mouth, etc…), rather than the features themselves (Barton, Press et al. 2002; Joubert, Felician et al. 2003).

Having provided a basic account of prosopagnosia, the focus will shift back to BY's model. We previously talked about the distinct roles carried out by the FRUs and PINs. The former entail only visual information of a given face identity; while the latter are concerned with several aspect of a person's identity, including their face, voice and distinctive sematic information. As explained earlier the diverse functional profiles of these two units allows the conceptualization of two independent and parallel processing routes leading to the identification of an individual. Perhaps one of the most convincing lines of evidence supporting the existence of two distinct processing routes leading to the identification of an individual is the work carried out on prospopagnosic patients. The face processing deficit displayed by this group hinders their ability to recognize a person through information carried by the face's internal features, yet they achieve identification by maximizing the use of other information, such as clothing, voice or even face shape.

An important implication of the independency of these routes, and perhaps to date the most controversial, is that identity-related and identity-unrelated information (such as gender, facial expression, mouth shape, gaze direction) are processed by independently in a parallel fashion (Bruce and Young, 1986, Calder et al, 2001). The rationale behind the conceptualization of independent routes for processing different facial dimensions comes from the understanding that representations of identity should be relatively independent of the representations of changeable aspects of faces. The lack of such independency could lead to misinterpreting change in expression or speech-related movements of the mouth as a change of identity. Empirical data directly tackling this issue have mainly focused on gender judgment and expression judgment (Ganel and Goshen-Gottstein 2002). Behavioural studies on gender judgement have produced results that are clearly dissonant with the parallel route hypothesis (Goshen-Gottstein and Ganel 2000; Calder, Burton et al. 2001; Baudouin and Tiberghien 2002; Ganel and Goshen-Gottstein 2002). For example, Goshen-Gottstein and Ganel (Goshen-Gottstein and Ganel 2000) reported repetition-priming effects to identity when gender judgment was performed. They concluded that the processing of gender and facial identity are performed by a common cognitive route. Further evidence for the idea that gender and identity are not processed by independent routes comes from the study of Ganel (2002). The authors, by means of Garner's speeded-classification task, found that selective attention to either gender or identity could not be achieved independently of one another.

As explained above, an overwhelming wealth of evidence seems to point towards the cognitive dependency in processing identity and gender information. On the other hand however, a number of studies have provided data supporting a parallel route for the processing of identity and expression (Tranel, Damasio et al. 1988; Young, Newcombe et al. 1993; Breiter, Etcoff et al. 1996; Campbell, Brooks et al. 1996; Schweinberger, Baird et al. 2003). Neuropsychological data provide support for the existence a parallel-route of identity and expression. Prosopagnosic patients for example are impaired in recognizing faces, and yet they maintain the capacity to process expression relatively intact (Tranel, Damasio et al. 1988; Parry, Young et al. 1991; Humphreys, Donnelly et al. 1993). Moreover, several studies report patients showing the reverse dissociation (Kurucz and Feldmar 1979; Kurucz, Feldmar et al. 1979; Humphreys, Donnelly et al. 1993; Hornak, Rolls et al. 1996). Behavioural data from healthy subjects also suggest that identity and expression are processed independently. Repetition priming effects have been reported for facial identity, but not for expression judgement (Ellis, Young et al. 1990). Somewhat contrasting however, are the results of Young et al (Young, Newcombe et al. 1993). They described the case of a patient, D.R., with amygdalotomy, who was severely impaired in performing expression judgement, with a relatively intact ability to perform identity matching. Critically though, when presented with 2 simultaneous image of the same identity with different emotional expression, D.R. reported the images to belong to different individuals. Young et al. concluded that the failure of the patient correctly classify the expressions of the images somehow interfered with their face identification skills. Furthermore studies on aftereffects (e.g. Fox, Oruc et al. 2008) and recognition (e.g. Kaufmann and Schweinberger 2004) also show a degree of processing interactions between facial identity and expression. Schweinberger (1998) for example showed that changes in facial identity required to be ignored significantly increase participants' RTs to categorise facial expressions. Interestingly, however the opposite was not found to be true (Schweinberger and Soukup 1998). Finally Ganel (2004) showed in a series of experiment that familiarity increases the perceptual integrality between identity and expression. In order to accommodate their findings as well as those reported within the academic literature, the authors explain that there are indeed two separate systems for processing identity and expression as originally suggested by Bruce (1986), but that these are not completely independent. The two systems in fact interact with identity, which functioning as a reference point from which expressions can be easily derived.

Moreover, according to BYs model, depending on the task demands, visual attention may have to be selectively directed to different features. This is the role of the "directed visual processing" unit, which strategically directs visual attention to the task-relevant aspects of the target face. The data put forward by Eisenbarth (2011) support this claim. In recognizing a specific emotion, different facial features may be more or less diagnostic. Examining eye scan patterns of healthy participants, Eisenbarth (2011) recently showed that in sad facial expressions, individuals are more likely to fixate the eyes compared to all other expressions. In happy facial expressions, however, participants fixated the mouth region for a longer time.

It is worth noting that as Bruce (1986) argued the "cognitive system" deeply involved in all the processes carried out within the model. Several modules, such as the PINs and "directed visual processing", have been posited as residing outside the cognitive system to emphasize the "logically distinct role that they play in person recognition […] and not because they are seen as fundamentally different from other nodes in semantic memory" (Bruce and Young, 1986:313). The "cognitive system" is in fact intrinsically linked with all stages of recognition and identification: it determines the degrees of similarity of the representations stored in the FRUs and the description generated in the "expression-independent" module; it interacts with the "directed visual processing" in focusing visual attention directed towards specific features or ensemble of features; it accesses association and episodic information in achieving recognition and identification; and it is heavily involved in the analysis of facial expression and speech. It is this very system that generates semantic codes from visual inputs using information from the analysis of expressions, structural encoding, directed visual processing and face recognition units.

In this first chapter we have described and evaluated one of the most influential models of face processing. The contribution of this model to the field of face processing is undeniable. Although BY's model was formulated over 20 years ago, to date it still remains the most widely accepted functional model of face processing, capable of withstanding many criticisms and providing the best overall account of face research (Calder and Young 2005). The model though falls short in one key aspect. While it describes very well the different stages of face processing, it fails to provide a satisfactory answer to a crucial issue such as that regarding the computational mechanisms leading to the formation of an abstract face representation that is triggered by any view of someone's face (Phillips, Scruggs et al. 2010).

1.2 Face specificity

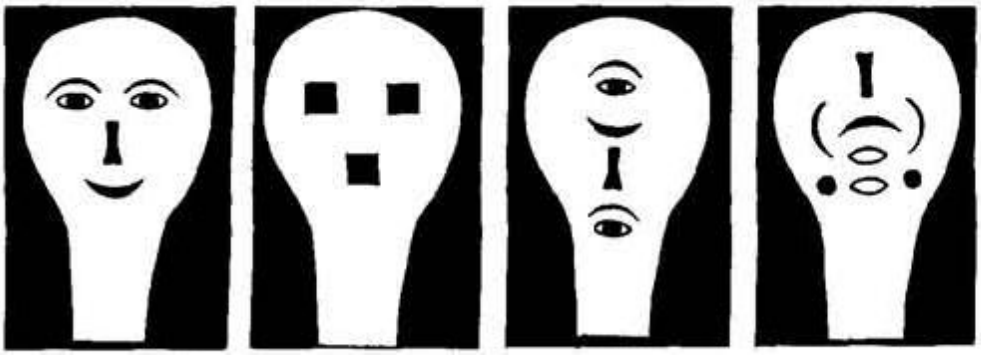
Preamble

In the following paragraphs we will be focusing on whether faces can be considered "special". To this end a wealth of evidence from several fields of cognitive neuroscience, stemming from behavioural psychology, through developmental and cognitive neuroscience will be reviewed. The bulk of this section will focus on neuroimaging studies, including functional neuroimaging (fMRI), transcranial magnetic stimulation (TMS) and electrophysiological data in both humans – by means of electro (EEG)– and primates – with single cell recordings.

The question of whether faces can be regarded as a special category compared to other visual stimuli may very well seem trivial. This object category, if one can call it so, conveys an incredible amount of social cues, such as identity information, gaze direction and emotional expression, which are extremely meaningful and crucial for daily interactions. Within this context thus, it is easy to assert that, yes, faces are indeed special. Framed in the milieu of cognitive neuroscience though, the word "special" whit regards to faces historically assumes a different meaning that refers to their functional uniqueness. One of the most controversial debates within the field revolves around whether faces can indeed be regarded as functionally unique, or whether the difference with other visual category is a mere consequence of differential level of expertise. A wealth of empirical evidence supporting the functional uniqueness of faces can be divided in three main strands. Firstly, a considerable amount of studies seem to suggest that the processing of faces is *innate* and *automatic.* Secondly, somewhat supporting this view, neuroimaging data suggest the existence of a *dedicated and specialised cortical network* - probably developed through evolution or throughout childhood - devoted to the neurocognitive processing of this category. Thirdly, substantial evidence advocates that faces processing are underpinned by *specific visual processes*. Within this chapter we will be reviewing the evidence for and against face specificity, with a particular focus on brain imaging data, although behavioural and developmental studies will also be addressed.

1.2.1 Is face processing innate?

Strong evidence supporting the view of the existence of an innate predisposition towards processing of faces comes from developmental studies carried out on infants. To begin with, a number of studies show that, as little as 9 minutes after birth, infants display a preference for face-like stimuli (Goren, Sarty et al. 1975; Maurer 1983; Johnson, Dziurawiec et al. 1991; Johnson and Morton 1991). When presented with palettes approximating the oval shape characteristic of face contours (Figure 2), new-borns display a preference for schematic faces (Figure 2a) and stimuli with black squares disposed in a face like configuration (Figure 2b).



a) b) c) d)

Figure 2 – palette stimuli representing faces (a); schematic faces (b); scrambled faces (c); and random patterns (d) (Goren et al., 1975)

Along the same line, Walton (1993) also shows preference for face stimuli in new-borns. The authors presented 4 images to infants, observing that, after as little as one minute of exposure, they show a clear preference for faces as opposed to other non-face stimuli. Importantly, it has been reported that until 2 months of age, infants do not have the same visual capabilities of adults (Johnson and Morton 1991; Brown, Lindsey et al. 1995). New-borns are sensitive to low spatial frequencies and have impoverished colour vision (Johnson and Morton 1991; Brown, Lindsey et al. 1995). These characteristics are in accordance with the results showing infants' preference to schematic face like images, in which low spatial frequencies are dominant. However, in spite of the imperfections of their visual system, which should be hindering intra category differentiation, new-borns exhibit a surprising ability to distinguish amongst faces of different identities (Turati, Macchi Cassia et al. 2006; Turati, Bulf et al. 2008). This is true even when faces are novel, cropped for external features, and are displayed under different viewpoints (Turati, Macchi Cassia et al. 2006; Turati, Bulf et al. 2008). Such ability is astonishing, even more so in light of the fact that faces are a highly homogeneous category, which renders the computational mechanisms underlying their recognition extremely complex. Accordingly, a number studies show that new-borns display a preferential attention to their mothers' compared to others' face (Field, Cohen et al. 1985; Bushnell, Sai et al. 1989; Pascalis, de Schonen et al. 1995). These data further corroborate the idea that infants are indeed able to differentiate amongst individual faces, in that, without such ability, no preference for one face or the other should be observed. Similar results have been found in young monkeys, raised without visual face exposure (Sugita 2008), strengthening the view that the processing of faces in primates and humans is indeed innate.

To fuel even further the "innateness strand", considerable evidence supports a degree of perceptual narrowing for faces across the course of development (Pascalis, de Haan et al. 2002; Kelly, Quinn et al. 2007; Sugita 2008). Perceptual narrowing in other domains (such as for example language), has been regarded as strong evidence for innate mechanisms (McKone and Robbins 2011). Within the face field, for example, perceptual narrowing has been found across races. A conspicuous amount of studies show how early experience with one race significantly increases recognition performance with faces of that same race. This is one of the main facets of the phenomenon known as the other-race effect (ORE, Feingold 1914 , which will be dealt with in details in section 1.3).

A plausible explanation accounting for the surprising proficiency in recognising faces displayed by infants has been put forward by Johnson (1991). The authors suggested that new-borns possess an innate abstract structural representation of faces, which allows them to differentiate across exemplars (Johnson and Morton 1991). Accordingly, Meltzoff (1977) observed that 2 to 3 weeks old new-borns are capable of imitating facial movements. Although this result may at first sight appear rather trivial, it further substantiates the idea of the existence of an innate face representation, as the latter is necessary in order for the baby to reproduce facial movements. Neuropsychological and neuroimaging studies also support the idea that face processing is innate. For example, Farah (2000) studied the case of a 16 year old patient who, at the age of 1 suffered occipital and occipito-parietal damages. In spite of 15 years of experience with faces, the patient sill exhibited significant impairment in face recognition performance, while object recognition well within norm. Further evidence comes from twin studies. The first neuroimaging twin study on face recognition using functional magnetic resonance imaging (fMRI) was carried out by Polk and collaborators (Polk, Park et al. 2007). The authors investigated the neural signal of monozygotic (i.e. with identical genetic patrimony) and dizygotic (i.e. different genotype) twins, while participants were observing pictures of faces, phase scrambled faces, chairs, written words and pseudo-words. Results showed that neural patterns within the ventral stream of monozygotic compared to those of dizygotic twins were more similar only in response to face stimuli (Polk, Park et al. 2007). The data suggests a genetic (and therefore innate) influence on the functional neural architecture of face processing.

1.2.2 A dedicated face network

Before reviewing the evidence for and against the existence of a dedicated neural network to face processing, it would seem appropriate to spend a couple of sentences on the choice of words adopted in this next section. While it is convention within the academic literature to refer to cells displaying larger responses to faces than another object category as "face specific", here we will call these neural populations *face preferential.* The choice of a more lineant term stems from the fact that, although showing larger responses to face stimuli, face cells in humans have been shown to be activated also by other visual stimuli, thus rendering the word "specific" misleading.

The fMRI and neuropsychological studies described in the last section, as well as providing evidence for the view that face processing is innate, also hint towards an important aspect of the processing of this particular category. As explained above, damages to occipito-parietal areas observed by Farah (2000) have been paired with face processing impairments; also, Polk (2007) reported distinct neural patterns of activation to faces within the ventral stream. From this, one might gather that these areas are important for the neural processing of faces. But can these cortical regions be considered as *crucial* and *necessary* for the neural organization and processing of this particular visual category? Can they even further be regarded as dedicated to and specialised for processing faces? These are interrogatives which to date constitute one of the main debated within the neurocognitive field of face processing. The next section will examine the empirical evidence supporting the existence of a dedicated neural network devoted to processing faces, looking at patient studies, brain imaging data in humans and single cell recording in monkeys.

1.2.3 Face preferential neurons in non-human primates

The first evidence for the existence of face preferential neurons was discovered almost by chance. While Rolls and hi collaborators (1976) were recording the response of single neurons in awake, behaving non-human primates with the intent of investigating the neural reward system, they came across an interesting finding. They discovered that a cells within the lateral hypothalamus responded to the sight of food (Rolls, Burton et al. 1976). From this astonishing finding the authors began questioning whether abstract representation did in fact exists in high level cortical areas. Rolls (1977) later reported that neurons in the inferior temporal cortex (IT) where excited by more complicated stimuli – such as faces – compared to simple geometric forms. It was 1979 when the same group reported face preferential neurons in the amygdala and IT. In the same year, Perrett (1979) localized face preferential neurons in the inferior temporal visual cortex. Further research on the response profile of these cells revealed that these neurons display distinctive high level cognitive properties such as invariance to size, colour, distance and rotation (Perrett, Rolls et al. 1982). Frequent tuning to a particular view point or specific facial features, such as eyes or mouth, and to their configuration (i.e. the spatial relation) was also described (Perrett, Rolls et al. 1982). Since then, many studies have replicated these finding, further strengthening the idea of the existence of face preferential cells in high level cortex of non-human primates (Sanghera, Rolls et al. 1979; Leonard, Rolls et al. 1985; Desimone 1991; Nakamura, Mikami et al. 1992; Wilson and Rolls 1993; Quiroga, Reddy et al. 2005; Gothard, Battaglia et al. 2007). Single unit recording studies in macaque monkey, for example, have identified neurons in the superior temporal sulcus and the inferior temporal cortex responding preferentially to faces (Haxby, Hoffman et al. 2000)

1.2.4 Face preferential neurons in human

Having argued for the existence of face preferential cells in non-human primates, the focus will now switch to human research. The beginning of the twenty-first century saw an unprecedented development of fMRI techniques. This rapid improvement significantly enhanced the spatial resolution and anatomical precision in investigating functional maps of intact human brains; as well as facilitating access to MR scanners. A logical consequence of such development was an overwhelming production of empirical brain imaging data. Studies using fMRI in humans have shown the existence of neural populations responding preferentially to faces (e.g. Sergent and Signoret 1992; Puce, Allison et al. 1995; Kanwisher, McDermott et al. 1997; Gauthier, Tarr et al. 1999; Halgren, Raij et al. 2000). While this is now generally accepted, one of the main debates within the field revolves around whether face perception is modular in nature – with specific modules or cortical regions specialised for processing unique facial dimensions (e.g. one area dedicated to identity, another to expression – Kanwisher, McDermott et al. 1997); or whether it is mediated by distributed processing (e.g. Haxby, Hoffman et al. 2000). Although differing in some key processing aspects, these two approaches are not necessarily mutually exclusive. In assessing the evidence for and against face preferential cortical structures this next section will be looking at one of the most influential neural models of face processing – the Distributed Neural System for Face Perception (Figure 3 – Haxby, Hoffman et al. 2000) – as well as focusing on empirical evidence arguing for neural modularity of face processing.

1.2.5 A Distributed Neural System for Face Perception

The need to incorporate the numerous brain imaging data in a comprehensive neural model of face perception was answered by Haxby et al. (2000). These authors put forward a neural model of face perception linking behavioural, neuroimaging and neuropsychological data. The model comprises of a core system and an extended system (Figure 3). The core system includes the Fusiform Face Area (FFA), the Occipital Face Area (OFA) and a portion of the posterior Superior Temporal Sulcus (pSTS). The extended system (which will not be dealt with in details as regarded as beyond the scope of this thesis) includes the intraparietal sulcus (IPS – Cowan 2011), a portion of the auditory cortex (Price 2010), regions within the amygdalae complex, insula and limbic system (Adolphs 1999; Adolphs 2002; Adolphs 2002; Dolan and Vuilleumier 2003), and anterior temporal cortex (AT – Gainotti 2007 Figure 3). The extended system interacts with the core one to extract different types of facial information (Haxby, Hoffman et al. 2000).

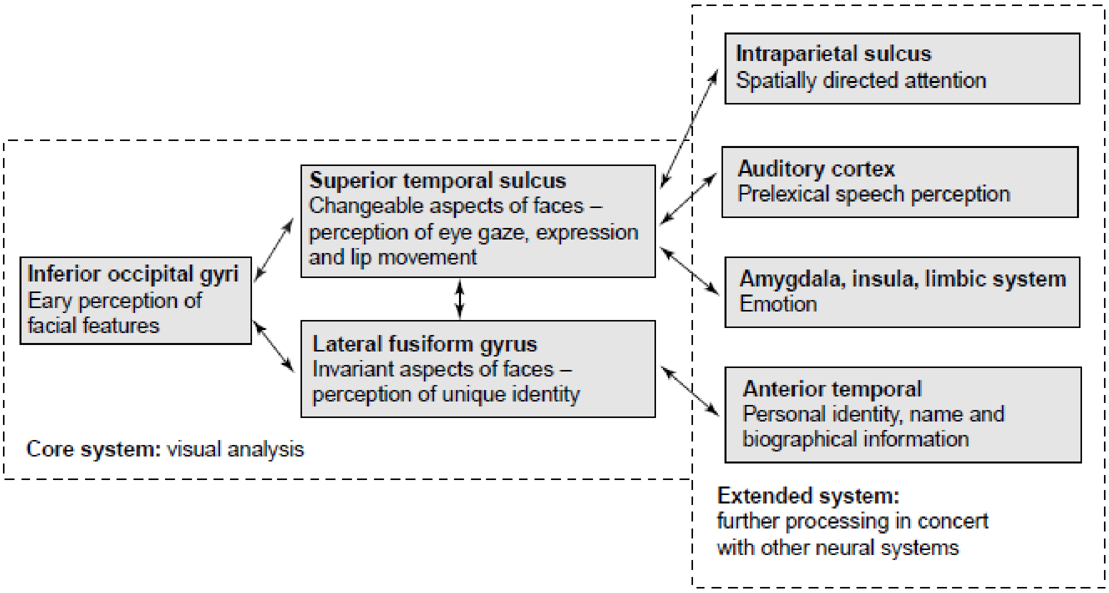


Figure 3 – Haxby core and extended face cortical network (Haxby, Hoffman et al. 2000; Haxby, Gobbini et al. 2001).

With the term "distributed" Haxby et al. refer not only to the involvement of a number of cortical areas communicating amongst each other to process facial information; but also to locally distributed population codes within these areas (Haxby, Hoffman et al. 2000; Haxby, Gobbini et al. 2001). A parallel can be drawn between this model and Bruce and Young's model of face perception. As explained earlier, according to Bruce and Young, the processing of facial identity and that of expression and speech-related facial movements are cognitively separated and carried out by independent parallel routes. Likewise, Haxby (2000), strongly emphasises a dissociation within the core system between two main facial dimensions: *invariant* features, required for identification; and *changeable* features, needed for the recognition of dynamic aspects of faces, such as expression and gaze. Individuals, for example, are able to identify a face regardless of changes in expression, information which, within this context, becomes irrelevant. However, for an accurate perception of facial expression, the very same facial dimensions that are deemed to be irrelevant during identification are instead crucial. Therefore, these aspects, although complementary, are thus distinct and have the potential to interfere with each other. Supporting this claim, one lesion study shows that prosopagnosic patient R-ST1 – displaying damages to the STS, but with the rFFA and rOFA intact – performs within the norm in identification tasks, while being impaired in judging expressions (Fox, Iaria et al. 2009). In addition, face identification was negatively affected when the stimuli contained irrelevant changes in expression, seemingly interfering with identity information (Fox, Iaria et al. 2009).

Single cells recordings in macaque monkeys also appear to be in line with the idea that these two classes of facial information are segregated not only functionally, but also anatomically. Hasselmo (1989) reported neural tuning to identity in the inferior temporal (IT) cortex; and tuning to expression in the STS (see also Perrett, Smith et al. 1984 for similar results). In humans, perception of eyes and mouth has been reported to evoke activation in the pSTS but not in the FFA (Puce, Allison et al. 1998). Furthermore, selective attention to identity leads to an increased activation in the FFA but not the pSTS, while selective attention to eye gaze direction increases activity in the pSTS but not in the FFA (Hoffman and Haxby 2000). Engell (2006) also reported stronger activation to identity in the FFA, while preferential pSTS activation to eye gaze. To further corroborate Haxby et al.'s claim, it has been reported that functional localizer using dynamic faces increases activity in pSTS but has little effect on the FFA (Hasson, Nir et al. 2004). While the data reviewed above support Haxby et al.'s model, a number of studies have produced somewhat contrasting results. Identity related information, for example, seem to be coded in cortical regions outside the core system (Kriegeskorte, Formisano et al. 2007; Rajimehr, Young et al. 2009). Kriegeskorte (2007), using multivariate pattern analysis (MVPA), have shown that it is possible to successfully classify faces of different identities based on the neural codes elicited within the anterior inferior temporal (aIT) cortex, but not in the FFA. Other than showing that face identity information may be coded outside the FFA and the core system (see also Grill-Spector, Knouf et al. 2004), Kriegeskorte's data raise an important issue that has been dominant in the fMRI field over the last decade: MVPA is more sensitive than conventional univariate analysis and may lead to different patterns of results. For example Tong (2000) reported no differences in activity within the FFA between human and non-human faces. Connolly (2012), however using MVPA demonstrated that the FFA and additional ventral areas that respond maximally to other visual stimuli do in fact distinguish between human and non-human faces. Moreover, data against the independency of expression and identity processing comes from primate studies. Sugase (1999), by means of single cell recording, assessed the relationship between neurons coding for identity information and those computing facial expression. They reported that cells within the STS responded with different latencies to the identity and the expression. These data suggest not only a degree of overlap between the two systems, but that an accurate perception of expression relies on input regarding the identity of faces (Sugase, Yamane et al. 1999). In addition, lesion studies carried out on prosopagnosic report cases presenting deficits in processing both identity and expression (e.g. Rossion, Caldara et al. 2003).

The last paragraphs have discussed Haxby et al.'s distributed neural model of face processing, focusing on the cortical regions comprising the core system. We have explained how the prerogative of this model is the assumption of an independent processing of invariant (i.e. identity) and changeable (i.e. expression and eye gaze) dimension of face perception; and how empirical evidence has produced both data supporting and challenging this stand. The next session will be focusing on the functional role of FFA, OFA and STS – regarded as face preferential modules of processing – in the attempt to provide a background within which framing the modular view of face processing.

1.2.6 The Fusiform face area (FFA)

a) *A face preferential region?*

Perhaps the most studied face preferential cortical region is the Fusiform Face Area (FFA – Kanwisher et al., 1997, McCarthy et al., 1997). The FFA, located within the fusiform gyrus in the ventral stream (Figure 4), has been reported to show significantly larger response to faces compared to other object category (Kanwisher, McDermott et al. 1997; McCarthy, Puce et al. 1997).

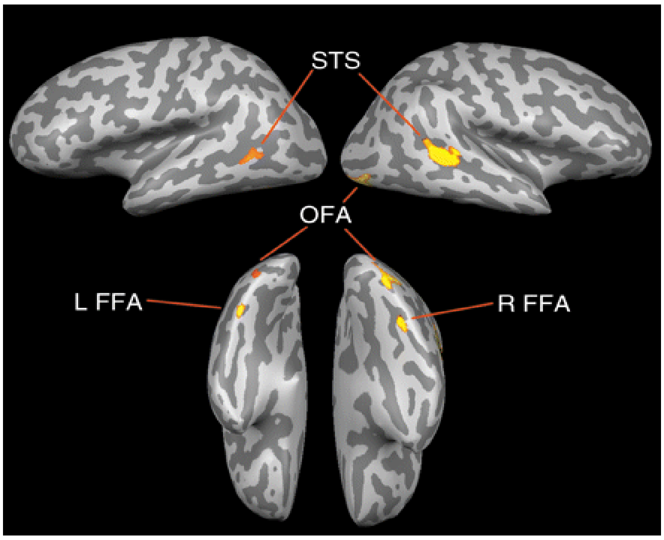


Figure 4 – FFAs OFAs and STS average location on inflated brain

This response profile has been observed for a variety of face stimuli, including full front and profile image (Tong, Nakayama et al. 2000), line drawings (Spiridon and

Kanwisher 2002), schematic faces (Tong, Nakayama et al. 2000; Loffler, Yourganov et al. 2005) and “Mooney faces” (Figure 5 Kanwisher, Tong et al. 1998; Rhodes, Byatt et al. 2004). The consistency of these results, in spite of the considerable differences in the low-level visual properties across the stimuli used, indicates that the larger response observed in the FFA for faces compared to non-face stimuli seems to be genuinely related to a degree of “face preferentiality” of this region. To further corroborate this view, research carried out with bi-stable stimuli produced similar data (e.g. Tong, Nakayama et al. 1998; Hasson, Hendler et al. 2001; Andrews and Schluppeck 2004; Pasley, Mayes et al. 2004; Williams, Moss et al. 2004). For example, Hasson (2001) exploited the advantages conferred by visual illusions – in this case the Rubin face-vase illusion (Figure 5) – to show larger FFA activation when participants reported perceiving a face as compared to when they did not.

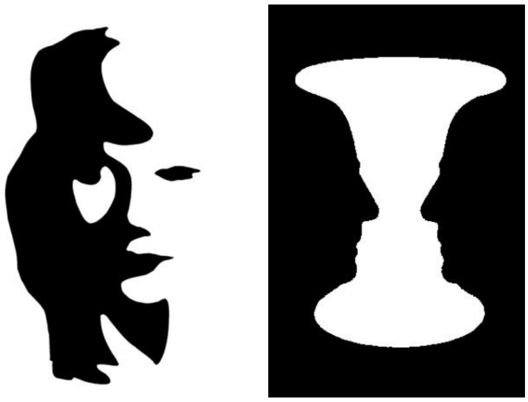


Figure 5 – example of a Mooney face (left), and the Rubin vase illusion (right)

Along the same lines are a number of studies on binocular rivalry (Tong, Nakayama et al. 1998; Pasley, Mayes et al. 2004; Williams, Moss et al. 2004). In these studies participants were presented with a face stimulus to one eye and a non-face one to the other. Larger FFA activation was observed for trials were individual reported perception of a face compared to those where they reported perceiving the non-face object (Tong, Nakayama et al. 1998; Pasley, Mayes et al. 2004; Williams, Moss et al. 2004), even though the retinal image across conditions did not change (Andrews, Schluppeck et al. 2002).

While these findings provide strong support for face preferentiality of the FFA, an alternative hypothesis has been proposed. Gauthier (1999, 2000) for example argued that the FFA responds to categories we are expert of, rather than uniquely to faces. The expertise hypothesis has been tested within several domains leading to contradictory results. FFA activation of experts in the fields of birds (Gauthier, Skudlarski et al. 2000), cars (Gauthier, Skudlarski et al. 2000; Grill-Spector, Knouf et al. 2004; Gauthier, Curby et al. 2005; Xu 2005), butterflies (Rhodes, Byatt et al. 2004), and novel objects classes such as greebles (Gauthier, Tarr et al. 1999) have been assessed. Gauthier (1999) for example trained individuals with a novel category: greebles (Figure 6).

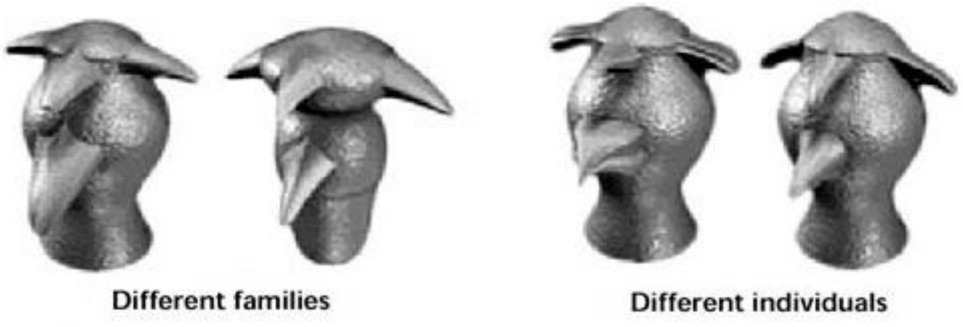


Figure 6 – example of greebles (Gauthier et al., 1999)

Greebles are objects possessing the same number of parts in a common spatial configuration. This renders intra-exemplar identification challenging, encouraging the use of all features and the relationships between them to achieve exemplars recognition. Behaviourally, participants trained to be greebles experts exhibited similar response profiles as those displayed with faces, such as intra-category identification and higher recognition accuracy for upright compared to inverted images (Gauthier, Anderson et al. 1997). Importantly, acquisition of expertise with greebles led to significantly larger activation in the right FFA for experts compared to non-experts (Gauthier, Tarr et al. 1999). Larger activation in the right FFA was also observed only for greebles experts in response to upright compared to inverted stimuli (Gauthier, Tarr et al. 1999). Moreover, to further fuels the expertise hypothesis, data from the same group showed larger FFA activation for car and birds experts compared to novices (Gauthier, Skudlarski et al. 2000). Interestingly, two studies, consistently with the expertise hypothesis, also reported larger activation within this ventral region for SR compared to OR faces (Golby, Gabrieli et al. 2001; Kim, Yoon et al. 2006). Controversially though a number of studies failed to replicate these patterns of results. Rhodes (2004) looked at activation patterns within the FFA in butterflies experts and compared it to those of faces. They reported two key findings: firstly a larger activation to faces compared to butterflies; secondly only 15% of the active voxels following butterflies presentation fell within the fusiform gyrus. While these findings may appear to be in stark contrast with those supporting the expertise hypothesis, there are a number of considerations deserving attention. Even though the authors studied neural activations of butterflies' experts, one can argue that the level of expertise these individuals have with faces is nonetheless larger than that with butterflies. This would account for the observed larger activation reported for face compared to butterfly stimuli. In addition, in spite of the fact that the overlap between the cortical areas activated by faces and butterflies within the fusiform gyrus was reported to be small, such overlap was larger for butterflies experts. This, although suggesting a stronger involvement of the FFA in face processing, seems to indicate at least a degree of expertise sensitivity of the area. However, adding fuel to the controversy, both Grill-Spector (2004) and Op de Beeck (2006) showed no significant effect of training on FFA activity.

b) Functional role in face processing

In light of the evidence discussed so far, it is clear that the face activate the FFA more than any other object category. However, it may yet seem unclear whether this response profile is an outcome of experience – if one accepts that faces are indeed the visual category humans have the most experience with – or reflecting a specific modularity in processing this category. One observation is undisputable observation though: the FFA does respond preferentially to faces. But what function does this region actually sub-serve?

Face detection – The greater response to faces than other visual categories seems to suggest and implication of this region in face detection. However, data from patients with acquired prosopagnosia – developed following brain damages – (e.g. Bruyer, Laterre et al. 1983; de Gelder and Rouw 2000; Rossion, Caldara et al. 2003; Schiltz, Sorger et al. 2006) and developmental prosopagnosia –lifelong deficit, manifesting in early childhood, and not accountable for by acquired brain damages – (de Gelder and Rouw 2000; Duchaine, Nieminen-von Wendt et al. 2003; Duchaine and Nakayama 2006; Le Grand, Cooper et al. 2006) may challenge this view. A perfect example is the case of PS, a patient with acquired prosopagnosia who has structural damages to the right FFA only and yet, displayed no impairment in face detection tasks (Rossion, Caldara et al. 2003; Schiltz, Sorger et al. 2006). Moreover, several studies with both acquired and developmental prosopagnosic individuals reported no face identification deficits (Bruyer, Laterre et al. 1983; de Gelder and Rouw 2000;

Duchaine, Nieminen-von Wendt et al. 2003; Rossion, Caldara et al. 2003; Duchaine and Nakayama 2006; Le Grand, Cooper et al. 2006; Schiltz, Sorger et al. 2006). While this report seems to rule out the involvement of the FFA in face detection mechanisms, there are at least 2 points to take into consideration. Firstly, collapsing results from acquired and developmental prosopagnosia may be erroneous. While cases of acquired prosopagnosia, such as that of PS, show a clear structural damage to the FFA (e.g. Rossion, Caldara et al. 2003), developmental prosopagnosic do not display visible damages to this region (Avidan, Hasson et al. 2005). Secondly, all the studies mentioned above featured detection tasks where participants had to perform upon the sole appearance of a centrally presented face. However, as argued by Lewis (2003), the absence of distractors and context does not epitomize face detection occurring in everyday life, which is far more complex. To this end, further tests were carried Garrido (2008). They studied fourteen individuals with developmental prosopagnosia under more demanding tasks constraints, such as perception of hidden faces embedded in complex scenes or Mooney faces. Their results showed that, compared to controls, developmental prosopagnosic patients were less efficient in detecting the presence of a face (Garrido, Duchaine et al. 2008). The question of whether the FFA is involved in face detection thus remains unanswered, with further evidence required to elucidate the matter.

Structural encoding –before turning to the empirical evidence suggesting the implication of the FFA in structural encoding of faces, it would seem appropriate to clarify what are these structural properties. For the scope of this chapter the term "structural" will be used to refer broadly to the structure of a face, including the configuration of facial features in their correct order and the metric distance among them.

A number of studies support the involvement of the FFA in the structural encoding of faces. Liu (2010) for example reported FFA sensitivity to the physical structure of a face, including the presence of face features – such as eyes, nose and mouth – as well as their correct configuration. Furthermore, one of the principal behavioural markers of configural processing, – i.e. processing not just the individual features of a face in isolation, but the relationship amongst them (more details in the following paragraphs - for a review Maurer, Grand et al. 2002) – which sub-serves structural encoding, is considered to be the composite face effect (Young, Hellawell et al. 1987; Carey and Diamond 1994; Hole 1994; Hole, George et al. 1999; Le Grand, Mondloch et al. 2004; Michel, Rossion et al. 2006). This phenomenon refers to the observation that adults find it difficult to recognize the top half of a face when the latter has been aligned to the bottom half of a different face, even when they are instructed to ignore the bottom half of the face in question (Young, Hellawell et al. 1987 – Figure 7; Hole 1994). However, when the two halves are misaligned, performance increases significantly. Given that a neural correlate of the composite face effect has been shown in the FFA (Mazard, Laou et al. 2005; Schiltz and Rossion 2005), the latter has been proposed as a primary candidate to carry out structural encoding of faces.

Figure 7 – example of face composite effect. In both the aligned and the misaligned stimuli, the top parts are identical, but they are perceived as different only for aligned stimuli. This “illusion” is thought to be an outcome of configural processing

Moreover, a number of studies have reported neural adaptation within the FFA to the identity of faces (e.g. Gauthier and Nelson 2001; Avidan, Hasson et al. 2005; Eger, Schweinberger et al. 2005; Pourtois, Schwartz et al. 2005; Rotshtein, Henson et al. 2005), even when the stimuli where of different size (Andrews and Ewbank 2004), spatial scale (Eger, Schyns et al. 2004) and position (Grill-Spector, Kushnir et al. 1999). Neural adaptation (also known as neural repetition suppression) is a phenomenon whereby neural activity in stimulus sensitive regions is reduced when two or more stimuli are subsequently presented (for a review see Miller, Li et al. 1991; Wiggs and Martin 1998; Henson 2003; Grill-Spector, Henson et al. 2006). While the mechanisms underpinning this neural occurrence are still unclear (for more details see Grill-Spector, Henson et al. 2006), neural adaptation is generally regarded as a marker of *preferential* processing for a specific stimulus category (Grill-Spector, Henson et al. 2006). Adaptation within the FA has been reported also for faces that were perceived to be from the same identity, despite morph-induced changes in the image (Rotshtein, Henson et al. 2005). On the other hand, no adaptation was observed when participants perceived changes in identities (Rotshtein, Henson et al. 2005). Fox (2009) showed similar patterns of results with release from adaptation only when individuals perceived identity changes in the face stimuli. Taken together, these findings suggest that the FFA is not only sensitive to low level properties of faces images, but to the structure of faces, which, as indicated also by Bruce (1986) is itself necessary to process identity related information. A final line of evidence supporting the involvement of the FFA in the structural encoding of faces comes from apperceptive prosopagnosic patients. As explained in chapter 1, apperceptive prosopagnosia consists of a deficit in forming an accurate face percept, possibly as a consequence of difficulties in extracting configural relationship of facial features (Barton 2008). Within Bruce and Young's model of face perception, patients affected by this specific case of prosopagnosia would therefore exhibit damages at the structural encoding stage. Coupled with fMRI evidence showing loss of the FFA in at least one apperceptive prosopagnosic (de Gelder, Frissen et al. 2003), these findings strongly indicates the involvement of the FFA in structural encoding stages of ace processing.

Identity encoding – it has also been shown that the FFA is sensitive to identity coding. For example, Ewbank (2008) recorded the Blood Oxygen Level Dependent (BOLD, see chapter 1.4 for more details) signal of their participants while displaying faces of different or same identities across diverse viewing angles. Their results showed larger adaptation across viewpoints for faces of the same identity. These data suggest not only that the FFA is in facts sensitive to identity coding, but also that this area responds to perceived rather than physical changes in a face stimulus. Large (2008), by means of change blindness paradigm, further corroborated these findings by reporting FFA sensitivity to perceived changes – namely whether the subjects reported a change in identity between first and second stimulus presented – as opposed to physical changes in the image stimuli. Along the same line Rotshtein (2005) and Fox (2009) exploited the advantages conferred by morphing two famous faces of different identities. They assessed how participants perceived different stages along the morph continuum, while measuring their BOLD signal. The authors contrasted BOLD signal changes to morph steps crossing categorical boundaries of identity (physical changes) against those causing the subjects to perceive an identity change (perceptual changes). Their results also showed that the FFA sensitivity to perceived rather than physical properties of the stimuli presented. Winston (2004) also reported FFA sensitivity to identity, but not expression (but see Fox et al., 2009, who showed FFA sensitivity to both identity and expression). The evidence discussed so far seems to suggest an involvement of the FFA in higher level perceptual processing (of faces), responding to perceived as opposed to physical properties of face stimuli. However, pinpointing the exact contribution of this area to processing identity related information is still a matter of debate. Specifically it remains unclear whether face identity is processed only by the FFA; whether the FFA carries out a primary role in encoding identities concomitantly with other cortical areas; or whether it only plays a secondary part in this process.

1.2.7 The Occipital face area (OFA)

The Occipital Face Area (OFA – Puce, Allison et al. 1996; Gauthier, Tarr et al. 2000) is arguably the least understood face preferential region, as it has not been studied as extensively as the FFA (Pitcher, Walsh et al. 2011). As the name itself suggest, the OFA is located in the occipital cortex, and more specifically on the lateral surface of the occipital lobe, within the inferior occipital gyrus (Figure 4). The OFA also responds more strongly to faces than any other object category (Puce, Allison et al. 1996; Gauthier, Tarr et al. 2000), however its face-preferentiality is less pronounced compared to that of the FFA (Schwarzlose, Swisher et al. 2008). Due to its anatomical location – significantly closer to early visual areas, compared to the FFA – the OFA's neurons are believed to have smaller receptive fields (e.g. Pitcher, Walsh et al. 2011); and the area is believed to be involved in earlier stages of face processing, possibly representing the first face preferential cortical region (Liu, Harris et al. 2002; Pitcher, Walsh et al. 2007; Pitcher, Garrido et al. 2008; – however see Rossion 2008; Sadeh, Podlipsky et al. 2010). Empirical evidence seems to confirm this claim. Pattern analysis, for example, has revealed that the OFA is more sensitive to position (Kovacs, Cziraki et al. 2008; Schwarzlose, Swisher et al. 2008), and it displays stronger contralateral field bias (Hemond, Kanwisher et al. 2007). Moreover, unlike the FFA, a number of studies suggest that the OFA responds to physical as opposed to perceived face properties (e.g. Rotshtein, Henson et al. 2005; Large, Cavina-Pratesi et al. 2008; Fox, Moon et al. 2009). Both Large (2008) and Rotshtein (2005) have shown that the OFA was sensitive to identity changes across face stimuli regardless of the participants' awareness. Another important difference between these two face preferential areas lies in that, while the FFA is sensitive to variation in metric distance across facial features, the OFA responds to the nature of these features, rather than their spatial position (Liu, Harris et al. 2002; Pitcher, Walsh et al. 2007; Liu, Harris et al. 2010; Nichols, Betts et al. 2010). These results are further supported by a transcranial magnetic stimulation (TMS) study by Pitcher et al. (2007). The authors produced a number of face stimuli either varying in distance across internal features (such as eyes, nose and mouth) or replacing these features with ones of different faces. They then presented the stimuli to their participants while delivering TMS pulses to the right OFA (rOFA) and other control areas (such as vertex) at varying time intervals following stimulus onset. They reported participants' impairments in accurate discrimination of face parts but not on the discrimination of spacing between these parts when TMS pulses were delivered to the rOFA between 60 and 100 ms after stimulus onset (Pitcher, Walsh et al. 2007).

Patient's studies also provide invaluable information regarding the functional role of the OFA. It has to be noted however that inferences drawn on the basis of empirical evidence based on prosopagnosic patients' has to be carefully interpreted. Most patients with lesions to the OFA in fact present either functional or structural damages to several other cortical areas. This is the case for PS, who has lesions to the r rOFA and left FFA (lFFA) (Rossion, Caldara et al. 2003); R-IOT1, with damages to the rOFA and rFFA (Fox, Iaria et al. 2008); and DF presenting lesions to the right and left OFAs, but also right and left lateral occipital complex (Steeves, Culham et al. 2006).

PS showed severe impairment in identity judgment and face matching task, while milder deficit to expression and gender judgement (Rossion, Caldara et al. 2003). R-IOT1 instead reported selective impairments in identity processing (Fox, Iaria et al. 2008). DF displayed the ability to discriminate between face and non-face objects, only within natural context and not with more demanding stimuli. The behavioural deficits displayed by DF however are more difficult to interpret due to the extensive nature of the lesions, which led the patient to suffer from a more general type of visual agnosia, rather than prosopagnosia. The data gathered from PS and R-IOT1 strongly suggest that lesions to the OFA impact upon identity processing, suggesting a level of involvement of the OFA in facial identity computation. If we accept that the OFA represents the earliest area of face processing, then it would seem plausible to postulate that this area may send information to the FFA, contributing to several facets of face perception. fMRI studies have shown face preferential rFFA activation in PS as well as right and left FFA activation in DS (Sorger, Goebel et al. 2007). These results suggest that the OFA is not the sole provider for input to the FFA as, while for PS one could argue that FFA activation may derive from signal stemming from the lOFA (which is intact in this patient), DF presents lesions to both OFAs. However, regardless of an absolute neural activity elicited by face stimuli within this region, PS did not show identity adaptation in the FFA (Schiltz, Sorger et al. 2006; Dricot, Sorger et al. 2008), suggesting no identity sensitivity within this area. Thus face identity discrimination would seem to require intact functionality of the OFA. Further evidence of the involvement of the OFA in identity computation comes from fMRI studies in normal (Hoffman and Haxby 2000; Yovel and Kanwisher 2004). While its exact role still remains largely unknown, it is believed that the OFA is involved in structural description of a face prior to deeper processing occurring within the FFA (Haxby, Ungerleider et al. 1999; Haxby, Hoffman et al. 2000; Hoffman and Haxby 2000). Finally there is also some evidence suggesting OFA involvement in the processing of facial expression. While R-IOT1 performed well on expression judgment, both PS and DF display deficit in this very same aspect (Rossion, Caldara et al. 2003). Moreover TMS studies have further corroborated this claim, by showing that pulses delivered directly to the rOFA impair expression judgment (Pitcher, Walsh et al. 2007; Pitcher, Garrido et al. 2008).

1.2.8 The Superior Temporal Sulcus (STS)

Unlike the FFA, which can be reliably located in most, if not all normal subjects, face preferential regions within the Superior Temporal Sulcus (fSTS) have been reported in half, or at best three quarters of the scanned individuals (Kanwisher, McDermott et al. 1997; Yovel and Kanwisher 2005; Fox, Moon et al. 2009). It is for this very reason that this region has not been studied as extensively as the FFA. The available evidence however suggests that the functional role carried out by the fSTS is extremely important within the realm of face processing. A number of studies have shown the involvement of the fSTS in emotional expression (Andrews and Ewbank 2004; Winston, Henson et al. 2004; Simon, Craig et al. 2006; Furl, van Rijsbergen et al. 2007; Fox, Moon et al. 2009; Said, Moore et al. 2010; Said, Moore et al. 2010). Winston (2004) for example reported sensitivity to facial expression and not identity within the fSTS. Along the same lines, Fox (2009) by means of an fMRI adaptation paradigm showed sensitivity within the fSTS to perceived changes in expression, but only when participants were attending to the expression. Another facial dimension that has been suggested to be coded in this area is eye gaze (Puce, Allison et al. 1998; Wicker, Michel et al. 1998; Hoffman and Haxby 2000). Specifically, it has been demonstrated that this region is sensitive to the social context within which a gaze shift occurs, i.e. whether the gaze is perceived to be consistent or inconsistent with the subject's expectation regarding the intention of the person making the eye movement (Pelphrey, Singerman et al. 2003). Moreover, the fSTS has also been found to respond to dynamic face stimuli in which either gaze direction or expression changes (e.g. Calvert and Campbell 2003; Thompson, Hardee et al. 2007). Finally, discrepant data have been produced with regards to coding of facial identity. A number of studies have found that the neural activity within the FFA but not fSTS correlates with successful identification of faces (Andrews and Schluppeck 2004; Grill-Spector, Knouf et al. 2004; Yovel and Kanwisher 2005). On the other hand, though, empirical data have shown that identity information may be also coded within the fSTS: Fox (2009) and Winston (2004) used fMRI adaptation to reveal sensitivity to identity in the posterior STS, while the anterior portion of this cortical region was found to respond selectively to expression. Furthermore, Fox (2009) described the only case of a patient, R-ST1, presenting lesions to the STS with rFFA and rOFA intact. R-ST1 showed impairment in judging facial expression, while performing within normal range in identity judgment tasks. Face identification however was deficitary when the stimuli contained irrelevant changes in expression (Fox, Iaria et al. 2009).

1.2.9 Are faces sub-served by a specific visual processing?

The last of the three strands underpinning the functional uniqueness of faces is the claim that this category is subserved by a specific visual process. A wealth of evidence suggests that the mechanisms for face perception are *qualitatively* different than those of any other visual category. Such a claim would seem plausible in light of the amount of visual and social information conveyed by this highly homogeneous stimulus, which is processed extremely accurately and with unprecedented proficiency. Unlike other objects faces are thus believed to be processed configurally (for a review see Maurer, Grand et al. 2002). As opposes to "featural" or "analytic" processing – encompassing the perception of features isolation - configural processing refers to perceiving the relationship amongst the features composing a given stimulus (Maurer, Grand et al. 2002). According to Maurer et al. (2002) it involves three types of processes: (1) sensitivity to first-order relations –i.e. the configuration of two eyes above a nose and a mouth; (2) holistic processing – perceiving the features into a gestalt allowing to see the face as a whole; and (3) sensitivity to second-order relations – i.e. the distances among features. As Maurer notes though, no formal consesnus upon a comprehensive definition has been reached, with some authors using the terms configural and holistic interchangeably to refer to one or more these facets. The afore mentioned behavioural composite effect represents an example of how first-order relations affects face processing (Young, Hellawell et al. 1987; Carey and Diamond 1994; Hole 1994; Hole, George et al. 1999; Le Grand, Mondloch et al. 2004; Michel, Rossion et al. 2006). In addition, it has been shown that adults are better at identifying facial features when these are within the context of the whole face (the whole/part advantage – Tanaka and Farah 1993). These findings demonstrate that facial features are not only represented individually, but are also integrated into a holistic representation that interferes with access to the representation of any individual feature. Moreover, whether configural processing is specific to faces, or is expertise related still represents one of the main debates within the field of high level vision e.g. Gauthier et a., 1999). Compelling evidence seems to suggest that configural processing is indeed a prerogative of faces. One such line of work is that carried out exploiting the advantages conferred by the so-called face inversion effect (FIE – Yin 1969). The FIE is a phenomenon whereby picture plane inversion dramatically impairs configrual processing leading to a significant decrease in recognition performance for faces compared to any other object category (Yin 1969). Although the putative neural mechanisms underlying this phenomenon have yet to be clarified, visual expertise is generally regarded as one of the main causes of the effects of face inversion (e.g. de Haan, Pascalis et al. 2002; Rossion and Gauthier 2002). One view holds that the extraordinary level of expertise humans have with faces leads to distinct neural mechanisms in processing upright and inverted face (i.e. configural mechanisms for upright and featural for inverted - Rossion 2008). However, a quantitative account – arguing that the same neural putative processes are at play while perceiving of upright and inverted faces – has also been proposed (see Sekuler, Gaspar et al. 2004 for more details). Another example of how inversion impacts upon configural processing and thus the perception of faces is the "Thatcher Illusion" (Thompson 1980). The latter consists of the difficulty of detecting changes in local features embedded in a face presented upside-down. The inverted face with eyes and mouth in the canonical upright orientation is not perceived as grotesque until the stimulus is presented in their upright (Figure 8).

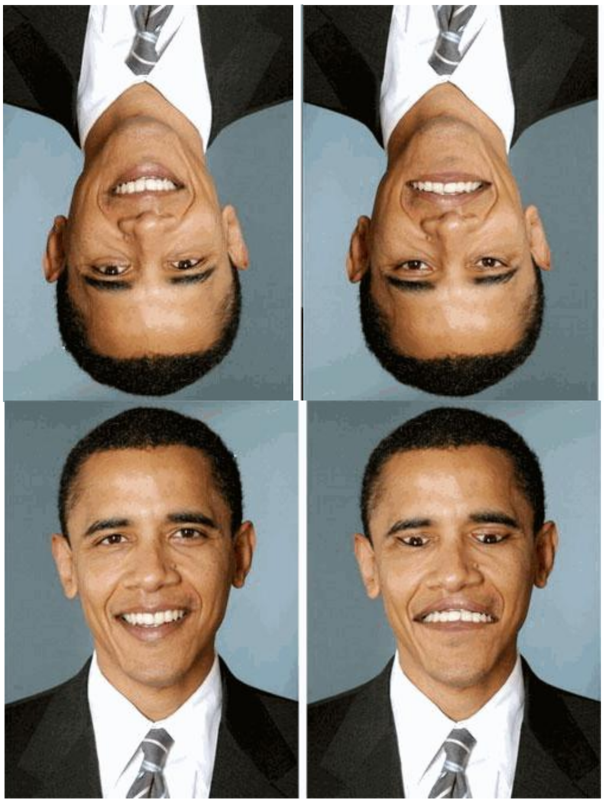


Figure 8 – example of Thatcher illusion – the upside down eyes and mouth are perceived as grotesque only when faces are in their canonical orientation

The N170 – further evidence corroborating the view that faces are processed by a specific neural mechanism comes from electrophysiological data; specifically from electro-encephalography (EEG) – i.e. electrical neural signal recorded at the scalp level (more details on this technique will be provided in paragraph 1.4). EEG studies consistently report a negative deflection in the Event Related Potential (ERP – more details in paragraph 1.4) signal occurring roughly 170 milliseconds (ms) after stimulus onset, peaking at occipitotemporal sites, which is larger for faces compared to any other visual category: the N170 (Figure 9 – Bentin, Allison et al. 1996; – for a review see Rossion and Jacques 2008).

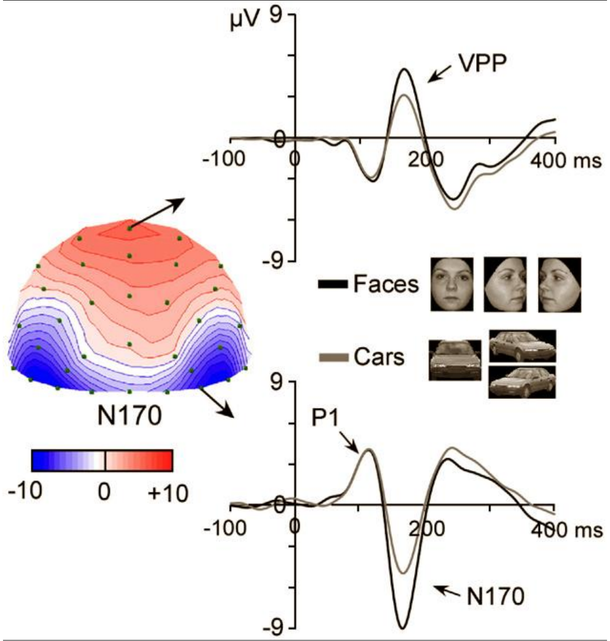


Figure 9 – the N170

While the N170 is regarded as one of the (if not the) earliest face preferential ERP components (Rousselet, Gaspar et al. 2011) and it has hence been extensively studied (Eimer 2000; Rossion, Curran et al. 2002), the putative mechanisms underlying its generation are yet to be fully understood. Empirical research has thus far produced contrasting results. Originally this component was believed to reflect the structural encoding of faces prior to individual face recognition (Bentin, Allison et al. 1996). One line of evidence supporting this view comes from studies with schematic and Mooney faces. Schematic faces, for example, retaining the overall spatial configuration of a face while lacking other types of information (such distinctiveness of the eyes across exemplars), have shown to elicit N170 comparable in amplitude and latency to that triggered by natural face stimuli (Sagiv and Bentin 2001). These data suggest that the N170 is sensitive to the configuration of facial features, rather than the features in isolation. Further corroborating the link between the N170 and configural processing, Latinus (2005; Latinus and Taylor 2006) reported larger N170 to Mooney faces, only when the participants perceived the stimulus as a face. Mooney faces do not possess specific information about internal facial features, nor about the canonical first order orientation of faces (Figure 5). It is therefore the gestalt perception of these stimuli that leads to perceiving them as a face. The findings reported by Latinus and Taylor can thus be regarded as strong evidence for the involvement of the N170 in holistic processing. Along the same lines, Eimer (2011), exploiting the advantages conferred by adaptation paradigms – manifested as a reduction in amplitude of the ERP signal (see Chapter 3 for more details) – showed N170 sensitivity to both schematic and Mooney faces. Importantly, electrophysiological FIE has also been reported (Bentin, Deouell et al. 1999; Rossion, Delvenne et al. 1999; Rossion, Gauthier et al. 2000). Face inversion has been found to elicit significantly delayed (Bentin, Deouell et al. 1999; Rossion, Delvenne et al. 1999; Rossion, Gauthier et al. 2000) and larger N170 (Rossion, Gauthier et al. 2000; Rossion, Joyce et al. 2003; Itier and Taylor 2004; Itier and Taylor 2004). George (2005) showed N170 amplitudes increase to inverted Mooney faces only when these stimuli were identified as faces. The effects of face inversion on the N170, together with the behavioural patterns to inverted faces (as reported above), have been interpreted as evidence for a disruption of configural face processing (Rossion and Gauthier 2002), strengthening the existence of a link between the latter and the N170. Recent evidence has also reported N170 modulation to identity (Jacques and Rossion 2006; Jacques, d'Arripe et al. 2007) and levels of expertise (Tanaka 2001; Rossion, Curran et al. 2002). These findings can be regarded as evidence that the face preferential N170 component is associated with configural face processing, supporting the idea that faces are underpinned by a specific neruo-visual process. However, Harris (2008) recently challenged this view. The authors showed equal amount of adaptation on the M170 component – the magneto-encephalographic (MEG) counterpart of the N170 – to faces preceded by full faces, scrambled faces, or isolated face parts. They therefore suggested that the M170 is linked to the detection of individual face parts, rather than the processing of face-specific first-order relational properties. Somewhat accordingly, Schyns (2003) also showed that the N170 responds preferentially to facial features, specifically, to the eyes. The authors used Bubbles (Gosselin and Schyns 2001), which, by means of image classification technique, exploits distinctions across spatial frequency bands to pinpoint the specific diagnostic visual information required for a perceptual decision. Their results show that, independently of task demands, the most negative amplitude on the N170 correlates with the appearance of the eyes, suggesting that this ERP component responds preferentially to this facial feature. Nevertheless Task demands (e.g. Okazaki, Abrahamyan et al. 2008; Wronka and Walentowska 2011), as well as other top down influences, such as perceptual load (Mohamed, Neumann et al. 2009) and spatial attention (e.g. Eimer, Holmes et al. 2003; Holmes, Vuilleumier et al. 2003; Crist, Wu et al. 2008), have been lined to modulation of the amplitude of the N170. A number of studies though have challenged these findings by reporting no top-down effects on the N170, concluding that the latter represent stages of pure visual encoding (Cauquil, Edmonds et al. 2000; Guillaume and Tiberghien 2001; Carmel and Bentin 2002; Lueschow, Sander et al. 2004; Furey, Tanskanen et al. 2006; Philiastides, Ratcliff et al. 2006; Rousselet, Husk et al. 2007; Rousselet, Gaspar et al. 2011). Recent EEG studies using Bubbles in an expression categorization tasks showed that the N170 integrates facial features over time (Schyns, Petro et al. 2007). The process begins at the eye level, roughly 50 ms prior to the N170 peak, and it moves downwards on the face, until the information required for the correct expression categorization is encoded (see also van Rijsbergen and Schyns 2009). In light of what argued so far, it can be concluded that, although the putative mechanisms underlying the N170 are yet to be fully understood, the latter seems to be involved in the perception of first order relationship amongst facial features. Moreover, regardless of whether uniquely responding to faces, it has been consistently shown that this visual category leads to systematically larger amplitude for this ERP component.

Throughout this chapter we have reviewed evidence for and against the view that faces are a special visual category. We have seen how a large number of studies have reported that face processing is innate, subserved by a dedicated cortical network and a specific visual processing. While the debate revolving around whether these mechanisms are solely dedicated to faces or they stem from high level of expertise with this visual category has yet to be resolved, an overwhelming wealth of data indeed suggests that faces are in fact special, in that they convey an incredible amount of social information that must be processed quickly and efficiently in order to engage in daily interactions. The next chapter will be looking at how race affects face recognition, specifically examining a phenomenon known as the other-race effect.

1.3 The other race effect

Preamble

While the previous chapter aimed to provide an understanding of the mechanisms underlying face processing in general, the following paragraphs will be focusing on a specific aspect that impacts upon the perception of this visual category, namely race. Specifically we will be looking at a renowned phenomenon firstly reported almost a hundred years ago by Feingold (1914): the Other Race Effect (ORE). After a general theoretical context, the chapter will be looking at the different hypothesis and models arguing that different aspects cause the ORE. In doing so behavioural, electrophysiological and neuroimaging data will be reviewed.

The remarkable proficiency displayed by human beings in identifying faces, as well as extracting relevant information crucial in everyday interaction, brings us to sometimes take for granted how demanding face processing really is. In just a fraction of a second the human brain processes the overwhelming wealth of social cues conveyed by a face –such as eye gaze, mouth movements, identity and so on – regardless of the different viewing and lighting conditions, which greatly impact upon low level visual information. To begin to barely grasp the complexity of the computational mechanisms at play throughout the neural processing of faces let us consider, for example, the highly renowned computer metaphor. Unparalleled technological progress have led to unprecedented amount of computational power, to such an extent that it is now possible in matters of minutes to carry out functions that are unthinkable for a human brain, such as the analysis of extremely large data sets (such as brain imaging data). Yet computers are still not able to accurately identify the same face under different viewing conditions (like viewing angles or changes in size), within an amount of time and precision comparable to that of a human brain. It is probably in light the effortlessness with which face processing occurs that we tend to underestimate its complexity. One in facts begins to ponder upon the intricacy of a reliable mechanism only when the latter fails us. With regards to face processing, one such instance is the renowned other-race effect (ORE). The ORE is a phenomenon whereby individuals display higher accuracy in recognizing same-race (SR) compared to other-race (OR) faces (Malpass and Kravitz 1969; for a review see Meissner and Brigham 2001). This SR recognition advantage is paired with a faster OR categorization (Valentine and Endo 1992; Levin 1996 ; Caldara, Rossion et al. 2004). The scope of this chapter will be to provide a theoretical account within which the ORE can be framed. In doing so behavioural, EEG and fMRI evidence will be reviewed and the main hypothesis accounting for the neuropsychological basis of this phenomenon will be elucidated.

1.3.1 What is the ORE – some behavioural evidence

As mentioned earlier, the ORE was first reported by Feingold, almost a hundred years ago (1914). The author noticed that "other things being equal, individuals of a given race are distinguishable from each other in proportion to our familiarity, to our contact with the race as whole. Thus, to the uninitiated American all Asiatics look alike, while to the Asiatics, all White men look alike" (Feingold, 1914, p.50). Over half a century after Feingold's claim the first experimental study was published: Malpass (1969) reported that both Western Caucasian (WC) and African-American (AA) students were more accurate at identifying faces form their SR compared to the OR. Since then, a vast number of studies replicated Malpass' finding (Malpass 1981; Shepherd and Deregowski 1981; Lyndsay and Wells 1983; Brigham and Malpass 1985; Brigham 1986; Bothwell, Brigham et al. 1989; Anthony, Copper et al. 1992), emphasizing the robustness of this effect. With an ever-growing interest around this topic, the first review was published by Shepherd (1981), quickly followed by a number of meta-analysis. Lyndsay (1983) for example analysed thirteen experiments, where subjects were engaging in recognition tasks with SR and OR faces. Importantly, only six of these studies showed a full cross-over interaction between the race of the participants and that of the face stimuli. This observation is quite unfortunate in that a full cross-over interaction is indeed required to reliably and genuinely link the observed effects to race, and exclude any potential (low level) confound, which may be intrinsic in the stimulus set. While this may seem to question the robustness of these findings, a finer-grained analysis on the same data set revealed that out of the 1445 subjects tested (693 AA and 752 WC) roughly 80% of the sample population displayed a genuine ORE (Bothwell, 1989). Interestingly, all of the studies reported above only employed WC and AA stimuli. However, Luce (1974) and Shapiro (1986) also utilised East Asian (EA) faces, producing the same pattern of results (see also Valentine and Endo 1992; Ng and Lindsay 1994; O'Toole, Deffenbacher et al. 1994). Moreover, behavioural ORE was been reported whit participants tested with Spanish (Tanaka and Pierce 2009) and Mexican (Platz and Hosch 1988) faces. These data further corroborate the robustness of this phenomenon, which can thus not be limited to a specific set of race stimuli. A recent meta-analysis, representing a major proof of the genuinity of the ORE, was carried out by Meissner (2001). The authors tested the ORE on a sample of 5000 subjects, confirming the reliability of the effect. In addition this meta-analysis not only revealed that participants were significantly more accurate at identifying SR faces, but also that OR faces led to a greater number of false alarms. Another important finding on the realm of the ORE was that presented by Barkowitz (1982). The authors tested their subjects in and old-new recognition task, illustrating that individuals, regardless of their race, are more likely to erroneously perceive newly presented OR faces as previously seen.

While the ORE is mainly renowned as an OR identification deficit, a number of studies have shown that race impacts upon perception of other dimensions of faces.. Together with the afore mentioned OR race categorization advantage (Valentine and Endo 1992; Levin 1996 ; Caldara, Rossion et al. 2004), it has been reported that race affects gender categorization (e.g. O'Toole, Peterson et al. 1996). O'Toole (1996) showed that WC and EA participants performed significantly better in gender categorization task for SR compared to OR faces. Importantly, the authors reported full crossover interaction between the race of the observers and that of the face stimuli. Moreover, similar results concerning behavioural performance in judging the age of a face were described by Dehon (2001). The study investigated the effect of race on age judgement in WC and AA observers. The results revealed that WC are more accurate at estimating SR compared to OR age. The same pattern however was not observed for AA participants, who displayed no differences across races. The authors concluded that the lack of a full cross over interaction had to be attributed to AA's time of residence in a WC country, which significantly increased their level of expertise with WC faces, leading to better performance. This study touches upon one of the main theoretical framework accounting for the mechanisms underpinning the ORE: visual expertise (see paragraph 1.3.2.1.3).

In light of the evidence discussed so far, the ORE can thus be regarded as an all-round sound perceptual phenomenon. Crucially though, the ORE is not a mere theoretical construct, but it has important repercussion on several aspects of everyday life. One such consequence is directly rooted into criminal justice. Sporer (2001) described the impact of the ORE on eyewitness identification, emphasizing how OR recognition impairment greatly contributes to false convictions. In the United States for example it has been reported that erroneous guilty verdicts led to a significant number (i.e. over a third) of convictions of innocent individuals due to misidentification of OR eyewitness (Scheck, Neufeld et al. 2003). Similar reports were observed in the United Kingdom and in Canada (Smith, Stinson et al. 2004).

1.3.2 Explicative Hypotheses of the ORE

In spite of the vast amount of research on the ORE, the neuropsychological mechanisms underpinning this phenomenon are still poorly understood. A number of theoretical hypotheses attempting to account for the causes underlying this effect have been postulated. However, research has thus far failed to provide consistent evidence for one account over another. Based on of the nature of the explanation offered, these accounts can be broadly categorised into two main strands: one focusing on perceptual and different levels expertise across races; and the other emphasizing social cognitive and motivational factors leading to the differences in behavioural performances between SR and OR faces. Belonging to the first of these tow strands are:

1) The visual expertise hypothesis
2) The contact hypothesis
3) The Multidimensional Face Space Model (Valentine and Endo 1992)

Although emphasizing diverse aspects of processing, these hypotheses are united by the core assumption that a lack of experience with OR faces leads to differences in encoding OR and SR faces, and translates into the observed OR recognition impairment (e.g. Rhodes, Tan et al. 1989; Valentine 2001; Sangrigoli and De Schonen 2004; Tanaka, Kiefer et al. 2004).

The social cognitive accounts instead share the view that individuals tend to process out-group faces in a categorical way, while individuating in-group members (see Brewer 1988; and Fiske and Neuberg 1990; Levin 1996 ; Levin 2000; Hugenberg and Sacco 2008). Importantly, unlike the expertise related hypotheses, according to this theoretical stand the ORE is not due to perceptual differences across faces of different races, which is only a consequence of different categorization processes (e.g. Ostrom, Carpenter et al. 1993). The social cognitive hypotheses include:

1) The Prejudice hypothesis
2) The in-group/out-group hypothesis
3) The feature selection model (Levin 2000)

The following paragraphs will be focusing on these six main explicative hypotheses of the ORE.

1.3.2.1 Expertise Based Accounts

While differing in some key aspects, all expertise-based accounts of the ORE share the view that lower levels of experience with OR compared to SR faces is the cause of the observed OR recognition impairment (e.g. Chance and Goldstein 1981; Tanaka, Kiefer et al. 2004; Hancock and Rhodes 2008; Rhodes, Ewing et al. 2009).

1.3.2.1.1 The Visual Expertise Hypothesis

As the name itself suggests, the visual expertise hypothesis regards visual expertise with one race or the other as the main cause for the ORE. Different levels of expertise lead to a preferential neural tuning to SR faces. Evidence supporting this claim comes from a variety of studies. Developmental research on infant and young participants constitutes one such example. It has been shown that infants as young as three months display a clear SR gaze bias (Sangrigoli and De Schonen 2004; Kelly, Quinn et al. 2005; Bar-Haim, Ziv et al. 2006; Kelly, Liu et al. 2007). Additionally, de Heering (2010) reported that young observers between six to fourteen years of age show a pronounced ORE (see also Walker and Hewstone 2006). Moreover, research carried out with Korean children adopted by European families demonstrates that the ORE can be reversed if children are extensively exposed to OR faces (Sangrigoli, Pallier et al. 2005). A different line of research focusing on adult subjects also supports the visual expertise view. It has been suggested that individuals can significantly improve their recognition performance with OR faces consequently to naturalistic exposure (e.g. Hancock and Rhodes 2008; Rhodes, Ewing et al. 2009). Both self-reported contact with OR individuals (Hancock and Rhodes 2008) as well as living in OR societies (Rhodes, Ewing et al. 2009) correlates with the magnitude of the ORE.

One possible explanation for these findings is that exposure – leading to higher level of expertise with one race or another – leads to differential processing mechanisms for SR and OR faces. As a consequence of greater level of expertise, SR faces are processed configurally, while OR faces in a featural manner (Rhodes, Tan et al. 1989; Tanaka, Kiefer et al. 2004; Michel, Rossion et al. 2006). As explained earlier, strong evidence suggests that configural processing occurs with stimulus classes with which the perceiver hold higher degrees of expertise (e.g. Diamond and Carey 1986; Gauthier, Williams et al. 1998). This type of processing is more efficient as it allows to perceive first and second order relationship amongst facial features as well as processing the face as a whole, leading to better identification (Maurer, Grand et al. 2002). Evidence that SR and OR faces are processed in a qualitatively different way comes from three main lines of research. Firstly, as explained earlier, one of the main behavioural marker of configural processing is the inversion effect (e.g. Rossion and Jacques 2008). Inversion leads to greater recognition impairment for object categories we are expert of (e.g. Rossion and Gauthier 2002). According to this logic, if it is true that SR faces are processed more configurally than OR faces, inverting SR stimuli should lead to a greater impairment compared to OR ones. This is exactly what Rhodes (1989) showed. Unfortunately though a number of studies have failed to produce consistent patterns of results (e.g. Buckhout and Regan 1988), leaving a need for clarification. A second line of evidence supporting the visual expertise view comes from studies exploiting the composite effect paradigm (Young, Hellawell et al. 1987; Goffaux and Rossion 2006). This paradigm rests on the idea that, given that faces are perceived configurally, first order relationship amongst internal facial features would lead to perceiving the same features differently once their spatial relationship is altered. Therefore, when presenting two stimuli composed by the same top halves and different bottoms aligned, participants would perceive the eyes as being different cross images, leading to a perception of two different identities. Michel (Michel, Rossion et al. 2006; 2007; Michel, Corneille et al. 2010) employed this paradigm with WC and EA observers looking at WC and EA faces. She showed a larger composite effect for SR compared to OR stimuli. The third and last line of research makes use of the whole/part paradigm to show differential processing styles for SR and OR face (e.g. Tanaka and Farah 1993; Tanaka and Sengco 1997; Tanaka 2001; Tanaka, Kiefer et al. 2004). In the whole/part paradigm observers are exposed to a target face, immediately followed by the same whole face or by an isolated facial feature (e.g. the eyes). Using this paradigm, Tanaka (2004) reported that WC participants were better at recognizing SR than OR whole faces, but not face parts, which showed the opposite pattern (i.e. better recognition performance for OR than SR facial features). Interestingly however, EA observers recognised whole faces better than face parts regardless of race. The lack of the whole/part face advantage displayed by EA participants though can be explained by one important factor. Tanaka (2004) measured the level of contact participants had with OR individuals, to find that while WC reported extensive experience with WC compared to EA faces, EA observers reported no such difference, claiming the same amount of exposure across racial groups. This observation serves as preparatory ground to introduce the next ORE explicative account: the contact hypothesis.

1.3.2.1.2 The Contact Hypothesis

The contact hypothesis can be regarded as an extension of the visual expertise account. Just like the latter, the contact hypothesis emphasizes the importance of expertise developed through interracial contact in explaining differences in recognition performance across races. Accordingly, a number of studies have documented not only that that interracial contact can improve OR recognition (e.g. Elliott, Wills et al. 1973; Goldstein and Chance 1985; Hancock and Rhodes 2008; Rhodes, Ewing et al. 2009), but also that these observed changes in behavioural performance reflect a change in the type of face processing. For example, Hancock (2008) assessed EA and WC interracial contact by means of self-reports, observing a negative correlation between contact with the OR and the magnitude of the ORE. Importantly, the authors also measured the FIE, reporting that the latter was predicted by the level of contact with OR individuals (i.e. augmentation of OR contact increased OR FIE). Given that the FIE is regarded as a marker of configural processing (in that larger FIE is associated to stimuli processed configurally – see Chapter 2), this last finding creates a direct link between contact with OR and the type of face processing. However, several studies failed to produce a consistent relationship between interracial contact and OR recognition accuracy (e.g. Malpass and Kravitz 1969; Luce 1974; Barkowitz and Brigham 1982; Brigham and Malpass 1985; Ng and Lindsay 1994). In their meta-analysis for example, Meissner (2001) explained that differential levels of contact with the OR only accounted for 2% of the observed variance in the ORE, questioning the robustness of the relationship between the two. These data lay the ground for introducing the main aspect distinguishing the contact from visual expertise hypothesis. Contact alone does not suffice to predict the magnitude of the ORE; it is the quality of the interaction with OR individuals serving as a reliable predictor for this phenomenon (Sporer 2001). Walker (2006) for example emphasized how the mere amount of contact is unlikely to directly reflect increase in expertise unless the type of interaction with OR individuals requires effortful encoding of OR faces. In line with this view, Lavrakas (1976) found a negative correlation between OR recognition impairment and the number of OR friends of their participants. The nature of the relationship individuals have with friends suggests a deeper level of interaction with OR faces, compared to that resulting from mere exposure. Moreover, Rhodes (2009) tested EA participant who had been living in a WC country (i.e. Australia) for a varying period of time, ranging between a week and twenty-six years. They also assessed the quality of contact with OR individuals by means of self-report. Their data showed that quality and quantity of interaction with OR individuals significantly predicted configural processing of OR faces recognition performance. Carroo (1986) compared the magnitude of the ORE in geographically distinct areas, testing AA and Nigerian participants in their country of residence. OR recognition deficit was only found in Nigerian and not in AA observers, who had significantly more contact, both in terms of amount and quality, with WC individuals. Evidence presented by Tanaka (2009) also provides strong support for this view. The authors trained participants to either identify or categorize OR faces by race. Their results showed that, despite the same amount of exposure to OR faces, individuals trained in identification task were significantly better compared to those trained in categorization task. These results seem to constitute a major proof for the importance of the quality of exposure to OR faces in predicting OR recognition performance. However, one must be careful in drawing strong conclusion from these data. The effects of laboratory training in fact are still difficult to explain. It has been shown for example that training individuals in discriminating amongst OR faces can only temporarily reduce OR recognition deficit (e.g. Elliott, Wills et al. 1973; Lavrakas, Buri et al. 1976; Goldstein and Chance 1985; Meissner and Brigham 2001); and that these training effects improve OR recognition with surprising speed (Elliott, Wills et al. 1973; Goldstein and Chance 1985).

Importantly, a number of studies failed to report a significant correlation between the quality of contact with OR individuals and OR recognition performance. Ng (1994) for example tested a group EA participants leaving in Canada and a different group residing in Singapore. The authors reported no differences in the magnitude of the ORE across groups, questioning the validity of the contact hypothesis.

1.3.2.1.3 The Multidimensional Face Space Model

Both the visual expertise and the contact hypotheses provide an account for only one of the facets of the ORE, namely the observed OR recognition impairment. However they fail to offer a valid explanation for the faster OR race categorization. Valentine (1991; Valentine 1991; Valentine and Endo 1992) proposed a comprehensive theoretical model accounting for both facets of the ORE. According to the author, faces are encoded in a multidimensional face space as a function of their perceived difference. The dimensions of the space represent the diagnostic dimensions of faces and may vary across individuals and races (Valentine 1991). Such a space is thus shaped by subjective experience in that the latter affects perceptual differences across face exemplar (i.e. even though the physical physiognomic variance is the same across races, OR faces all look alike!). Psychological representations of faces are depicted multidimensional vectors within an n dimensional space, with the distance between these vectors representing their perceived similarity. The properties of this space thus lead to diverse distributions of SR and OR representations. Therefore, contrary to the highly distinctive SR faces, similarly perceived OR faces will be tightly clustered (see Figure 10).

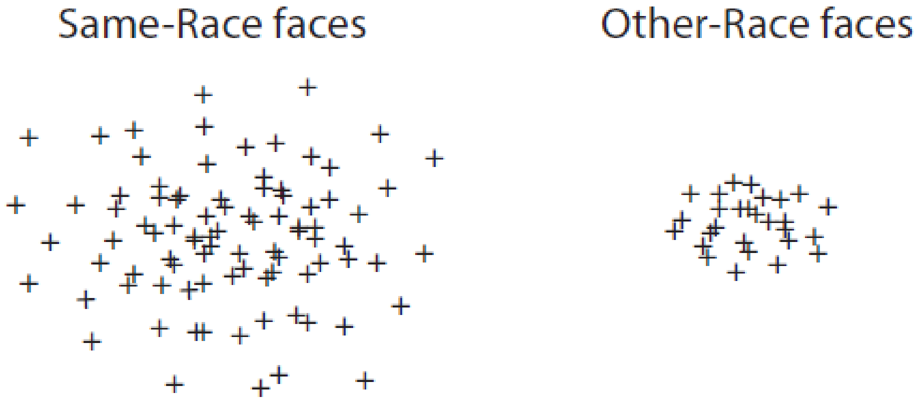


Figure 10 – schematic 2D representation of the Valentine's multidimensional face space model. The crosses represent psychological representation of faces. Note the different density distribution across races, symbolising the perceived distinctiveness of face exemplars. The (multidimensional) space is represented in 2D for simplicity of presentation (from Valentine,1991).

According to Valentine the recognition process is divided into two stages. The first stage involves the encoding of a target face as an n-dimensional vector. The second requires determining whether the encoded vector matches that of a known face. Depending on the viewing conditions (which will be affected by factors such as viewing angle, light contrast etc.) a given amount of noise is expected to affect the encoding process. Within this framework, the decision process (leading to face recognition) is modulated by three main factors: 1) the noise associated to the encoded vector; 2) the level of dissimilarity between the encoded vector and that of a stored representation (which is reflected by its spatial proximity); and 3) the dissimilarity between the stimulus vector and its nearest neighbour (Valentine 1991). The density properties of a given region within the space constitute thus a main aspect impinging upon face recognition performance. In recognizing a distinctive face, the newly encoded target vector will be less likely to be closely located to any other vector than the one corresponding to its stored representation. This will promote recognition speed and accuracy. On the other hand, the encoded vector of a non-distinctive target exemplar will fall in a high density region, increasing the likelihood of multiple closely located neighbours and thus negatively affecting recognition performance. Unlike identification tasks, categorization does not require distinguishing amongst face exemplar. In categorizing faces (by race for example) density properties of the region around the encoded stimulus are used to determine category membership (Valentine 1991). The greater the density in the region, the faster the stimulus will be categorised. These properties are to be held responsible for both the observed differences in recognition performance between SR and OR faces; and the faster race OR face categorization (Valentine 1991; Valentine 1991; Valentine and Endo 1992).

In his original work, Valentine (1991) put forward two variants of this theoretical account: the exemplar-based and the norm-based models. Valentine (1991) argued that both accounts can be seen as “nearest neighbour exemplar” models, but they differ in the role played by a norm (i.e. average face) in encoding faces, from which distinctiveness is measured. The norm-based account holds the existence of an average face, representing the origin of the multidimensional. This average face is the outcome of all the faces encountered in life, weighted by the frequency of the encounter (for example a mother’s face would contribute to the formation of the average significantly more than that of a newly acquired friend). Faces are encoded relatively to the norm, and distinctiveness is thus a function of the distance and direction from the norm (i.e. the origin of the space). The Dissimilarity amongst two face representations can thus be quantified as the cosine between the two n-dimensional vectors. Like the norm-based, the exemplar-based model still assumes that faces are encoded as a function of their perceived distinctiveness (represented by their spatial distance), however the central tendency is irrelevant in the encoding process. Here, exemplars dissimilarity is epitomised as a function of the monotone distance separating two face representations (Valentine 1991). Originally an unresolved debate revolved around which one of the two models was the most empirically sound, with a number of studies supporting the exemplar-based account (e.g. Hintzman 1986; Nosofsky 1988; Nosofsky 1991; Valentine 2001); and others promoting norm-based encoding (Hebb 1949; Hochberg 1978; Goldstein and Chance

1980; Diamond and Carey 1986; Rhodes, Brennan et al. 1987; Valentine 1991; Rhodes 1996; Leopold, O'Toole et al. 2001; Loffler, Yourganov et al. 2005). Recently though, exhaustive evidence from adaptation after-effects studies have discarded the exemplar based in favour of the norm-based encoding of faces (Rhodes and Jeffery 2006).

Valentine’s model is regarded not only as a valid account for the ORE, but it is largely considered as a robust framework for face processing in general. Evidence supporting the multidimensional face space model comes from a variety of sources. Behavioural data (e.g. Leopold, O'Toole et al. 2001), brain imaging in humans (e.g. Loffler, Yourganov et al. 2005), and single cell recording in monkeys (Leopold, Bondar et al. 2006) all strongly support norm-based encoding of faces. Importantly, with regards to the ORE, while this model quite distinctively falls within the expertise based account category, it differs from the previously described hypotheses in one important aspect. This theoretical framework does not make direct predictions regarding qualitatively differences (i.e. configural vs. featrural) in processing SR and OR face; rather it accounts for the behavioural aspects of the ORE on the basis of the experience-dependent frequency with which SR and OR faces are represented in memory. Perceptual training paradigms support the multidimensional face space model. Hills et al. (2006) for example specifically tested the model’s predictions on WC participants. They showed that training individuals on previously identified salient OR faces dimensions (Ellis, Deregowski et al. 1975) led to a reduction of the magnitude of the ORE. The authors thus suggested that developing a finer sensitivity to OR cognitively meaningful facial dimensions produced a finer-grained representation of OR faces, decreasing the density of their distribution within the space. While appealing, the study only assesses the effect of perceptual training on WC participants on AA faces. This is unfortunate as the lack of AA participants makes it impossible to assess a crossover interaction between the race of observers and that of the face stimuli, inducing prudence on any conclusion. Moreover, it has been shown that it is possible to shift the centre of the face space by showing observers a number of distorted face stimuli (Rhodes, Jeffery et al. 2003). Extending this paradigm to include SR ad OR faces Jaquet (2007; Jaquet, Rhodes et al. 2008) adapted participants to convex WC faces (i.e. eyes far apart) and concave EA faces (i.e. eyes close together). Following this manipulation, they reported that their observers perceived WC faces with eyes far apart and EA faces with eyes close together as being more normal compared to non-manipulated stimuli. These findings suggest the existence of separate “norms” for SR and OR faces d (see also Papesh and Goldinger 2010). Although the multidimensional face space model has been proven useful to account for a large number of empirical data, this account has also been questioned. Levin (1996) for example criticizes Valentine’s model on the ground that it does not specify which features are to be held accountable for how face representations are stored within the space. Furthermore, it has been reported that manipulating aspects that do not directly impinge upon diagnostic facial dimensions or density distribution strongly impact upon recognition performance. For example, OR recognition accuracy has been found to improve significantly by means of evaluative incongruence (e.g. presenting OR faces with positive expressions – Corneille, Hugenberg et al. 2007), or attributing faces to arbitrary created groups (Corneille, Goldstone et al. 2006). These findings suggest that social cognitive dimensions may have a major impact on the ORE. The next paragraphs will thus be devoted to exploring these alternative explanatory views of the ORE.

1.3.2.2 The Social Cognitive Accounts

Social cognitive accounts of the ORE share the view that individuals tend to think about SR and OR faces in psychological different ways. SR faces are processed at the individual level, promoting the extraction of individuating information; while OR faces are treated categorically (e.g. Brewer 1988; Fiske and Neuberg 1990; Bodenhausen, Macrae et al. 2003). This notion has been around for a long time and it is not exclusive to the face domain. For example the out-group homogeneity effect (i.e. the tendency of perceiving out-group members more homogenous than in-group ones) is well documented within the academic literature (e.g. Judd and Park 1988). Importantly, beyond the generic assumption of considering the way of thinking differentially about in-group and out-group members as the main cause of the observed OR face recognition impairment (Anthony, Copper et al. 1992), social cognitive theories of the ORE differ in a number of key aspects. The following paragraphs will review some of the main social cognitive accounts of the ORE

1.3.2.2.1 The Racial Prejudice Hypothesis

A number of theorists have proposed that high degrees of prejudice towards OR groups can affect OR recognition performance (e.g. Lavrakas, Buri et al. 1976; Brigham and Barkowitz 1978; Carroo 1987). For example, Carroo (1987) argued that the observed deficit in identifying OR individuals stems from the fact that prejudiced observers focus on race stereotype rather than individual differences amongst OR faces. Galper (1973) also attempted to assess the relationship between prejudice and WC participants recognition performance on AA faces. The tested sample was formed by students enrolled in a Black Studies course. The results showed that participants recognized AA faces more accurately than WC faces. Galper concluded that this data support the prejudice hypothesis assuming that individuals taking part in the Black Studies course held positive attitudes towards AA individuals. While at first glance these results would seem to favour the prejudice hypothesis, Galper's study is fundamentally flawed in two key aspects: firstly the level of prejudice of their participants was never directly assessed; secondly, experience with OR faces was not tested. Moreover, Black Studies students are likely to possess higher level of OR expertise, developed through interracial contact. These considerations seriously undermine Galper's study. Importantly, empirical research failed to reveal a significant relationship between levels of prejudice and the magnitude of the ORE. Lavrakas (1976) directly measured WC participants' prejudice employing the Racial Attitudes Scale. The authors reported no correlation between racial attitudes and AA identification performance. Along the same lines, Brigham (1978) assessed racial attitudes by means of the Multifactor Racial Attitude Inventory, showing that scores on the latter had no effects on OR recognition accuracy. Ferguson (2001) though argued that, while these two studies represent a step forward from to Galper's work (as they directly attempt to measure participants' prejudice), they still present a number of limitations. Firstly, the authors employed self-reports to assess levels of prejudice. However, Fazio (1995) argued that when participants are aware that their racial attitudes are being tested, they are likely to censor their responses. Moreover, Wittenbrink (1997) pointed out that subjects may be unable to accurately self-assess their racial attitudes. In addition, it has been suggested that self-reports, measuring explicit aspects of prejudice, may not tap into the dimensions that are likely to affect face recognition (Dovidio, Kawakami et al. 1997). Dovidio (1997) showed that implicit (as opposed to explicit) prejudice, is a better predictor of spontaneous judgement, and thus it may more accurately account for face recognition performance. Finally, the studies reported above failed to assess the relationship between prejudice and the difference in recognition performance between SR and OR faces, which is one of the key aspects the ORE. Some authors in facts tested observers' OR identification only (e.g. Lavrakas, Buri et al. 1976); while others selectively assessed whether racial attitudes predicted SR or OR faces recognition in isolation (e.g. Brigham and Barkowitz 1978; Carroo 1987). To account for these limitations, Ferguson (2001) measured the relationship between both implicit and explicit prejudice and differences in identification performance between OR and SR faces. They showed that either measures of prejudice failed to significantly predict the magnitude of the ORE in both WC and AA subjects, thus discarding the prejudice hypothesis.

1.3.2.2.2 The In-group/Out-group hypothesis

The lack of robust evidence for the prejudice hypothesis, paired with the shortcomings of the expertise accounts led researcher to further investigate the impact of social cognitive dimensions on OR face recognition. Amongst these, Sporer (2001) put forward the In-group/Out-group (IO) hypothesis. According to the latter, when individuals encounter a face they first assess whether it belongs to an in-group (i.e. SR) or an out-group (i.e. OR) member. This classification affects subsequent stages of face processing. In-group faces elicit deeper levels of processing, leading to automatic extraction of configural information, in the attempt to spontaneously identify the face in question (e.g. Rhodes, Tan et al. 1989). Conversely, out-group faces lead to basic group (or race) categorisation, emphasizing the processing of typical out-group features. These can be either facial dimensions, such as skin colour, or categorical group labels. This categorization process has been suggested to trigger a qualitatively different type of face processing (i.e. featural), which is associated to low-levels of expertise (Tanaka and Farah 1993). The superficial levels of (featural) encoding for out-group faces (Chance and Goldstein 1981) can attributed to a number of reasons: it can be prompted by cognitive disregard (see Rodin 1987); alternatively it can be considered a consequence of the perceived lower utility of out-group members (Malpass 1990); or even a combination of the two. Young et al. (2012) argue that one of the main strength of the IO hypothesis is that it accounts for cross-category effects beyond race. For example this model accounts well for data reflecting same age (e.g. Anastasi and Rhodes 2006; Harrison and Hole 2009), gender (Cross, Cross et al. 1971) and social group (e.g. Bernstein, Young et al. 2007; Rule, Ambady et al. 2007) effects. Moreover this account seems to be strongly supported by several lines of research. A number of studies for example have evidenced a quick extraction of category defining information (e.g. Levin 1996 ; Levin 2000; Cloutier, Mason et al. 2005; Ge, Zhang et al. 2009). It has further been shown that racial in-group faces are processed more configurally than out-group exemplar (e.g. Tanaka, Kiefer et al. 2004; Michel, Rossion et al. 2006; Hancock and Rhodes 2008; Rhodes, Ewing et al. 2009). Hugenberg (2009) tested WC participants on WC faces. They divided their stimuli in arbitrary in-group and out-group categories that were thus equated for levels of expertise. The authors found that in-group faces were processed more configurally than out-group ones, supporting the importance of social cognitive aspects in face processing and concluding that expertise alone cannot account for the full spectrum of the ORE. Along the same lines, Corneille (2006) presented to their participants racially ambiguous face stimuli, showing that these required equal amount of configural processing. However when these stimuli were labelled as out-group members, configural processing was disrupted.

1.3.2.2.3 The Feature Selection Hypothesis

Levin's (1996 ; Levin 2000) feature selection hypothesis shares the main assumption of social cognitive models, holding that the ORE stems from thinking categorically about out-group, and individually about in-group members. Specifically, according to Levin, when viewing in-group (i.e. SR) faces, the psychological differences in thinking about SR and OR exemplars cause individuals to actively search for diagnostic facial information that allow distinguishing amongst SR members. Concomitantly, the tendency to categorically think about OR faces triggers a search for category specific information (i.e. features common to all members), which are extracted before other social and individuating features. This process thus interferes with extracting identity-diagnostic information of out-group faces. Having encoded only the race-specifying feature, OR faces are difficultly distinguished. Essentially, this model rests on the argument that differential search processes (focusing on different facial features) operate for SR and OR faces. Race defining information (e.g. skin tone for AA individuals) are seen as a "feature-positive" target and hence quickly extracted. While Levin was the first to import this idea within the face domain, the view that feature-positive targets are more easily identified than feature-negative ones comes from a long standing tradition of visual research task research (e.g. Treisman and Souther 1985). Treisman (1985) showed that participants are faster and more accurate at finding targets defined by the presence of basic features (i.e. feature-positive) amongst feature-negative distractors (which are defined by the absence of specific features) than vice-versa (Figure 11)

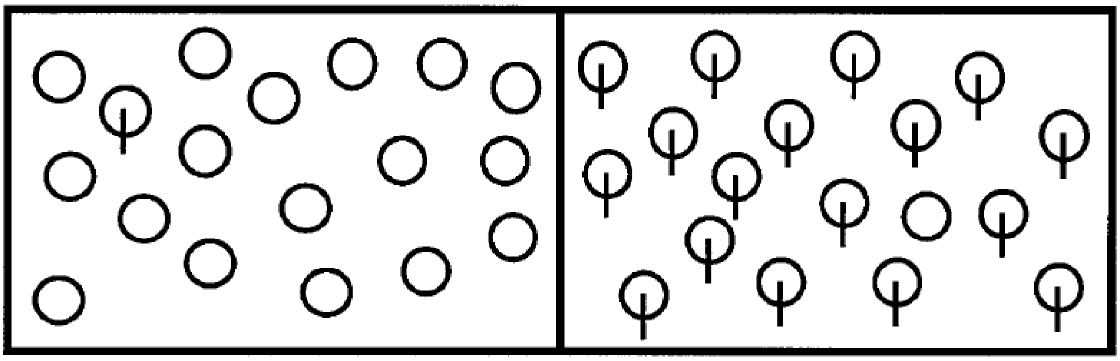


Figure 11 – example of visual search "feature positive" task. It is easier to identify the feature positive target (a circle with a line) amongst feature negative distractor (circles without lines – left quadrant) than vice versa (right quadrant)

Extending this hypothesis to SR and OR faces, Levin thus postulated that it would be easier to identify an OR face amongst SR distractors (Levin 1996 ; Levin 2000). This is exactly what his results showed (Levin 1996 ; Levin 2000). Moreover, Levin (2000) further found that only participants with OR recognition deficit displayed an advantage in search time for OR faces. These data led Levin to conclude that the ORE indeed occurs because of the tendency to overemphasize race-specifying information in OR faces at the cost of individuating information. Ge (2009) and Susa (2010) recently replicated Levin's findings. They reported faster reaction times for OR face categorization by race paired with slower and less accurate OR recognition. These data further corroborate the view that categorization and individuation processes compete during face encoding. Contrastingly though, it has been shown that manipulations leading to out-group categorization of racially ambiguous faces (Rhodes, Lie et al. 2010) do not always translate in poorer recognition performance. This finding is difficult to interpret within Levin's model, thus questioning the comprehensiveness of the feature-selection hypothesis. Further challenging this model, Levin himself (1996) reported that AA participants displayed SR categorization advantage. This finding is incongruent with the prediction of the model, in that, for AA participants, the white colour of OR faces should be perceived as feature-positive and hence lead to faster identification in a search task where the requirement is finding a WC face amongst AA ones. More evidence questioning the validity of the feature-selection model comes from Lipp (2009), who showed that preferential attention to SR or OR faces is at least partly due to task variables such as stimulus size. Furthermore, Zhao (2008) asked their participants to categorise SR and OR faces based on gender and age. They reported that task performance was not affected by the race of the face stimuli, suggesting that in facts race does necessarily precede the processing or other information (such as age and gender).

1.3.3 The ORE: Neurophysiological Evidence

EEG - Even though, as documented throughout this chapter, the ORE has been widely and robustly supported by abundant behavioural evidence, neuroimaging studies (including EEG and fMRI) have thus far failed to produce consistent results in the understanding of this phenomenon. Within the ERP literature, the main on-going debate revolves around whether the N170 face preferential component is in facts sensitive to the race of face stimuli. Contrasting data have been reported. A number of studies have failed to reveal sensitivity of the ERP signal within the N170 time window (e.g. Caldara, Thut et al. 2003; Caldara, Rossion et al. 2004; Tanaka and Pierce 2009). These results seem to suggest that race is not extracted until later stages of face processing. Caldara (Caldara, Thut et al. 2003; 2004) and Tanaka (*2009*) for example both report race sensitivity on the ERP signal roughly 250 to 300 ms after stimulus onset. This is the time window of occurrence of the N250. This component has been related to active categorization of visual stimuli (e.g. Latinus and Taylor 2005; Philiastides, Ratcliff et al. 2006; Philiastides and Sajda 2006; Harel, Ullman et al. 2007), as well as to long term memory of faces (e.g. Schweinberger, Pickering et al. 2002). Modulations on this component would therefore seem to fit with social cognitive accounts of the ORE. On the other hand though, several lines of research have reported N170 modulation to race. Amongst these, some have shown that OR faces elicit larger N170 amplitude (e.g. Stahl, Wiese et al. 2008; Walker, Silvert et al. 2008); while others reported larger N170 amplitude for SR faces (e.g. Ito and Urland 2005; Herrmann, Schreppel et al. 2007). A number of factors may be held accountable for this reported heterogeneity of the ERP results. Firstly considerable methodological differences exist across reports. Some studies employed active old/new recognition paradigm (e.g. Stahl, Wiese et al. 2008); while others employed passive orthogonal tasks, such as identifying two same subsequently presented stimuli (e.g. Walker, Silvert et al. 2008). As explained earlier (e.g. Okazaki, Abrahamyan et al. 2008; Wronka and Walentowska 2011), the N170 seem to be modulated by task demands (see also Caldara, Thut et al. 2003; Ito and Urland 2003; Caldara, Rossion et al. 2004; Herrmann, Schreppel et al. 2007), therefore, the considerable differences in the nature of the tasks employed may partially account for some of the inconsistencies reported. Secondly, global low level properties of the stimuli (such as luminance, contrast and amplitude spectrum), which are known to affect the amplitude of early ERP components (e.g. Dakin, Hess et al. 2002; Rousselet, Pernet et al. 2008) were not controlled across studies, even though these co-vary with the race of the stimuli. Thirdly different types of OR stimuli, including EA, AA and Hispanic (e.g. Caldara, Thut et al. 2003; Ito and Urland 2003; Caldara, Rossion et al. 2004; Ito and Urland 2005; Herrmann, Schreppel et al. 2007; Walker, Silvert et al. 2008; Tanaka and Pierce 2009) faces have been employed. Finally, all the studies that have reported modulation to race on the N170 have only relied on data gathered from a single population: the WC population. This methodological shortcoming undermines generalizations of the results as, as explained earlier, a crossover interaction across the race of the observers and that of the face stimuli is fundamental to rule out any potential confound intrinsic in the stimulus set

fMRI – Even though, compared to EEG data, considerably less evidence exists within the literature, a number of fMRI studies have offered indications that neural activity within the FFA is modulated by race. For example, by means of “classic” univariate approach, Golby (2001) showed that the rFFA responded more strongly to SR compared to OR faces. Kim et al. Kim (2006), reported a similar patterns of results, by demonstrating greater BOLD signal response to the bilateral FFAs for SR compared to OR unfamiliar faces. These findings indicate the involvement of the FFA in the organization of face representations with regards to race. Natu et al. (2010) however recently challenged this view, arguing that the neural activity elicited within FFA alone is not sufficient to distinguish among races. The authors showed that that SVM multi-voxel pattern classifiers can only discriminate faces by race when taking into account the activation elicited within the broader ventro-temporal (VT – Natu, Raboy et al. 2010). Natu (2010) also highlight differences in the neural dynamics of FFA as a function of race: the FFA activation time course is characterized by an initially stronger response to SR faces, which attenuates over time to ultimately produce the opposite pattern (i.e. larger activation for OR compared to SR faces). These findings are in stark contrast with previous reports, compelling further clarification on the role of the FFA in processing the race of faces.

1.4 The purpose of this thesis

Before discussing the aims of this thesis it is essential to clarify some of the key concepts distinguishing different accounts if the ORE. As explained throughout this chapter, in the attempt to account for the different facets of the ORE, a number of hypotheses have been postulated. These can be grossly divided in two categories: the experience based accounts; and the social cognitive accounts. As previously argued, these two categories differ on a number of key aspects; primarily on what are considered to be the main factors causing the behavioural ORE. Expertise based models hold that experience leads to differences in perceiving SR and OR faces. Expertise with one race or another in facts shapes the neural tuning to faces, causing it to be shifted and optimised to process SR exemplars. The "un-optimised" neural tuning for OR faces consequentially leads to perceiving the latter as highly homogeneous. Therefore, expertise based accounts see the ORE as a direct experience-related consequence of the inability of the human brain to efficiently process the OR diagnostic facial dimension that are crucial to distinguish amongst individuals. On the other hand, social cognitive accounts consider the behavioural magnitude of the ORE to be a consequence of different motivational factors, which cause differential information to be processed across races. Unlike expertise based hypotheses, these theories do not conceptualise that individuals are incapable of processing OR individuating facial information; rather that differences in psychological thinking across races (i.e. categorically for OR and individually for SR faces) favour the extraction of certain information over others (i.e. race defining and individuating features respectively for OR and SR faces). The main purpose of this paragraph is to highlight one implicit difference across these perspectives, which is essential for this thesis. The assumptions of the expertise based accounts, resting on the idea of the inability of individuals to efficiently process OR faces, see the ORE as originating at *early perceptual level of face processing*: OR faces are *perceived* as looking alike. Contrarily, social cognitive theories see the ORE as stemming from the fact that, the automatic prioritisation of the extraction of given facial features over other leads to differences in stored mental representation of faces. Therefore according to model belonging to this strand, the ORE is caused by *differences in later stages of face processing* that are related to categorization processes: OR faces are *categorised* as a homogenous outgroup and thus look alike.

Although, as seen earlier, research has thus far produced contrasting findings, neuroimaging techniques, such as EEG and fMRI, can reveal a great deal of information regarding the neurophysiological basis of the ORE. These techniques can help shed light upon the debate reigning within the academic literature as to which strand (i.e. social cognitive or expertise based) best accounts for this phenomenon. EEG for example can elucidate whether the ORE is a perceptual or categorisation based effect. It is hypothesised that, if the ORE originates at early perceptual levels of face processing, the race of the faces should modulate the early ERP face preferential N170 component. These patterns of results would promote expertise based accounts. On the other hand, observing race modulations on later ERP components – like for example the P2 or the N250 – would favour the social cognitive account, supporting the memory based origins of the ORE. Moreover, the reliable spatial resolution offered by fMRI can clarify the cortical location where SR and OR faces are encoded, as well as reveal important insights onto their neural organization.

The purpose of this thesis is to clarify the neurophysiological basis of the ORE. Specifically, this work promises to answer tree fundamental question within this framework: *when, how* and *where* the ORE occurs in the human brain. Two EEG studies have been designed to tackle the first interrogatives, namely when and how the ORE originates. A third fMRI study attempts to answer the second two questions: how and where SR and OR faces are encoded in the human brain.

The first study exploits the advantages conferred by the FIE in conjunction with the high temporal resolution offered by EEG to assess two issues: 1) whether the N170 face preferential component is sensitive to race, 2) whether SR and OR faces are processed in qualitatively different ways (i.e. configurally or featurally). We reasoned that if SR are processed more configurally than OR faces, the former should elicit lager behavioural and electrophysiological FIE, compared to the latter. Because of the specificity of the hypothesis the statistical analysis will be component based.

The second EEG study makes use of adaptation (or repetition suppression), which is considered to be a well-established paradigm to assess the nature of information coding at the perceptual and neurophysiological levels. In light of recent evidence showing N170 sensitivity to identity (e.g. Jacque and Rossion, 2007), it is hypothesised that this components should display differential levels of repetition suppression (and thus sensitivity) across identities of different races. Specifically it is expected that SR, but not OR, faces of different identities would be distinguishable at the N170 level.

The third and final study uses fMRI to assess the nature of the neural organization of SR and OR faces within four functionally defined regions of interest (ROIs): the right and left FFAs and the right and left OFAs. The aim of the study is to assess whether and where the neural representations of SR and OR faces follow the laws predicted by the ORE and the norm-based multidimensional face space model.

1.5 Methods

1.5.1 EEG

Electro-encephalogram (EEG) is one of the most commonly used non-invasive techniques for measuring humans' neural activity. EEG possesses an extremely accurate temporal resolution (i.e. in the millisecond space), at the costs of poor spatial resolution. It measures electrical changes recorded by electrodes placed on the scalp surface caused by the summed activity of pyramidal neurons with their axons aligned and pointing towards the scull (Figure 12). Given that the measured neural activation is resulting from the average firing of thousands of neurons (Nunez and Srinivasan 2005), it is difficult to pinpoint the exact neural generator. While it is generally accepted that the measured brain potential reflects excitatory post-synaptic neural activity, the specific contribution of "primary" and "secondary currents" to the recorded signal is yet to be fully clarified (Niedermeyer and Lopes da Silva 2005; for a recent review see Kirschstein and Kohling 2009). Primary currents are small changes in the electrical field directly caused by neuronal activity. Secondary currents are the residual activity of primary current "trapped" within a conductive medium (e.g. the brain tissue and brain liquor). Since changes in the electrical field induced by primary currents are too small and transient to be detected by scalp level electrodes, EEG is believed to measure primarily neuronal activity stemming from secondary currents (Niedermeyer and Lopes da Silva 2005; Nunez and Srinivasan 2005).

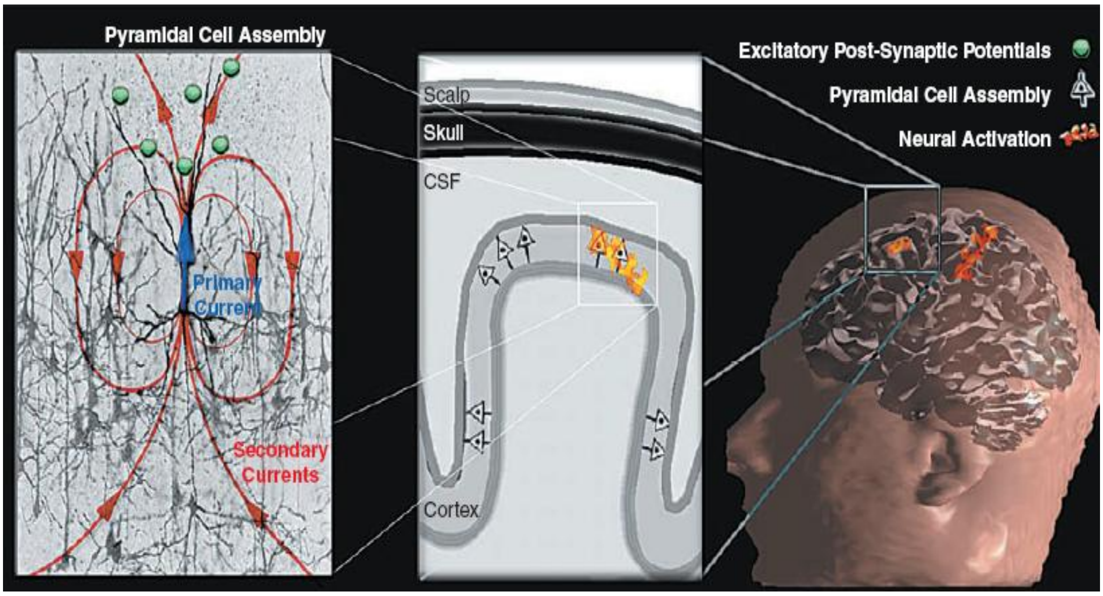


Figure 12 - a diagram reflecting the neural activity measured by EEG

The electrical signal is recorded and transformed (from analogical to digital) through differential amplifiers measuring the differences between the scalp electrodes and a given reference. The latter can be: 1) a single electrode usually placed in locations of low neuro-electrical activity (such as the nose or the earlobe); 2) an average reference, consisting of a balanced high-resistance network that connects the electrode inputs together and creates a virtual ground site; 3) a bipolar reference, where electrical activity is measured as the difference between two adjacent electrodes. The validity of the chosen reference depends on the resulting signal-to-noise ratio of the EEG signal, thus, in order to attempt to improve the quality of the recorded data, the signal can be re-referenced off-line (Essl and Rappelsberger 1998; Hagemann, Naumann et al. 2001). An increasing consensus among EEG experts is emerging favouring of common average ground reference (AR) , which represents the zero potential point in the brain and offers a relatively silent ground site for the measurement (Picton, Bentin et al. 2000; Rosenfeld 2000).

The electrodes usually are placed on the scalp most commonly following a configuration known as the international 10-20 system (Jasper 1958). The latter specifies the electrode positions in relation to fixed markers on the skull (i.e. the nasion and the inion). The number of electrodes usually ranges between sixteen up to three-hundreds and are incorporated in a nylon cap (although net configurations also exists), which facilitates a standardized measurement of EEG activity (Niedermeyer and Lopes da Silva 2005; Nunez and Srinivasan 2005).

The digital signal is filtered offline (as well as usually online with a band-pass filter of arbitrary frequency) by means of high-pass and low-pass filters (such as for example a butterworth filter) to remove noise generated by unwanted electrical activity.

This thesis exploits the advantages conferred by one of the main EEG techniques: Event Related Potentials (ERPs). ERPs are measured brain activities that are stimulus locked (i.e. observed after stimulus onset), and hence directly related to the stimulus at hand (Nunez and Srinivasan 2005). The onset of a stimulus thus becomes the time zero and an epoch of arbitrary length (e.g. from 200 ms before to 600 ms after stimulus onset) is chosen and extracted from the continuous signal. Given that one of the main assumptions for ERPs is that no activity (of interest) should be observed before stimulus onset, baseline correction is applied by subtracting from each single trial the mean activity of the defined baseline (e.g. from 200 ms before stimulus onset to 0). Noisy trials are rejected and artefact correction is applied. A popular way to correct for artefacts caused by, for example, muscle activity is by means of independent component analysis (e.g. Delorme and Makeig 2004). The latter allows modelling and segregating the different components generating the signal in order to remove the unwanted ones.

ERP waveforms consist of a series of positive and negative voltage deflections, called components. These components are usually named with a P or an N, indicative the valance of the deflection (i.e. P if positive and N if negative), followed by a number referring to the latency of occurrence in milliseconds. Therefore the N170 for example stands for N – negative deflection – occurring 170 ms after stimulus onset (Figure 13).

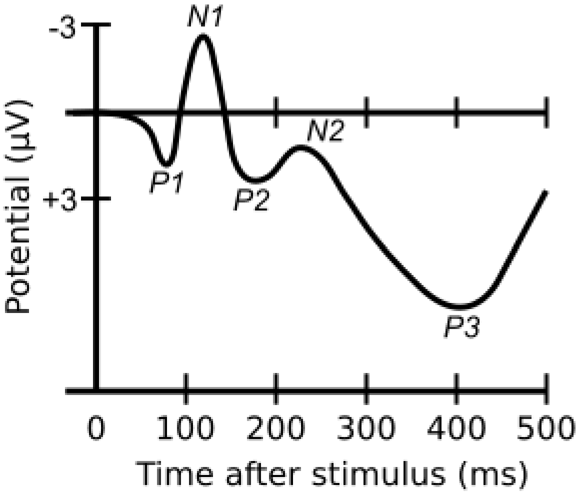


Figure 13 – example of ERP nomenclature

Amplitude and latency of the ERP signal are the variables of interest, compared across conditions by means of inferential statistical tests. Conventional analysis measures either peak or mean amplitude of a given component of the average ERP (computed by performing the mean across trials). Peak amplitude is defined as the most positive or most negative deflection of the component of interest; mean amplitude is the average of all the time points of an arbitrary time window centred on the peak of a given component. Unless aiming to test a specific hypothesis though (like assessing a specific component's sensitivity to a given stimulus dimension), focusing on the mean or peak amplitude/latency of one or more components can be restrictive and potentially lead to missing meaningful differences across conditions (Rousselet, Pernet et al. 2011). Important effects occur between peaks, and they are quantifiable by applying analyses at all time points and electrodes (Delorme, Westerfield et al. 2007; Schyns, Petro et al. 2007; Rousselet, Pernet et al. 2008; Schyns, Petro et al.

2009; Pernet, Chauveau et al. 2011 – see also chapter 3; Schyns, Thut et al. 2011). Moreover, peaks may signal the end of a process rather than its information processing mechanism (Schyns, Petro et al. 2007).

1.5.2 fMRI

How does it work - Magnetic Resonance Imaging (MRI) scanners for humans are built with powerful magnets generating electromagnetic fields varying from 1.5 to 12 Tesla (T); however 3T (with growing popularity of 7T) scanners are most commonly used for academic research. These machines exploit the composition of bodily tissues, which contain large amount of water and hence H+ ions. The magnetic moments of these protons are precessed (i.e. change in the orientation of the rotational axis) and become aligned with the direction of powerful magnetic fields, such as that generated by the MR scanner. Radio frequency (RF) pulses are intermittently delivered by RF coils. When on, these pulses create another magnetic field that is applied perpendicularly to that of the main coil and it oscillates at resonance (also known as Larmor) frequency. This causes the spin of the protons in the magnetic field to flip to high energy state. When the RF pulse is turned off, the protons return to thermodynamic equilibrium becoming re-aligned with the static magnetic field. It is during this relaxation period that radio frequency signals are sampled from the receiver coil and stored as a function of time during the data acquisition of an MR imaging sequence. The emission of energy in the form of an electromagnetic resonance signal of a nucleus after its excitation is referred to as echo. Once the protons are fully realigned with the static magnetic field, another RF pulse is applied and the cycle begins again (detailed information about the process described above can be found in Toga and Mazziotta 2002; Lee 2006).

MRI raw data are thus the result of this magnetisation (i.e. a measure of the intensity of the induced magnetic moments) and are usually acquired as transversal slices. Within these slices the resonance of the excited protons are stored as sinusoid functions of different encoding frequencies, with the direction of the encoding frequency represented by the horizontal axis, and its phase along the vertical axis. Importantly the Larmor equation sates that the resonant frequency is proportional to the field strength (Toga and Mazziotta 2002; Lee 2006). Therefore, by applying linear changes (i.e. gradients) in the magnetic field it is possible to alter the resonant frequency of the spins, rendering it spatially dependent. This is done to spatially encode the positions of the MRI spins which allows accurate 2D/3D image reconstruction. A gradient pulse is thus delivered through gradient coils creating non-uniformity in the field and varying the Larmor frequency as a function of spatial position, so that spins at different location precess at frequencies unique to their location (Toga and Mazziotta 2002; Lee 2006).

The 2D matrix (covering the phase and frequency encoding data) is known as k-space and it therefore represents the full spectrum of the spatial frequency information the imaging object. A Fourier transform is finally applied to the k-space to reconstruct the final MR image of a given slice of the brain. A 3D image (i.e. a volume) is then compiled from multiple 2D images (Toga and Mazziotta 2002; Lee 2006).

MRI sequences consist of different combinations of RF pulses and gradients, to favour the resonance (and hence the acquisition) of protons within a particular tissue (contrast), while limiting images artefacts, without altering the signal to noise ratio. There are three main components for any imaging sequence:

1) An RF excitation pulse (to induce electromagnetic resonance)
2) Gradients for spatial encoding (2D or 3D), whose arrangement will determine how the k-space is filled.
3) A combinations of echo types determining the type of contrast (i.e. relaxation times – T1, T2 and T2*).

Other parameters that have to be selected by the user include:

- TR (repetition time) – the amount of time (usually in seconds) between consecutive excitation pulses
- TE (time echo) – time interval between the application of a RF pulse and the peak of the echo signal (usually in milliseconds)
- Flip angle – the angle to which the net magnetization is tilted relative to the direction of the main magnetic field (as a consequence of RF excitation pulse at the Larmor frequency).
- Turbo factor – the number of echoes acquired after each excitation.
- Field of view matrix (FOV) –the size (usually in mm^2) of the 2D or 3D spatial encoding area of the image

What does it measure – While the previous section was related to MRI in general, the following paragraphs will focus on fMRI. As explained earlier, fMRI detects changes in blood oxygen level dependent (BOLD) signal. The main assumption upon which this technique rests is that increase in neural activity within a given cortical region is coupled with increase in flow of oxygenated haemoglobin. In order to properly function, neurons need energy, which is produced in the mitochondria. These make use of oxygen to extract energy from glucose and fat and synthesize the adenosine triphosphate (ATP) enzyme. The latter, often referred to as the "molecular unit of currency" of intracellular energy transfer (Knowles 1980), is essential for initiating a chain of chemical reactions within the neuron, leading the cell to "fire". Consequently, when neurons are active, larger volumes of oxygenated blood flow in the capillaries adjacent to the cells in question. Importantly, haemoglobin, when oxygenated, creates a magnetic field, which is in opposition to an externally applied magnetic field (i.e. it is diamagnetic). However deoxygenated haemoglobin repulses externally applied magnetic fields (i.e. it is paramagnetic). This oxygen-dependent difference in the magnetic properties of blood molecules produces small differences in the MR signal.

Given that neural activation requires oxygen consumption, it may therefore seem legitimate to expect a relative decrease in the magnitude of the BOLD signal; however this is not exactly the case. While after an increase in neural activity an "initial dip" in the signal is observed (Figure 14), the haemodynamic response actually increases. This occurs not only to meet the oxygen demands required to synthesize enough ATP needed by the neurons to fire; but because the increased oxygen demands lead to an overcompensation. The BOLD signal response in facts peaks after roughly six seconds, taking six to fourteen more seconds to return to baseline. This return to baseline is often accompanied by a "post-stimulus undershoot" (Figure 14). These properties of the BOLD signal are summarised in the haemodynamic response function (HRF – Figure 14).

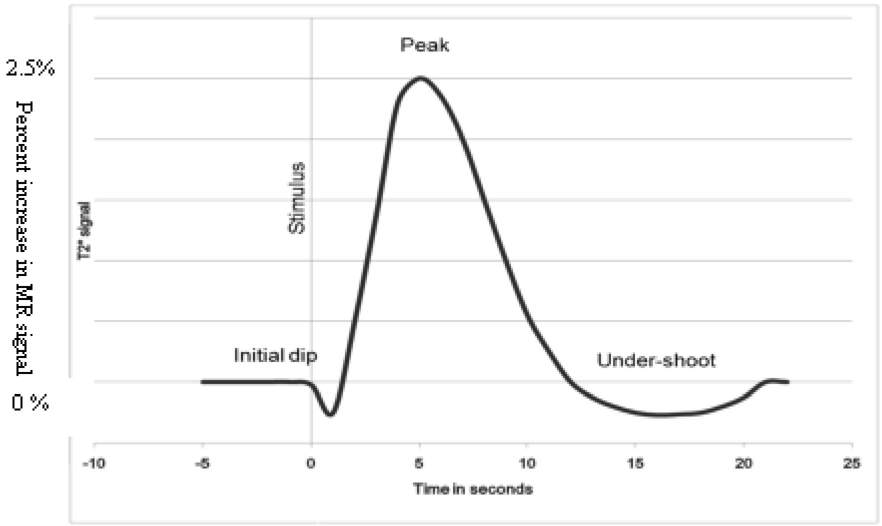


Figure 14 – the Haemodynamic Response Function (HRF)

Although beyond the scope of this thesis, it is worth spending a few sentence highligitng one of the main problems in fMRI, stemming from the fact that the BOLD signal, reflects neural activity indirectly. As explained earlier, the coupling between the oxygen level and increase in neural activity is at the core of fMRI. But what is the nature of the neural activity reflected by the BOLD signal? Is the BOLD signal more strongly related to neuronal action potentials or to local field potentials (LFP)? Early studies comparing human BOLD response and monkey electrophysiological data reported compelling evidence suggesting that the BOLD response reflect primarily increase in oxygen blood levels used to generate action potentials (e.g. Heeger, Huk et al. 2000). More recently however, these data have been strongly challenged. An ever increasing number of studies in facts have consistently and robustly reported a strong coupling between local field potentials (LFPs) and changes in tissue oxygen concentration in the absence of spikes (Logothetis, Pauls et al. 2001; Nir, Fisch et al. 2007; Viswanathan and Freeman 2007). These results imply that the BOLD signal is more closely related to synaptic activity.

fMRI Analysis - While many techniques have been proposed to statistically analyse fMRI data, many rely on parametrically modelling the BOLD signal with the afore described HRF by means of general linear model (GLM). The following section will lightly touch upon some of the issues in using the GLM for fMRI data as well as the different ways of exploiting this technique.

The HRF accounts for the dispersion and delay of the BOLD signal, however, in modelling BOLD responses there are other factors that need to be taken into account.

fMRI scans have to be considered as a function of time and analysed as a timeseries (Friston, Jezzard et al. 1994). The BOLD signal in facts is not independent across events and tends to be correlated between consecutive scans. This is because the acquisition time (i.e. TR) is usually relatively fast, ranging in most studies between one and four seconds. As explained earlier however, BOLD responses need between twelve and thirty seconds before returning to baseline. This observation leads to a summation across BOLD signal events that is not taken into account by canonical HRF. Importantly, Boynton et al. (1996) argued that the BOLD signal can be considered as an output of a linear time-invariant (LTI) system. The response elicited by consecutive stimuli implies that the BOLD responses are independent of time and that activity elicited by consecutive stimuli is thus superimposed in a linear fashion. The linearity assumption holds only for relatively long stimulus onset asynchronies (sot). However, whit short sots (less than approximately 3 seconds) non-linearities are predominant (Friston, Josephs et al. 1998). These observations are crucial in modelling the BOLD signal. BOLD signal events can be modelled linearly by means of General Linear Model (GLM). Importantly, the GLM has to be expressed as a function of time and take into account the autocorrelation patterns (Friston, Jezzard et al. 1994). These issues are summarised in the equation:

$$y(t) = x_c(t)\ \beta_c + \varepsilon(t) \qquad \varepsilon(t) \sim N(0,\sigma^2\ \Sigma)$$

where y(t) represents the fMRI timeseries (each timepoint representing one scan);, xc(t), c=1..Nc are the explanatory variables (also known as predictors) described as a function of time; βc (beta) represent the Nc parameters which is itself time-invariant; ε is the error term; and Σ is the noise autocorrelation (Henson 2003). ε is minimised with the use of some stress function (e.g. least squared residuals)
Importantly, in order to model BOLD responses as a function of a stimulus, under LIT assumption, the HRF has to be convolved with a finite impulse response (FIR – Friston, Jezzard et al. 1994). FIR can vary from basic “boxcar”, to more complex sinusoid and cosinusoid functions (see Henson 2003 for more details).

The analysis described above is performed independently per voxel. Importantly, as explained earlier, in the GLM each predictor time course X is associated coefficient or beta weight β, quantifying its contribution in explaining the voxel time course y. This simplifies statistical analysis comparing differences across conditions, in that it reduces the dimensions of BOLD data. It is thus possible to compute an activation map summarizing the neural activity of a given condition across the whole timecourse.

Once computed, the beta weights only provide a descriptive map of neural activation. However in order to pinpoint a specific function of a given brain regions, these maps are further used as inputs to second level statistical tests. In traditional univariate approaches, beta maps are smoothed by applying arbitrary Gaussian kernels of 4-8 mm in order to further eliminate unwanted noise from the signal. In classical fMRI paradigms, focusing on activation based analysis, spatially smoothed maps are considered as signal, while fine grained components as noise (Kriegeskorte and Bandettini, 2007). After being spatially smoothed, functional maps are contrasted across conditions to identify relevant regions of interest (ROIs). The timecourse within these ROIs is then averaged across voxels and the whole region is thus treated as one big voxel. This procedure, as well as removing what is regarded as unwanted noise, also reduces the effective number of comparisons (decreasing the "threats" of appropriately choosing a multiple comparison correction technique that will minimise both type I and II errors). Moreover, it helps combining data across subjects by improving interbrain functional (and to some extent structural) correspondence. This procedure has been proved robust and useful in a number of situations. One such example is the localization of functionally defined cortical regions. Face preferential cortical patches for example have been consistently reported using a variety of paradigms by means of univariate approach (e.g. the face preferential FFA – Kanwisher, McDermott et al. 1997; McCarthy, Puce et al. 1997).

However, univariate approaches are rapidly losing favour amongst researchers. This is partly due to the fact that a growing consensus is emerging within the fMRI literature considering fMRI patterns as distributed codes (see Kriegeskorte and Bandettini 2007). It has been shown for example that unsmoothed patterns of activation contain meaningful information. These patterns (and most importantly the difference amongst them) are even capable of revealing columnar level information (Haynes and Rees 2005; Kamitani and Tong 2005). Furthermore, as argued by Kriegeskorte (2007), the rapid technological advances that have led to the production of more powerful MR scanners does indeed increase fMRI spatial resolution but it brings along a number of challenges. The authors highlight four possible limitations related to such a development: 1) high resolution fMRI may produce inaccurate (for example as a consequence of blurring or distortion) picture of neuronal activity; 2) small voxel are likely to be more noisy; 3) the larger number of voxels complicates the interpretation of neural patterns as well as imposing statistical restrictions due to the large number of comparison, significantly increasing the chance of both type I and II errors (i.e. multiple comparison correction problem); 4) it further complicates functional interbrain correspondence . In order to overcome these problems and fully exploit the advantages conferred by high resolution fMRI, the authors suggest not to focus on the magnitude of voxels' activation per se, rather to make use of the information conveyed by the patterns of activity (for more details see Kriegeskorte and Bandettini 2007). Examples of information based analyses include representational Dissimilarity methods (Kreigeskorte, Goene et al. 2006) and multivariate pattern analysis (MVPA) such as pattern classifiers (Pereira, Mitchell et al. 2009).

The processes described above do not aim to provide a complete picture of all the possible analytical tools available for fMRI data (other include for example principal component analysis, independent component analysis, partial least square). The above section aimed to offer a basic understanding of what a beta weight represents, why the GLM is a popular analysis tool for BOLD data, and different ways of exploiting the information conveyed by beta maps. The reason for this was to deliver a basic theoretical framework that would allow the reader to later understand the choice of analysis implemented in Chapter 4. It is important to acknowledge that many issues concerning BOLD signal analysis (such as pre-whitening, low pass filtering, artefactual movement related noise etc.) are not discussed as regarded beyond the scope of this thesis.

2. Inverting Faces Elicits Sensitivity to Race on the N170 Component: a Cross-Cultural Study

(Published in Journal of Vision (2010) 10(1):15, 1–23)

Preamble

Human beings are natural experts at processing faces, with some notable exceptions. Same-race faces are better recognized than other-race faces: the so-called other-race effect (ORE). Inverting faces impairs recognition more than for any other inverted visual object: the so-called face inversion effect (FIE). Interestingly, the FIE is stronger for same- compared to other-race faces. At the electrophysiological level, inverted faces elicit consistently delayed and often larger N170 compared to upright faces. However, whether the N170 component is sensitive to race is still a matter of ongoing debate. Here we investigated the N170 sensitivity to race in the framework of the FIE. We recorded EEG from Western Caucasian and East Asian observers while presented with Western Caucasian, East Asian and African American faces in upright and inverted orientations. To control for potential confounds in the EEG signal that might be evoked by the intrinsic and salient differences in the low-level properties of faces from different races, we normalized their amplitude-spectra, luminance and contrast. No differences on the N170 were observed for upright faces. Critically, inverted same-race faces lead to greater recognition impairment and elicited larger N170 amplitudes compared to inverted other-race faces. Our results indicate a finer-grained neural tuning for same-race faces at early stages of processing in both groups of observers.

2.1 Introduction

Human beings are natural experts at recognizing faces. Brain imaging studies have shown that this visual expertise is implemented by a specialized cortical network located in the occipital temporal cortex (Haxby, Hoffman et al. 2000), optimally tuned to process this particular visual category (Caldara, Seghier et al. 2006; Caldara and Seghier 2009). However, such a highly developed biological skill is markedly impaired in processing two specific face categories: other-race and inverted faces.

The face recognition impairment observed for other-race (OR) compared to same-race (SR) faces has long been reported in the literature (Feingold 1914), a phenomenon often referred to as the Other-Race Effect (ORE – Feingold 1914; for a review see Meissner and Brigham 2001). Although the neural mechanisms at play are yet to be understood, it is widely accepted that visual expertise plays a crucial role in shaping this recognition deficit. Many studies advocate the existence of finely tuned mechanisms to process SR faces, probably developed as a by-product of visual experience (Walker and Tanaka 2003; Tanaka, Kiefer et al. 2004; Caldara and Abdi 2006; Michel, Caldara et al. 2006; Michel, Rossion et al. 2006), which can plausibly be held accountable for SR face identification advantage. This identification advantage is paired with faster performance in race categorization tasks for OR faces (Valentine and Endo 1992; Levin 1996 ; Caldara, Rossion et al. 2004). To account for these findings, Valentine & Endo (1992) suggested a model in which individual faces are stored in a multidimensional space as a function of experience. Within this space, OR faces are more closely clustered together than SR faces. These differences in the spatial distribution of the face exemplars would translate in be responsible for faster OR race categorization but impaired identification. A different account was provided by Levin (2000) who suggested that race information is a feature that is quickly extracted from OR faces at the cost of the information required for fine individual discrimination.

Picture plane inversion of faces also affects face recognition. Inverting faces has been consistently linked to a significantly greater recognition deficit compared to any other visual category (Yin 1969): the so-called Face Inversion Effect (FIE). The FIE is thus regarded as one of the strongest evidence for specialized face processing. Although the putative neural mechanisms underlying this phenomenon have yet to be clarified, some level of consensus seems to reign around the idea that visual expertise may be accountable for the effects of face inversion (e.g. de Haan, Pascalis et al. 2002; Rossion and Gauthier 2002). One of the main hypotheses involving qualitative processing differences holds that, as a byproduct of experience, the human brain engages into distinct mechanisms in processing upright and inverted faces: holistic mechanisms for upright and featural mechanisms for inverted faces; or at least that picture plane inversion significantly impairs holistic processing of faces (Rossion 2008). One can thus infer that the greater level of expertise with SR faces, which translates in higher levels of holistic processing (e.g. Michel, Caldara et al. 2006; Michel, Rossion et al. 2006), should elicit a stronger FIE compared to OR faces. This prediction is supported by converging evidence showing that inverting SR faces leads to a greater impairment in recognition performance compared to OR faces (Buckhout and Regan 1988 ; Rhodes, Tan et al. 1989; Murray, Rhodes et al. 2003; McKone, Brewer et al. 2007). To date, only a single study reported the opposite pattern of results: Valentine (1986) found a larger FIE for OR faces compared to SR faces. However, these authors attempted to equate performance by modulating the time of exposure for encoding SR and OR faces (of 2 and 5 seconds respectively), rendering these findings incomparable across groups of observers.

Electrophysiological studies in humans have significantly contributed to clarify the time course of visual processing. With regards to faces, a critical time window occurs between 130 to 200 ms after stimulus onset, in which the early Event-Related Potential (ERP) N170 component takes place. The N170 is a negative deflection in the ERP signal occurring roughly 170 ms after stimulus onset, peaking at occipitotemporal sites, which tends to be larger for faces than any other visual object categories (for a recent review see Rossion and Jacques 2008). Since Bentin (1996) seminal work, the speculative debate on the putative mechanisms underlying the N170 has yet to be resolved. While originally this component was believed to reflect the structural encoding of faces prior to individual face recognition (Bentin, Allison et al. 1996), recent evidence has shown N170 modulation to identity (Jacques and Rossion 2006; Jacques, d'Arripe et al. 2007) and levels of expertise (Tanaka and Curran 2001; Rossion and Gauthier 2002), suggesting that it may reflect more advanced stages of face processing. Earlier studies have identified a positive component peaking in the time window of the N170 at central and frontal sites: the Vertex Positive Potential (VPP – Botzel and Grusser 1989; Jeffreys 1989). Like the N170, the VPP has been reported to respond with larger amplitude to faces than other visual category, suggesting that both components reflect the same neural process (Joyce and Rossion 2005).

Despite the large amount of behavioral findings supporting the ORE, electrophysiological studies have as yet failed to achieve a degree of consistency in the understanding of this phenomenon. The main ongoing debate lies in whether the early N170 face-preferential component is sensitive to race. Research has thus far produced contrasting results. A number of studies have failed to report sensitivity to race on the N170 (e.g. Caldara, Thut et al. 2003; Caldara, Rossion et al. 2004; Tanaka and Pierce *2009*), or on the related VPP (Ito, Thompson et al. 2004), suggesting that the race of the stimuli is not processed until later stages (i.e. roughly 250-300 ms after stimulus onset – Caldara, Thut et al. 2003; Caldara, Rossion et al. 2004; Tanaka and Pierce *2009*), or that the N170 is not be sensitive enough to capture race information (Caldara, Thut et al. 2003). However, other studies have found OR faces eliciting larger N170 amplitudes than SR faces (Stahl, Wiese et al. 2008; Walker, Silvert et al. 2008), with two studies reporting larger N170 amplitude for SR faces (Ito and Urland 2005; Herrmann, Schreppel et al. 2007).

The heterogeneity of the N170 results described above may be explained by considerable methodological differences across studies. Indeed, race modulation of the N170 appears to depend on task demands (Caldara, Thut et al. 2003; Ito and Urland 2003; Caldara, Rossion et al. 2004; Herrmann, Schreppel et al. 2007). Another point of interest is that albeit global low-level visual properties of face stimuli, such as amplitude spectrum, luminance and contrast, might affect early electrophysiological components such as P1 and N170 (Dakin, Hess et al. 2002; Rousselet, Pernet et al. 2008), none of the previous studies attempted to control for or even address all these factors. This is surprising considering the low-level differences that co-vary with different races of faces. Furthermore, previous studies have used different types of OR stimuli, including EA, AA and Hispanic (e.g. Caldara, Thut et al. 2003; Ito and Urland 2003; Caldara, Rossion et al. 2004; Ito and Urland 2005; Herrmann, Schreppel et al. 2007; Walker, Silvert et al. 2008; Tanaka and Pierce *2009*) faces, leading to contrasting results. Critically, all the studies that have reported modulation to race on the N170 have only relied on data gathered from a single population: the WC population. This methodological shortcoming undermines generalizations of the results, because any effect could be confounded by differences in the face stimuli. A full cross-over interaction between races of observers and face stimuli is crucial to assess genuine ORE modulations on the ERP signal.

Although behavioral research has extensively investigated the mutual effects of ORE and FIE, to date only one electrophysiological study has exploited the conjoint advantages offered by the combinations of these two phenomena (Wiese, Stahl et al. 2009). Wiese (2009) tested the effects of the ORE and FIE on the N170 using EA and WC faces on WC observers only. They reported a general amplitude increase for inverted compared to upright faces and latency delays on the N170 for inverted faces as a function of race. However, Wiese (2009) only tested one group of observers (the WC population) and did not control for low-level visual properties of the stimulus' set. These limitations hinder any possible conclusion on the conjoint effects of the FIE and the race of the faces on the ERP signal, leaving this issue in need of further clarifications.

In summary, The FIE is regarded as a well documented marker of visual expertise for faces (Yin 1969) both at the electrophysiological (Bentin, Allison et al. 1996; Rossion, Delvenne et al. 1999; Rossion, Gauthier et al. 2000) and the behavioral level (e.g. Freire, Lee et al. 2000). Observers respond less accurately and with longer reaction times when recognizing inverted faces. Moreover face inversion elicits significantly delayed N170 (Bentin, Allison et al. 1996; Rossion, Delvenne et al. 1999; Rossion, Gauthier et al. 2000) and VPP (Jeffreys 1996), often accompanied by amplitude increases (Rossion, Gauthier et al. 2000; Rossion, Joyce et al. 2003; Itier and Taylor 2004; Itier and Taylor 2004). These effects have been interpreted as a disruption of holistic processing for faces (Rossion and Gauthier 2002).

Here we took advantage of the conjoint effects of the ORE and FIE to investigate whether the N170 is sensitive to race in two groups of observers. We recorded scalp EEG in WC and EA observers presented with WC, EA and AA faces in upright and inverted orientations. Participants were required to perform an orthogonal task, consisting in the detection of colored faces in the stimulus sequence. Moreover, to control for potential low-level confounds in the ERP signals that would relate to differences in the low-level properties across faces from different races, we normalized the amplitude-spectrum, luminance and contrast of the entire image set (see Figure 16). In addition, we used a second “other race” category of stimuli (i.e., AA faces) as the absence of differences across the two OR faces (i.e. EA and AA for WC observers and WC and AA for EA observers) would further strengthen the claim that any observed ERP modulations are related to the ORE. A separate behavioral experiment was designed to assess the levels of ORE and FIE in both groups of observers. Possibly due to higher levels of expertise, SR faces have been reported to be processed more holistically than OR faces. We therefore hypothesized that SR faces would elicit a larger inversion effect compared to OR faces. At the electrophysiological level, we predicted FIE modulations as a function of the race of the faces on the face preferential N170 component.

We did not find any significant difference in the upright conditions. However, our data show sensitivity to race on the N170 across both groups of observers for inverted faces, with larger N170 amplitude modulations between upright and inverted faces (i.e. the magnitude of the FIE) for SR compared to OR faces. Moreover, although a significant delay for the onset of the N170 was observed for inverted compared to upright faces, we did not observe latency differences across races. The electrophysiological modulation was paired with greater recognition impairment for inverted same-race faces compared to other-race faces.

2.2 Methods

Participants – 30 subjects (15 East Asians (EA) and 15 Western Caucasian (WC), with an age range of 19–30 and a mean of 23) took part in the experiment. All the EA participants were Chinese; they had been in the country for less than 1 month and had previously never lived in a Western society. All participants provided written informed consent and had normal or corrected-to-normal vision. All subjects were right handed and 15 (8 EA and 7 WC) were female. The experiments received the approval of the local ethical committee.

Stimuli – The stimuli consisted of 30 front-view grayscale photographs of WC, EA and African American (AA) faces (5 identities x 2 genders x 3 races) occupying approximately a visual angle of 3.75° x 4.25°(see Figure 16). We used the WC and EA face database used in previous studies (Michel, Caldara et al. 2006; Michel, Rossion et al. 2006). The AA face stimuli were obtained from a subset of identities of the Productive Aging Lab Face Database (Minear and Park 2004). The inclusion of a second "otherrace" category (i.e. AA faces) represented a further control on the ERP signal.

Each identity was equally presented in 2 orientations (upright and inverted). All faces were cropped to remove external features; none had particular distinctive features and male faces were clean-shaven. The stimuli were centered in a 5.2°x5.2° background of average luminance (25.4 cd/m2, 23.5°x30.1°). The stimuli were equated in terms of spatial frequency content by taking the average of the amplitude spectra of all 30 stimuli and combining that average spectrum with the original phase spectra to reconstruct each individual stimulus. The RMS (root mean square) contrast (i.e. the standard deviation of the pixel intensities) was also kept constant across faces. Because form information is largely carried by phase rather than amplitude (Rousselet, Husk et al. 2008), individual faces remain easily recognizable after this manipulation, however still ensuring that any race related differences in the EEG is not simply a function of differences in the relative visibility of specific frequency components in the stimuli.

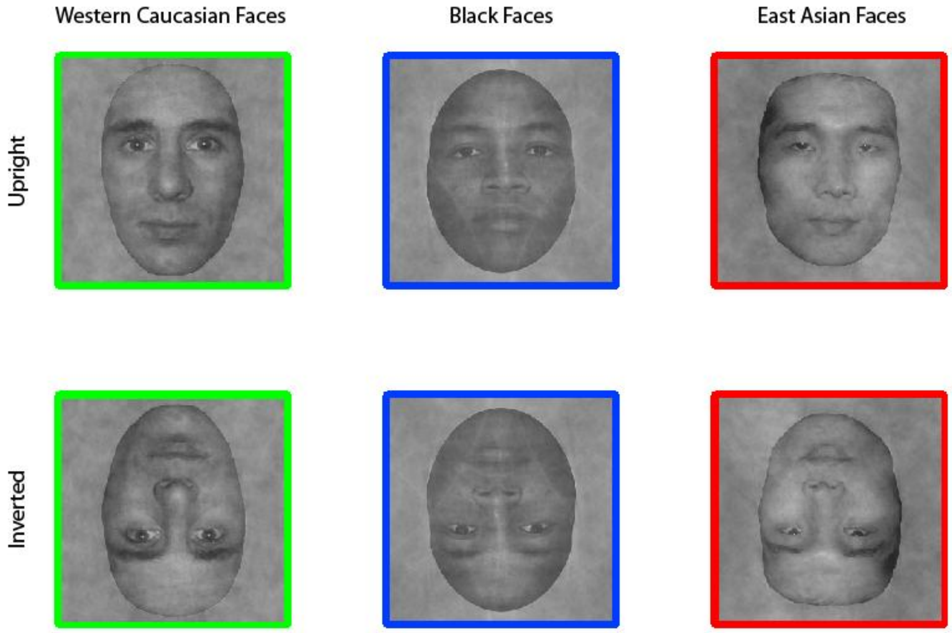


Figure 16 – Example of the face stimuli used in the experiment. To avoid potential low level confounds on the ERP signal, amplitude spectrum, luminance and contrast were normalized to all images' mean.

2.2.1 Experimental design

EEG study – Participants were seated in a dimly lit, sound-attenuated electrically shielded room. Viewing distance was maintained at 80 cm by use of a chinrest. Stimuli were randomly interspersed and sequentially presented for 200 ms (16 frames at 80 Hz) on a Samsung SyncMaster 1100 MB monitor (resolution 2048 x 1536), with an inter-stimulus interval (ISI) randomly varying between 2200 and 3200 ms. A black 0.3° fixation cross was presented in the middle of the screen before stimulus onset and remained on the screen during the whole ISI duration. Each trial had thus a random duration ranging between 2400 and 3400ms.

Participants were instructed to perform an orthogonal task that required pressing the "s" key on the keyboard every time a green face appeared on the screen and the "k" key for a red face. This orthogonal task was designed to avoid potential signal modulations due to attentional confounds linked to the race of the stimuli (Golby, Gabrieli et al. 2001). Red and green faces appeared in approximately 8% of the trials (i.e. 15 red and 15 green faces). Each face appeared once either as a red or a green stimulus.

The experiment consisted of 5 blocks of 78 trials each (360 trials in total with 60 trials x condition x orientation and 30 red and green faces) and lasted approximately 20-25 minutes.

Behavioural Study – Subsequently to the EEG experiment, to directly assess the level of ORE and FIE, we recalled the same subjects asking them to take part in a small behavioural experiment. 9 out of 15 subjects per group participated in this experiment; the others failed to reply to our query. Participants sat in the same dimly lit room with the same viewing conditions, and were presented with 20 new faces for each race, one at the time (3s each, 5s ISI). The faces were obtained from the KDEF (Lundqvist, Flykt et al. 1998) and AFID (Bang, Kim et al. 2001) databases. All faces were selected from a set of stimuli different from the set used in the EEG experiment, and were also equated for global amplitude spectrum, luminance, and contrast. Stimulus size subtended 3.75° x 4.25° of visual angle. Participants were told explicitly to memorize the faces. The encoding phase was followed by a forced-choice old-new recognition task whereby 40 faces (20 old and 20 new) were presented individually. Participants underwent two blocks of the old/new face recognition task per race with faces displayed in two orientations (i.e., upright and inverted). The blocks were counterbalanced across participants. Faces were blocked by race during both the encoding and the recognition phase. The encoding stage was followed by a 1 minute pause, after which participants had to indicate whether each face was old or new by pressing the "s" key on the computer keyboard for old faces and the "k" key for new faces. Each face remained on the computer screen until the participant's response, or for a maximum of 200 ms (3s ISI). Participants did not know the ratio of old to new faces and did not receive any feedback on their responses. The order and the number of presentation of SR and OR stimuli were pseudorandom, changing across subjects.

As in previous studies (e.g. Carroo 1986), d' indices (Swets, Tanner et al. 1961) for WC and EA faces were calculated for each participant to assess accuracy.

2.2.2 EEG Recording and Analysis

EEG Recording – EEG data were acquired by means of a 128-channel Biosemi Active Two EEG system (BioSemi, Amsterdam, Netherlands). Electrodes were placed in a nylon cap according to the 10–5 system (Oostenveld and Praamstra 2001). Vertical and horizontal electro-oculograms were recorded by attaching 4 additional electrodes (UltraFlat Active electrodes, BioSemi) below and at the outer canthi of both eyes. Analog signal was digitized at 1024 Hz and band-pass filtered online between 0.1 and 200 Hz. An active electrode (common mode sense — CMS) and a passive electrode (driven right leg — DRL) were used to comprise a feedback loop for amplifier reference, and electrodes impedances were kept between +/– 20 kΩ. Subjects were asked to minimize blinking, head movement, and swallowing.

EEG Pre-processing – EEG analysis was performed using EEGLAB (Delorme and Makeig 2004), Matlab 7.5 (2007b) and BESA 5.2. In BESA, EEG data were referenced on-line to an average reference. Noisy electrodes were rejected on a subject-by-subject basis. The signal was low-pass filtered offline at 40 Hz with a slope of 6dB. Baseline correction was performed using 150 ms of pre-stimulus onset. Artefacts were rejected based on absolute abnormal values larger than 120 μV. Trials were averaged across an epoch of -200 ms to +600 ms. Trials including red or green faces were excluded from the analysis.

Before averaging, single trials were corrected for horizontal and vertical eye movement and blinking artefacts by means of PCA. Due to their specific topographical configuration, we first identified these artefacts on the continuous signal. We then manually selected portions of the segment showing the topographical configuration of interest. We thus averaged the selected epochs to create a subject-specific template for that particular artefact. The first PCA component (accounting for 89% to 99% - mean 92% - of the variance for individual subjects) was removed.

Across subjects and conditions, the minimum number of trials accepted after artefact rejection was 252, the maximum 360, and the mean 343. The rest of the analyses were performed in EEGLAB and Matlab.

Amplitudes and peak latencies were measured at electrodes O1 and O2 for the P1 and P2 components (i.e. where the amplitude of such components was maximal), and at 9 pairs of occipitotemporal electrodes over the left and right hemisphere for the N170, and N250. To select the electrodes of interest, we performed the mean average of the ERPs scalp topography at the mean latency of the N170 for upright and inverted stimuli across all the subjects and selected the electrodes with maximal amplitudes (see Figure 1s in the supplementary section). The channels previously excluded consequently to artifact rejection were interpolated using the EEGLAB topoplot function. The electrodes selected, consistently with the N170 literature (e.g. Bentin, Allison et al. 1996; Rossion and Jacques 2008), were: P4, P6, PPO6h, P8, P8h, PO8, P10, PO10h, PO10 in the right hemisphere; and P3, P5, PPO5h, P7, P7h, PO7, P9, PO9h, PO9 in the left hemisphere (see Figure 1s in the supplementary section).

For each subject, each component amplitude was quantified as the maximal positive (for P1 and P2) or negative (for N170 and N250) voltage measured within a 40 ms time window centred on the Grand Average ERP latency.

Statistical Analysis – In terms of statistical analyses, we employed canonical methods (i.e. ANOVA and t-tests) as well as robust approaches (i.e. bootstrap). Bootstrap has higher statistical power and makes fewer assumptions on the distribution of the data compared to more canonical statistical methods. Our goal was to address a growingly popular issue that has often been overlooked within the electrophysiological literature: the examination of the number of subjects showing a similar pattern of results (e.g. Rousselet, Pernet et al. 2008). It is worth noting that most EEG and MEG papers do not report the number of subjects showing a given effect, although there is a recent trend in the literature favouring this view (e.g. Philiastides and Sajda 2006; Schyns, Petro et al. 2007; Smith, Gosselin et al. 2007). Ensuring that an effect is observed across all or most subjects is essential because in some situations an effect might be driven by a minority of subjects (for instance the early P1 difference reported by Rousselet, Husk et al. 2008). This is not to say that such effects are not interesting, rather that they should be interpreted with caution.

A first statistical analysis was performed on the P1 N170, P2 and N250 peak amplitudes and latencies. We carried out a mixed model repeated measures 5 way ANOVAs on the N170 and N250 components. The 5 factors included in the ANOVA were: 2 groups of observers (i.e. WC and EA participants); 3 races of the stimuli (i.e. stimulus race: WC, AA and EA); 2 orientations in which the stimuli were presented (i.e. upright and inverted); 2 hemispheres; and the electrodes of interest (as described above). Mixed model repeated measures 4 way ANOVAs (group x stimulus race x orientation x hemisphere) were carried out on P1 and P2 components. These analyses did not include the electrode factor as only one electrode per hemisphere was considered. A further 5 way ANOVA (group x stimulus race x orientation x electrode x hemisphere) was carried out with the latency of the above mentioned components as the dependent variable.

In light of the results, we then further carried out two 4 ways ANOVA (hemisphere x electrodes x stimulus race x group) on the N170 peak amplitude, one for the upright and one for the inverted conditions.

We finally assessed the difference between two conditions across subjects at each electrode independently using t-tests. The differences assessed were WC vs. AA, WC vs. EA, and EA vs. AA for WC Observers; and EA vs. AA, EA vs. WC, and WC vs. AA for EA Observers.

Given the rather heterogeneous, asymmetrical nature of the distributions of ERP differences (computed both between upright minus inverted faces per each condition independently – i.e. the magnitude of the FIE – and between conditions for each orientation independently), and the d’ scores, which were also limited in sample size, we carried out percentile bootstrap analyses. We sampled subjects with replacement, averaging the means across participants independently for each condition, and then computing the difference between the means for the two conditions (for instance inverted WC vs. AA). This process was repeated 999 times, leading to a distribution of bootstrapped estimates of the mean difference between two ERP conditions, averaged across subjects. Then the 95% per-cent confidence interval was computed (alpha = 0.05). Finally, the difference between the two sample means was considered significant if the 95% confidence interval did not include zero. Note that this bootstrap technique, relying on an estimation of H1, tends to have more power than other robust methods like permutation tests and related bootstrap methods that evaluate the null hypothesis H0 (Wilcox 2005).

We then carried out correlation analyses to assess the relationship between the N170 and behavioural magnitudes of the FIE. FIE indexes were calculated at the N170 – by subtracting the N170 peak amplitude elicited by inverted to that elicited by upright faces - and behavioural - the d’ scores for upright minus those for inverted faces - levels. Pearson correlation coefficients were calculated between the 2 FIE indexes for each group of observers and for each race of the faces. Again, because of the limited sample size and the asymmetrical nature of the distribution of the data, bootstrap tests of independence were also carried out. We sampled with replacement pairs of data points (i.e. the N170 and d' FIE indexes), and then computed the Pearson correlation between these pairs, across subjects, for each stimulus race independently. This process was repeated 599 times, leading to a distribution of bootstrapped Pearson correlation coefficients between the two FIE indexes. Then, 95% confidence intervals were computed using the special adjustments suggested by Wilcox (2005). Finally, correlations were considered significant if their 95% confidence intervals did not include zero (alpha = 0.05).

Our second statistical analysis was data driven. Because we were interested in any significant interaction on the early cerebral dynamics evoked by faces of different races (across groups of subjects) (i.e. the first 600ms after stimulus onset), we carried out an ANOVA independently at all the electrodes and all the time points. First we calculated the index of the magnitude of the FIE at the electrophysiological level by computing the differences between the amplitude of ERPs elicited by upright minus those elicited by inverted faces independently for each stimulus' race, at all the electrodes and all the time points. We then carried out a 2 way ANOVA (group x stimulus race) on these differences across all electrodes and all time points independently. Post-hoc bootstrap tests were subsequently carried out between paired conditions by sampling subjects with replacement, as described earlier. Again 95% percent confidence intervals were computed, with the difference between the means considered significant if a confidence interval did not include zero.

No correction for multiple comparisons was applied. However, significant differences were not randomly scattered (as it might be expected with the significant points being the result of random type I errors) but formed consistent spatiotemporal clusters.

2.3 Results

We found four main results. First, both groups of observers were significantly less accurate at recognizing inverted compared to upright same race faces (SR), but showed no behavioural inversion effect for other race (OR) and African American (AA) faces. Second, regardless of the group of observers, the race of the face stimuli modulated the magnitude of the N170 amplitude face inversion effect (FIE), which was largest for SR faces, with no differences between OR and AA stimuli. No race effects were observed on P1, P2, and N250. Third, no race effects were observed on the peak amplitude of the N170 for upright faces in both groups of observers. Finally, the behavioral FIE positively correlated with the N170 FIE for SR faces only. We report the analyses of all the behavioural and ERP results below.

2.3.1 Behavioural Results

We observed significant main effects for orientation (F(1,16)=216.28;p<.01), with both groups being significantly more accurate at recognizing upright compared to inverted faces; and race of the stimuli (F(1,16)=39.24;p<.01), with the lowest d' for AA faces.

As shown in Figure 17, both groups of observers exhibited a larger FIE (represented by the differences between d' scores for upright and inverted stimuli) for SR compared to OR and AA faces. Consistently, the 3-Way ANOVA (groups x orientations x stimuli) showed significant interactions between Group x Stimuli (F(2,15)=131.03; p<.01) and group x stimuli x orientation (F(2,15)=16.11; p<.01). Although, within both groups, all subjects but one consistently displayed larger d' for upright compared to inverted SR faces only, a paired t-test contrasting upright and inverted SR faces showed a significant difference for WC (t(8)=3.72, p<.01), but not for EA participants (t(8)=2.16, p=.06). These low t values seem to be due to small sample sizes and violations of homoscedasticity. Bootstrap confidence intervals, which are less sensitive to these factors, showed that regardless of the group of observers, participants were significantly impaired at recognizing inverted compared to upright SR faces (WC: mean difference = .53, bootstrap CI of the mean difference = [.27, 8], p<.01; EA: 0.29, [.07, .59], p<.01]). No differences between upright and inverted d' score were observed for OR (WC: t(8)=.47, p>.05; mean difference = 0.12 [-.34, .58], p>.05; EA: t(8)=.93, p>.05; mean difference = 0.13 [-.13 .39], p>.05) and AA faces (WC: t(8)=.33, p>.05; mean difference = .06 [-.26, 37], p>.05; EA: t(8)=.34, p>.05; mean difference = .09 [-.43, .56], p>.05).

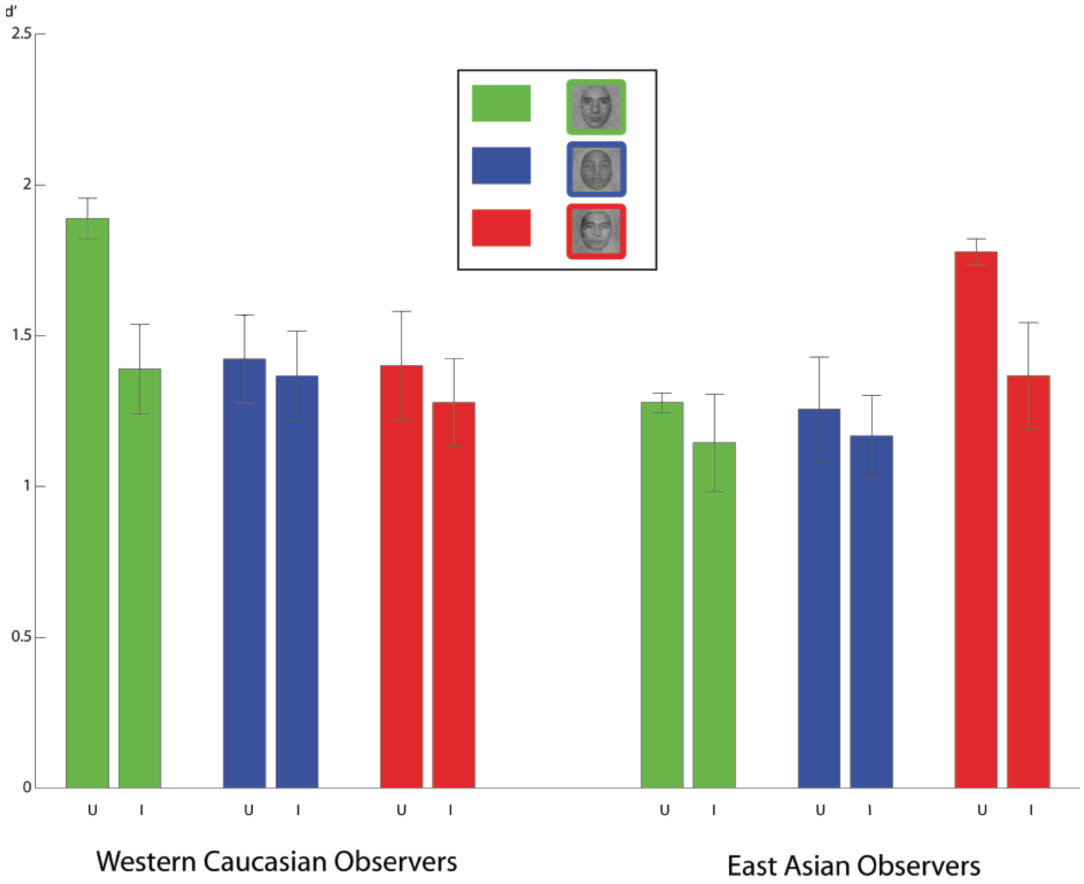


Figure 17 – Mean d' scores and standard errors of the old/new face recognition task, for Western Caucasian (green), East Asian (red) and African American (blue) faces for the upright (U) and inverted (I) orientations.

2.3.2 EEG Results

P1 – Table 1 shows P1 results. P1 amplitude was significantly modulated by face orientation (F(1,28) = 30.21; p<.01 – Figure 18). Inverted faces elicited significantly larger P1 (mean = 3.62 µV; std = 1.63 µV) compared to upright faces (mean = 2.96 µV; std = 1.43 µV). Importantly, no effect of stimulus race was observed on the amplitude elicited by faces presented in either orientation (groups x stimuli F(2,27) = .56; p>.05; groups x stimuli x orientations F(2,27) = .741; p>.05) .

P1 elicited by inverted faces (mean lat. = 111 ms; std = 7.4 ms) was significantly delayed by 3.4 ms compared to that elicited by upright faces (mean lat. = 108 ms; std = 7.3 ms; F(1,28)= 31.907; p<01). The latency of this component, like its amplitude, was not modulated by stimulus race in either orientation (group x stimuli - F(1,28)=.35; p>05; group x stimuli x orientations - F(2,27)=1.42; p>05). No other significant differences were observed.

Table 1

P1

Groups	Electrode	Orientation	Stimuli	Mean Amplitude	Std. Deviation	Mean Latency	Std. Deviation
Wester Caucasian Observers							
	O2						
		upright					
			Western Caucasian	3.51	1.89	108	9
			African American	3.30	2.01	108	15
			East Asain	3.21	2.11	109	12
		Inverted					
			Western Caucasian	4.21	2.26	115	11
			African American	4.03	2.12	111	14
			East Asain	3.97	1.97	114	11
	O1						
		upright					
			Western Caucasian	4.27	4.10	109	13
			African American	3.87	4.07	109	14
			East Asain	3.58	3.41	108	11
		Inverted					
			Western Caucasian	4.67	4.32	110	14
			African American	4.51	4.08	109	14
			East Asain	4.63	4.70	112	13
East Asian Observers							
	O2						
		upright					
			Western Caucasian	2.71	1.41	104	11
			African American	2.69	1.16	107	11
			East Asain	2.52	1.23	107	9
		Inverted					
			Western Caucasian	3.16	1.88	110	9
			African American	3.00	1.25	109	9
			East Asain	3.02	1.56	108	11
	O1						
		upright					
			Western Caucasian	2.10	1.33	108	11
			African American	1.80	0.88	108	13
			East Asain	1.89	1.14	111	12
		Inverted					
			Western Caucasian	2.95	1.58	113	11
			African American	2.36	1.32	111	10
			East Asain	2.80	1.72	114	12

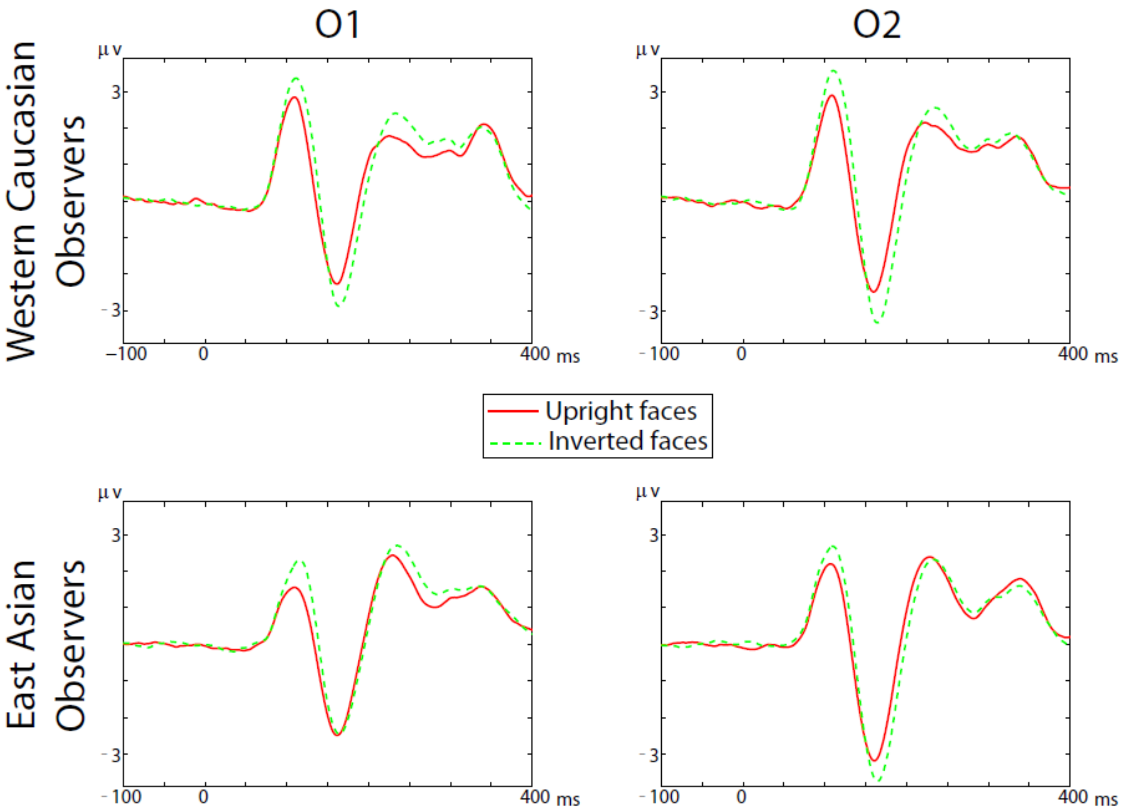


Figure 18 – Grand average ERP waveforms of Western Caucasian and East Asian observers elicited by Upright (red) and Inverted (dotted green) faces at two occipital sites showing the largest P1 amplitude (O1, left hemisphere; O2, right hemisphere). The ERPs were obtained averaging together faces across conditions (i.e. Western Caucasian, East Asian and African American) independently per each orientation. While P1 was not modulated by the race of the faces in either orientation, a significant inversion effect was observed regardless of the race of the face stimuli, with inverted faces eliciting larger P1 compared to upright faces. No latency differences were observed across orientations.

N170 – The mean peak amplitudes, latencies and standard deviations in each condition are reported in Table 2.

Table 2

N170

Groups	Electrode	Orientation	Stimuli	Mean Amplitude	Std. Deviation	Mean Latency	Std. Deviation
Wester Caucasian Observers							
	PO8						
		upright					
			Western Caucasian	-5.20	4.77	159	10
			African American	-5.37	4.69	159	14
			East Asain	-5.06	4.25	158	11
		Inverted					
			Western Caucasian	-7.56	5.20	165	11
			African American	-6.40	4.89	164	15
			East Asain	-6.90	5.16	165	13
	PO7						
		upright					
			Western Caucasian	-4.45	3.81	160	12
			African American	-4.21	3.83	162	14
			East Asain	-4.42	3.54	162	13
		Inverted					
			Western Caucasian	-5.57	4.12	165	9
			African American	-4.81	4.29	164	11
			East Asain	-5.33	4.00	165	9
East Asian Observers							
	PO8						
		upright					
			Western Caucasian	-5.91	3.41	160	9
			African American	-5.73	3.39	161	9
			East Asain	-5.57	2.99	161	12
		Inverted					
			Western Caucasian	-6.90	3.53	166	11
			African American	-6.61	3.67	167	11
			East Asain	-7.40	3.58	165	10
	PO7						
		upright					
			Western Caucasian	-4.35	3.45	160	10
			African American	-4.30	3.59	161	9
			East Asain	-3.78	3.34	161	10
		Inverted					
			Western Caucasian	-4.33	4.40	165	9
			African American	-4.34	3.82	164	10
			East Asain	-4.43	4.42	165	10

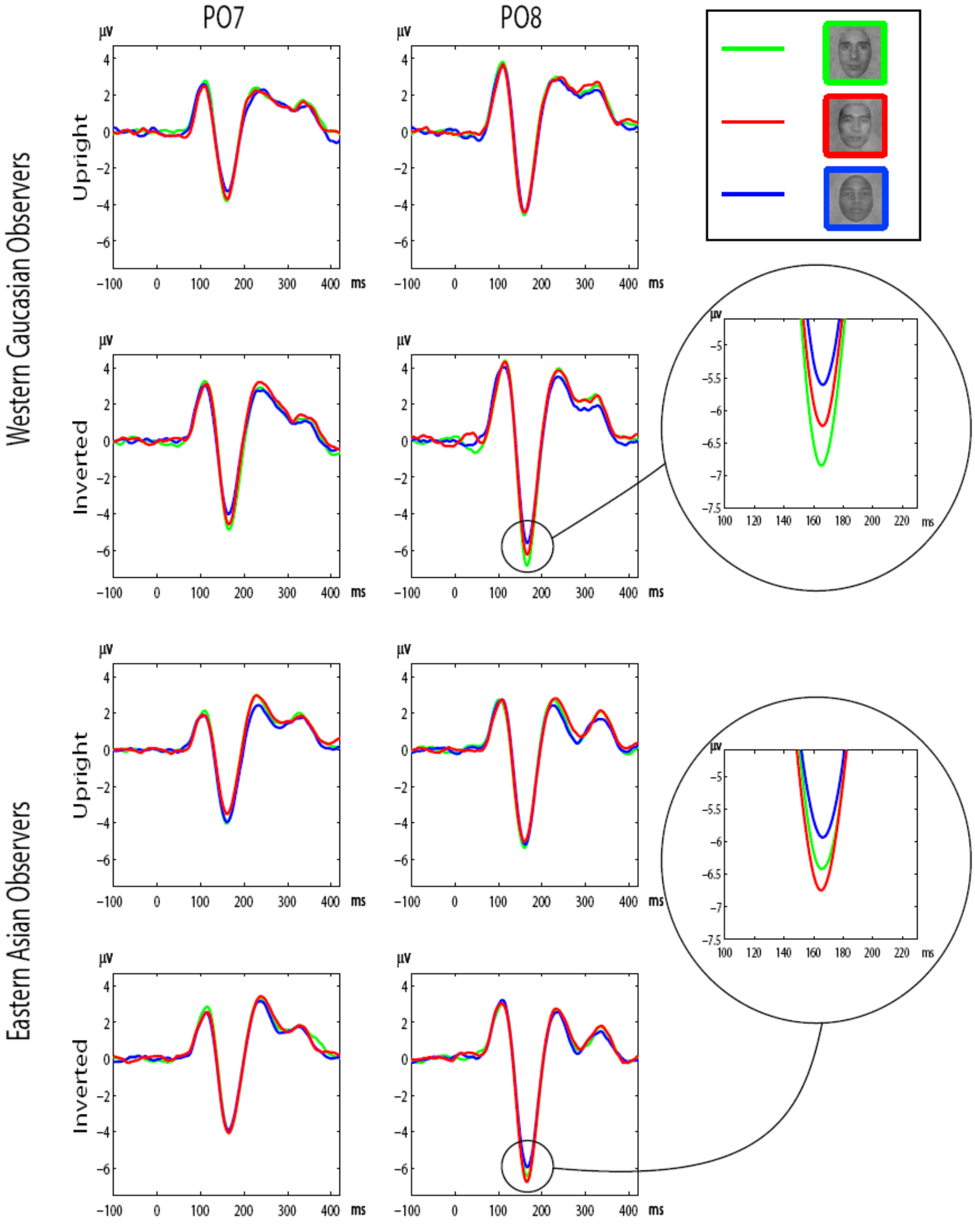


Figure 19 – shows the mean ERPs at the right hemisphere electrode PO8, where the N170 amplitude was largest (F(8,21) = 4.14, p<.01), and the left hemisphere electrode PO7, for both stimulus orientations and both subject groups. Our main result indicates that stimulus race systematically modulates the FIE magnitude of the N170 amplitude across groups, which was largest for SR compared to OR or AA faces (orientation x stimulus x group - F(2,27) = 4.62, p<.05 – Figure 19 and Figure 21). Moreover, inverted faces elicited significantly larger N170 compared to upright faces regardless of stimulus race and the group of observers (F(1,28) = 60,41, p< .01). Bonferroni corrected t-tests carried out between the peak amplitudes elicited by upright and those elicited by inverted faces independently for each stimulus race show that this effect was significant for all conditions (p<.05).

We also observed a main hemispheres effect, with larger amplitudes over the right hemisphere (F(1,28) = 6.15, p<.05); and a main effect of stimulus race (F(2,27) = 6.7, p<.01). Bonferroni corrected paired t-tests showed that AA faces elicited the smallest amplitude (p<.05), while no differences were observed between WC and EA faces. The 5 way ANOVA further showed significant interactions between hemisphere x orientation (F(1,28) = 20.04, p<.01), orientation x stimulus (F(2,27) = 6.32, p<.01); electrode x stimulus (F(16,13) = 4.06, p<.01); and hemisphere x stimulus x orientation (F(2,27) = 3.49, p<.05).

To clarify these results, we carried out two 4 way ANOVAs on the N170 amplitudes (hemisphere x electrodes x stimulus x group), one for each orientation. Crucially, this analysis indicated that for the upright orientation, stimulus race did not modulate the N170 amplitude (stimuli x groups - F(2,27) = 1.89, p>.05). However, inverted SR faces elicited the largest amplitude regardless of the group of observers (stimuli x groups - F(2,27) = 9.15, p<.01). A significant electrode effect indicated that the largest N170 was measured at PO8 for both orientations (upright: F(8,21) = 4.29, p<.01; inverted: F(8,21) = 34.75, p<.01). ERPs elicited by inverted, but not upright faces were also found to be significantly larger over the right hemisphere (upright: F(1,28) = 3.51; p>.05; inverted: F(1,28) = 8.72; p<.01). Finally, for inverted, but not upright, we observed a main effect of stimulus race (upright: F(2,27) = 2.38, p<.05; inverted: F(2,27) = 8.10, p<.01). Bonferroni corrected t-tests showed that inverted AA faces elicited the smallest N170 amplitude (p<.05). This effect, as shown by the stimuli x hemisphere interaction (F(2,27) = 5.46, p<.01) was stronger over the right hemisphere.

In light of the ANOVAs' results, paired sample t-tests and bootstrap confidence intervals were used to estimate effects of stimulus races on the N170 peak amplitude elicited by inverted faces. No significant amplitude differences were observed (Figures 19 and 20) among stimulus races over the left hemisphere.

Over the right hemisphere, regardless of the group of observers, SR inverted faces elicited the largest amplitude. For both groups the amplitude differences between SR and AA inverted faces (at PO8: t(14) = -3.92, p<.01 for WC Observers, and t(14) = -3.66, p<.01 for EA Observers) was consistently larger than those between SR and OR (at PO8: t(14) = -3.24, p<.01 for WC Observers and t(14) = -3.81, p<.01 for EA Observers). No significant differences were observed between OR and AA faces (at PO8: t(14) = 1.49, p>.05 for WC Observers, and t(14) =1.61; p>.05 for EA Observers). Bootstrap confidence intervals showed the same patterns of results (Figure 20 displays effect size and data distribution at PO8 and PO7).

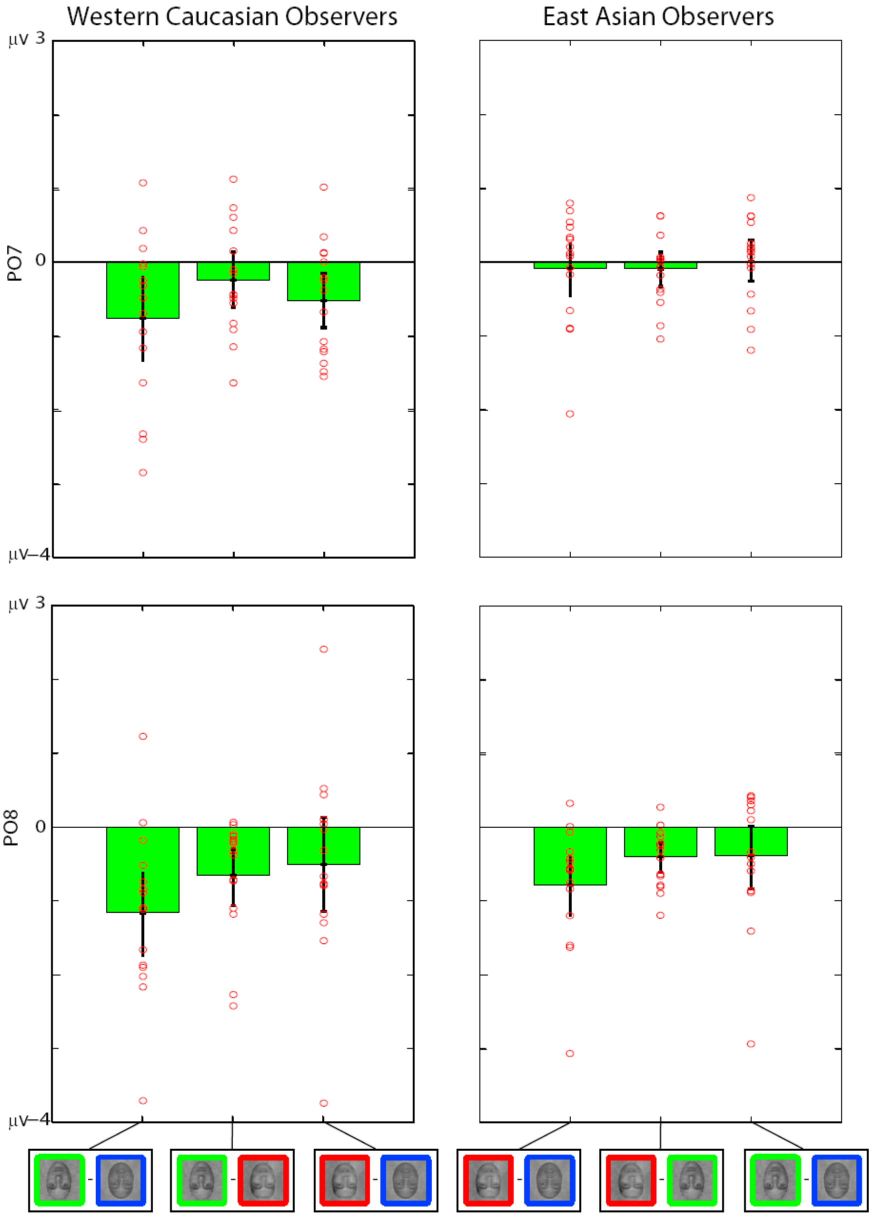


Figure 20 – Bar plots of all paired differences of the N170 peak amplitudes at PO7 and PO8 for both groups of observers for the inverted condition. Red circles represent individual data points. The error bars denote the 95% bootstrapped (Wilcox, 1995) confidence interval (CI) of these differences. Statistically significant differences are conveyed by CI not including zero. Note that amplitudes differences at electrode PO8 show a consistent pattern of results, with both groups of observers responding to the law: Same-Race vs. African American > Same-Race vs. Other-Race > Other-Race vs. African Americans. The difference between Other-Race vs. African Americans is non-significant.

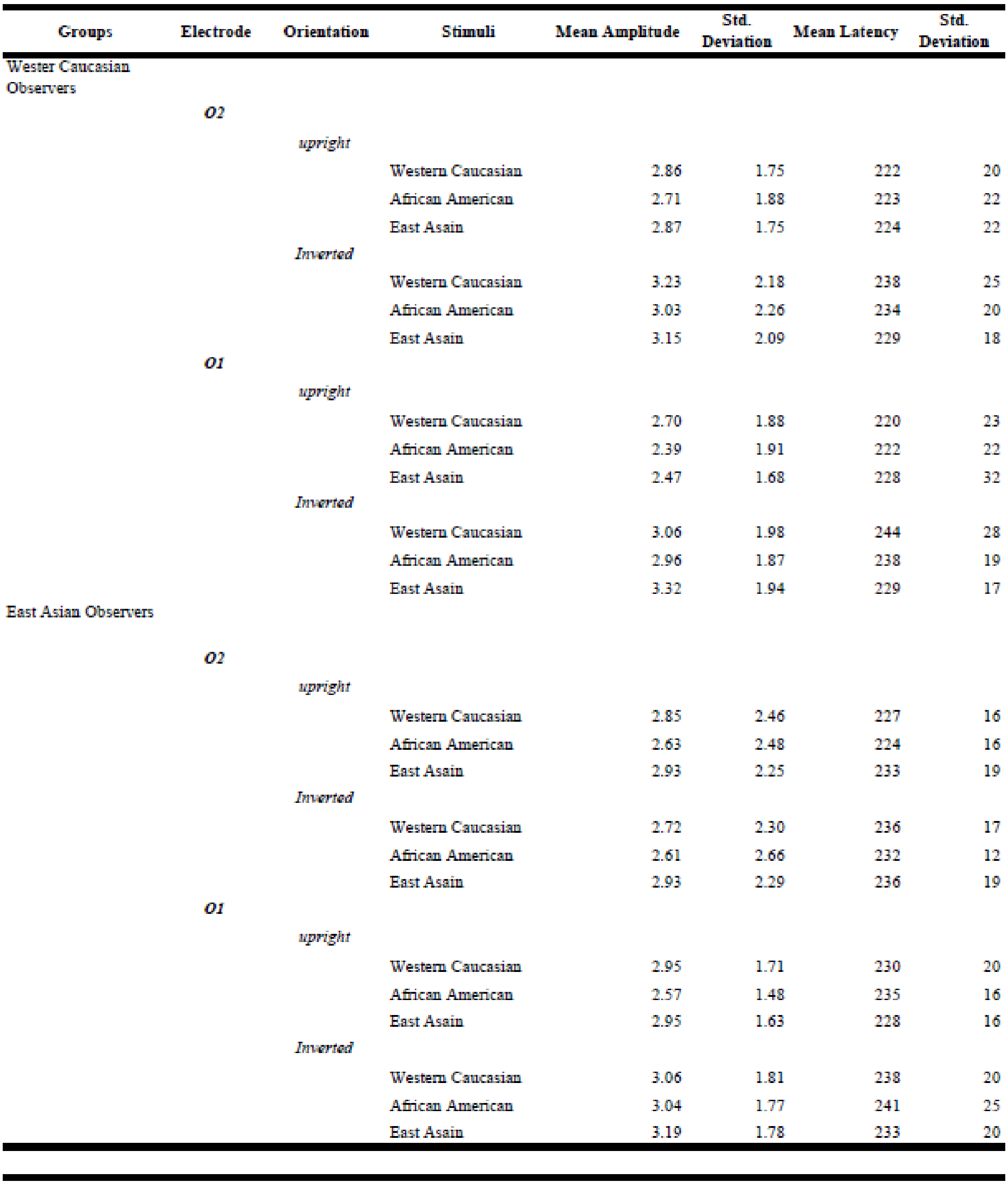
The latency of the N170 was significantly delayed by 6 ms for inverted (mean = 166 ms; std = 10 ms) compared to upright (mean = 160 ms; std = 10 ms) faces (F(1,28) = 18.83, p<.01 – see Figure 21). Importantly, there were no significant latency differences among the races of stimuli (F(5,24) = .33, p>.05); and no significant interaction between the race of the stimuli and the groups of observers in either orientation (stimuli x groups - F(2,27) = .07; p>.05; stimuli x groups x orientation -

F(2,27) = 1.2; p>.05). No other significant latency differences were observed on this component.

P2 – P2 results are reported in table 3. The absence of significant groups x stimuli (F(2,27) = .33; p>.05) and groups x stimuli x orientations (F(2,27) = .36; p>.05) interactions on P2 amplitude indicated that stimulus race did not systematically modulate the amplitude of this component across groups in either orientation. Moreover, a main effect of stimulus race was observed on amplitude (stimuli - F(2,27) = 4.13; p>.05). Pairwise comparisons revealed only one significant differences between EA and AA faces, which was true for upright and inverted faces (Bonferroni corrected t-tests, p<.05). In addition, P2 amplitude was modulated by face orientation (F(1,28) = 8.48; p<.05 – Figure 18). Inverted faces elicited significantly larger amplitudes (mean = 3.03 μV; std = 1.91 μV) compared to upright faces (mean = 2.74 μV; std = 1.75 μV). However, this effect was observed only over the left hemisphere. (orientation x hemisphere - F(1,28) = 5.08; p<.05).

The latency of P2 elicited by inverted faces (mean = 235.5 ms; std = 14.85ms) was significantly delayed by 5.8 ms compared to that elicited by upright faces (mean = 226.5 ms; std = 16.9 ms; F(128) = 22.96; p<.01). Importantly, the race of the face stimuli did not modulate the latency of this component in either orientation (stimuli x groups - F(2,27) = .55; p>.05; stimuli x groups x orientation - F(2,27) = 1.14; p>.05). No other significant differences were observed.

Table 3
P2



Groups	Electrode	Orientation	Stimuli	Mean Amplitude	Std. Deviation	Mean Latency	Std. Deviation
Wester Caucasian Observers							
	O2						
		upright					
			Western Caucasian	2.86	1.75	222	20
			African American	2.71	1.88	223	22
			East Asain	2.87	1.75	224	22
		Inverted					
			Western Caucasian	3.23	2.18	238	25
			African American	3.03	2.26	234	20
			East Asain	3.15	2.09	229	18
	O1						
		upright					
			Western Caucasian	2.70	1.88	220	23
			African American	2.39	1.91	222	22
			East Asain	2.47	1.68	228	32
		Inverted					
			Western Caucasian	3.06	1.98	244	28
			African American	2.96	1.87	238	19
			East Asain	3.32	1.94	229	17
East Asian Observers							
	O2						
		upright					
			Western Caucasian	2.85	2.46	227	16
			African American	2.63	2.48	224	16
			East Asain	2.93	2.25	233	19
		Inverted					
			Western Caucasian	2.72	2.30	236	17
			African American	2.61	2.66	232	12
			East Asain	2.93	2.29	236	19
	O1						
		upright					
			Western Caucasian	2.95	1.71	230	20
			African American	2.57	1.48	235	16
			East Asain	2.95	1.63	228	16
		Inverted					
			Western Caucasian	3.06	1.81	238	20
			African American	3.04	1.77	241	25
			East Asain	3.19	1.78	233	20

N250 – Table 4 shows the N250 results. Because all the electrodes of interest showed the same pattern of results, we only report the values for PO8 and PO7, those sites where the N250 was largest. We observed a main effect of stimulus race (F(2,27) = 3.87; p<.05) on the N250 amplitude. However, Bonferroni corrected t-tests showed only a significant amplitude difference between EA and AA faces for the 2 orientations (p<.05). Furthermore, unlike all the previous components, the N250 showed no significant amplitude modulations by face orientation (orientation - F(1,28) = .93; p>.05). There was also no significant stimuli x groups (F(2,27) = .09; p>.05) and stimuli x groups x orientation (F(2,27) = 1.91; p>.05) interaction.

Similarly to the N250 amplitude, the N250 latency showed no sensitivity to orientation (F(1,28) = .21; p>.05) and to race (F(2,27) = 3.23; p>.05). Race effects did not interact with groups (stimuli x groups - F(2,27) = .64; p>.05) in either orientation (stimuli x groups x orientation - F(2,27) = 1.5; p>.05). No other significant differences were observed for this component

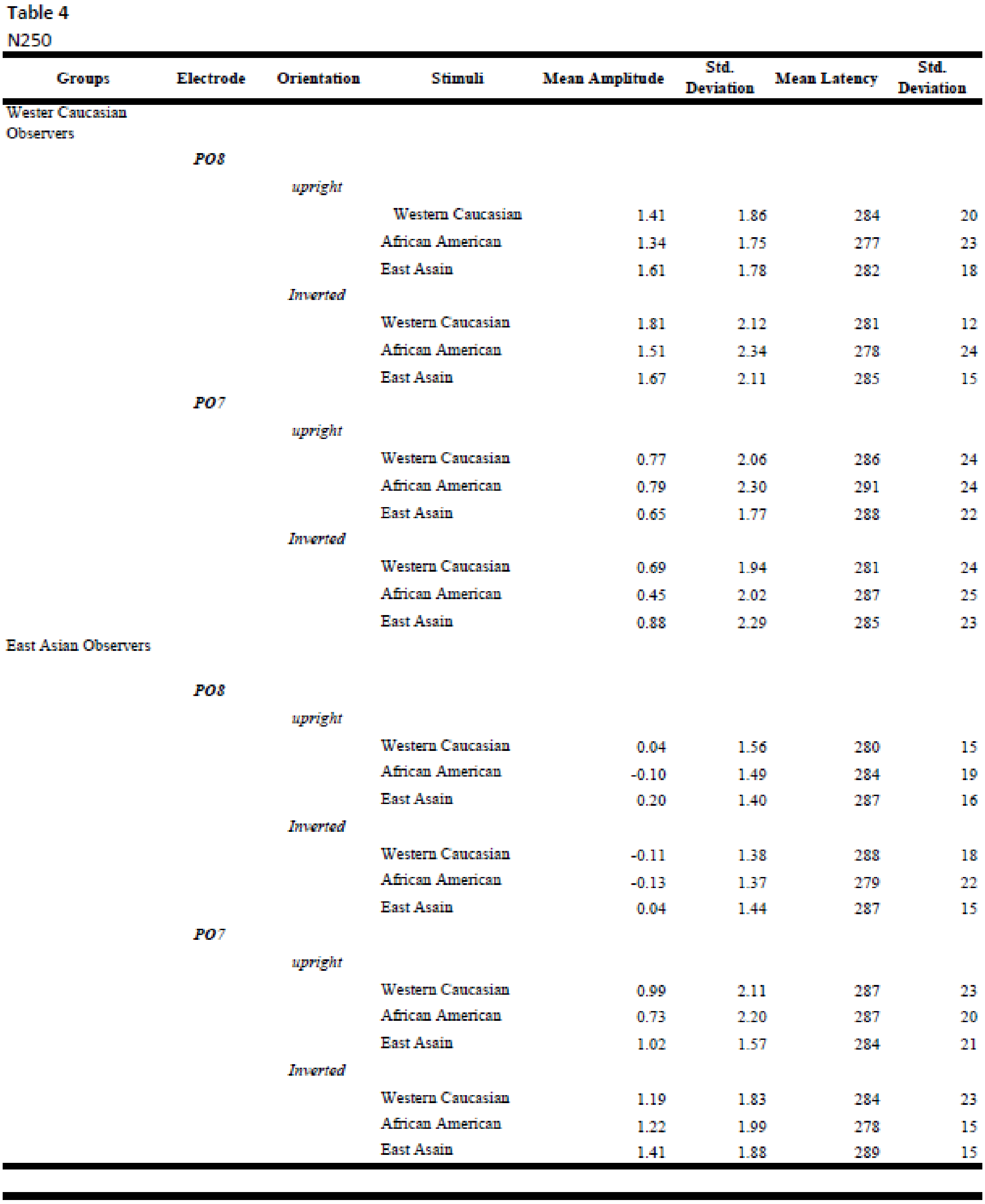


Table 4
N250

Groups	Electrode	Orientation	Stimuli	Mean Amplitude	Std. Deviation	Mean Latency	Std. Deviation
Wester Caucasian Observers							
	PO8						
		upright					
			Western Caucasian	1.41	1.86	284	20
			African American	1.34	1.75	277	23
			East Asain	1.61	1.78	282	18
		Inverted					
			Western Caucasian	1.81	2.12	281	12
			African American	1.51	2.34	278	24
			East Asain	1.67	2.11	285	15
	PO7						
		upright					
			Western Caucasian	0.77	2.06	286	24
			African American	0.79	2.30	291	24
			East Asain	0.65	1.77	288	22
		Inverted					
			Western Caucasian	0.69	1.94	281	24
			African American	0.45	2.02	287	25
			East Asain	0.88	2.29	285	23
East Asian Observers							
	PO8						
		upright					
			Western Caucasian	0.04	1.56	280	15
			African American	-0.10	1.49	284	19
			East Asain	0.20	1.40	287	16
		Inverted					
			Western Caucasian	-0.11	1.38	288	18
			African American	-0.13	1.37	279	22
			East Asain	0.04	1.44	287	15
	PO7						
		upright					
			Western Caucasian	0.99	2.11	287	23
			African American	0.73	2.20	287	20
			East Asain	1.02	1.57	284	21
		Inverted					
			Western Caucasian	1.19	1.83	284	23
			African American	1.22	1.99	278	15
			East Asain	1.41	1.88	289	15

2.3.3 Component free analyses

Figure 21 shows the N170 and the VPP.

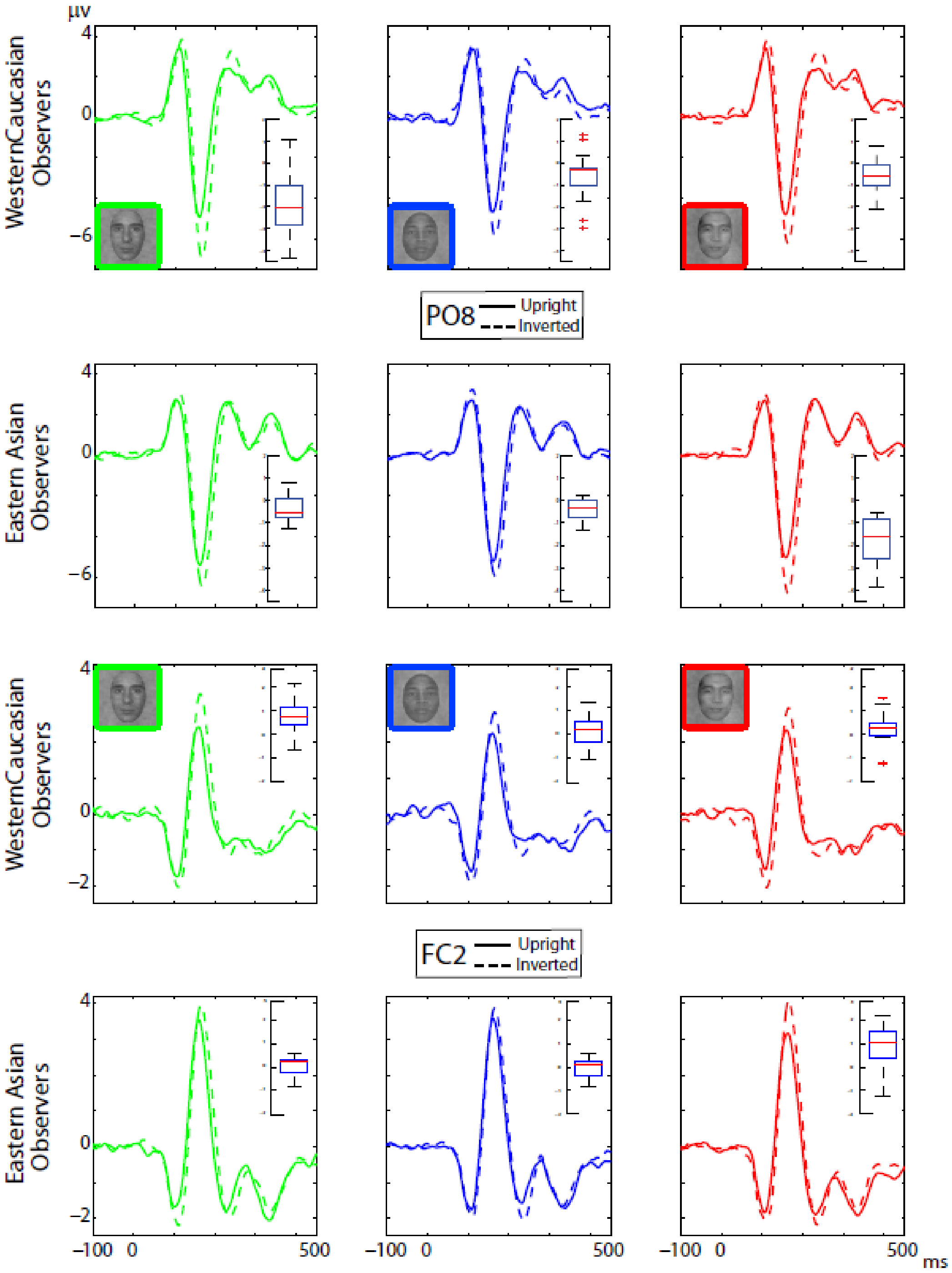


Figure 21 – Grand average ERPs at PO8 and FC2 for the upright and inverted (dotted) conditions, electrodes showing respectively the largest amplitudes for the N170 and VPP components. Note that the maximal difference between Inverted and Upright faces occurs at the N170 latency for both the occipitoparietal and frontal site. Both groups of observers showed largest amplitudes for Same-Race > Other-Race > African Americans. The box plots represent the distribution of individual data point around the median (red line); red crosses indicate outliers.

The 2 way ANOVA (group x stimuli) carried out independently at each electrode and at each time point on the FIE index revealed significant interactions only in the N170 time window ($p<.05$).

The scalp topography in Figure 22 shows the significant F values (p<.05) for the group x stimuli interaction. SR faces elicited the largest electrophysiological FIE at the N170 peak latency, regardless of the group of the observer. Significant effects were observed over four clusters of electrodes: left occipital, right occipital, left frontotemporal and frontal sites. Because all the electrodes within each cluster showed the same pattern of results, for display purposes, we only selected the electrodes with the largest amplitude in each group.

Bootstrap tests revealed a stronger FIE for SR compared to AA faces in the clusters of electrodes around PO8 and FC2 (Figure 22; PO8: mean difference = .82, CI = [.41, 1.18] for WC; mean difference = .65 [.10, 1.18] for EA; FC2: mean difference = -.55 [-.20, -.90] for WC; mean difference = -.20 [-.02, -.45] for EA). Similarly, the FIE was stronger in SR compared to OR faces (PO8: mean difference = .63 [.10, 1.11] for WC; mean difference = .31 [.05, .56] for EA; FC2: mean difference = -.30 [-.10, -.50] for WC; mean difference =-.10 [-.05, -.30] for EA). No significant differences were observed between OR and AA faces (PO8: mean difference = .27 [-.32, .67] for WC; mean difference = .32 [-.15, .83] for EA; FC2: mean difference = -.25 [.05, -54] for WC; mean difference = -.10 [.10, -.28] for EA). Although the left occipital and frontotemporal clusters showed respectively the same patterns as the right occipital and left frontal clusters, pairwise comparisons did not reveal any significant differences (Figure 22).

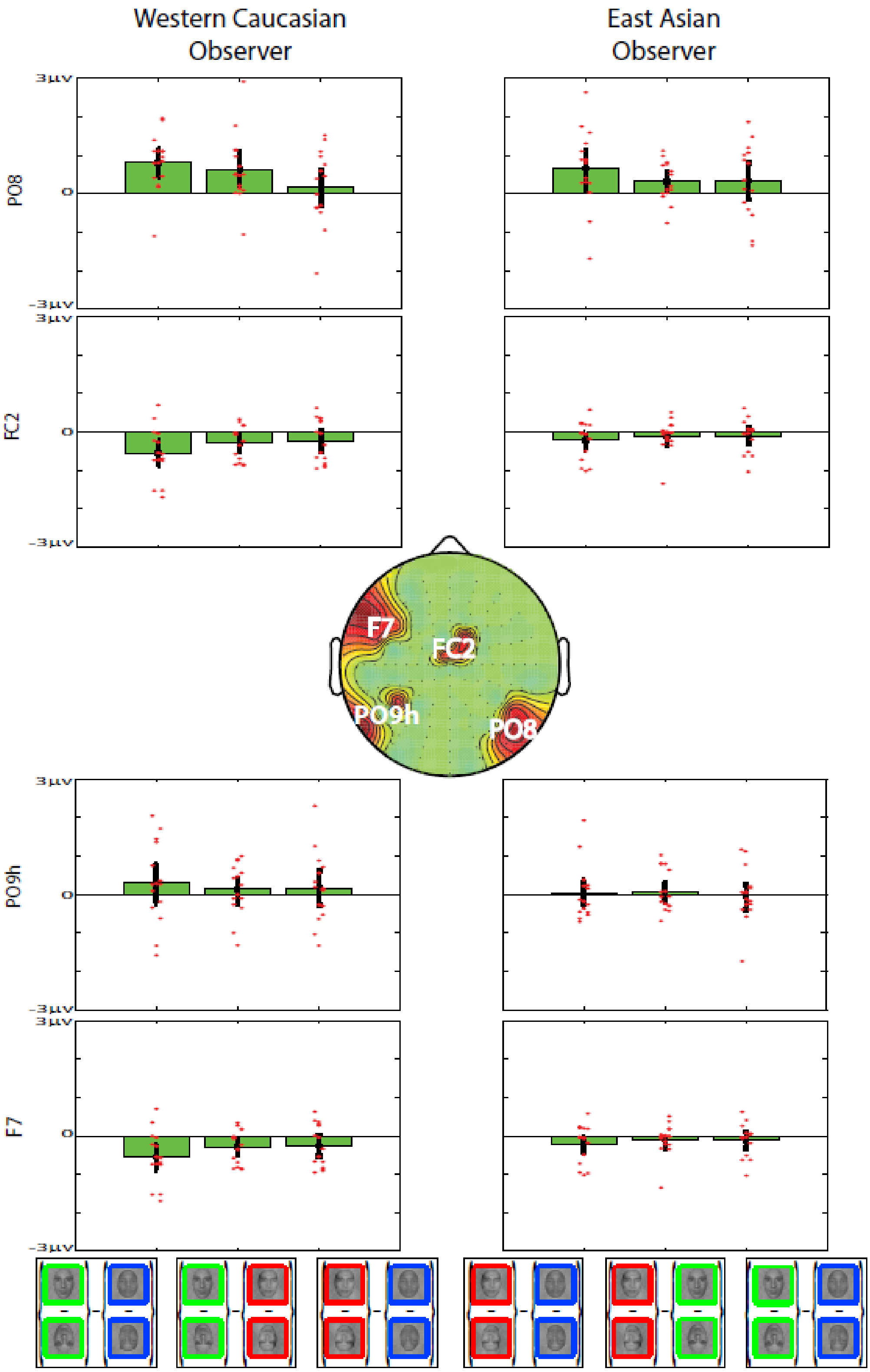


Figure 22 – Centre: Scalp topography at the N170 latency of significant F values for the ANOVA computed on the differences between Upright minus Inverted faces on all electrodes, across all time points and all conditions. The red clusters highlight significant F values distributions (p<.05). Note that high significant F values clustered around the N170 latency at four sites (i.e. left and right occipitoprietal, frontal and right frontotemporal). Top and bottom: Bar plots reporting the results of the post-hoc tests computed on the pair-wise differences (i.e. Same-Race vs. African American, Same-Race vs. Other-Race, Other-Race vs. African Americans) for inverted vs. upright conditions at the time

window where significant F values clustered (i.e. N170 window). Within each cluster all the electrodes show a similar pattern of results. We report here only the electrodes showing the largest differences per cluster. The red dots represent single data points. The error bars show the 95% bootstrapped (Wilcox, 1995) confidence interval (CI) of these differences. Statistically significant differences are conveyed by CI not including zero. Both groups of observers on these clusters respond to the law: Same-Race vs. African American > Same-Race vs. Other-Race > Other-Race vs. African Americans. The difference between Other-Race vs. African Americans is always non-significant.

2.3.4 EEG and Behavioural results

As shown in Figure 23, in WC observers there was a significant correlation between the N170 amplitude and the behavioural FIE for SR (r(8)=.82, p<.01), but not for OR (r(8)=.56, p>.05) and AA (r(8)=.23, p>.05) faces. Moreover, while the same pattern of results was observed for EA participants, the correlation detected for SR faces was non significant (r(8)=.63, p=.06), even though all subjects but one showed the effect; correlations for AA (r(8)=-.19, p=.62) and OR faces (r(8)=-.50, p>.17 - Figure 23) were also non significant. A more robust percentile bootstrap test of independence showed significant correlations (p<.01) between behavioral and electrophysiological FIE indexes, for both groups of observers (WC – CI = [0.28, 0.98]; EA –CI = [0.35, 0.94]).

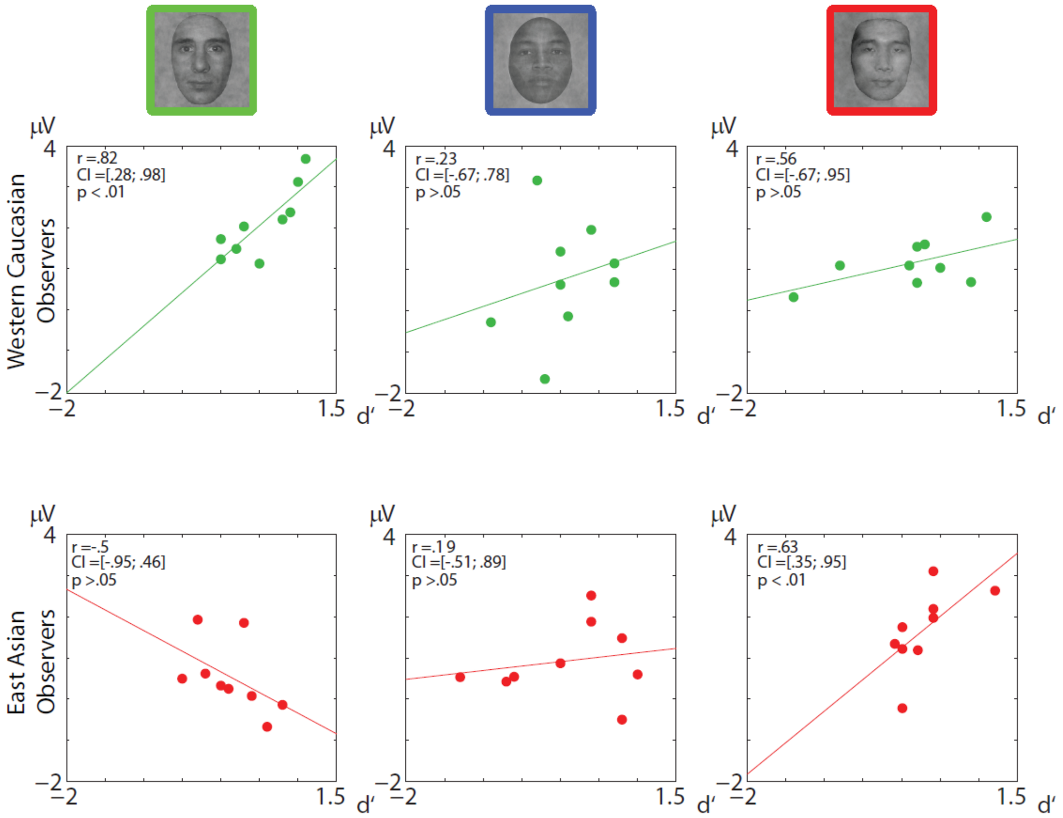


Figure 23 – Correlations between the magnitude of the FIE on the N170 (i.e. N170 amplitude elicited by Inverted minus those elicited by upright faces per each condition) and the magnitude of the FIE on the d' scores. Pearson coefficient, bootstrap confidence interval and respective p values are reported in the top left corner

2.4 Discussion

We investigated whether the early ERP face-preferential N170 component (and its positive counterpart, the VPP) was modulated by the race and orientation of faces as a function of the race of the observers.

Consistent with previous behavioral studies (e.g., Rhodes, Tan et al. 1989; Walker and Tanaka 2003; Tanaka, Kiefer et al. 2004; Michel, Rossion et al. 2006; Blais, Jack et al. 2008), Western Caucasian (WC) and East Asian (EA) observers were more accurate at recognizing same-race (SR) compared to other-race (OR) faces. Importantly, in accordance with past reports (Buckhout and Regan 1988 ; Rhodes, Tan et al. 1989; Murray, Rhodes et al. 2003; McKone, Brewer et al. 2007) face inversion had greater detrimental effects on the recognition of SR compared to OR and African-American (AA) faces in both groups of observers. Moreover, in line with previous electrophysiological findings (Bentin, Allison et al. 1996; Jeffreys 1996; Rossion, Delvenne et al. 1999; Rossion, Gauthier et al. 2000; Itier and Taylor 2004; Rossion and

Jacques 2008), inversion increased and delayed the N170 and the VPP. Importantly, while the race of the faces did not affect the latencies of these components in either orientation, we observed a modulation the magnitude of the face inversion effect (FIE) as a function of race across groups of observers - this is the main novel finding of our study. Specifically, the magnitude of the FIE (i.e., the amplitude difference between upright and inverted faces) was largest for SR, compared to OR and AA faces, with no differences between the latter two categories. This effect cannot be accounted for by low-level visual differences among faces from different races for three reasons. First, amplitude spectrum, luminance, and contrast were equated across all the stimuli; second, we observed a full crossover interaction between groups showing that, regardless of the groups of observers, SR faces elicited larger FIE compared to OR and AA faces; third, our statistical analyses showed no significant amplitude differences between the two respective OR categories. These observations strengthen the claim that the modulations observed on N170 and VPP components are genuinely related to race.

Interestingly, while both P1 and P2 were sensitive to stimulus orientation, exhibiting larger amplitudes and delayed latencies for inverted compared to upright faces, the N250 was not modulated by this factor. Importantly, the P1, P2 and N250 components were not sensitive to race, as demonstrated by the absence of an interaction between the race of the faces and the groups of observers.

The electrophysiological results were consistent with the behavioral data. Both groups of observers showed a significant positive correlation between the magnitude of the FIE on the N170 and recognition accuracy only for SR faces. In line with previous observations (Jacques, d'Arripe et al. 2007), these positive correlations indicate that larger N170 amplitudes elicited by inverted faces are associated with lower recognition accuracy.

It is worth noting however that these correlations are driven by different components of the inversion equation. The behavioral FIE is due to the superior recognition of SR faces in their upright orientation. In contrast, the electrophysiological FIE is due to the enhanced N170 negativity elicited by SR faces in their inverted orientation. However, in our study the electrophysiological (i.e., orthogonal) and the behavioural (i.e., active) findings relied on different task constraints. Therefore, future studies are necessary to clarify the very nature of this paradox and precisely identify the mechanisms underlying the relationship between these measures.

The analyses of the conjoined effects of face inversion and race on the ERP signal were underlined by a rigorous and comprehensive statistical approach. We carried out both canonical statistical tests (i.e. t-tests) as well as robust statistics (i.e. bootstrap confidence interval) on behavioral data. From a methodological point of view, the importance of implementing such a statistical approach on our data is illustrated by the behavioural results. Canonical statistical tests (i.e. t-tests) did not capture significant effects (i.e., p=.06) for the FIE for SR faces in EA observers, and the correlation between this index with the electrophysiological data. However, as clearly shown by the standard errors in Figure 17, the absence of significant effects seems to arise from the large variance for the inverted orientation (with all participants but one showing the effects). The power of parametric tests is significantly affected by both the limited sample size and the asymmetrical distribution of the population. By using bootstrap confidence intervals, which are less sensitive to sample size and outliers, both statistics reached significance.

In the face processing literature, it has been suggested that the recognition impairment observed for inverted faces reflects a qualitative switch from holistic to featural processing, or at least an impairment of holistic processing (e.g. Rossion and Gauthier 2002). Undeniably, due to the lack of experience with inverted faces, these stimuli are more difficult to process than those presented in their canonical (upright) orientation. Concurrently, the amplitude enhancement on the N170 and VPP components could be related to the relative processing impairment associated with inverted faces (e.g. Rossion, Gauthier et al. 2000). It has also been argued that SR faces are processed more holistically than OR faces (e.g. Michel, Caldara et al. 2006; Michel, Rossion et al. 2006). Thus, if face inversion triggers a switch from holistic to featural processing mode, it should lead to a greater impairment for the category processed more holistically: SR faces.

Importantly, regardless of these theoretical interpretations, our data show that the relatively larger behavioral recognition impairment for SR faces due to stimulus inversion is associated with electrophysiogical modulations, with both measures correlating positively. The sensitivity of the N170 to race during face inversion suggests that differences in processing SR and OR faces begin early, at the perceptual level. These early perceptual differences fit well with ORE theoretical frameworks. In the face space model proposed by Valentine (1991), which recently found objective support in neural network simulations (Caldara and Abdi 2006), faces are encoded in an arbitrary psychological multidimensional space. Variations in exemplar density between races account for SR face recognition advantage, because SR face representations are more widely distributed in the face space than the representations of OR faces. The physical distance between points, symbolizing psychological representations of individual faces, is a function of the perceived difference between faces, which determines the density of the cloud. It would therefore make sense that differences in processing SR and OR faces arise at the perceptual level. Unlike Valentine's multidimensional face space model, Levin (1996 ; Levin 2000) postulates that for OR faces, race is extracted as a feature at the cost of individuating information. Therefore, according to Levin, performance for SR and OR faces can be accounted for by differences in coding features for faces of different races (Levin 2000). This account would also be consistent with our data showing modulations of face processing as a function of race at early perceptual stages.

In keeping with several previous studies (e.g. Caldara, Thut et al. 2003; Caldara, Rossion et al. 2004; Tanaka and Pierce *2009*), race did not affect the N170 amplitude for upright faces. However, we failed to replicate the delayed N170 latency for inverted OR compared to SR faces (Wiese, Stahl et al. 2009), as well as previous modulations of race on the N170 amplitude for upright faces (Ito and Urland 2005; Herrmann, Schreppel et al. 2007; Stahl, Wiese et al. 2008; Walker, Silvert et al. 2008). We also failed to replicate race effects at earlier latencies than that of the N170. Ito (2003) reported race modulations between AA and WC faces in WC observers on early ERP components (i.e. 100 ms after stimulus onset). In their experiment, however they used color pictures of faces of different races that differed markedly in skin color and were not equated in spatial frequency content. Despite these physical differences, Ito (2003) interpreted their findings as evidence for early race categorization. Alternatively, P1 effects might be due to differences in global low-level visual properties, which are known to modulate early ERP components (e.g. Johannes, Munte et al. 1995; Hillyard, Teder-Salejarvi et al. 1998; Luck 2005), even independently of attention (Hillyard, Teder-Salejarvi et al. 1998). In our study, we equated some important global low-level visual properties across stimuli, and we failed to observe any P1 categorical race effect. In line with previous studies (e.g. Itier and Taylor 2004; Itier and Taylor 2004; Lueschow, Sander et al. 2004), we only observed a general amplitude and latency increase on the P1 component for inverted compared to upright faces. Indeed, amplitude modulations on this component have been associated with low-level differences in the stimuli (Debruille, Guillem et al. 1998; Halit, de Haan et al. 2000). In a nutshell, despite the fact that controlling for low-level visual properties of the stimuli may reduce their ecological validity, our findings suggest that this control abolishes potentially spurious effects related to salient differences in faces from difference race. In addition, these studies relied on only one group of observers. Importantly, we show that the investigation of sensitivity to race requires the use of at least two groups of observers and the presence of a crossover interaction.

Contrary to previous findings, our data failed to reveal P2 (Caldara, Rossion et al. 2004) and N250r (Tanaka and Pierce *2009*) race effects. Although controlling for global low-level visual properties might have abolished P2 and N250 race effects, it seems more likely that the lack of race effects on these components in our experiment may result from differences in task constraints. Indeed, our subjects were instructed to perform a passive orthogonal task, whereas Caldara (2004) used a direct race categorization task with interspersed catch trials, and Tanaka (*2009*) employed an active old-new recognition task, directly tapping into face memory. The N250 and the P2 have been related to the active categorization of visual stimuli (Latinus and Taylor 2005; Philiastides, Ratcliff et al. 2006; Philiastides and Sajda 2006; Harel, Ullman et al. 2007), and long term memory of faces (Schweinberger, Pickering et al. 2002). If the task demands do not entail active categorization of face stimuli, or retrieval of face representations, the effect on these later components may thus be abolished.

An important question that would require further investigation is whether the N170 is sensitive only to race for inverted faces. How can race affect the early electrophysiological dynamics only in a given unfamiliar upside-down orientation, while producing no effects in its more canonical upright orientation? This surprising result could be explained by a ceiling effect. First, humans' proficiency in processing upright faces is so high that the ERP signal might not be sensitive enough to detect any subtle differences that may exist. However, situations that is more demanding in terms of visual processing — as it is the case for inverted faces — may render such subtleties to become more easily identifiable. Second, the tasks and paradigms used so far may be unable to confer enough power to measure early amplitude modulations to race. Our data however do not allow speculation in either direction. Further research with more sensitive paradigms (e.g., neural adaptation) and task constraints (e.g., face identification) tapping into the roots of the ORE is necessary to clarify whether early neural markers of processing upright faces (i.e. the N170) are sensitive to race, or to confirm that race sensitivity occurs uniquely for inverted faces.

2.5 Conclusion

Given its actuality in everyday life, the thoroughly documented ORE remains an interesting topic to be studied in the field of cognitive and vision science. Although, behavioral data have shown high levels of consistency, the neural mechanisms underlying this visual effect have yet to be fully understood. Electrophysiological studies have reported highly contrasting data. In the present study we sought to investigate whether it was possible to relate modulation of the ERP signal in the early neural dynamics of face processing to behavioral differences associated with the ORE. We addressed some of the methodological inconsistencies displayed in previous research by controlling for low level visual properties of our stimuli, which are known to modulate the ERP signal and by adding a set of other-race faces common to both group of observers (i.e., AA faces). Since any (significant) effect could be confounded by differences in the face stimuli, which would critically impact on the generalization of the results, we adopted 2 groups of observers: EA and WC. We observed a full cross-over interaction between the races of the observers and the race of the faces, which positively correlated with our behavioral data. These findings indisputably represent a genuine ORE on the ERP signal. Our results showed that while race did not elicit differences across the whole ERP for uptight faces, the race of the faces systematically modulated the amplitude of the N170 and VPP in the inverted condition. The neural face system is sensitive to race at early perceptual stages of processing, at least when faces are presented upside-down.

3. Neural repetition suppression to identity is abolished by other-race faces

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Preamble

Human beings are remarkably skilled at recognizing faces, with the marked exception of other-race faces: the so-called other-race effect. As reported nearly a century ago (Feingold CA (1914) Journal of Criminal Law and Police Science 5:39-51), this face recognition impairment is accompanied by the popular belief that other-race faces all look alike. However, the neural mechanisms underlying this high-level "perceptual illusion" are still unknown.To address this question, we recorded high-resolution electrophysiological scalp signals from East Asian (EA) and Western Caucasian (WC) observers while they viewed two EA or WC faces. The first adaptor face was followed by a target face of either same or different identity. We quantified Repetition Suppression (RS), a reduction in neural activity in stimulus-sensitive regions following stimulus repetition. Conventional electrophysiological analyses on target faces failed to reveal any RS effect. However, to fully account for the paired nature of RS events, we subtracted the signal elicited by target to adaptor faces for each single-trial and performed unbiased spatiotemporal data-driven analyses. This novel approach revealed stronger RS to same-race faces of same identity in both groups of observers on the face-sensitive N170 component. Such neurophysiological modulation in RS suggests efficient identity coding for same-race faces. Strikingly, OR faces elicited identical RS regardless of identity, all looking alike to the neural population underlying the N170.Our data show that sensitivity to race begins early at the perceptual level, providing, after nearly one hundred years of investigations, the first neurophysiological correlate of the all look alike perceptual experience.

3.1 Introduction

Almost a hundred years ago, Feingold (Feingold 1914, p. 54) reported that human beings living in different geographical locations perceive individuals belonging to “other-races” (OR) as all looking alike: "Other things being equal, individuals of a given race are distinguishable from each other in proportion to our familiarity, to our contact with the race as whole. Thus, to the uninitiated American all Asiatics look alike, while to the Asiatics, all White men look alike." This commonly experienced all look alike “perceptual illusion” for OR faces is at the root of one of the most robust empirical finding in face recognition: the other-race effect (ORE) for faces, which refers to the marked behavioural impairment displayed by humans in recognizing OR compared to same-race (SR) unfamiliar faces (i.e., lower accuracy coupled with higher false identifications for OR faces). The scientific literature has provided clear evidence that the ORE and the popular belief that OR faces all look alike are not accounted for by the paucity of anthropometric variations in OR faces, but by a genuine lack of expertise with them. Although this theoretical explanation has been supported by numerous behavioural (for a review see Meissner and Brigham 2001), computational (e.g., O'Toole, Deffenbacher et al. 1991; O'Toole, Deffenbacher et al. 1994; Caldara and Abdi 2006) and neuroimaging (Golby, Gabrieli et al. 2001; Caldara, Thut et al. 2003; Ito and Urland 2003; Caldara, Rossion et al. 2004; Ito, Thompson et al. 2004; Kim, Yoon et al. 2006; Herrmann, Schreppel et al. 2007; Stahl, Wiese et al. 2008; Walker, Silvert et al. 2008; Tanaka and Pierce *2009*) studies on the ORE, the neurophysiological correlates of the all look alike perceptual experience, have never been directly investigated.

This observation is even more surprising considering that the rapid development of neuroimaging techniques has dramatically increased our knowledge of how the brain achieves visual categorization. Studies employing single-cell recordings in primates and functional Magnetic Resonance Imaging (fMRI) in humans have shown the existence of neural populations responding preferentially to faces (e.g., Sergent and Signoret 1992; Puce, Allison et al. 1995; Kanwisher, McDermott et al. 1997; Halgren, Raij et al. 2000) and face identity (Winston, Henson et al. 2004; Quiroga, Reddy et al. 2005; Gothard, Battaglia et al. 2007; Kriegeskorte, Formisano et al. 2007). Importantly, genuine race effects require an interaction between the race of the observer and the race of the faces. Only one fMRI study has employed two groups of observers, revealing greater responses for SR compared to OR faces in the face sensitive cortex during a face memorization task (Golby, Gabrieli et al. 2001). Crucially, however, the all look alike effect takes place in the subsequent face recognition stage during which mechanisms related to individual face identification are engaged. For example, it is common experience to misidentify personally familiar individuals belonging to an OR group (i.e., misidentify your Chinese friend on the street, if you are Westerner), whereas this perceptual misidentification related to the all look alike effect does not occur during the memorization of familiar faces. In addition, fMRI prevents from drawing any conclusion on the time course of neural sensitivity to race.

Human faces elicit also a particular electrophysiological signature: the N170 Event-Related Potential (Botzel and Grusser 1989; ERP, Bentin, Allison et al. 1996; for a review see Rossion and Jacques 2008). The N170 is a bilateral occipitotemporal negative deflection peaking roughly 170 ms after stimulus onset, larger for faces compared to other visual categories. Activity in this time window is associated with the early accumulation of perceptual information leading to visual categorization, which is necessary for post-sensory, decision, and motor stages (Philiastides, Ratcliff et al. 2006; Schyns, Petro et al. 2007).

Numerous electrophysiological studies have investigated the early electrophysiological dynamics of the ORE (Caldara, Thut et al. 2003; Ito and Urland 2003; Caldara, Rossion et al. 2004; Ito, Thompson et al. 2004; Herrmann, Schreppel et al. 2007; Stahl, Wiese et al. 2008; Walker, Silvert et al. 2008; Tanaka and Pierce *2009*). Several studies have failed to show any sensitivity to race on the N170 (6, 7, 14), or on its frontal counterpart the vertex positive potential (11). These results suggest that brain activity in the N170 period codes only for the detection of a face shape, whereas race information from faces is extracted in post perceptual stages occurring roughly between 250-300 ms after stimulus onset (6, 7, 14). On the other hand, several studies have reported larger N170 amplitudes for OR faces compared to SR faces (10, 13, 15). This finding might be due to uncontrolled physical differences (30). It is also at odd with many studies that have shown larger N170 to object categories of expertise (see Rossion, Curran et al. 2002), a result that would lead to the prediction of a larger N170 to SR faces. The heterogeneity of these results and the lack of sensitivity of the N170 may also be explained by the use of diverse task constraints: the detection of catch trials (7, 15), detection of colored faces (30), explicit race categorization (6), and an old-new face recognition design (14). Furthermore, previous studies used different types of OR stimuli, including Western Caucasian (6, 7, 10-13, 15, 30), East Asian (6, 7, 10, 13, 30), African American (11, 12, 14, 15, 30) and Hispanic faces (14). More importantly, all these ERP studies relied exclusively on data from the WC population. This is a serious methodological problem, because any effect could be confounded by physical differences in the face stimuli, preventing any firm conclusion on the ORE. A full cross-over interaction between races of observers and the race of faces is mandatory to assess genuine behavioural and neurophysiological ORE. To the best of our knowledge, only one electrophysiological study used two groups of observers and reported sensitivity to race for inverted faces in two groups of observers (Vizioli, Foreman et al. 2010). But critically, none of these neuroimaging studies has yet employed a paradigm optimally tapping into mechanisms devoted to face recognition, which leaves the neurophysiological bases of the all look alike effect unexplored.

Adaptation is a well-established paradigm to reveal the nature of information coding at the perceptual and neurophysiological levels (for a review see Grill-Spector, Henson et al. 2006). Neural activity in stimulus-sensitive regions is typically reduced when a stimulus is repeated, a phenomenon known as Repetition Suppression (RS, Miller, Li et al. 1991; Wiggs and Martin 1998; Henson 2003; Grill-Spector, Henson et al. 2006). RS was initially observed in monkey single-cell recordings (e.g., Miller, Li et al. 1991; Li, Miller et al. 1993; Sobotka and Ringo 1994). More recently it has been reported in human electrophysiological (e.g., Puce, Allison et al. 1999; Eimer 2000; Doniger, Foxe et al. 2001; Schendan and Kutas 2003; Henson, Rylands et al. 2004) and fMRI BOLD studies (e.g., Henson, Rylands et al. 2004; Winston, Henson et al. 2004; Loffler, Yourganov et al. 2005) using a variety of cognitive tasks. Although the precise neural computations of RS remain unclear, RS elicited by two stimuli presented in rapid succession indicates the engagement of the same (or at least a largely overlapping) neural population in the processing of both stimuli (Grill-Spector, Henson et al. 2006). Therefore, the amount of RS is related to the capacity of a neural population to discriminate stimuli and could be compared to a novelty detection mechanism (Grill-Spector, Henson et al. 2006), decreasing neural responses' redundancy while increasing coding efficiency (Sobotka and Ringo 1994; Muller, Metha et al. 1999; Dragoi, Sharma et al. 2002; Grill-Spector, Henson et al. 2006; Gutnisky and Dragoi 2008). Interestingly, the face sensitive N170 component shows preferential RS to faces but not to other visual categories (Kovacs, Zimmer et al. 2006), as well as to face identity (Jacques and Rossion 2006; Jacques, d'Arripe et al. 2007; Caharel, d'Arripe et al. 2009). Thus, RS represents a powerful tool to elucidate the time course and the nature of the neural representations leading to the all look alike effect. In this context, it seems logical to predict stronger RS for SR compared to OR faces in the N170 time window.

To address this question, we recorded high-temporal resolution scalp ERP signals in East Asian and Western Caucasian observers while they viewed sequences of two faces: an adaptor face and a target face (Figure 24). In each sequence, the two faces were either East Asian or Western Caucasian, and from the same or different identities. To minimize the use of trivial image matching strategies, we changed the facial expression displayed by the adaptor and the target faces. As expected, Westerner and Easterner observers showed an ORE, as assessed in a separate face recognition task. Previous electrophysiological adaptation studies compared the ERPs to target faces, ignoring the response to adaptor faces (Jacques and Rossion 2006; Kovacs, Zimmer et al. 2006; Jacques, d'Arripe et al. 2007; Caharel, d'Arripe et al. 2009). In our experiment, this conventional approach failed to reveal any significant difference across conditions. However, because RS is a signal reduction to the second stimulus of a pair, we developed a novel single-trial analysis method. We subtracted the signal elicited by the presentation of the target face to that elicited by the adaptor face independently for each pair, resulting in a single-trial RS (stRS) electrophysiological response (Figure 25). We also used unbiased spatiotemporal data-driven analyses at all electrodes and time points. In line with previous findings (Jacques and Rossion 2006; Jacques, d'Arripe et al. 2007; Caharel, d'Arripe et al. 2009), stRS responses in the N170 time-window showed larger RS for SR faces of the same identity compared to any of the other conditions in both groups of observers. This result suggests a more effective coding of identity for SR faces than OR faces. Strikingly, however, in both group of observers OR faces elicited similar RS responses regardless of a change in facial identity, suggesting that the neural populations underlying the early face sensitive N170 responses cannot discriminate OR face exemplars.

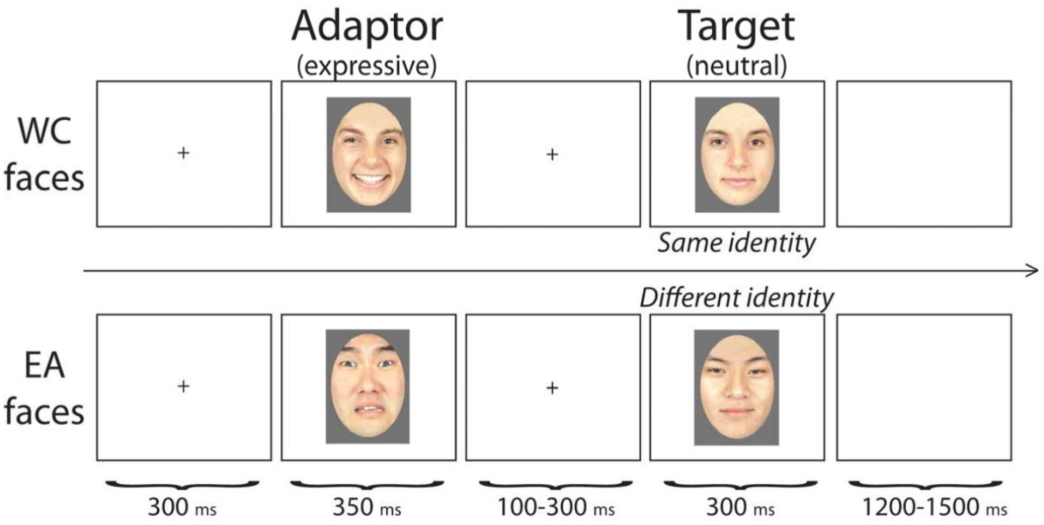

Figure 24 – Example of the face stimuli used in the experiment and the time course of the experimental design.

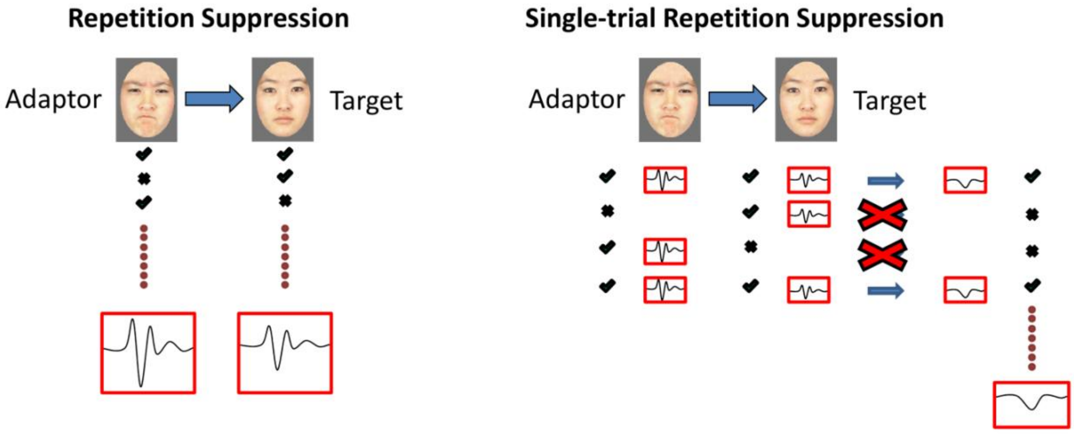

Figure 25 – Conventional and single-trial repetition suppression analyses. For both analyses, the same artifact rejection criteria are used to remove noisy trials. However, in conventional Repetition Suppression (RS) analyses (left), adaptor and target trials are processed independently, whereas in single-trial RS (stRS, right), adaptor and target trials are processed as dependent pairs. Concretely, in conventional RS, the trial rejection criterion is applied independently for adaptor and target (rejected trials are marked as '▯'). The remaining trials (marked as '▯') are then averaged separately for the adaptor and the target conditions. This procedure breaks the association between adaptor and target trials, which would not be problematic if no trials were rejected. Because there are always some noisy trials in EEG recordings, a different strategy is necessary to preserve the association between adaptor and target trials. Hence, in stRS, the trial rejection criterion is applied to pairs of events: we reject both adaptor and target trials if artifacts contaminate any one of the two epochs. We then subtract the signal elicited by target to adaptor faces for each single-trial before averaging the differences. Formally, averaging independently the adaptor and target signals and then performing a subtraction would lead to the same results because of the associative and commutative property of the average. The average of series of numbers is simply the average of the numbers, no matter what order they are inputted in. Performing a subtraction does not compromise the commutative property of the average. To sum up,

the stRS procedure relies on a paired trial rejection criterion, which effectively preserves the paired nature of the RS design, in keeping with the definition of RS as a stimulus specific reduction of neural activity.

3.2 Methods

Participants – Twenty-four right handed subjects took part in the experiment: 12 East Asians (EA - 6 female), with an age range of 18–33 and a mean of 25; and 12 Western Caucasian (WC - 6 female), with an age range of 19–31 and a mean of 23. All EA participants were Chinese who had been in the country for less than 1 month and had previously never been in contact with a Western society. All participants provided written informed consent and had normal or corrected-to-normal vision. The local ethical committee approved the experiments.

Stimuli – The stimuli consisted of 20 front-view grayscale photographs of WC and EA faces (5 identities x 2 genders x 2 races), approximately 3.75° x 4.25° of visual angle, taken from the JACFEE database (**Matsumoto** and **Ekman 1988**).

To limit the possibility that ERP repetition effects were the result of pixel based low level adaptation, instead of high level adaptation to face identity, each identity was equally presented as a neutral face, or a face displaying 5 possible emotions: happy, anger, sad, disgust and surprise. All emotions were counterbalanced across face races and conditions. All faces were cropped to remove external features by the application of the same oval mask; none had particular distinctive features and male faces were clean-shaven. The stimuli were centered in a 5.2°x5.2° and color normalized with Adobe Photoshop ® CS4, by constraining all the images in the same average template color space.

EEG Study – Participants sat in a dimly lit, sound-attenuated electrically shielded booth. Viewing distance was maintained at 80 cm by a chinrest. Each trial consisted of 2 faces of same or different identities (Figure 24) presented sequentially on a Samsung SyncMaster 1100 MB monitor (resolution 2048 x 1536 pixels, 23.5°x30.1°, background of average luminance 25.4 cd/m2, refresh rate 80 Hz). A trial started with a black fixation cross approximately 0.3° of visual angle, presented at the centre of the screen for 300 ms. The first face, the adaptor, was then presented for 350 ms, followed by an interval of random duration (100 to 300 ms), and then by the second face, the target, for 300 ms. The offset of the second face was followed by a randomized intertrial interval between 1,300 to 1,500 ms. Target and adaptor faces' identities matched in half of the trials. To minimize low-level adaptation, the adaptor face portrayed an emotion, whereas the target face was neutral. Face race and gender were consistent within trials. There were 4 conditions (2 races – EA and WC x 2 identities – same and different): SR same, SR different, OR same and OR different (where same and different refers to the identities of the 2 subsequently presented faces). Each identity equally appeared in the same and different conditions. There were 80 trials per condition, and the order of the conditions was randomized within each block.

Subjects performed an orthogonal task that required pressing the "s" key on the keyboard every time one of the 2 faces within a trial was presented upside-down and the "k" key when both faces were inverted. This orthogonal task was designed to avoid potential signal modulations due to attentional confounds linked to the race of the stimuli (Golby, Gabrieli et al. 2001). Inverted faces appeared in approximately 12.5% of the trials: 20 with the adaptor or the target face inverted and 20 with both faces inverted. Each identity appeared twice as inverted.

The experiment consisted of 8 blocks of 45 trials each (360 trials in total with 80 trials x 4 conditions and 40 trials with inverted faces) and lasted approximately 20 minutes.

Behavioural Study – Subsequently to the EEG experiment, the same participants performed a behavioural task that directly assessed the ORE. In an encoding phase, participants had to memorize 20 faces of each race, presented for 3s each, with 5s ISI. Subsequently, subjects performed a forced-choice old-new recognition task with 20 old and 20 new faces.

Faces were selected from a set of stimuli different from the set used in the EEG experiment (Bang, Kim et al. 2001). Participants did two blocks of the old/new face recognition task per race. The order of the blocks was pseudo-random and counterbalanced across observers. Faces were blocked by race during both the encoding and the recognition phase. The encoding stage was followed by a 1 minute pause, after which participants pressed the "s" key on the computer keyboard for old faces and the "k" key for new faces. Each face remained on the computer screen for 200 ms (3s ISI). Participants did not know the ratio of old to new faces and did not receive feedback on their responses.

EEG Recording and Analysis – We acquired EEG data with a 128-channel Biosemi Active Two EEG system (BioSemi, Amsterdam, Netherlands). Four additional electrodes (UltraFlat Active electrodes, BioSemi) attached below and at the outer canthi of both eyes measured the vertical and horizontal electro-oculograms. Analog signal was digitized at 1024 Hz and band-pass filtered online between 0.1 and 200 Hz. Electrode offsets were kept between +/– 20 µV. Participants were asked to minimize blinking, head movement, and swallowing.

We used EEGLAB (Delorme and Makeig 2004), Matlab 7.5 (2007b) and BESA 5.2 to perform EEG analyses. In BESA, EEG data were referenced to an average reference. Noisy electrodes were rejected on a subject-by-subject basis. The signal was low-pass filtered at 40 Hz with a slope of 6dB. Single trials were corrected for horizontal and vertical eye movements and blinking artifacts by PCA, as implemented in BESA. First, we identified eye movements on the continuous signal using their specific topographical distribution. Then, we manually selected portions of the signal showing the topographical configuration of interest. Finally, we averaged the selected epochs to create a subject-specific template for each artifact. The first PCA component of each artifact was removed. This component accounted for 89% to 99% of the variance (mean = 91%). Artifacts were rejected based on absolute abnormal values larger than 120 µV. Trials were averaged across an epoch of -100 ms to +500 ms and the average 100 ms of pre-stimulus activity was removed from every time point, independently at each electrode. Trials including inverted faces were excluded from the analysis. Channels contaminated by artifacts were interpolated using the EEGLAB topoplot function.

Consistently with previous studies, we first analyzed the ERP amplitude to the adaptor and to the target faces separately. For adaptor faces, we carried out a 2 way ANOVA with 2 groups of observers (WC and EA) x 2 races of faces (WC and EA). We performed another 2 way ANOVA for target faces, with 2 groups of observers (WC and EA) x 4 conditions (WC faces same identities, WC faces different identities, EA faces same identities, EA faces different identities). These ANOVAs were performed independently at all electrodes and time points, with ERP amplitude as dependent variable. This analysis makes no a priori assumption about where and when to look for effects in the ERP signal. Post hoc t-tests were then carried out between paired conditions.

The ANOVA on both the target and adaptor faces failed to demonstrate any RS effects across the whole ERP. However, this type of analysis makes the implicit assumption that adaptor and target faces are independent, and therefore fails to recognize the paired nature of the experimental design. We thus developed a single trial Repetition Suppression (stRS) response. Based on the definition of RS, which refers to a stimulus specific reduction of neural activity, we computed the stRS response by subtracting the activity elicited by the target face from the activity elicited by the adaptor. We rejected from the analysis the signal elicited by both adaptor and target face if either one of the two epochs was contaminated by artifacts (for more details about the procedure see Figure 25).

We then carried out a 2 way ANOVA (2 race of the observers – EA and WC – x 4 conditions - WC faces same identities; WC faces different identities; EA faces same identities; EA faces different identities) independently at all electrodes and time points, with stRS as dependent variable.

To correct for the increase in type I errors due to multiple comparisons we used bootstrap (Wilcox 2005) and a multivariate clustering technique (Maris and Oostenveld 2007). We centered the data so that each condition had a mean of zero; then we used the bootstrap to derive an estimate of the sampling distribution of our statistic in a condition in which the null hypothesis of no difference in means is true. In each bootstrap, we sampled subjects with replacement and carried out the repeated measures ANOVAs described above, independently at all electrodes and time points. Then the significant F values (p<.05) were grouped in spatiotemporal clusters (Maris and Oostenveld 2007). For each bootstrap, we computed the sum of F values in every cluster and saved the maximum cluster sum across clusters. We repeated this procedure 599 times, leading to 600 F cluster sums for each main effect and for each interaction. After sorting the 600 cluster sums we selected the 95th percentile as our cluster threshold to assess statistical significance. The significant F values from the original ANOVAs were clustered, and the sum of F values inside each cluster was compared to the bootstrap cluster threshold for that test. If an observed cluster sum was equal or larger than the threshold sum obtained under H0, all the time points and the electrodes inside that cluster were considered significant.]

3.3 Results

We carried out ANOVAs independently at all electrodes and all time points (see methods for details). This approach led to a large number of F, t and p values. For clarity, we report here only the minimum and maximum F or t values and their associated p values. Exact p values are reported for significant effects, unless they were smaller than .001.

3.3.1 Behavioural results

Western Caucasian (WC) observers were better at recognizing SR (d'=2.2; s.d.=0.44) than OR faces (d'=1.7; s.d.=0.4). Likewise, East Asian observers (EA) were better at recognizing SR (d'=2.1; s.d.=0.41) than OR faces (d'=1.6; s.d.=0.49). A repeated-measures ANOVA performed on d' scores, with race of the observers (WC and EA) as a between-subject factor, and race of the face (WC or EA) as within-subject factor, confirmed the significance of this observation (F(2,32)=7.19; p<.001).

3.3.2 ERP Results

Descriptive Statistics – Consistent with previous research (Rossion and Jacques 2008), for both groups of observers, the N170 peaked bilaterally over parietal-occipital electrodes, being largest at the right hemisphere electrode PO8h (see Supporting Table 1). After artifact rejection, the mean number of trials per condition was 72 (s.d.=9.2).

Repetition Suppression results – Following the conventional RS analysis, we performed a 2 way ANOVA of the amplitude of the ERPs to target faces, independently at all electrodes and time points (race of the observer (2): WC, EA x condition (4): WC same identity, WC different identity, EA same identity, EA different identity). This ANOVA revealed no significant effect across the whole epoch (p>.05, corrected for multiple comparisons (MC) by a multivariate cluster analysis, as described in the methods – Figure 27). A 2 way ANOVA of the amplitude of the ERPs to adaptor faces also led to null results (race of the observer (2): WC, EA x race of the face (2): WC, EA; p>.05, MC corrected).

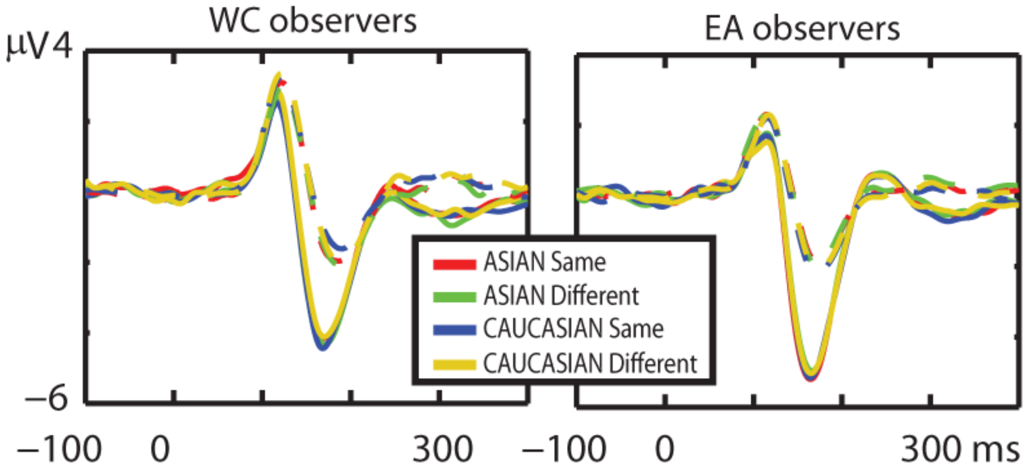

Figure 26. Mean ERPs elicited by the adaptor (continuous line) and the target faces (dotted line) measured at PO8h for the four conditions (Asian faces of same identities, red line; Asian faces of different identities, green line; Caucasian faces of same identities, blue line; Caucasian faces of different identities, yellow line) for WC and EA observers. No significant differences were observed across all conditions for the ERPs elicited by both adaptor and target faces.

We carried out a 2 way ANOVA of the peak latency of the P1, N170 and P2 components elicited by the target face. The race of the observer was the between-subject factor and the 4 conditions (as described above) were the within-subject factor. We performed the ANOVA at the electrodes where the components were the largest: PO8h and PO7h for the N170, and O2 and O1 for P1 and P2. No significant latency differences were observed for P1 (F(2,11)=1.12; p>.05), N170 (F(2,11)=2.11; p>.05) or P2 (F(2,11)=1.06; p>.05).

We also carried out a 2 way ANOVA on the peak latency of P1, N170 and P2 components elicited by the adaptor face at the electrodes described above. The factors of the ANOVA were race of the observers and conditions. Once again, no significant latency differences were observed for P1 (F(2,11)=2.31; p>.05), N170 (F(2,11)=.51; p>.05) or P2 (F(2,11)=1.2; p>.05).

Single-trial Repetition Suppression results – Only trials accepted for both adaptor and target faces were included in the computation of the stRS ERP (see results at electrode PO8h in Figure 27a). The mean number of trials accepted per condition thus dropped from 72 to 54 (min. = 46; max. = 68; std = 6.4).

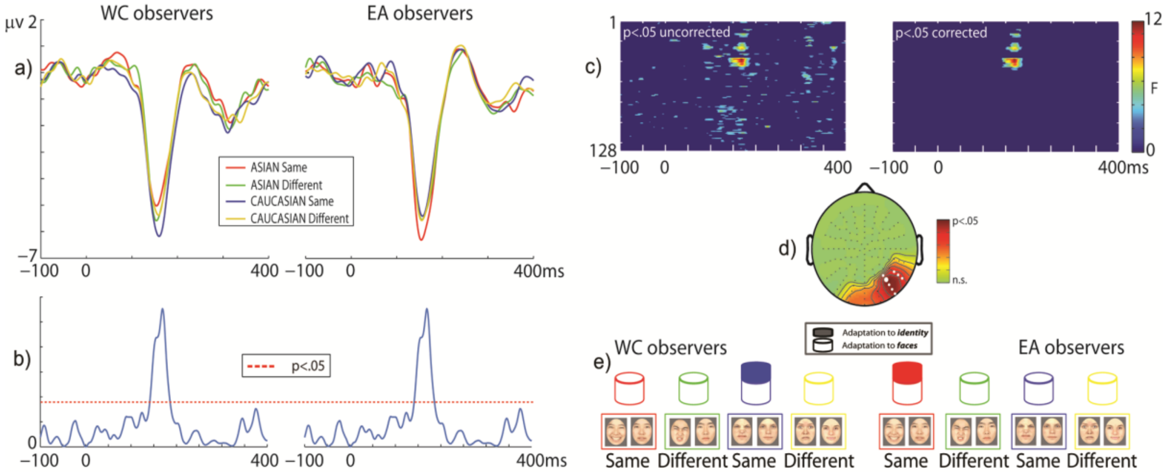

Figure 27 - a) Single-trial RS responses measured at PO8h, the electrode with the largest N170 for WC and EA observers. The stRS responses are obtained by averaging the single-trial differences between adaptor and target faces. Note that the more negative is the amplitude, the stronger the adaptation. b) Timecourse of the F values for the group × condition interaction from the ANOVA on the stRS amplitude at PO8h, the electrode with the largest effect size. Note the burst of significant F values coincided with the stRS peak latency. c) Significant F values of the group × condition interaction on the stRS amplitude obtained from the ANOVA carried out independently at all electrodes and time-points, uncorrected (Left) and corrected (Right) for multiple comparisons. Electrodes are stacked up along the y axis and time is shown along the x axis. The electrode order is not based on their spatial topographical position (which instead is correctly shown in d). d) Topography of the F values at the latency of the maximum F, showing the electrodes displaying a significant group ×condition interaction on the stRS amplitude. The white dots are the right occipito–temporal electrodes that displayed significantly larger RS responses for SR same identity faces compared with any other condition. The largest white dot indicates the electrode showing the largest effect. e) Model. A general level of adaptation to faces is observed for all conditions (empty bars). The stRS specific to identity is only observed for same-race faces (filled bars), which is related to greater coding efficiency for this visual category.

The ANOVA (race of the observer x condition) carried out on the stRS amplitude independently at all electrodes and time points revealed a significant interaction (max. F(2,11)=11.06, min. F(2,11)=2.75, p=.049, MC corrected), which was maximal at the latency of the stRS peak amplitude at PO8h, Figure 27). This interaction was significant over a cluster of center and right occipito-parietal electrodes (Figure 27d). The time-course of the F values of the race of the observer x condition interaction revealed a burst of significant F values in the N170 time window, synchronous with the largest RS responses (Figure 27b). Post hoc paired t-tests revealed that regardless of the race of the observers, SR same identity trials elicited significantly larger stRS responses compared to the other conditions (at PO8h – min.: WC: t(11)=-2.73; p=.02;

EA: t(11)=-2.29; p=.04; max.: WC: t(11)=-3.92; p=.002; EA: t(11)=-4.22; p=.001) over a cluster of right occipito-parietal electrodes only (i.e. P8, P8h, P10h, PO6, PO8, PO8h, PO10h, PO10 – see Figure 27d). RS was equivalent across the remaining conditions (Figure 27a). Moreover, stRS responses were time-locked to stimulus onset and reliably present throughout the duration of the experiment (Figure 28). No other significant amplitude differences were observed.

We also carried out a 2 way ANOVA (race of the observer x condition) on the peak latency of the stRS response at the electrodes showing significant race of the observer x condition interaction on the stRS amplitude (as described above). No significant latency differences were observed.

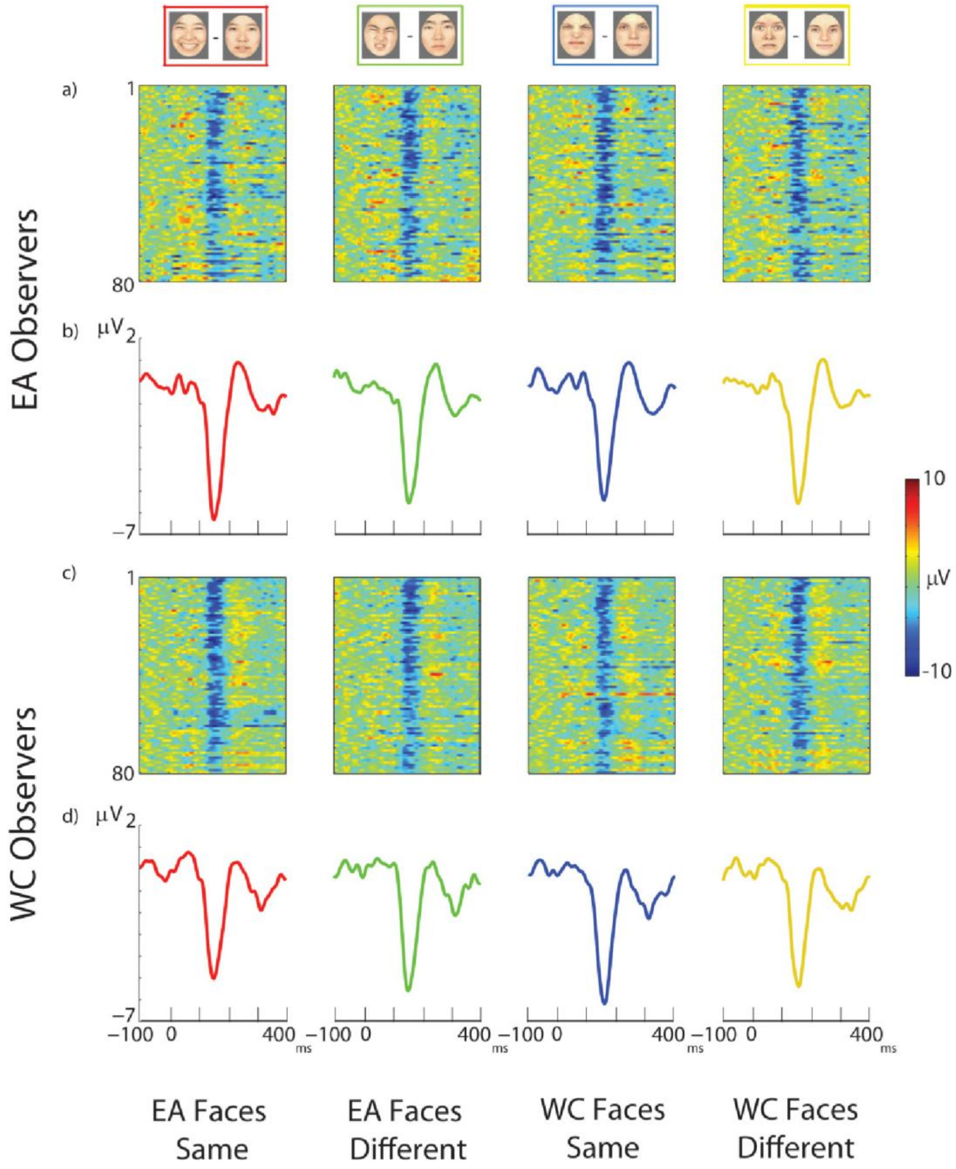

Figure 28 – ERP image for Western Caucasian (WC - a) and (EA - c) observers at electrode PO8h. For each condition, each horizontal line shows the single trials averaged across subjects – i.e., row 1 shows the average across subjects of their first trial. Red represents positive activity and blue negative activity. The number of subjects used for averaging varied from 9 to 12 across trials, depending on the

single trials rejection as explained in the methods section. b) & d) Single-Trial Repetition Suppression (stRS) responses for WC and EA observers at electrode PO8h.

Finally, to rule out any potential significant contribution of the different facial expressions portrayed in the target faces in modulating the stRS responses, we carried out 2 way ANOVAs (2 groups of observers – WC and EA – x 5 facial expressions of emotion – angry, sad, happy, surprised, disgust) at all electrodes and time points on stRS signals. Our data revealed that facial expressions did not modulate stRS signals ($p<.05$, MC corrected).

3.4 Discussion

This cross-cultural study investigated the early neural dynamics of the all look alike perceptual phenomenon, the root of the marked recognition impairment observed in humans for other-race (OR) faces. We used an adaptation paradigm and recorded electrophysiological signals. In line with previous behavioral studies on the other-race effect (e.g. Rhodes, Tan et al. 1989; Tanaka, Kiefer et al. 2004; Michel, Caldara et al. 2006; Michel, Rossion et al. 2006; Blais, Jack et al. 2008; Walker, Silvert et al. 2008; Vizioli, Foreman et al. 2010), our Western Caucasian (WC) and East Asian (EA) observers were more accurate at recognizing same-race (SR) than other-race (OR) faces. Importantly, in both groups of observers, our component-free spatiotemporal EEG analyses revealed larger repetition suppression (stRS) following adaptation to SR faces of the same facial identity compared to SR faces of a different identity. Consistently with previous electrophysiological studies, adaptation to face identity occurred in the N170 time window (Jacques, d'Arripe et al. 2007; Caharel, d'Arripe et al. 2009).

In addition, we found a novel result: Repetition Suppression (RS) responses did not discriminate between same and different identities for OR faces in both groups of observers. This crossover interaction can be considered as an early neurophysiological signature of the perceptual all look alike effect, occurring in a time window typically associated with early categorical face processing (e.g., Jacques and Rossion 2006; Jacques, d'Arripe et al. 2007; Schyns, Petro et al. 2007; Rousselet, Husk et al. 2008; Caharel, d'Arripe et al. 2009). Importantly, the full crossover interaction between the race of the observers and the race of the faces demonstrates that the differences in stRS are genuinely related to race and culture of the observers, and not a consequence of differences in the visual properties of faces from different races (see also Vizioli, Foreman et al. 2010). It is also worth noting that RS and the all look alike perceptual phenomenon were not modulated by the facial expression of the adaptor faces.

Identity dependent RS occurred at right occipitotemporal electrodes only, in line with lesion studies suggesting that the right anterior temporal cortex is critical for face identification (e.g., Evans, Heggs et al. 1995; Tranel, Damasio et al. 1997; Gainotti, Barbier et al. 2003). These early scalp electrophysiological effects were similar in observers from two cultures. This suggests that the consecutive presentation of any pair of faces elicits a comparable stRS (represented in Figure 27e by the non filled bars). Neural populations coding for face shapes might be involved in these early RS responses. Whereas the presentation of any face caused some level of adaptation, the presentation of faces with same identity was responsible for an additional amount of adaptation only if faces were from the same race as the observer (represented in Figure 27e by the plain bars). This race preferential adaptation might be due to the recruitment of a supplementary neural population coding selectively for SR facial identity. Importantly, our results converge with evidence showing the existence of face-preferential cortical areas (e.g. Kanwisher, McDermott et al. 1997; Afraz, Kiani et al. 2006; Leopold, Bondar et al. 2006), as well as distinct populations specifically coding for face identity (e.g., Winston, Henson et al. 2004; Quiroga, Reddy et al. 2005; Gothard, Battaglia et al. 2007; Kriegeskorte, Formisano et al. 2007). It then becomes natural to ask why identity dependent RS responses are abolished by OR faces.

According to an influential theoretical model of the ORE (Valentine 1991; Valentine and Endo 1992), individual faces are represented in an arbitrary multidimensional space shaped by visual and social experience. In this space, location codes for facial identity and distance from the mean face (i.e., a prototypical average face) codes for distinctiveness. In the model, SR faces have a wide multidimensional distribution whereas OR faces have a denser, more clustered distribution. For instance, SR faces are coded along many diagnostic dimensions such as hair and eye colors. In contrast, OR faces tend to lack diagnostic information (i.e., all East Asian faces have black hairs and dark eyes), which leads to more prototypical coding, hence harder to discriminate faces (Caldara and Abdi 2006). This encoding strategy emerges through experience and increases coding efficiency for SR identity to the detriment of OR faces. Evidence for such norm-based face encoding has been found in single cell recordings in monkeys (Leopold, Bondar et al. 2006) and fMRI in Western Caucasian observers confronted with SR faces (Loffler, Yourganov et al. 2005). In particular, both studies show that neural responses to face identity increase with distinctiveness (i.e., the distance from the face prototype). Such evidence is in line with our observations, because we found larger stRS responses to SR faces, but not to OR faces.

At the neurophysiological level, numerous adaptation studies have interpreted RS as reflecting decreased neural redundancy and sharpening of sparser stimulus' representation (for a review see Grill-Spector, Henson et al. 2006), which would result in more efficient neural information coding (Sobotka and Ringo 1994; Muller, Metha et al. 1999; Dragoi, Sharma et al. 2002; Gutnisky and Dragoi 2008). Within this framework, RS has been considered as a neural mechanism devoted to novelty detection (Grill-Spector, Henson et al. 2006). The lack of stRS to OR faces suggests that they trigger prototypal responses preventing novelty detection in face exemplars. On the contrary, stRS to SR faces suggests a more efficient coding of this visual category.

The explanations offered above are also compatible with two major theoretical accounts of the ORE in psychology: the social experience model (Levin 1996 ; Levin 2000) and the visual expertise framework (Tanaka and Taylor 1991; Tanaka and Pierce *2009*). The social experience model holds that the rapid extraction of race information, at the cost of individuating information, would account for the OR recognition deficit. Following this logic, OR faces would not tap into the neural population coding for identity. This prediction is clearly supported by our electrophysiological data. Along the same lines, the visual expertise framework (Tanaka and Taylor 1991; Tanaka and Pierce *2009*) postulates that SR faces are categorised at the subordinate level (i.e., John, Jack, etc.), whereas OR faces are categorised at the basic level (i.e., East Asian, Black American, etc.). This theoretical account is also compatible with our data, in which SR faces only tap into individual face recognition.

It is worth noting that conventional electrophysiological RS measures are based on amplitude differences for target faces only (i.e., amplitude differences on target faces Jacques and Rossion 2006; Jacques, d'Arripe et al. 2007; Caharel, d'Arripe et al. 2009) and have so far failed to show any significant effect for both groups of observers in the N170 time window. Using this approach, we also failed to replicate previously reported RS differences for SR faces of the same identity (e.g. Jacques, d'Arripe et al. 2007) (Figure 26). The use of different images of the same individual between the adaptor and the target face (expressive vs. neutral) might explain this observation.

This control increased the validity of the face recognition task, while decreasing the sensitivity of conventional electrophysiological RS measures on the target face.

To increase the sensitivity of RS analyses we implemented a novel approach. Because RS is a reduction in neural response to a target stimulus following the presentation of an adaptor stimulus, we subtracted the signal elicited by the presentation of the target face to that elicited by the adaptor face. This analysis was only performed for trials not contaminated by artefacts for both events. The amplitude of the stRS increases the signal to noise ratio and reflects a genuine amount of RS per event, which is a function of both amplitude and latency differences between the signals elicited by the two successively presented faces. Changes in amplitude, synchrony, or both, of local field potentials may explain the modulations across events (Grill-Spector, Henson et al. 2006). Therefore, the novel stRS approach may help to elucidate the nature of the neural information coding underlying responses in electrophysiology, magnetoencephalography (MEG) and single-cell recordings, as all these techniques can finely exploit the temporal dynamics of single events.

3.5 Conclusion

The present study investigated the neural correlates of the perceptual all look alike effect, which represents the core facet of the ORE. We used an adaptation paradigm involving Western and Eastern faces and quantified single-trial spatiotemporal electrophysiological RS responses in Western Caucasian and East Asian observers. Our data show RS in the time window of the early face-sensitive N170 component, with sensitivity to face identity only for SR faces. OR faces did not show RS modulation, indicating a lack of sensitivity to face identity for this category. These results show that the discrimination of same- and other-race faces begins early at the perceptual level. After nearly one hundred years of investigations, our results provide also the first neurophysiological correlate of the all look alike perceptual experience.

4. Neural Face Coding is Shaped by Race

Preamble

Human populations can be categorized by salient phenotypic traits, a visual process defining the social concept of race. Race markedly impairs one of the most critical and specialized skills humans possess: the recognition of conspecifics. Humans are significantly better at recognizing Same-Race (SR) than Other-Race (OR) faces, feeding the popular belief that OR faces all look alike. Theoretical (Valentine 1991) and computational (e.g.Caldara and Abdi 2006) norm-based multidimensional face-space models have provided a consistent account for this universal Other-Race Effect (ORE). As a by-product of visual experience, efficient SR face identification is achieved by sparser coding across diagnostic dimensions for SR compared to OR face-exemplars. The present study investigates whether and where neural face coding subserves the laws predicted by this theoretical framework. Western Caucasian (WC) and East Asian (EA) observers' BOLD signals was measured in functionally defined face-selective Region of Interest (ROIs – Fusiform Face Areas (FFA) and Occipital Face Areas - OFA) while they perceived normalized WC and EA faces. Representational Dissimilarity Matrix (RDMKriegeskorte, Mur et al. 2008) showed significant higher values for OR compared to SR neural face representations in the FFA only. These results suggest prototypical (less distinctive) activation patterns of neural representations of OR faces in both groups of observers. This multidimensional voxel mapping quantifies coding efficiency in the FFA for individual SR faces.

4.1 Introduction

A fraction of a second is all human beings need to correctly recognize a face. This remarkable ease and accuracy overshadow the complexity of the cortical mechanisms underpinning face recognition, which have been puzzling cognitive and computer scientists alike for decades. The extent of such complexity only begins to emerge in scenarios where this seemingly undemanding identification proficiency comes to be challenged. One such case is the robust other race effect for faces (ORE –Feingold 1914; Malpass and Kravitz 1969; for a review seeMeissner and Brigham 2001). The ORE is a well-established cognitive phenomenon by which individuals are more accurate at recognizing same-race (SR) compared to other-race (OR) faces. This recognition impairment leads to the widely experienced high level perceptual illusion by which OR individuals "all look alike" (Vizioli, Rousselet et al. 2010). Cracking the neural code at the basis of this illusion has important implications both for the general understanding of the neural substrates of face processing, and for everyday life events, like for example, the reliability of eye witness testimonies.

The all look alike effect, which is one of the core facets of the ORE (Vizioli, Rousselet et al. 2010) has been long reported in the literature (Feingold 1914; Malpass and Kravitz 1969; Carroo 1986). The latter cannot be accounted for by the paucity of anthropometric variations in OR faces, but it is due to a genuine lack of expertise (e.g.Carroo 1986; Golby, Gabrieli et al. 2001; Meissner and Brigham 2001; Vizioli, Rousselet et al.).

The conceptualization of the expertise account, supported by an abundance of behavioural (Malpass and Kravitz 1969; Carroo 1986; for a review, see ref.Meissner and Brigham 2001), computational (O'Toole, Deffenbacher et al. 1994; Caldara and Abdi 2006) and neuroimaging (Golby, Gabrieli et al. 2001; Caldara, Thut et al. 2003; Ito and Urland 2003; Caldara, Rossion et al. 2004; Ito, Thompson et al. 2004; Kim, Yoon et al. 2006; Herrmann, Schreppel et al. 2007; Stahl, Wiese et al. 2008; Walker, Silvert et al. 2008; Tanaka and Pierce *2009 ;* Vizioli, Foreman et al. 2010; Vizioli, Rousselet et al. 2010) data, finds its theoretical grounding in the multidimensional face space (MDFS) model – (Valentine 1991). According to this psychological model, face representations are coded and stored within an arbitrary multidimensional space, centred on the average of all faces (i.e., the prototypical face). Within this space, location codes for facial identity, while distance from the centre represents facial distinctiveness. The expertise dependent neural tuning to SR faces leads to coding the latter along several diagnostic dimensions, rendering their representations highly distinctive and hence sparsely distributed (Figure 30a). In contrast, the inadequate level of experience with OR faces induces a lack of sensitivity to their diagnostic information, which results in a more prototypical coding, and therefore less distinctive representations. Within this context, visual and social experience-dependent modulations of the MDFS architecture account for the robustly reported OR recognition impairment (Valentine 1991; Caldara and Abdi 2006).

At the neurophysiological level, the notion that neural representations of faces are organized according to norm based experience dependent (and thus race dependent) coding has only recently found indirect empirical support (Vizioli, Rousselet et al. 2010). However, for SR only, numerous studies directly corroborate the idea that norm-based coding is the main organizing principle of the neural architecture underlying face representations. Neural responses to face identity, for example, have been reported to systematically increase with distinctiveness (i.e. the distance from the face prototype) in monkeys IT (Leopold, Bondar et al. 2006) and in the Fusiform Face Area (FFAKanwisher, McDermott et al. 1997) of Western Caucasian (WC) observers presented with SR faces (Loffler, Yourganov et al. 2005).

The FFA is a brain region located in the infero-temporal cortex responding preferentially to faces compared to any other object category (Puce, Allison et al. 1995; Kanwisher, McDermott et al. 1997; Tong, Nakayama et al. 2000). A wealth of data consistently points towards the involvement of this cortical area in face identification. Lesion studies, for example, show that damages to this region can be associated with deficits in recognizing individual faces (prosopagnosiaDamasio, Damasio et al. 1982; Barton, Press et al. 2002; Hadjikhani and de Gelder 2002). Moreover, in the FFA sequences of different, compared to same face identities elicit larger responses for healthy subjects (Gauthier, Skudlarski et al. 2000; Andrews and Schluppeck 2004; Loffler, Yourganov et al. 2005; Pourtois, Schwartz et al. 2005; Rotshtein, Henson et al. 2005; Schiltz, Sorger et al. 2006), but not for individuals with face processing impairments (acquired prosopagnosia:Schiltz, Sorger et al. 2006; Dricot, Sorger et al. 2008; visual agnosia:Steeves, Dricot et al. 2009). In line with these findings, responses in the FFA have been found to co-vary with identification performance (Grill-Spector, Knouf et al. 2004; however seeCaldara and Seghier 2009), and differ as a function of visual expertise and level of categorization (Gauthier, Skudlarski et al. 2000).

Importantly, a number of studies have offered indications that neural activity within the FFA is modulated by race. Golby et al (Golby, Gabrieli et al. 2001), for example, using a "classic" univariate approach, report stronger fMRI BOLD responses to SR compared to OR faces in the rFFA. Kim et al. (Kim, Yoon et al. 2006) also found greater neural activity in bilateral FFAs for SR compared to OR unfamiliar faces. These findings indicate the involvement of the FFA in the organization of face representations with regards to race. A recent study carried out by Natu et al (Natu, Raboy et al. 2010) however suggests that the neural activity elicited within FFA alone is not sufficient to distinguish among races. The authors report that SVM multi-voxel pattern classifiers can discriminate faces by race only when considering responses elicited within the broader ventro-temporal (VT – Natu, Raboy et al. 2010). Natu et al. also highlight differences in the neural dynamics of FFA as a function of race: the FFA activation time course is characterized by an initially stronger response to SR faces, which attenuates over time to ultimately produce the opposite pattern (i.e. larger activation for OR compared to SR faces). These unexpected findings are somewhat in contrast with previous reports, compelling further clarification on the role of the FFA in processing the race of faces.

Surprisingly, to the best of our knowledge, no study has directly investigated the underlying nature of the neural representations of faces of different races and its relation to the FFAs. As explained earlier, the MDFS accounts extremely well for differences in face recognition performances observed between SR and OR faces. According to the model's predictions, it would therefore be plausible to expect that the organization of abstract neural representations is not invariant, but susceptible to experience, and hence race. Moreover, as explained so far, empirical evidence suggests that the FFA is modulated by race and expertise, and, that norm-based coding is an organizing principle of this region in particular.

In the present study we aim to investigate the nature of the neural code underlying face percept. Specifically we are interested in where faces are represented and how they are shaped and organized within the human cortex. In light of what has been described so far, we reason that abstract representations should be shaped by levels of expertise and follow the laws predicted by the MDFS model within the ORE context. We further hypothesise the major involvement of the FFA in processing race of faces, and intend to clarify weather neural activity elicited within this specific cortical area alone is in fact sufficient to discriminate across races.

To this end we measured WC and EA observers' BOLD responses elicited by SR and OR faces in four functionally defined face preferential ROIs: right and left FFA and right and left Occipital Face Area (OFASergent, Ohta et al. 1992; Gauthier, Tarr et al. 2000). We then computed Representational Dissimilarity Matrix (RDM – Kriegeskorte, Mur et al. 2008) for each ROI independently, by correlating the multi-voxel patterns of activity elicited by each identity within a race with the remaining 9. We found significant higher RDM r-values for OR compared to SR faces in the dominant FFA in both groups of observers, relating to prototypical (less distinctive) activation patterns of OR identities.

4.2 Methods

Participants – Twenty healthy right handed subjects aged 18 to 31 (10 Western Caucasian (WC), of which 5 females, mean age 24; and 10 Eastern Asian (EA), of which 4 females, mean age 22) took part in the experiment. All subjects had normal or corrected to normal vision and provided written informed consent. Importantly EA participants had been in the UK for no longer than 1 month and had no previous direct experience with the western culture. The ethical committee of College of Medical, Veterinary and Life Sciences at the University of Glasgow approved the experiments.

Stimuli – All visual stimuli consisted of front-view grayscale photographs of faces, houses and textures of noise. For the FFA and OFA localizer, we employed 10 WC and 10 EA faces (5 identities × 2 genders × 2 races) taken from the JACFEE database (Matsumoto and Ekman 1988); 20 images of houses (Husk, Bennett et al. 2007); and 20 different textures of noise. The latter were created by combining the mean amplitude spectrum across faces and houses with random phase spectra sampled from a Gaussian distribution. Thus, the noise textures had the same amplitude spectrum as the faces and houses. In the main slow event related experiment, we used a different set of 20 front-view grayscale photographs of WC and EA faces (again 5 identities × 2 genders × 2 races), which we used in previous studies (e.g. Michel, Caldara et al. 2006). All images subtended approximately 3.75° × 4.25° of visual angle. All faces were cropped to remove external features; none had particular distinctive features and male faces were clean-shaven. The stimuli were centered in a 52 x 52 background of average luminance (25.4 cd/m2, 23.5- 30.1). All images were equated in terms of luminance, contrast and spatial frequency content by taking the average of the amplitude spectra of all stimuli and combining that average spectrum with the original phase spectra to reconstruct each individual stimulus. The RMS (root mean square) contrast (i.e. the standard deviation of the pixel intensities) was also kept constant across stimuli. Because information is largely carried by phase rather than amplitude (Rousselet, Pernet et al. 2008), individual stimuli (i.e. faces and houses) remained easily recognizable after this manipulation, while still ensuring that any differences in the BOLD signal related to the race of the face stimuli were not confounded by global low level visual properties of the images.

4.2.1 MRI Data Acquisition

The stimuli were projected from the back of the scanner on a round screen situated in the scanner tunnel and occupying the whole of the tunnel (i.e. 60 cm of diameter). Participants viewed the images through a mirror placed on the head coil.
MRI data were collected with a 3-T Siemens Tim Trio System with a 32-channel head coil and integrated parallel imaging techniques (IPAT factor: 2). Blood oxygen level-dependent (BOLD) signals were measured with an echo-planar imaging sequence (Localizer block design runs: TE: 52 ms, TR: 2,000 ms, field of view: 210 mm, flip angle: 62°, 10% gap, 36 axial slices; Event Related runs: TE: 30 ms, TR: 1,000 ms, field of view: 210 mm, flip angle: 77°, 10% gap, 16–18 axial slices). Spatial resolution was kept constant throughout the experiment with a voxel size of 3 × 3 × 4.5 mm for the main event related experiment, and 3 x 3 x 3 mm for the localizer. Furthermore, the slices were positioned to maximize coverage of occipital regions. inale a high-resolution 3D anatomical scan (3D MPRAGE, 1 × 1 × 1-mm resolution) was recorded in the same session as the functional scans. For participants who were re-scanned due movement artefacts, separate anatomical scans were recorded in each scanning session to facilitate realignment of the functional data

4.2.2 Paradigm

All participants performed 2 runs of the block design localizer fMRI experiment to define the areas responding preferentially to faces (i.e. ‘FFAs’ and ‘OFAs’), and 3 runs of the main event-related design experiment aimed at measuring the neural activity elicited by individual identities. A number of runs were rejected due to large degree of movements (see results for more details). Participants with more than 1 run per experiment rejected were called back for additional scans.

4.2.3 Block Design Localizer

In the scanner participants viewed blocks of WC or EA faces, houses and noise textures.

Each run begun with a 20 seconds black fixation cross and consisted of 24 randomly presented blocks of images (6 blocks per stimulus category, 12 seconds per block), with 12 seconds black fixation cross between the blocks. Within each block 10 different stimuli were randomly presented for 800 msec, with an ISI of 400 msec. To avoid potential attentional confounds on the BOLD signal related to the race of the stimuli we implemented an orthogonal task: participants were instructed to respond by pressing a button on a response pad held in their right hand, to red or green stimuli which were represented 10% of the images (i.e. one red or green stimulus per block).

4.2.4 Event Related Experiment

Each event lasted approximately 12 seconds, throughout which a fixation cross was constantly on screen. In the scanner participants viewed images of WC or EA faces presented to them for 850 msec. followed by a fixation cross for 11.250 seconds. To avoid potential attentional confounds on the BOLD signal related to the race of the stimuli here too we implemented an orthogonal task. The black fixation cross changed colour, turning either red or green, for 200 to 1200 msec. at a random time within an event, before reverting to its original black. Participants were instructed to respond to the fixation cross colour change by pressing a button on the response pad held in their right hand.

Each run begun and ended with a 20 seconds black fixation cross and consisted of 80 trials/events (4 repetitions per identity – 10 identities per race). The whole experiment consisted of 3 runs lasting approximately 16 minutes each.

4.2.5 Behavioural Study

Subsequently to the fMRI experiment, participant took part in a behavioral task designed to assess the observers' ORE. Subjects sat in a dimly lit room with the same viewing conditions as the fMRI experiment. They were presented with 20 new faces for each race, one at the time (3s each, 5s ISI). The faces were obtained from the KDEF (Lundqvist, Flykt et al. 1998) and AFID (Bang, Kim et al. 2001) databases. All faces were selected from a different set of stimuli than that used in the fMRI experiment, and were also equated for global amplitude spectrum, luminance, and contrast. Stimulus size subtended 3.75°x4.25° of visual angle. Participants were told explicitly to memorize the faces. The encoding phase was followed by a forced-choice old-new recognition task whereby 40 faces (20 old and 20 new) were presented individually. Participants underwent two blocks of the old/new face recognition task per race. The blocks were counterbalanced across participants. Faces were blocked by race during both the encoding and the recognition phase. The encoding stage was followed by a 1 minute pause, after which participants had to indicate whether each face was old or new by pressing the "s" key on the computer keyboard for old faces and the "k" key for new faces. Each face remained on the computer screen until the participant's response, or for a maximum of 200 ms (3s ISI). Participants did not know the ratio of old to new faces and did not receive any feedback on their responses. The order and the number of presentation of SR and OR stimuli were pseudorandom, changing across subjects. As in previous studies (e.g.Carroo 1986), d' indices (Swets, Tanner et al. 1961) for WC and EA faces were calculated for each participant to assess accuracy.

4.3 Analysis

fMRI data were analysed in Brain Voyager QX software package (Brain Innovation, Masstricht, Netherlands) and Matlab 2007b. The following steps were carried out independently for each participant and run of both the event related and block design experiments. Functional data for each run were corrected for slice time and 3D motion, temporally filtered (high-pass filtered at 0.01 Hz and linearly detrended), and spatially normalized into the Talairach space with Brain Voyager QX.

The data from all runs were then independently subjected to a standard general linear model (GLM) with 4 predictors (i.e. WC faces, EA faces, houses and noises) per run for the localizer and 20 predictors (i.e. 10 EA and 10 WC identities) per run for the main experiment.

4.3.1 Block Design Localizer

The data collected in the block localizer were spatially smoothed with a 4 mm Gaussian and used to identify 4 face preferential regions of interest (ROIs): right and left OFA and right and left FFA. These areas were defined by subtracting the neural response elicited by blocks of houses and noises from the conjoint activity of blocks EA and WC faces. We thus created 4 masks – one per ROI – which were subsequently exported into matlab.

4.3.2 Event Related Experiment

To maximally exploit the advantages of multivariate analysis, which treats all voxels independently, no spatial smoothing was performed on the data collected in the main event related experiment. We extracted independently per voxel the beta weights obtained from the previously described GLM. These beta weights estimate activation for each single trial/event of stimulation, assuming a standard 2γ model of the hemodynamic response function.

We imported the beta weights of all the voxels in the brain into matlab and used the ROIs mask obtained in the localizer to determine the voxels of interest.

To assess the nature of the face representations for SR and OR, we computed Representational Dissimilarity Matrix (RDM) independently per subject and per ROI. We first extracted the beta weights elicited by individual faces within the 4 ROIs, and created 20 vectors of betas (10 identities x 2 races) independently per each ROI. Each vector thus epitomises the underlying neural representations of a given identity. We then computed Pearson correlation coefficients between the vector of beta weights elicited by each identity and the remaining 19. This led to 4 RDMs (i.e. 1-r – one per ROI) per subject. Each cell of a given RDM (e.g. Figure 30a) compares the response patterns elicited by a pair of faces by measuring the dissimilarities (i.e. 1 - Pearson correlation) across the voxel populations. In order to perform parametric statistical tests on the RDMs we further normalised the data computing fisher Z transform, by calculating the arc-tangent of the 1-r scores within a matrix. Finally we computed the trimmed mean (25%) of each RDM per ROI per subject and fed these values into repeated measures (one per ROI) 2 x 2 ANOVAs (2 races of participants x 2 races of stimuli).

We used two criteria to group the ROIs across subject for inclusion in the ANOVAs. Firstly we looked at the group effect within each ROI grouped by hemisphere (i.e. one independent ANOVA for the rFFAs, one for the lFFAs, one for the rOFA and one for the lOFA). We also grouped the ROIs by dominance: we defined a ROI (i.e. left or right) based on their face preferentiality. We thus chose either the right or the left FFA/OFA depending on which area showed the largest difference in the (WC+EA faces) > (Houses+Noise) contrast.

We also carried out robust statistic (i.e. bootstrap confidence interval on the trimmed mean – 25 % - of the RDM), which is less susceptible to extreme values, to ensure that the observed effects were not driven by a few data points. We sampled subjects with replacement, averaging the trimmed means across participants independently for each condition and ROI, and then computing the difference between the trimmed means for the two conditions. This process was repeated 999 times, leading to a distribution of bootstrapped estimates of the trimmed mean difference between two conditions, averaged across subjects. Then the 95% percent confidence interval was computed (alpha = 0.05). Finally, the difference between the two sample trimmed means was considered significant if the 95% confidence interval did not include zero. Note that this bootstrap technique, relying on an estimation of H1, tends to have more power than other robust methods like permutation tests and related bootstrap methods that evaluate the null hypothesis H0 (Wilcox 2005).

A 2 x 2 ANOVA (2 races of participants x 2 races of stimuli) was also carried out with the behavioural d' responses as dependent variable.

Finally, we carried out unsupervised (i.e. not requiring a categorical structure) classical multidimensional scaling independently per ROI, following the metric stress criterion.

4.4 Results

4.4.1 Representation Dissimilarity Matrix

Lateralised ROIs – Within the rFFA only, the 2 x 2 repeated measures ANOVA yielded a significant crossover interaction between the race of the observers and that of the face stimuli (F(1,18)=4.4. p<.05). Correlational distance (i.e. 1- r) computed on OR faces (WC mean 1-r = .44; WC std=.12; EA mean 1-r = .36; EA std =.11) was smaller (i.e. more similar patterns) compared to those for SR faces (WC mean 1-r = .45; WC std=.14; EA mean 1-r = .56; EA std =.17), regardless of the race of the observer. No significant main effects were observed (p>.05). The ANOVAs on the three remaining ROIs (lFFA and right and left OFA) led to null results (p>.05).

While conventional parametric analysis carried out on the ROIs based on their lateralization showed that the neural representations of SR faces are more distinct (i.e. smaller r values) than those of OR faces in the rFFA only, Bootstrap Confidence Interval (bCI) failed to lead to the same results, with all bCIs differences including zero (WC: WC-EA faces bCI [-.82 .017]; EA: WC-EA faces bCI [-.032 .09]).

Dominant ROIs –The dominant (as defined in the methods section) FFA was found to be the right one for 7 out of 10 WC observers and 9 out of 10 EA observers. For the dominant FFA only the 2 x 2 repeated measures ANOVA yielded a significant crossover interaction between the race of the observers and that of the face stimuli (F(1,18)=21.91; p<.0001). Correlational distance (i.e. 1- r) was smaller for OR faces (WC mean 1-r = .51; WC std=.1; EA mean 1-r = .32; EA std =.13) (i.e. more similar patterns) compared to those for SR faces (WC mean 1-r = .41; WC std=.16; EA mean 1-r = .61; EA std =.16), regardless of the race of the observer (Figure 30a). The ANOVAs on the three remaining ROIs led to null results.

Bootstrap Confidence Interval (bCI) computed on the trimmed mean of the RDM led to the same patterns of results (WC: WC-EA faces bCI [-.06 -.02]; EA: WC-EA faces bCI [.01 .12]).

Importantly, when taking into account the dominant FFA, 9 out of 10 WC observers and 9 out of 10 EA observers showed the expected patterns of result (i.e. larger correlations amongst OR compared to SR neural representations of faces)

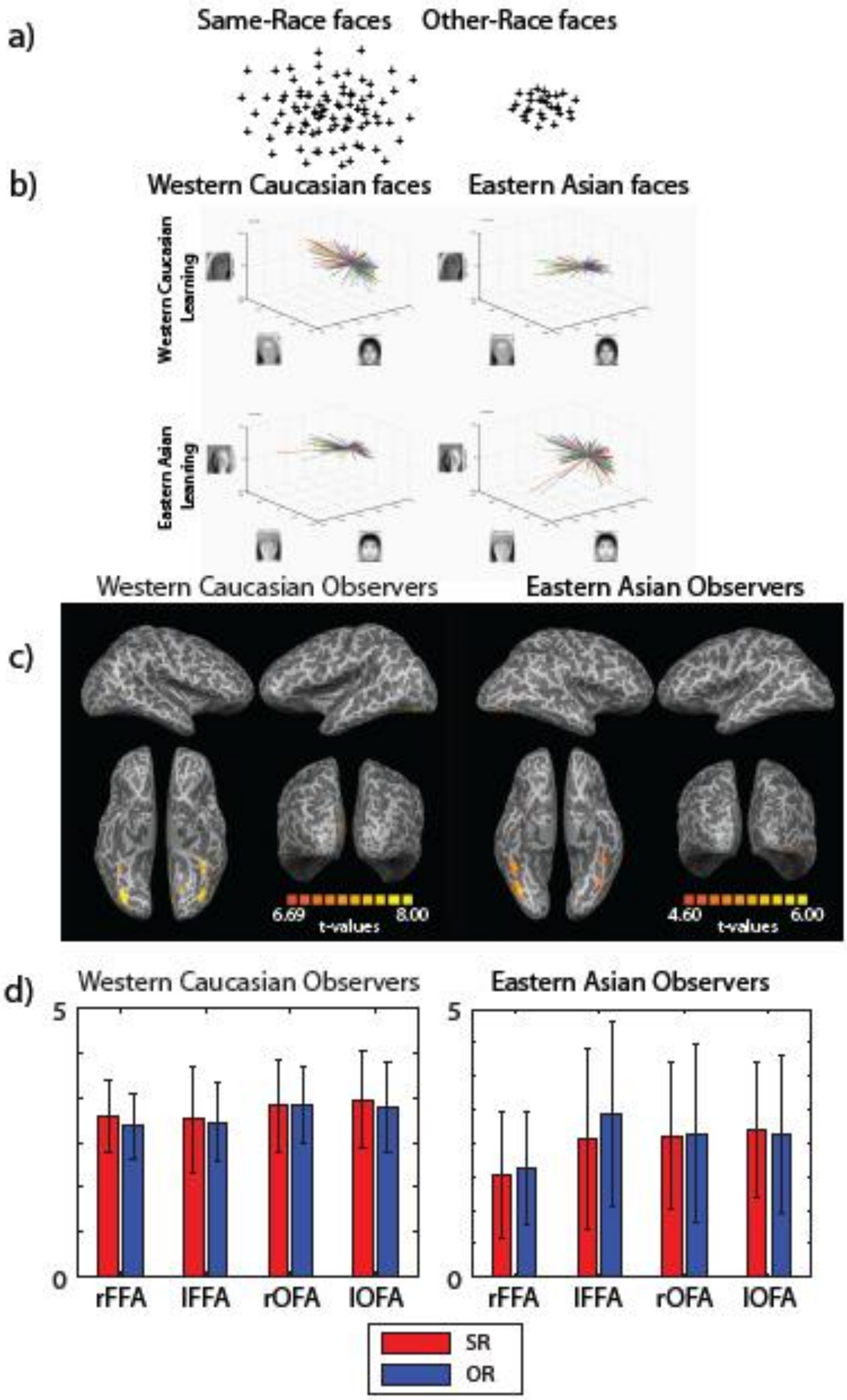

Figure 29 – a) schematic 2D representation of Valentine's multidimensional face space model; b) neural network simulating valentine's multidimensional face space; c) average ROIs per group of observer (right and left FFAs and right and left OFAs); d) Bar plot displaying to overall activation (beta weights) per each ROI, group of observers and race of the face stimuli

Multidimensional scaling – Figure 30b shows the spatial arrangement on a 2D plane (defined by the data first and second eigenvectors) of neural face representation within the dominant FFA as described by classical unsupervised multidimensional scaling. Closely positioned points represent stimuli that elicited similar response patterns; data points placed far apart instead elicited dissimilar response patterns. As it is clearly visible in Figure 30b, regardless of the group of observers, SR neural face representations are loosely clustered compared to those representing OR faces.

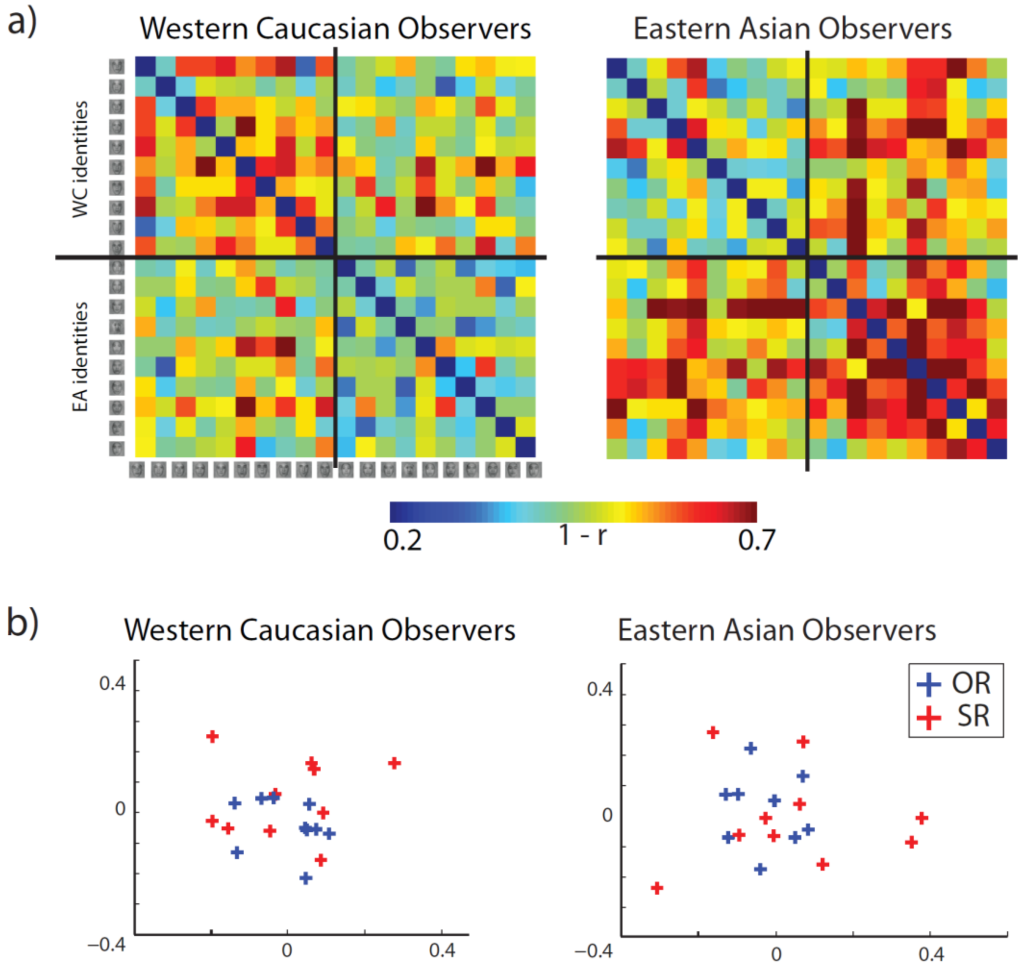

Figure 30 – a) average RDM for the dominant FFA. High values (i.e. red) indicate large correlational distance across points (i.e. dissimilar), while low values (i.e. blue) reflect small correlational distance (i.e. similar). Note that, regardless of the race of the observers, SR faces elicit more distinct (i.e. red) neural representations; b) Multidimensional scaling of correlational patterns for neural representations within the dominant FFA

4.4.2 Face Localizer

The 4 Regions of Interest (ROIs – i.e. right and left FFA and OFA – Figure 29c) were functionally determined independently across subjects (Table 4). Functional ROIs were defined by performing F-tests on all the voxels in the brain. Face-preferential regions were delineated in each individual (in Talariach space) using the peak voxel of the activation clusters identified by the contrast (WC + AC) faces > (Houses +Noise) in the functional face localizer (e.g.Kanwisher, McDermott et al. 1997). FFAs were defined as the region within the bilateral fusiform gyrus for which the differences in BOLD signal elicited by face minus those of house and noise was largest. OFAs were defined as the region within the bilateral inferior occipital gyrus for which the differences in BOLD signal elicited by face minus those of house and noise was largest. In order to control for type I errors (i.e. rejecting the null hypothesis when the latter is in fact true), False positive Discovery Rate (FDR) was implemented as multiple comparison correction. The significance threshold was set to q<.05 for all ROIs and participants.

Region-of-interest	subject	# of subjects	X	Y	Z	number of voxels
Right FFA	WC	10	36.65±3.04	-49.98±7.11	-18.83±5.08	502±143
	EA	10	39.14±3.56	-47.17±8.14	-17.00±4.16	495±253
	ALL	20	37.89±3.47	-48.58±7.57	-17.91±4.61	499±200
Left FFA	WC	10	-37.13±2.82	-48.07±7.10	-16.96±4.06	543±170
	EA	9	-39.88±4.50	-47.91±4.63	-17.19±3.38	445±592
	ALL	19	-38.43±3.87	-48.00±5.90	-17.07±3.65	496±416
Right OFA	WC	10	38.54±2.69	-75.42±4.39	-16.33±7.52	594±198
	EA	9	38.90±5.17	-72.27±4.75	-6.44±5.73	637±485
	ALL	19	38.71±3.94	-73.93±4.75	-11.65±8.28	614±353
Left OFA	WC	10	-40.07±4.44	-73.95±6.99	-16.25±5.79	670±253
	EA	7	-40.49±4.11	-76.80±3.87	-8.74±5.20	835±507
	ALL	17	-40.24±4.18	-75.12±5.93	-13.16±6.60	738±374

Table 4 – ROIs size and 3dimensional coordinated (in Talaraich Space)

4.4.3 Behavioural Experiment

Both WC and EA observers were consistently more accurate at recognizing SR than OR faces. WC observers had higher d’ for upright SR faces (mean=1.91, std=0.53), compared to OR faces (mean=1.52, std=0.3). The same pattern was observed for EA observers (SR: mean=1.86, std=0.35; OR: mean=1.51, std=0.47).

The 2-Way repeated measures ANOVA (i.e. races of participants x 2 races of stimuli) revealed a significant interaction of races of participants x races of stimuli (F(1,18)=16.9; p<.01), reflecting the greater accuracy for SR faces across groups of observers. No other significant interaction was observed.

4.5 Discussion

The present study aimed to investigate how race impinges upon the nature and organization of the neural codes underpinning face representations. Specifically we were interested in whether and where such neural face coding sub-serves the laws of norm-based multidimensional face space model within the context of the ORE. To this end we measured BOLD signal elicited by individual WC and EA faces in WC and EA observers within four functionally defined face preferential ROIs (i.e. left and right FFAs and OFAs).

The two main results reported here stem from the representation Dissimilarity matrixes (RDM - Kriegeskorte, Mur et al. 2008) computed on the beta weights of the BOLD signal's GLM. RDMs were obtained by correlating the multivoxel patterns activity elicited by each identity within a race with the remaining 9. This was performed per each ROI independently.

We found 1) that RDMs displayed significantly (p<.05) larger values for OR compared to SR faces in both group of observers (Figure 30a); and 2) that this pattern was observed in the dominant FFA only of all but one EA and WC observers.

The data reported here demonstrate that within the FFA, patterns of activations elicited by SR identities are more distinctive compared to the highly similar ones of OR faces. Moreover, the full crossover interaction between the race of the observers and that of the faces proves that the differences in activation patterns are genuinely related to the race of the observers, and not a mere confound of low level visual properties of faces from different races (see also Vizioli, Foreman et al. 2010; Vizioli, Rousselet et al. 2010).

Our results fit perfectly with the norm-based multidimensional face space account (Valentine 1991) and provide important insights onto the neural substrates of the ORE for faces (Feingold 1914; – for a review see Meissner and Brigham 2001). According to the norm-based multidimensional face space model, face representations are encoded in an n-dimensional space as a function of their deviation from the face prototype, which represents the centre of the distribution.

Each percept is thus conceptualised as an n-dimensional vector of idiosyncratic features. Accordingly, here the neural representations of faces are characterised as n-dimensional (multi-voxels) vectors. In the norm-based multidimensional face space framework, the recognition impairment observed for OR faces stems from the lack of expertise individuals posses with this category. The constant exposure to SR shapes the choice and sensitivity of the diagnostic dimensions along which faces are encoded, leading to a fine neural running for SR faces. A WC observer gazing at the eyes of an unfamiliar SR conspecific is thus able to fully exploit the wealth of visual information carried by this region (such as shape, color, contrast, etc...), which contributes to the formation of a distinctive neural representation. This in turn renders the recognition of this newly encoded identity effortless, even amongst vast amounts of exemplars. When, however, the same WC observer looks at the eyes of an EA face, the lack of expertise with the OR leaves the nevertheless abundant amount of physiognomic information available within this facial feature unexploited. Within the WC observer's cortex, the neural code for the representation of EA identities will therefore lack distinctiveness. The different expertise dependent levels of sensitivity to the diagnostic dimensions shape therefore the nature of the distribution of face representations. Since location within the multidimensional space reflects the level of distinctiveness, the distribution of the highly distinguishable SR percept will be sparse, compared to the tightly clustered organization of the similar OR representations (Figure 29a, Figure 30b). This is exactly what is reflected in the RDMs of the dominant FFA (Figure 30a). The high correlations amongst OR identities indicate Dissimilarity between neural patterns and hence proximity of the representations in the multidimensional space. The lower correlations across pairs of neural vectors for SR faces reflect high distinctiveness across these neural representations that are therefore distantly situated (Figure 30a). Moreover, as shown on Figure 30b, the spatial organization of neural face representations in a 2 dimensional space (based on their first 2 eigenvectors) approximates the architectural disposition predicted by the theoretical multidemsional face space model (i.e. tightly clustered highly similar OR faces, compared to sparse distinctive SR faces).

Stimulus arrangements computed by multidimensional scaling are data driven and they can reveal important properties concerning the representations of the stimulus population. MDS computed on the RDM, thus provides further compelling evidence strengthening the existence of a direct link between the theoretical multidimensional face space model, and the neural architecture of SR and OR faces representations

These data corroborate a long lasting stream of behavioural evidence, providing the neural basis underlying the robustly reported OR recognition impairment. They further provide direct support for the predictions formulated over 2 decades ago by Valentine's model. Our research shows that the high level perceptual illusion leading human beings to perceive OR faces "all looking alike" (i.e. the "all look alike effect" Vizioli, Rousselet et al. 2010) and thus to erroneously identify OR individuals, is rooted in the very nature of the neural representations underlying face identities: the neural patterns of activity for OR face percept also "all look alike".

Converging evidence supporting our findings comes from distinct lines of work. Computational studies for example (e.g. Caldara and Abdi 2006) show that differential levels of a neural network's recognition accuracy across races depend on the race the network is firstly trained with. Caldara and Seghier (Caldara and Abdi 2006) trained a neural network to encode faces along their first three eigen vectors, obtained through PCA spectral decomposition. The results indicate that the network's identification performance is significantly higher for SR (i.e. the race with which it was trained) compared to OR faces. Moreover, the density properties of the 3 dimensional distribution of face vectors, just like the one of our MDS arrangement, match those predicted by the norm-based multidimensional face space model (i.e. sparser for SR compared to OR exemplars, Figure 29b).

Neuroimaging studies also support our data. Vizioli et al (Vizioli, Rousselet et al. 2010), for example report EEG repetition suppression (RS) to identity at early perceptual stages of face processing only to SR faces in both WC and EA observers. RS has been argued to reflect decreased neural redundancy and sharpening of sparser stimulus' representation (for a review, see Grill-Spector, Henson et al. 2006). This results in more efficient neural information coding and hence more distinctive SR percept. Furthermore, Golby et al. (Golby, Gabrieli et al. 2001) and Kim et al. (Kim, Yoon et al. 2006) reported sensitivity to race in the FFA. Within this setting is worth noting the advantages conveyed by the multivariate approach implemented here. Both Golby et al. (Golby, Gabrieli et al. 2001) and Kim et al. (Kim, Yoon et al. 2006) investigated the FFAs response properties by means of classic univariate methods. The latter builds upon activation, not information based analysis (Kriegeskorte and Bandettini 2007) of the BOLD signal, and treats neural responses within a given ROI as a single value. This reduces investigative spectrum to a simple comparison across levels of activation, revealing only higher or lower responses between 2 or more conditions. In contrast, information based multivariate analysis significantly enriches the quality and quantity of the details provided by the data set, allowing to further characterise the nature of the response profile of a given ROI. The studies carried out by Golby et al. (Golby, Gabrieli et al. 2001) and Kim et al. (Kim, Yoon et al. 2006), although informative, only provide insights on the overall differential levels of activity within the FFA as a function of race. This allows conclusions on the area's sensitivity to race, but it does clarifying the nature of such sensitivity. The data gathered here however support and expand previous univariate findings, by confirming the FFA sensitivity to race, and further demonstrating the norm based race dependent response characteristics of face encoding within this region.

Surprisingly, one contrasting finding comes from the work carried out by Natu et al. (Natu, Raboy et al. 2010), who reported that pattern classifiers can discriminate faces by race only within the broader realm of the ventro-temporal (VT) cortex, and not in the FFA alone. In relating these findings to those reported in the present paper however there are at least three points that need consideration. Firstly, unlike here, Natu et al. employed a face localiser including SR faces only to functionally define their ROIs. Because we were interested in the response profile of the FFA as a whole, and its relation to race, we defined this area on the basis of the neural activity to both WC and EA identities. We implemented such a measure as we reasoned that excluding stimuli of either race from the localiser might affect the size and location of a given ROI, which responds differentially to faces of different races (Golby, Gabrieli et al. 2001; Kim, Yoon et al. 2006). We further inferred that, given the response profile of the FFA, which has been shown to respond preferentially to faces as well as schematic faces (e.g Loffler, Yourganov et al. 2005) and faceness like characteristics of visual stimuli (Caldara and Seghier 2009), the presence of OR faces in the functional definition of the FFA should not induce the inclusion of face non-preferential voxels in the ROI. Secondly SVMs might not be sensitive enough to accurately classify faces by race. One of the SVM assumptions is the maximization of the margins for classifications. However, when there is no clear boundary between two classes, as it is the case in normally distributed data, SVM may fail to achieve successful classification. Finally, Natu et al. aimed to characterise the response profile of the FFA over time. In doing so, they uncover important findings concerning the dynamics of race processing. For example the report the initially stronger response to SR faces, which attenuates over time to ultimately produce the opposite pattern. However, the variance of single time points of the BOLD signal is considerably higher than that of the beta weights characterising the whole time-course, which were the object of our analysis. It is this larger variance which might lead to the null effects reported by Natu et al., within the FFA. These considerations may help accounting for the inconsistencies between the two studies. Importantly, we do not argue for the advantage of one dependent variable (DV – e.g. BOLD % change at each time point) over another (e.g. beta weights), as the appropriateness of the use of either DVs depends on the research question. Rather, we reason merely on the different sensitivity in computing analysis on these DVs.

In addition, our results further corroborate and expand neuroimaging studies tackling the general nature of face representations in both humans and primates. Loffler et al. (Loffler, Yourganov et al. 2005), for example show that within the human cortex representations of individual faces are encoded in the FFA by their direction (facial identity) and distance (distinctiveness) from the prototype. Accordingly, Leopold et al (Leopold, Bondar et al. 2006) – by means of single cell recordings – report evidence for norm-based encoding of face representations in the macaque IT. Specifically, both studies show that neural responses to face identity increase as a function of deviation from the mean (i.e. distinctiveness). Our data support the notion that faces are encoded according to norm based principles, and extend this account to include experience (and hence race) modulations of neural representations.

Moreover, it is worth noting the growing consensus within the neuroimaging field highlighting the limitations of averaging BOLD responses across subjects (Kriegeskorte and Bandettini 2007). The functional and structural correspondence between individual brains is extremely coarse and thus subject to high degrees of variation. In light of such variance, averaging BOLD responses across brains will distort the activation maps exhibited at the single subject level. To circumvent this limitation, we functionally defined our ROIs independently per subject, which produced areas of interests of different voxel sizes and location across observers. We then carried out groups level statistics on the neural information carried by each ROI. Specifically, we computed RDMs independently per ROI and subject. We thus performed statistical tests on the Fisher transformed mean values of each RDM (as described in the methods section). This measure avoids inter-subjects alignment confounds introduced by structural and functional differences across brains.

Interestingly the reported higher Dissimilarity of OR patterns of activity was observed within the dominant FFA, while its symmetrical counterpart and the bilateral OFAs showed no such neural characteristics. These results show that norm based encoding of face representations only occurs in higher level cortical regions, reflecting perceived (i.e. subjective) rather than actual (i.e. objective) differences across faces of different races. Within this context our data support the findings reported by Large et al. (Large, Cavina-Pratesi et al. 2008), who show FFA modulations to perceived changes in identity. The authors also described the response properties of the OFAs as being characterised by physical changes in the face stimuli, regardless of the observers' awareness to these changes (Large, Cavina-Pratesi et al. 2008). Large et al.'s data explain the reported lack of norm based encoding within the OFAs.

Furthermore, we chose implement an orthogonal task and measure the level of behavioural ORE of our participants outside the scanner. This measure was implemented to avoid any potential confound in the BOLD signal due to differential amount of attention the observers might have paid to faces of different races. Although we acknowledge the limitations of an orthogonal compared to a direct task (for example the fact that differences in task demands may modulate BOLD signal), we argue that attention is an amorphous concept and hence difficult to isolate. We therefore reasoned that, given that this study represents the first work investigating the impact of experience (i.e. race) upon neural representations, we wanted to ensure genuine race effects and avoid attentional confounds. Future studies should however aim to replicate our results exploiting the advantages conferred by a direct task.

Finally, it must be noted that the main findings reported here were strongly observed within the dominant FFA. In this respect there are a number of considerations that need to be taken into account. Let us firstly consider what it is meant by dominance. As explained in the methods section, we defined the dominant FFA as the region within the fusiform gyrus for which the differences in BOLD signal elicited by face minus those of house and noise was largest across hemispheres. Such a region was localised in the right hemisphere for seven out of ten WC observers and nine EA participants and in the left hemisphere for the remaining subjects. It is worth noting that the results within subordinate FFA showed a non significant trend in the same direction as its dominant counterpart. However, given the higher statistical reliability intrinsic in the definition of dominance, it is not surprising that the pattern in question was found significant only within the dominant FFA. Moreover, a number of studies (e.g. Grill-Spector, Sayres et al. 2006; Hanson and Schmidt 2010) advocate the heterogeneous response profile of the FFA, which reacts to objects as well as faces. The smaller differences in BOLD responses activation would seem to suggest a higher involvement of the subordinate FFA in object compared to face processing. While this may explain the different results observed between these bilateral cortical areas, further investigation is necessary to elucidate the matter.

4.6 Conclusion

In light of the evidence presented so far we argue that experience – via exposure – with SR faces characterises the sensitivity of the diagnostic dimensions employed to encode, as well as decode, abstract percept. This process begins at the neural level, where expertise shapes the nature of neural representations in the dominant FFA. The latter in turn affects the abstract psychological percept of faces and their organization within the multidimensional space.

Within the norm-based multidimensional face space framework, it is the nature of this multidimensional distribution to account for the widely experienced "all look alike" effect for OR faces (Vizioli, Rousselet et al. 2010). The data reported in the present paper not only reflect the density properties predicted by the norm-based multidimensional face space model, but further show that the high level perceptual illusion leading OR faces to be perceived as looking alike is reflected in the neural code of face representations: at least within the dominant FFA, the activation patterns of OR faces also all look alike.

5. General Discussion

The main purpose of this thesis was to clarify the neurophysiological basis of the ORE. Specifically, the core of this work attempted to answer three main questions: *when, how* and *where* in the human brain the ORE occurs. To do so I exploited the advantages conferred by EEG (and specifically ERPs) and fMRI. The high temporal resolution provided by the former allowed tackling the first two questions; while the spatial resolution, combined with an information-based analytical approach of the latter have been helpful in providing insights into the second two interrogatives. The first two EEG studies are therefore helpful in shedding light on when (i.e. at the perceptual or at later categorization based levels of processing) the ORE takes place; while the third fMRI study focuses on where (i.e. which cortical region) it happens. Importantly, all three studies provide useful information regarding how this phenomenon arises. Accordingly, this section will firstly discuss the EEG data in relation to answering the "when question"; secondly, fMRI data will be discussed with regards to the "where question". Finally the evidence from all three studies will be reviewed together to answer the final "how question"

All the studies reported here show differences in processing SR and OR faces. The results of the first experiment – which investigated the conjoint effect of race and inversion on face processing mechanisms – show not only that the N170 is somehow sensitive to the race of faces, but that behaviourally and electrophysiologically, faces of different races are processed in qualitatively different manners (see chapter 2). Accordingly, the second experiment also shows sensitivity to race on the N170 time window (i.e. larger repetition suppression to same identity only for SR faces and not for OR faces). The N170 is an early ERP component reflecting early perceptual stages of face processing (e.g. Rousselet, Gaspar et al. 2011). Therefore these results strongly suggest that the ORE takes place at the perceptual level, answering the first of the three questions: when does the ORE occurs. The results of the fMRI experiment (chapter 3) show that, across the four ROIs (i.e. right and left FFA and right and left OFA), SR and OR faces are encoded as a function of experience only within the dominant FFA. Just like for the behavioural ORE, neural representations of OR faces were found to be more similar than the highly distinctive SR ones. These data thus answer the question of where in the brain the ORE occurs. Moreover, all three studies reveal important information regarding the nature of SR and OR face encoding. The first experiment shows that the magnitude of the electrophysiological FIE is larger for OR compared to SR faces. As explained in Chapter 1, the FIE is regarded as a marker of configural/holistic face processing, in that inverting faces impairs their configural processing. These data therefore suggest that SR faces are processed more configurally than OR ones. In addition, as explained in Chapter 3, repetition suppression reflects amongst other things coding efficiency (Grill-Spector, Henson et al. 2006). Therefore the observed lack of repetition suppression to OR faces of same identity reported in experiment two suggests that this category triggers prototypical encoding, causing OR faces to be perceived as looking alike. On the contrary, the more finely tuned coding to SR faces leads this visual category to be perceived as highly distinctive. These data are further corroborated by the ones reported in Chapter 4 (i.e. similar neural representation to OR faces and distinctive neural representations for SR faces).

These results taken together fit very well with Valentine's norm based multidimensional face space model. According to this theoretical expertise based account the distance between the locations of face representations in the multidimensional space is directly proportional to the perceived distinctiveness across face exemplars. Highly similar OR faces are clustered together, while the distinctive SR faces are widely distributed. Accordingly, within the dominant FFA neural representations of SR faces are highly distinctive compared to the similar OR faces. Levin's (Levin 1996 ; Levin 2000) feature selection model also holds that SR are encoded in a more distinctive manner than OR exemplars. This view (and more in general social cognitive theoretical approaches) however does not attribute the differences in face coding across races to a lack of expertise with OR faces. Individuals perceive OR faces as looking alike as a consequence of an spontaneous categorization process, leading people to automatically extract race defining information (such as for example, skin tone)upon seen an OR member. This is in stark contrast with expertise based models proposing that the perception OR faces as highly homogeneous is a direct consequence of a genuine to a lack of neural tuning to the relevant diagnostic facial dimensions as a consequence of experience. So, for example, in Valentine's view people are unable to accurately encode OR faces as they do not possess the adequate capacity to extract relevant facia information; while in Levin's view, individuals impairment in accurately recognize OR faces dose not stem from an inability to process OR diagnostic information. Their brain does possess the required capability to efficiently process OR faces, however the automatic categorization process (leading them to focus upon different type of information – I.e. race relevant ones) prevent them from doing so. The data presented here, challenge Levin's feature selection, and more in general social cognitive hypotheses. The sensitivity to race of the N170 and its correlation to the behavioural ORE, together with a lack of race modulation on the P2 and N250 components (which have strongly been associated with categorisation mechanism – e.g. Latinus and Taylor 2005; Philiastides, Ratcliff et al. 2006; Philiastides and Sajda 2006; Harel, Ullman et al. 2007) reported in the first two experiments suggest that this phenomenon originates at perceptual levels of face processing, rather than being an outcome of categorization. These observations, coupled with the fMRI and EEG results showing differential coding efficiency across races, lead to assert that the SR and OR faces are encoded according to the laws predicted by the norm based multidimensional face space model of the ORE. This answers the final question regarding how the ORE occurs.

In light of what argued so far, it can be concluded that the neural substrates of the ORE are perceptually based and deeply eradicated into differential levels of visual expertise with SR and OR faces. Experience can be thus regarded as the originating cause at the core of the ORE. This however does not preclude nor underestimate the impact of social cognitive and motivational aspects on the manifestation of this phenomenon. A direct link between these aspects and the ORE has in fact been demonstrated by a large number of studies (see Chapter 1). The data presented here do not want to undermine nor challenge these findings; rather it is argued, that, with regards to the ORE, social factors come into play at later stages of face processing, only after the perceptual effects of visual expertise.

One possible limitation of this thesis is represented by the facts that, in determining the cortical region tuned to differentially encoding SR and OR faces, the search was limited to the four most commonly reported face preferential areas (i.e. OFAs and FFAs). While this observation does not undermine the validity of the results presented here, it does limit the reachable conclusion. The dominant FFA does indeed encode faces as a function of race according to the laws of the norm based multidimensional face space model, but it may not be the sole region presenting this response profile. There are a number of reasons though for limiting the analysis to four ROIs. Firstly, these areas are indicated by overwhelming empirical evidence as the main face cortical areas (see Chapter 1); as well as being included in the core face network (Haxby, Hoffman et al. 2000). The third area belonging to the core network is the pSTS. This region however could not be consistently localised across subjects and hence was excluded from the analysis. Moreover, to increase fMRI spatial resolution, the field of view was limited to the ventral and temporal cortices. An alternative approach to further explore whether further ventral or temporal regions display response profiles similar to that of the dominant FFA would have been by means MVPA. While this approach could have potentially revealed additional important information regarding the spatial cortical origin of the ORE, two issues have to be taken into account. One practical consideration is that, as explained in Chapter 4, due to excessive movement, some of the participants only had two usable runs. Such a number is not enough to exploits the advantages conferred by MVPA. This technique requires at least three, but desirably four runs two or three training and one testing run \Pereira, 2009 #24921}. Another theoretical problem may lie in the fact the MVPA may not be sensitive enough to detect subtle differences to accurately classify a relatively large number of identities. The RDM approach instead is deemed as more suitable to tackle this question, both in terms of its statistical sensitivity; and its theoretical proximity to the multidimensional face model.

Another important aspect needing to be discussed is the practical implication of this work. The anecdote told in this thesis preamble highlights the fact that the ORE has important repercussion on eye witness testimony. The impact of the ORE on the reliability of eye witnesses has in fact led a number of authors to propose a system-variable approach in which OR identification of guilty convicts would receive special preventive treatment at the time of the identification test. This measure would be adopted in order to prevent the misidentification of OR suspects (Wells and Olson 2001). Moreover preventive procedures have been suggested, such as, for example, the inclusion of same-race line-up constructors, larger numbers of fillers in other-race cases, dual line-up techniques in other-race cases (Wells and Olson 2001).

5.1 Future directions

The work throughout this thesis explores the neurophysiological basis of the well-known OR recognition impairment, successfully answering the three main questions related to where when and how the ORE occurs within the human brain. Having effectively demonstrated that OR and SR face are processed differentially at the neural level, future research should attempt to quantify these differences by pinpointing the amount and the type of information required across different tasks (e.g. identification and categorization) in encoding SR and OR faces. One way of achieving this goal would be by parametrically manipulating the amount of information available in the face stimuli by for example modifying the spatial frequency content of the images. An interesting technique, which has already been successfully applied behaviourally with SR emotional faces only (e.g. Smith and Schyns 2009) is the Laplacian pyramid approach (Simoncelli and Freeman 1995). This technique allows simulating the spatial frequency content (and thus the amount of fine grained information) at different viewing distances. Implementing this approach with SR and OR faces, while participants are required to perform an identity related task (i.e. old/new recognition paradigm) and a race categorization task could have number of potentially important implications. It could reveal for example important insights regarding the quantity of information required as a function of the task demands across faces of different races. Furthermore it would be possible to assess whether specific cortical regions (e.g. FFAs and OFAs) are tuned or differentially sensitive to diverse spatial frequency content across tasks and races.

An issue needing further investigation is faster categorization by race of OR faces. The visual information and the cortical correlates driving this speed categorization advantage for OR faces are still unknown. The conclusion drawn from the empirical evidence gathered within this thesis would suggest that the observed OR categorization advantage occurs as a consequence of differential levels of visual expertise across races. As explained earlier, visual expertise tunes the human brain to efficiently extract diagnostic facial dimensions needed for SR face identification. The observed lack of neural tuning to OR faces lead exemplar from this category to be perceived as highly similar. Consequently it would be plausible to hypothesis that the faster OR categorization by race is an outcome of the amount of information extracted from OR faces (which should be significantly less than that extracted from SR faces). In order to test this hypothesis, the percentage phase coherence of face stimuli could be parametrically manipulated (for example from 20% to 70% in incremental 5% steps) in order to control the amount of information available in the face stimuli. Concomitantly, EEG signal could be recorded from participants performing a race categorization task. This approach has been already implemented with SR faces only

(Rousselet, Pernet et al. 2008). The authors reported an increment of the N170 amplitude as a function of phase coherence information. By applying this paradigm to faces of different races it would therefore be expected that the N170 amplitude would display differential levels of sensitivity across races. Ideally, this face preferential ERP component should show a gradual amplitude increase at each step of the phase coherence continuum for SR faces, indicating a fine tuning to (additional) face information across steps. On the other hand, the N170 of OR faces should display a more categorical pattern, suggesting a less fine grained tuning to visual information for this category. Behaviourally, correct race categorization would ideally require less phase coherence information for OR compared to SR faces.

6. General Conclusions

The aim of this thesis was to clarify the neurophysiological basis of the ORE by means of neuroimaging techniques. I have shown throughout this work that the ORE is a perceptual phenomenon that stems from differential levels of visual expertise people have with faces of different races. I set out to answer three questions with regards to the ORE, namely *when where* and *how* it occurs in the human brain. EEG data showed that the ORE originates at early perceptual levels of face processing (*when).* I further showed by means of fMRI that SR and OR faces are coded within the dominant as a function of perceived distinctiveness (*where*). Finally, the data from all three studies consistently suggest that SR and OR faces are processed in a qualitatively different manner (SR more configurally, while OR more featurally), and that face encoding follows the laws predicted by the norm based multidimensional face space model in the dominant FFA (*how*).

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Supplementary Section

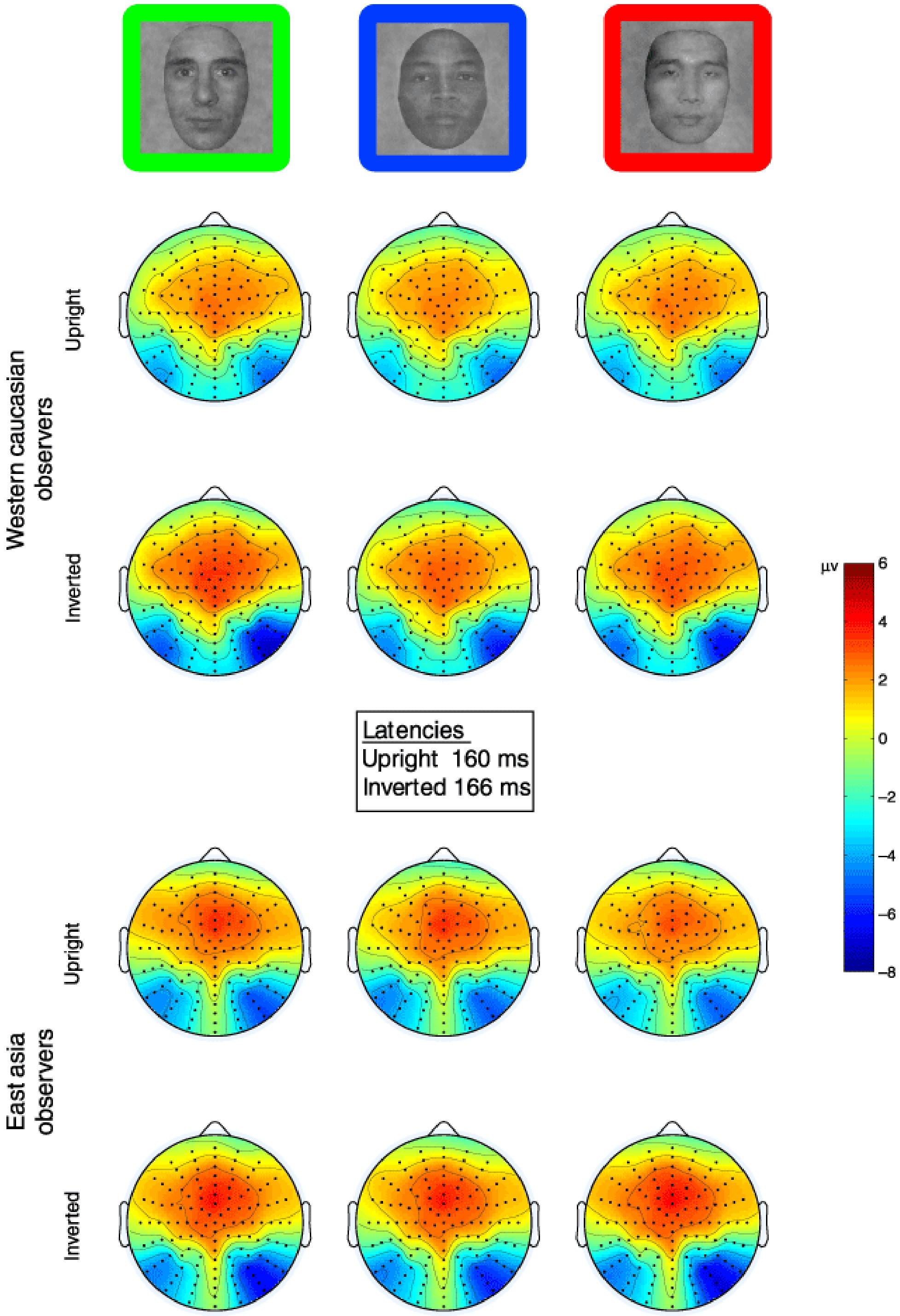

Figure 1s – Average scalp topographies and latencies elicited by upright and inverted stimuli in both groups of observers

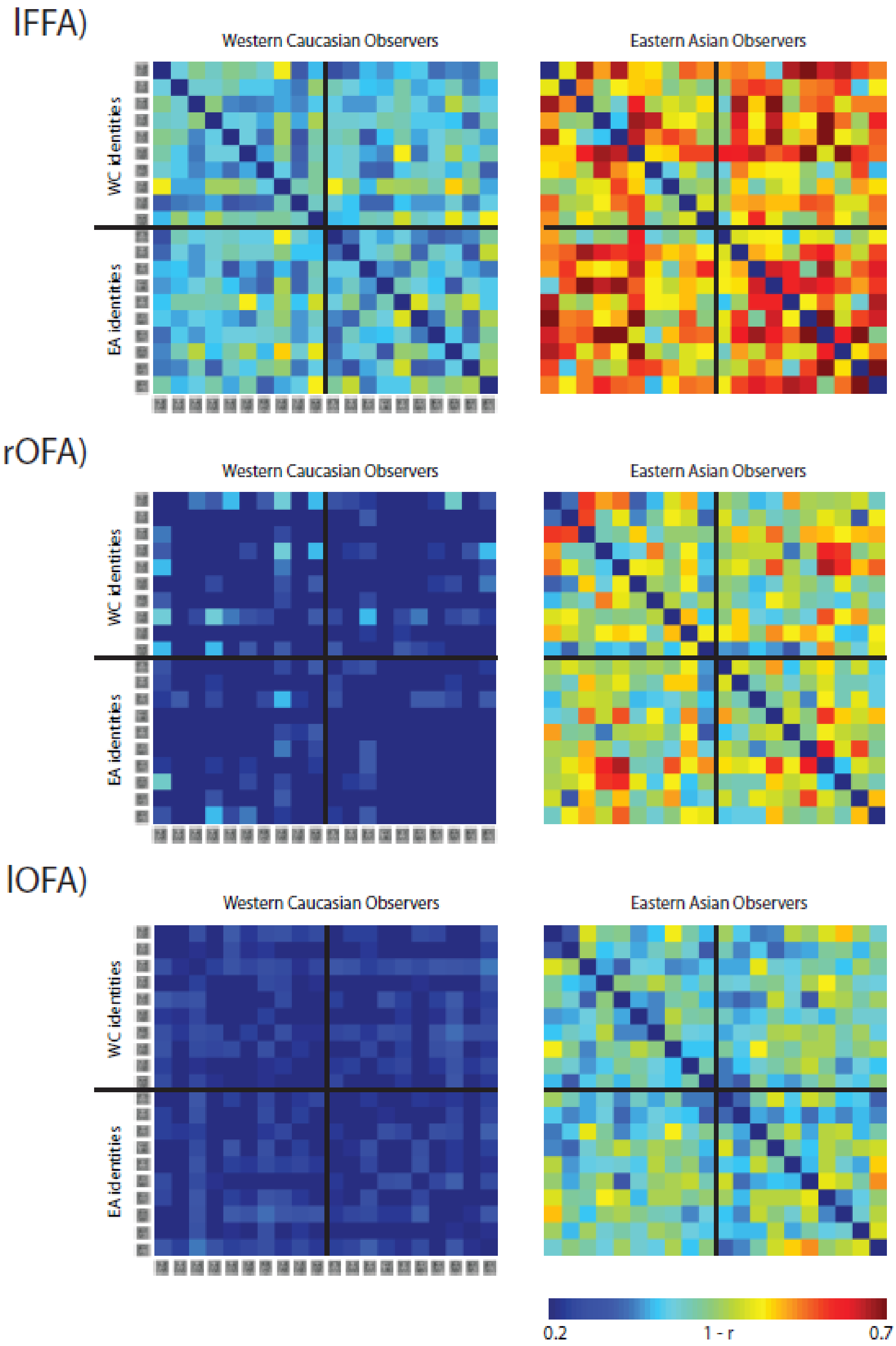

Figure 2s – top) RDM computed on the lFFA (see chapter 4); middle) RDM computed on the rOFA (see chapter 4); bottom) RDM computed on the lOFA (see chapter 4). Note that there are no clear differnces across correlational patterns for either race of faces and observers