INVESTIGATION OF NEURAL CORRELATES OF FACES AND EMOTIONAL EXPRESSIONS USING MAGNETOENCEPHALOGRAPHY

STEFANIE HASSEL

Doctor of Philosophy

ASTON UNIVERSITY

December 2004

Aston University

INVESTIGATION OF NEURAL CORRELATES OF FACES AND EMOTIONAL EXPRESSIONS USING MAGNETOENCEPHALOGRPAHY

Stefanie Hassel

Doctor of Philosophy

December 2004

The recognition of faces and of facial expressions is an important evolutionary skill, and an integral part of social communication. It has been argued that the processing of faces is distinct from the processing of non-face stimuli and functional neuroimaging investigations have even found evidence of a distinction between the perception of faces and of emotional expressions. Structural and temporal correlates of face perception and facial affect have only been separately identified. Investigation neural dynamics of face perception per se as well as facial affect would allow the mapping of these in space, time and frequency specific domains.

Participants were asked to perform face categorisation and emotional discrimination tasks and Magnetoencephalography (MEG) was used to measure the neurophysiology of face and facial emotion processing. SAM analysis techniques enable the investigation of spectral changes within specific time-windows and frequency bands, thus allowing the identification of stimulus specific regions of cortical power changes. Furthermore, MEG's excellent temporal resolution allows for the detection of subtle changes associated with the processing of face and non-face stimuli and different emotional expressions.

The data presented reveal that face perception is associated with spectral power changes within a distributed cortical network comprising occipito-temporal as well as parietal and frontal areas. For the perception of facial affect, spectral power changes were also observed within frontal and limbic areas including the parahippocampal gyrus and the amygdala. Analyses of temporal correlates also reveal a distinction between the processing of faces and facial affect. Face perception per se occurred at earlier latencies whereas the discrimination of facial expressions occurred within a longer time-window. In addition, the processing of faces and of facial affect was differentially associated with changes in cortical oscillatory power for alpha, beta and gamma frequencies.

The perception of faces and facial affect is associated with distinct changes in cortical oscillatory activity that can be mapped to specific neural structures, specific time-windows and latencies as well as specific frequency bands. Therefore, the work presented in this thesis provides further insight into the sequential processing of faces and facial affect.

KEYWORDS: Magnetoencephalography (MEG); Face perception; Facial Expressions; Synthetic Aperture Magnetometry (SAM)

Acknowledgements

I would like to thank my supervisor, Dr. Gina Rippon, for her guidance and valuable advice during my PhD. Your help throughout the development and completion of this thesis is greatly appreciated. I would also like to thank the MEG Research Group, particularly Dr. Gareth Barnes, Dr. Arjan Hillebrand and Dr. Krish Singh for all their help and constructive comments with the analyses of the data.

Thank you to all my fellow postgraduates for generating a very enjoyable working environment. Particular thanks to Alison for her encouragement, support and help when it was needed most, to Kim for being an inspiration and to Jenni for always smiling. Thank you to my parents, my family and friends for encouragement and support throughout, and to Sue & Martin, Annie, Alex, Matt & Sarah Hyde for being my family abroad.

Table of Contents

List of Figures

List of Tables

Chapter 1 The neuroscience of face perception

The recognition of faces, or face-specific perception, is an evolutionarily important skill, which allows us to distinguish stranger from family, friend from foe. In addition, appropriate interpretation of the facial expression of emotion is an integral part of social communication. Expressions are emotion specific and satisfactory interpretation of these allows us to gauge the feelings and responses of others and to respond accordingly. An inability to interpret emotional expressions correctly or a tendency to respond differentially to different emotions underpins a range of behavioural disorders such as alexithymia or unipolar and bipolar depression.

There has been much research into the neural substrates of face perception per se and key sites such as the fusiform gyri or the superior temporal sulcus have reliably been identified. In addition, further research has implicated additional sites in the perception of emotional expressions of faces, including subcortical regions such as the amygdala, hippocampus and parahippocampal gyrus (see section 1.4).

A range of models, both structural and functional have been developed from such findings, and these models are used to direct and inform research in the area of face perception and in the perception of emotional facial expressions.

1.1. Models of face processing

1.1.1. Structural Models of Face Processing

1.1.1.1. Bauer (1984): Two-Route Model of Face Processing

Bauer (1984) proposed a two – route model for face perception, which refers both to two neuroanatomical visual processing streams and to two cognitive pathways. Evidence in support of the two-route model has been taken from patient observations. Prosopagnosic patient LF was unable to recognise familiar faces from photographs, yet he showed greater autonomic skin responses when the photograph was shown with reference to the correct name. Bauer interpreted the greater SCR as a measure of unconscious (covert) recognition of the familiar face, which is separate from conscious (overt) face recognition. He proposed that such a dissociation between overt visual

recognition and autonomic arousal in response to familiar faces points towards two separate or independent processing routes with a distinct neuroanatomy. According to his model, overt face recognition occurs in the "ventral visual – limbic pathway", and covert recognition occurs in the "dorsal visual – limbic pathway" (**Figure1-1a**). The ventral visual – limbic pathway proceeds from the visual association cortex via the inferior longitudinal fasciculus to the temporal lobe and subsequently to the adjoining limbic system, with the target structure being the amygdala. This pathway subserves emotion, memory and learning functions that are more modality – specific to vision. The dorsal visual – limbic pathway involves projections from the visual association cortex to the superior temporal lobe, then to the inferior parietal lobe, with extensive reciprocal connections to the cingulate gyrus, and subsequent connections to the hypothalamus. This dorsal pathway was responsible for complex attentional functions, emotional arousal and orientation to stimuli of motivational significance (**Figure1-1b**).

Figure1-1a: Schematic representation

Hip = hippocampus; Amy = amygdala; Hyp = hypothalamus; Ant = anterior; Post = posterior
(Taken from Bear (1983) Archives of Neurology, 40, 195-202)

Hy

connections to CG and Hy.
(Taken from Bauer (1984), Neuropsychologia, 22 457-469)

The two – route model and the "ventral visual –" and "dorsal visual – limbic pathway" owe much to the account of the two visual pathways first described by Mishkin & Ungerleider (1982) and later by Milner & Goodale (1993).

Prior to Bauer (1984), Bear (1983) applied Mishkin & Ungerleider's work to propose a model for the representation of emotions and their hemispheric specialisation, with evidence largely drawn from observations of patients with temporal lobe epilepsy. Bear described two sensori-limbic connective pathways, one being the dorsal visuo-limbic structure, responsible for surveillance, attendance and arousal and a second one being a ventral system, responsible for stimulus identification, learning and emotional response. Arguing that the right hemisphere was dominant for emotions, Bear drew a clear distinction between the emotional functions of the dorsal and ventral visuo – limbic pathways in the right hemisphere. In Capgras delusions, damage seems to occur to the secondary affective pathway to face recognition (which they named "dorsal").

Bauer's account of the two-route model has received some criticism, as it has been stated that his model falls short of distinguishing between the dorsal and ventral pathways with respect to visual processing per se, hence enabling the notion of autonomic recognition via the dorsal visual pathway.

The notion of there being a neuroanatomical underpinning to the two cognitive routes seems, however, problematic as the functions of the proposed neuroanatomical pathways have yet to be fully developed. According to Young (1998 p44) "... even though they can be usefully combined, psychological and neurological hypotheses ... have some degree of independence from each other".

1.1.1.2. Haxby (2000): A Model of the Distributed Human Neural System for Face Perception

The model proposed by Haxby, Hoffman & Gobbini (2000) has some elements in common with the cognitive model put forward by Bruce & Young (1986) (see section 1.1.2.1). However, Haxby et al. suggest that the perception of expressions, of eye gaze and of facial speech share a common representation of the changeable aspects of faces, and that such a representation is different to that of facial identity and the recognition of facial identity. It appears to extend the cognitive model as it suggests that different face perception processes like the recognition of facial expressions, involve the integration of areas that are responsible for the visual configuration of the face with regions that are

responsible for inferring the meaning of such representations i.e. emotions and their significance. Therefore, like the Bruce & Young model it appears to have a branching structure, which highlights the distinction between representations of invariant aspects of faces (which initiate the recognition of unique identity) and representations of changeable aspects of faces (which initiate the perception of information regarding social communication). In addition, it also poses a hierarchical structure, as the existence of a core system is suggested which aids the visual analysis of faces and is different from an extended system that is responsible for processing the information, which is gathered from faces. Three bilateral regions comprise the core system - the inferior temporal cortex provides input for the lateral fusiform and the superior temporal sulcus. Neural systems, which mediate the processing of, for instance, emotions – such as the amygdala or inferior frontal areas, should be considered as extensions to the face processing system (Haxby et al. 2000) (**Figure1-2**).

the extended system are possible.
(Taken from Haxby, Hoffman & Gobbini (2000) Trends in Cognitive Sciences, 4, 223-233)

The functional roles of these separate regions are still somewhat unclear and will be discussed further in the next section. In short, it seems likely that there are degrees of separation, so, for instance, does it appear as if the lateral fusiform gyri play a more dominant role in the processing of facial identity, and only a supportive role in the

processing of emotional expressions, whereas the role of the superior temporal sulcus is more concerned with the processing of changeable aspects of faces (e.g. expressions).

1.1.2. Functional Models of Face Perception

1.1.2.1. Bruce and Young (1986): A Functional Model of Face Recognition

To clarify what needs to be understood in terms of face processing / face recognition, Bruce & Young (1986) proposed a functional model which aimed to explain the perceptual and cognitive processes involved in face recognition, and the model is considered to be reliant upon interactions of numerous different functional components (see **figure 1-3**). The involvement of specific brain areas, however, was not considered. According to Bruce & Young there are at least seven different and distinct types if information that can be revealed from faces, e.g., pictorial, structural, visually-derived semantic and identity-specific semantic information, as well as information regarding name, emotional state and facial speech.

The cognitive model needs to take into account that functional components different to the ones involved in the recognition of facial identity - which is the main aim of their model - are at work when it comes to the discrimination of facial expressions of emotions. As indicated by Bruce & Young, expression codes do not appear of great importance in the recognition of faces, and they insinuate that distinct functional components are involved in the generation of facial expressions. They describe facial expressions as a product of facial processing and propose suggestions regarding the procedures that generate such codes.

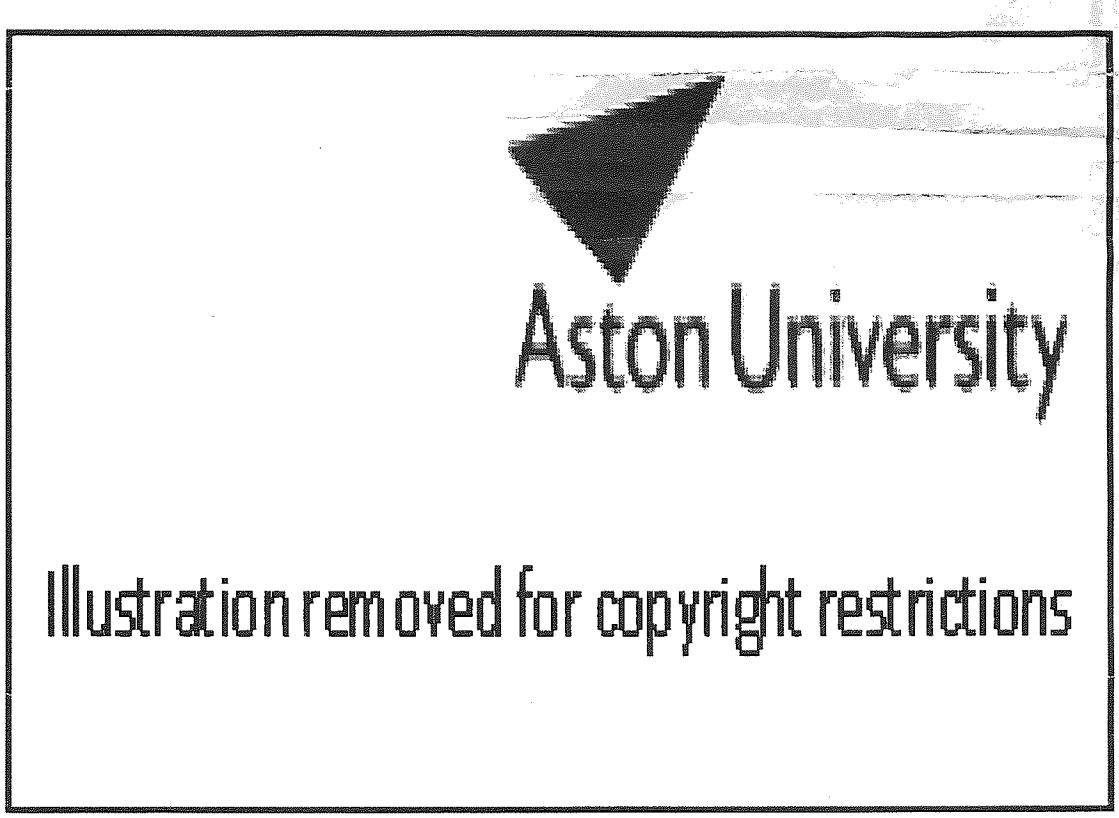


Figure1-3 is a schematic representation of the information – processing model of familiar face recognition.
(Taken from Bruce & Young (1986) British Journal of Psychology, 77, 305-327)

In accordance with the model, face recognition occurs along a single sequential pathway. In an initial stage the seen face is encoded using descriptions that are viewer – centred (angle of profile, lighting). These descriptions can be analysed by separate systems, independently for expressions, facial speech and information about gender, age and race. In the second stage, the seen face, if familiar, will initiate its representations in the Face Recognition Units (FRU), and subsequently activate information held at a third stage, the Person Identity Node (PIN), which store semantic and autobiographical information for familiar people. The final stage is the retrieval stage, here names of persons are saved independently of biographical details.

The system proposed is a hierarchical and branching organisation, mainly concerned with the recognition of identity and thus may use somewhat different organisational principles to a system that is used to identify emotional expressions or to recognise emotions. The role of functional models in understanding emotional recognition is less advanced. However, a later model of face perception incorporates the role played by facial emotions in somewhat more elaborate manner.

1.1.2.2. Ellis & Young (1990) Two-Route Model to Face Recognition

Ellis & Young (1990) adapt Bauer's (1984) model but take into account the described limitations by re-defining the model as incorporating two routes to face – recognition. One route subserves the visual recognition of face (as described by Bruce & Young 1986; above), and a separate route subserves an affective component that contributes to familiar face recognition.

This can be achieved in two separate ways: (i) by duplication of the FRU Module, one existing in the visual pathway, and one existing in the affective pathway; or (ii) by proposing a single route up to FRU, which then divides into separate pathways one leading to the PIN and one to the affective response (see also **Figure1-3**).

Ellis & Young (1990) used the model to explain the Capgras syndrome by demonstrating that patients suffering from the condition were able to recognise familiar faces but did not produce the autonomic response to these faces as has been observed in prosopagnosic patients and healthy controls (see Bauer 1984). Hence, contrary to prosopagnosic patients who cannot recognise familiar face but show an autonomic response to the presentation of photographs, patients suffering from Capgras Syndrome can recognise familiar faces by sight but do not show an affective response associated with it.

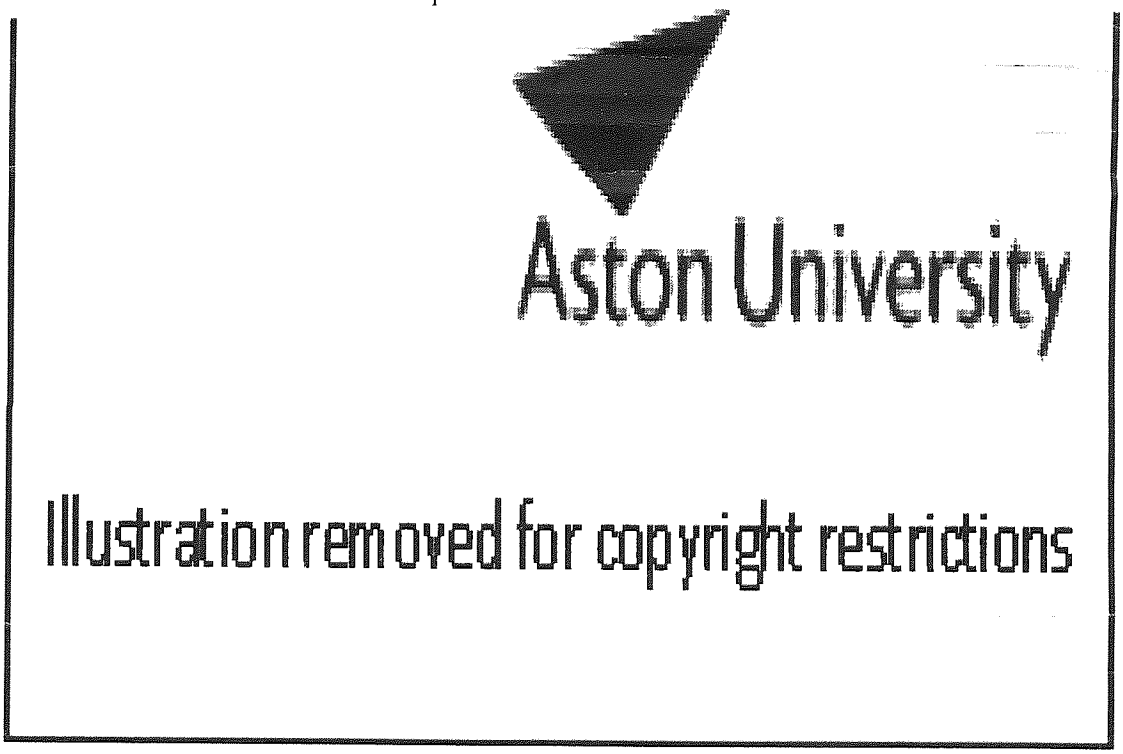
Ellis & Young state that the dorsal pathway is capable of some form of visual recognition, and that the dorsal limbic structures are able to contribute specific affective responses to familiar stimuli. Still, it lacks a clear description of exactly how the dorsal pathway explains face recognition, but since it appears that the affective response must be 'attached' to a particular face, the face must be recognised first.
It could also be stated that neither Mishkin & Ungerleider (1982) nor Milner & Goodale (1993) attributed the dorsal visual pathways with the capacity for object or particularly face recognition.

1.1.2.3. Breen, Caine & Coltheart (2003): Cognitive Model of Face Processing

Breen, Caine & Coltheart (2003), in agreement with Bauer (1986) and Ellis & Young (1990) state that, in an unimpaired brain, the ventral visual pathway mediates face recognition. It is carried out by ventral temporal lobe structures, a view consistent with Mishkin & Ungerleider (1982) and Milner & Goodale (1993). An affective component

of face recognition is provided by connecting ventral limbic structures, most prominently, the amygdala. When interference to normal face processing occurs, as in prosopagnosia, disruptions are most likely to be in the ventral pathway.

Breen, Caine & Coltheart propose a model which matches that of Ellis & Young (1990) but suggest that the model bifurcates after the FRU Module is reached (see **figure 1-4**). It then divides into two pathways, one leading directly to the PINs and a second one leading directly to the affective response. The stronger the emotional relationship is with the person whose photograph is presented, the stronger is the activation of the affective response.



(Taken from Breen, Caine & Coltheart (2000) Cognitive Psychology, 17(1/2/3) 55-71)

1.2. Non-human neurophysiological studies of face perception

Single – unit recordings in monkeys provide evidence for distributed mechanisms being implicated in the processing of complex visual objects (e.g. Tanaka et al. 1991), and face – selective cells have been described as being 'scattered' throughout the temporal lobe of the macaque, with a relative concentration in the superior temporal sulcus (STS) (e.g. Gross et al. 1972, Perrett et al. 1992, Baylis, Rolls & Leonard 1987). Perrett et al. (1992) identified five different types of cells within the temporal cortex of the macaque

that respond maximally to different facial characteristics, e.g. full face, profile, back of head, head up or head down). Other cells have been observed to respond selectively to one individual, regardless of pose or expression.

Discrepancies, however, are to be expected with respect to human observations in terms of 'location' of face-specific cells, and a face selective region analogue to the human 'fusiform face area' (FFA) has never been identified in the macaque.

A recent paper by Tsao et al. (2003) investigated the responses to faces and other visual stimuli in macaques, but also in human volunteers. They reported that in alert, fixating rhesus macaques, discrete face – selective cortical patches were observed within the lower region of the (STS) and in area TE (inferior temporal visual cortex). Smaller face – specific regions were also observed within upper regions of the anterior middle temporal sulcus, bilaterally. These regions appeared statistically robust and also responded to line drawings of faces.

Using the same face stimuli with human volunteers, activation was reported within two face – specific patches, the fusiform gyrus (bilaterally) and the left inferior temporal gyrus and the right superior temporal gyrus. Tsao et al. also tested the responses to macaque faces. In the macaques, patches selective for macaque faces responded more than twice as strongly to monkey faces, were larger than those for human faces and spread posteriorly into area TEO (posterior part of infero-temporal cortex). In humans, activation to macaque faces was observed in the same areas as for human faces.

The face specificity of the human FFA and of the macaque STS – TE area led to some speculation as to whether these areas could be regarded as homologous. Tsao et al. therefore computationally deformed the macaque face patches onto a human flat map and observed that their location was indeed quite close to that of the human FFA (Tsao et al. 2003). They concluded that humans and macaques share a strikingly similar neural architecture for the processing of different visual objects, particularly faces. Thus, evidence from non – human recordings can lead to hypothesise of the involvement of sub-processes, which may advance our understanding of human face processing.

1.3. Human brain studies of face perception

Research on emotional communication has suggested that emotions are asymmetrically organised in the brain. A first suggestion claims right hemisphere dominance for the

processing of all emotional stimuli (Bowers, Bauer & Heilman 1993). A number of neuropsychological investigations seem to provide some support for this argument (Bowers et al. 1985, Bowers et al. 1991, Bowers et al. 1993, Etcoff 1984). A study by Anderson et al. (2000), comparing the evaluation of facial expressions in patients suffering from either right temporal or left temporal lesions, found that only those with damage to the right hemisphere were significantly impaired in the evaluation of facial expressions. No evidence of impairment was apparent in patients with left temporal lobe lesions. A second suggestion states that left and right hemispheres make qualitatively different contributions, supporting the notion of affective dimensional specialisations such as negative versus positive valence (e.g. Silberman & Weingartner 1986) or approach versus withdrawal tendencies (e.g. Davidson 1992, Davidson et al. 1990). This is evidenced by lesion studies, as patients with right hemisphere lesions tend to be impaired more severely when performing expression evaluation tasks, with particular difficulties on unpleasant emotions. In contrast, left hemisphere lesions seem to cause greater difficulties with pleasant emotions (e.g. Silberman & Weingartner 1986).

Alternatively, electrophysiological measures demonstrate that left anterior brain regions are more involved in the approach – related affective expressions (happiness, pleasant surprise and anger) and right anterior regions are more involved with emotions of avoidance and withdrawal (sadness, fear and disgust) (Davidson 1993, Davidson et al. 1990, Tomarken & Davidson 1994). However, similar dissociations have not been reported for facial expressions so far. Anderson et al. (2000) reported that 25% of right temporal lobe lesion patients showed impaired evaluation of fearful faces, yet the appraisal of anger was unimpaired in that patient group. They claim that anger falls into the domain of attack – related approach behaviours and thus take this as support for Davidson's approach – avoidance behaviour model (rather than a negative versus positive distinction per se). A third suggestion states that independent emotions are supported by defined neural substrates (e.g. Adolphs et al. 1994, Calder et al. 1996). Evidence here is centred around findings that lesions of the human amygdala cause a corresponding impairment in the perception of facial expressions, in particular of fear (e.g. Adolphs et al. 1994, Broks et al.1998, Calder et al. 1996), and that the amygdala has been observed to be active when healthy controls view facial expressions of fear but also happiness (e.g. Breiter et al. 1996, Morris et al. 1996, Whalen et al. 1998). Anderson et al. (2000), in addition, observed impaired ratings of happiness in a sample of patients with right temporal lobe lesions, thus indicating that right temporal lobe

lesions could either be associated with deficits in the ability to process facial expressions of particular affective valence, or that lesions to the right temporal lobe do not exclusively lead to impairments for withdrawal related expressions such as sadness, but also to approach related ones as in happiness.

1.4. Neural correlates of face-perception and facial affect

The role of the right hemisphere in face perception has been highlighted by behavioural (e.g. Campbell 1978; Levy, Heller, Banich & Burton 1983), neuropsychological and functional imaging studies (e.g. Sergent, Ohta & MacDonalds 1992; Puce et al. 1995, 1996; Kanwisher, McDermott & Chun 1997). So, for instance, have right handed volunteers been found to judge faces as happier when the smile appeared in their left visual field (LVF), which suggests that information is judged more saliently when received by the right hemisphere (e.g. Levy, Heller, Banich & Burton 1983). There is also evidence for a dissociation between facial recognition (memory) and facial expression perception and the neural substrate underlying these processes (e.g. George et al. 1993; Sergent, Ohta & MacDonalds 1992).

Facial familiarity perception and unfamiliar face matching is linked to the right hemisphere (Young et al. 1993a), yet facial working memory has been linked to the left hemisphere (McIntosh et al. 1996) and facial recognition memory has been associated with left hippocampus activity (Kapur et al. 1995).

The effect facial expressions of emotions have within social interactions is likely to have a biologically 'pre-wired' neural basis, as it operates almost automatically, fast and repeatedly (Wild, Erb & Bartels 2001). Wild, Erb & Bartels (2001) put forward several suggestions as to why this might be, one being that there exists a functional network in which a direct input from higher visual areas such as the fusiform gyrus, projects to medial temporal, orbitobasal and dorsofrontal and insular cortices and the basal ganglia. Functional imaging and clinical studies support this notion (e.g. Borod et al. 1986; Ojemann, Ojemann & Lettich 1992; Allison et al. 1994; Morris et al. 1996; Sprengelmeyer et al. 1996; Kanwisher, McDermott & Chun; Lane et al. 1997; Phillips et al. 1997; Young 1997). Some of the results outlined above have led to the proposition that the processing of emotional faces preferentially engages the right hemisphere. Studies investigating facial expressions of emotions, however, have generated inconsistent results. Young et al. (1993) demonstrated the involvement of both

hemispheres, whereas Adolphs et al. (1996) reported evidence only for right hemisphere activation in lesion patients, with a bias for negative emotions. Using functional imaging to investigate activation to positive and negative emotional expressions, Gur, Skolnick & Gur (1994) and George et al. (1996) reported the involvement of the right hemisphere, Sergent, MacDonald & Zuck (1994) found activation within the cingulate cortex bilaterally, and the right anterior cingulate and bilateral frontal areas (inferior frontal cortex) have been observed by George et al. (1993).

As mentioned above there appear to be several regions which are proposed to play crucial roles in the perception of faces and facial expression. The role of some of these will now be briefly described. A summary table is provided (see **Appendix1**) outlining the spatial correlates of the processing of facial affect particularly those of happiness and sadness.

1.4.1. Occipito-temporal complex including lateral fusiform gyrus

Face – specificity has been observed in the fusiform gyrus by Halgren et al. (1994a) and Allison et al. (1994) using intra-cranial recordings. Sergent & Signoret (1992a) using PET, in addition reported activation within the lingual, parahippocampal gyrus, and anterior temporal cortex.

Furthermore, Sergent, MacDonald & Zuck (1994), Haxby et al. (1994), Courtney et al. (1996), Dolan et al. (1996) - all using PET – confirmed the involvement of ventral occipito-temporal regions and also implicated the right lateral occipital complex in the processing of faces and facial expressions.

Studies using fMRI have identified areas within ventral occipito-temporal cortex, the middle occipital gyri, the superior temporal and lateral occipital sulci for faces and scrambled images (e.g. Puce et al. 1996, Clark et al. 1996) but did not reach significant conclusions regarding lateralisation effects.

Using MEG, Lu et al. (1991) presented photographs of faces for 300ms and compared activity patterns generated to those generated by photographs of birds. They revealed early bilateral activity at about 150ms in inferior or occipito-temporal junction. Later components were not face – specific. Halgren et al. (1995b) attempted to localise face – specific activity by subtracting face responses from responses made to scrambled faces and reported an equivalent current dipole (ECD) in the right posterior fusiform gyrus with the maximum latency being at 166ms (to 256ms).

Halgren et al. (1995) also found strongest responses to photographs of faces in right occipito-temporal areas at a latency of 166ms, and reported activity of less intensity in responses to scrambled and schematic faces.

Confirmation for the above findings was also reported by Sams et al. (1997) and Swithenby et al. (1998). The latter reported the involvement of the right occipito-temporal regions in face – specific processing at latencies of about 140ms.

1.4.2. Superior temporal sulcus & inferior temporal cortex

Cell recordings in human and non – human animals render the temporal cortex surrounding the amygdala as an important site for the analysis of facial emotions (Hasselmo, Rolls & Baylis 1989; Ojemann, Ojemann & Lettich 1992).
Single neuron studies of the macaque have indicated the existence of a dissociation for face-selective cells in the temporal cortex. The superior temporal sulcus (STS) seems to be involved more in the processing of static images of changeable aspects of faces, e.g. facial expressions, or in facial movement. Involvement of the inferior temporal cortex however was observed when the perception of identity was studied.
In humans, activation has been observed in posterior regions of the STS in response to still pictures of faces (Haxby et al. 1999; Kanwisher, McDermott & Chun 1997; Halgren et al. 1999; Hoffman & Haxby 2000; Chao et al. 1999a, 1999b). Blair et al. (1999) reported evidence for the right inferior and middle temporal gyri being areas critical for the analysis of facial expressions of sadness.

1.4.3. Amygdala and limbic areas

In non-human primates and in rats, conditioning studies have provided much evidence for a dominant role of the amygdala in the processing of fear (LeDoux 1992; LaBar et al. 1998). Patients with bilateral damage to the amygdala have shown impairments in the recognition of negative emotion al expressions such as anger and fear (Calder et al. 1996; Adolphs et al. 1994). In studies investigating emotional expressions - with humans - responses within the left amygdala have consistently been reported to the presentation of fearful faces (Phillips et al. 1997; Breiter et al. 1996; Morris, Ohman & Dolan 1998; Whalen et al. 1998).

Work with psychopathic patients has put forward the suggestion that the amygdala may also be implicated in the processing of facial expressions of sadness, as it has been observed that selective autonomic responses were reduced in psychopathic patients compared to healthy controls (Chaplin et al. 1995; Blair et al. 1997). Psychopathic patients are hypo-responsive to facial expressions of sadness, and an amygdala dysfunction has been associated with this condition. Hence, Blair et al. (1999) regard it plausible that the amygdala may be involved in the processing of facial expressions of sadness, and report activation within the left amygdala in response to the presentation of facial expressions of sadness. A left lateralisation effect to facial expressions has also been reported by Morris et al. (1996) and Morris, Ohman & Dolan (1998), though to fear, and their interpretation of lateralisation proposed that it might reflect the modulation of amygdala activity by a left hemisphere system, similar to those mediating language.

The amygdala is also a candidate structure for the processing of (facial expressions of) anger. This is because of links to the amygdala, which plays a central role in the processing of threatening stimuli (Blair et al. 1999). Using PET, Blair et al. investigated the role of the amygdala in response to facial expressions of sadness and anger and reported activation within the left amygdala for expressions of sadness but not anger. Patients with damage to the amygdala do not consistently report difficulties with the recognition of sadness expressions, hence it might be that the amygdala responds either to a minimum of fear and sadness, or that an intact amygdala - though not a prerequisite for the recognition of sadness - appears necessary for the activation of the automatic response to this expression (Blair et al. 1999).

Functional imaging studies have also reported the involvement of the amygdala in response to facial expression of happiness; yet, patients with damage to the amygdala have not been reported as showing impaired performance with respect to happiness expressions on recognition tasks.

The involvement of the amygdala to several different emotions has lead researchers to consider a more general role of the amygdala in emotional processing. Generally it now seems accepted that the amygdala plays a role in emotional learning (e.g. Breiter et al. 1996; Davis 1986; LaBar et al. 1995; LeDoux 1998; Whalen et al. 1998). Thus, facial expressions of, e.g. sadness and anger, may act as unconditioned stimuli for behaviour patterns. In primates, as well as in humans, it has been observed

that newborns show fear of novel objects to which their mothers have expressed fear (transfer of valence information) (e.g. Mineka & Cook 1993).

1.4.3.1. Limbic dysfunction and emotional disorders

Abnormal neuronal firing patterns to emotional stimuli and subsequent difficulties in the perception and discrimination of emotional information have been observed in patients suffering from psychological disorders, such as depression or schizophrenia (Phillips et al. 2003b). A detailed review of these findings would go beyond the scope of this thesis and the interested reader is advised to seek out the following review papers for reference: Phillips et al. 2003a, Phillips et al. 2003b. Lawrence et al. (2004) observed that patients suffering from BD showed lateralised increases in activation within subcortical regions in response to facial expressions. Within the left amygdala, caudate nucleus and putamen, as well as the ventral prefrontal cortex signal increases could be observed in response to positive facial expressions (mild happiness) and also to mild and intense fear expressions. Bipolar patients also showed increased activation within the uncus and amygdala in response to facial expressions of mild happiness, and within the left hippocampus for facial expressions of mild sadness (Phillips et al. 2003a; Phillips et al. 2003b; Lawrence et al. 2004). Since regions such as the thalamus, caudate and the putamen have been reported to show increases in activation in BD patients in paradigms utilizing stimuli other than facial expressions, Lawrence et al. (2004) suggest that these areas might be implicated in the pathophysiology of bipolar depression.

Patients suffering from major depressive disorder showed increased responses within the putamen to expressions of mild sadness (compared to BD patients) as well as activation within the left hippocampus and the parahippocampal gyrus to expressions of mild sadness. Despite a general observation of "emotional blunting" (Lawrence et al. 2004; Elliot et al. 2004), increases in activation were observed to mildly sad facial expressions, indicating a bias towards the processing of negative emotional information (possibly unaffected by the what seemed to be general emotional blunting). In the Lawrence et al. (2004) study, amygdala activation (decreases or increases) were not observed (at all) to negative facial expressions (fear and sadness), thus it is assumed that other regions responsible for the processing of emotional information would have been recruited in addition instead.

1.4.4. Cingulate cortex

The anterior cingulate cortex (ACC) is part of the limbic system and has been implicated in sensory motor, cognitive and emotional processing (for a more detailed review see e.g. Critchley et al. 2003). The cingulate cortex integrates input from various sources, including representations from cognitive and emotional networks (connections of the affective subdivision include the amygdala, anterior insula and OFC; Devinsky, Morrell & Vogt (1995)) and influences activity in other brain regions by modulating cognitive, emotional, visceral and endocrine responses (Bush, Luu & Posner 2000). A guiding principle about ACC function is that cognitive and emotional information are processed separately. Hence, the ACC can be divided into an anterior and a posterior part, on grounds of different functions. The anterior part of the ACC is concerned with 'executive' functions (cognitive subdivision), whereas the posterior part of the ACC is referred to as 'evaluative' (affective subdivision) (Vogt, Finch & Olson 1992). Studies using two differing stroop-like inferences have demonstrated that point. The 'Counting Stroop' led to activation within the cognitive subdivision whereas the 'Emotional Stroop' led to activation within the affective subdivision of the ACC. The emotional Stroop-task shares surface similarities with the conventional Stroop-task as for both tasks the task-relevant part is the identification of the colour of the ink in which the word is written. In the emotional Stroop-task, the words presented, however, have either a neutral or an emotional meaning (e.g. Compton et al. 2003; Critchley et al. 2000; Whalen et al. 1998). Hence it emerged that the type of information to be processed can determine the recruitment of activity selectively in differing regions of the ACC. Drevets & Raichle (1992) and Mayberg et al. (1999) have reported evidence in support of a reciprocal suppression model (operating within the ACC). FMRI signal decreases were reported in the affective subdivision when dealing with the cognitively demanding neutral part in both tasks, e.g. the word reading, word counting and button pressing components; and it was also observed that limbic structures such as the amygdala and insular cortex showed decreased activity during these task components. In addition, the affective division of the ACC (as well as other structures of the 'emotional network') was (were) suppressed during the neutral part of the task, and conversely, was the only part that showed significant activation during the interference part of the task. This leads to the suggestion of the ACC having a specific role in the processing of more

complex emotional information (evaluation of emotional valence) (Bush, Luu & Posner 2000).

In animals, lesions within the ACC are associated with apathy and emotional instability (Tow & Whitty 1953), in humans, with striking personality changes including lack of distress, and emotional liability (Corkin, Twitchel & Sullivan 1979). Activity within the anterior cingulate cortex has been found in a number of studies investigating emotional expression (e.g. George et al. 1993; Sergent, MacDonald & Zuck 1994; Lane et al. 1997).

A study investigating the recognition of happy and sad facial expression (Phillips et al. 1998a) revealed the involvement of the left anterior cingulate gyrus as well as bilateral posterior cingulate gyri (BA23/30/31) in response to happy faces. The involvement of the anterior cingulate cortex in response to sad as well as angry faces has been reported by Blair et al. (1999) who interpret their finding of anterior cingulated involvement in response to anger in terms of greater attentional demands when processing angry expression or frightening stimuli.

1.4.5. Frontal areas

The role of the medial prefrontal cortex and the orbitofrontal cortex (OFC) in emotional behaviour has previously been highlighted by Rolls (1990).

Inferior frontal areas have also been associated with the judgement of the emotional content of facial expressions (Sprengelmeyer et al. 1998; Nakamura et al. 1999). Phillips et al. (1998) observed that patterns of activation within the medial frontal cortex bilaterally, and within the right dorsolateral prefrontal cortex (BA46) in response to happy faces differed in healthy and psychiatric populations (see section 5.3.1). Hornak, Rolls & Wade (1996) have reported the involvement of the orbitofrontal cortex in the processing of facial expressions in general and suggested it may play a mediating role in the processing of angry expressions in particular. They observed that patients with damage to the OFC showed impairments in the recognition of emotional expressions. An investigation by Blair et al. (1999) could substantiate these claims as they reported activation within in the right orbitofrontal cortex for anger expressions.

1.4.5.1. Davidson's model of brain asymmetry

The relatively clear evidence of a right hemisphere bias in the comprehension of emotional information has led to the claim that all aspects of emotional processing are favoured by the right hemisphere. This however was disputed by findings that claimed a hemispheric asymmetry in the processing of emotional information with the right hemisphere preferentially processing negative emotional information and the left hemisphere processing positive emotional information. This has become known as the *Valence Hypothesis* (Silberman & Weingartner 1986; Gainotti 1972). Evidence for this has been claimed by the observation that left hemisphere damage was associated with patients showing emotionally volatile behaviour, are prone to depression and crying. This has been termed *catastrophic reaction*. In patients with right hemisphere damage, on the other hand, inappropriate cheerfulness, lack of awareness to their disability and a proneness to laughter have been observed, this has been termed *euphoric – indifference*.

Tucker (1981) however, reversed the attribution of emotion to each hemisphere, as he offered that the observed behaviour was not a function of the intact hemisphere, but instead reflected the emotional one of subcortical areas on the damaged side that were released from cortical inhibition because of the lesion.

In addition, frontal lobe function has been associated with differential emotional responses. 60% of patients with left frontal lobe lesions were reported to fulfil the criteria of major affective disorder, with the increases in severity of the disorder being related to the more anterior regions (Lipsey et al. 1983). According to Davidson (1993) evidence for the asymmetry in frontal lobe activity has been observed in studies on negative affect using disgust, fear and sadness, which report findings of relatively greater activation in the right frontal lobe than the left. Positive affect in contrast was linked to greater activation of the left frontal lobe.

1.4.6. Additional cortical areas

Complex emotions and emotional expressions have been reported to involve structures such as somatosensory regions, particularly of the right hemisphere. According to Adolphs (1999) the interpretation of complex emotions and emotional expressions can be achieved by simulation of the perceived emotion, drawing upon the recruitment of somatosensory cortices and subsequently sensing that emotion.

A lesion analysis conducted by Adolphs et al. (1996 p7682) revealed that "...damage which includes the right inferior parietal cortex results in expression recognition impairments that correlate for most negative emotions, especially fear and sadness". Blair et al. (1999) found that right inferior and middle temporal gyri mediated responses to sad facial expressions, whereas Dolan et al. (1997) reported enhanced activity in these structures during perceptual learning of faces. Morris, Ohman & Dolan (1998) stated that the inferior and middle temporal gyri received greater contribution from the amygdala during the processing of fearful faces.

Adolphs et al. (1996) proposed that an extended neural system within the right hemisphere would need to be recruited for the successful processing of facial expressions.

1.4.7. Is there a fusiform face area (solely responsible for the processing of faces)?

FMRI studies have indicated that there is indeed an area within the lateral fusiform gyrus (known as the fusiform face area) specialised in the processing of face stimuli (e.g. Kanwisher et al. 1994; Kanwisher, McDermott & Chun 1997; Puce et al. 1995a; 1995b; Yovel & Kanwisher 2004). This area responds selectively and differentially to faces compared to houses or scrambled control stimuli. Puce et al (1995b) observed that for faces compared to scrambled images fusiform regions within the right hemisphere were more consistently activated, and showed larger volumes of activation, than corresponding areas within the left hemisphere. Other studies have shown that the region known as the FFA preferentially responds to faces compared to cars or butterflies (e.g. Allison et al. 1994), flower or common objects (McCarthy et al. 1997). However, Gauthier et al. (1999) present evidence that processes relying on 'expertise' rather than pure face processing per se also recruit the fusiform. Therefore, the role of a face-specific area is debateable (see chapter 3).

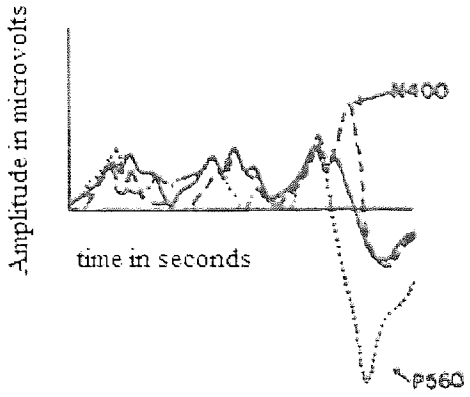
There appears to be sufficient evidence that indicates dissociable neural substrates that differentially respond to distinct emotional expressions (e.g. Adolphs et al. 1996). Aspects of the temporal organisation of such systems have not been receiving adequate attention so far. More recent developments in functional imaging methods which address the temporal development of emotional networks will allow to establish,

for instance, the order in which networks or separate components of networks can be accessed, and in what capacity face processing systems differ from systems that enable the detection and discrimination of facial expressions of emotions.

1.5. Temporal sequence of face perception and facial emotion processing

The investigation of temporal aspects of face processing has concentrated mainly on EEG and therefore studies examining event-related potentials (ERPs). To aid understanding of EEG and ERP findings a nominal trace of an ERP component is included for illustrative purposes (see **FigureA**).

Halgren et al. (1994a) conducted a study in which implanted electrodes were used to obtain recordings from occipital, temporal and parietal regions as well as from the limbic system (amygdala, hippocampal formation and posterior cingulate gyrus) of patients who were awaiting epilepsy elective surgery. They performed a declarative memory task in which patients were presented with unfamiliar faces. In addition to early components, N75-P105, most probably generated in visual cortical areas 17 and 18 (located in and around the lingual gyrus), and components N130-P180-N240 generated in the basal occipito-temporal cortex (fusiform gyrus, areas 19 and 37), Halgren et al. also demonstrated a N310-N430-P630 sequence for responses to faces, which was largest in the hippocampal formation and the amygdala, but was probably locally generated in many sites including the lingual gyri, lateral occipito-temporal cortex, middle and superior temporal gyri, temporal pole, supramarginal gyrus, and posterior cingulate gyrus.



N400 = large negative reflection in reponse to stimulus
P560 = large positive reflection in response to stimulus

FigureA: The EEG recording contains a signal that is extremely revealing about information processing in the brain. This signal can be obtained by time-locking the recording of the EEG to the onset of events such as a person reading a word or watching a face appear on a screen. The resulting activity is called an event-related potential (ERP), and consists of ERP components, which are positive and negative-going fluctuations that can be seen in any ERP waveform. These components are named by their polarity (N for negative; P for positive)

They proposed that during the N310, faces might be multiply encoded for form and identity (inferotemporal), emotional (amygdala), recent declarative mnestic (hippocampal formation) and semantic (supramarginal and superior temporal cortices) properties. These multiple characteristics may be contextually integrated across inferotemporal, supramodal associations, and limbic cortices during the N430, with cognitive closure following during the P630.

Allison et al. (1994) using subdural strip electrode recordings in patients who they presented with grey scale photographs as well as control images found face-specific responses bilaterally in central fusiform regions and in the inferior temporal gyrus with maximal latencies at about 200ms. Some electrodes that showed face – specificity also showed an earlier, non face – specific peak at 150ms.
Swithenby et al. (1998) stated that face – specific processing is broadly consistent across all task and sub – tasks, i.e. image categorisation, image comparison or emotional identification. This pattern of activation suggests that the activity is mainly automatic (i.e. not under conscious control) and cannot be dominated by the initial classification of the image as a face. In addition, they also point out that even though there is a reported dominance of the right hemisphere (right occipito-temporal cortex) over the left hemisphere, inspection of the raw signals indicate that similar processes are also evident in the left occipito-temporal regions, at similar latencies. The face – specific responses are compatible with predominantly bottom – up processing triggered by all objects that

meet some previous face – classification criteria. This seems harmonious with the structural encoding stage of the face – processing model by Bruce & Young (1986).

Swithenby et al.'s task involved a very short exposure time (100ms) that encourages parallel processing. Given the fact that other studies have mostly used longer exposure times, led to the suggestion that this may prompt different processes. This may also explain why the latencies reported here (140ms) are somewhat shorter as those reported in previous studies. The fact that MEG is preferentially sensitive to superficial tangentially oriented cells means that face – specificity will be observable when there are dominant contribution from appropriately oriented and distributed "face cells". The dipole model leaves open questions as to the probable coexistence of other sources within neighbouring cortical regions, individual variability and structural complexity of the brain's geometry and also the probability that the activity is relatively widespread.

Streit et al. (1997,1999), using MEG, observed that the processing of emotional expressions elicited stronger responses than a face detection task in the STS at a latency of 140-170ms, and in addition, at a later latency of 220ms the involvement of the right amygdala was reported in response to facial emotional expressions. Hence, it has been suggested by Haxby et al. (2000) that these regions interact during processing stages of emotions.

An investigation by Ioannides et al. (2000) looked into ways of inferring coupling between brain regions associated with cognitive tasks. By recording MEG data and using magnetic field tomography (MFT) and determining mutual information (MI) between established areas of interest they found that activation in the fusiform gyrus follows early processing within primary and association visual areas and is similar for both, complex objects and faces. They observed a face – specific latency interval at 100 – 200ms when comparing directly the activation within the FFG to faces to that of objects (see also Liu, Harris & Kanwisher 1999). Ioannides et al. (2000) claimed that face – specificity in terms of their MI analysis revealed only feed-forward mechanisms in the right hemisphere and they therefore suggest the existence of an early, automatic face – specific process. In an emotion recognition task they reported the main region of high average MI within the left hemisphere at latencies between 110 – 160ms. Within the right hemisphere linked activity period segments extended from 70ms to 200ms

Scalp electrode studies have demonstrated activity that is specific to faces, and the earliest latencies at which face – specificity has been reported ranges from 154ms

for repeated black and white drawings, to 180ms – to repeated presentation of black and white photographs (Seeck & Grüsser 1992).

1.6. Frequency variation in cortical activity in face and emotional processing

Investigating frequency specificity to emotional and facial stimuli, a study by Ponomarenko et al. (2003) revealed that depending on the behavioural state of an animal, various oscillatory patterns within the amygdala could be observed. In states of emotional arousal, increases in theta frequency have been reported in basolateral areas as well as in the perirhinal cortex of *rats* (Collins, Lang & Pare 1999; Pare & Gaudreau 1996; Pare, Collins & Pelletier 2002). In addition, beta and gamma oscillations were observed within the pre-piriform gyri.

Ray & Cole (1985b) attempted to investigate the effects of attention, emotion and cognition on EEG frequencies and recording sites. They asked their participants to remember sad and happy memories from the past and to imagine future ones, and they also presented their participants with slides showing positive and negative emotional content. Ray & Cole (1985b) observed that the different tasks reflected the differential involvement of parietal areas, observed at "*middle frequencies*" (including alpha). Significant main effects for emotional valence were observed in temporal and parietal areas, with increased beta in response to the positive than the negative conditions, in particular in right hemisphere regions. They concluded that differences in beta frequencies seem to reflect cognitive and emotional dimensions of a task, and that it would thus be useful to measure beta involvement in cognitive and emotional processing.

Nishitani (2003) conducted a study in which responses to pleasant and unpleasant human and primate baby faces were quantified in temporal spatial and frequency domains. They reported findings for MEG and MRS data. Their results revealed five main sources of activation, the middle frontal, hippocampal, superior temporal, inferior parietal and occipital areas in both hemispheres. To unpleasant faces significant peaks were revealed in occipital areas (e.g. BA19) at latencies of 160ms, in the superior temporal gyri (BA22) at latencies of about 214-223ms (left and right), in the middle frontal gyri (BA9/46) at latencies of 271ms and 236ms, in the hippocampal areas at 404ms and 431ms and for the inferior parietal lobules for latencies of 417ms

and 476ms. Pleasant stimuli were observed to evoke responses in the same areas. The Temporal Spectral Analysis (TSE; Salmelin & Hari 1994) (for quantification of event-related suppression or enhancement of rhythms as a function of time) revealed that theta amplitudes in both hemispheres seem to have increased during the presentation of unpleasant stimuli more than during the presentation of positive ones. The TSE curves with the most prominent peak in event-related synchronisation (ERS) (see section 2.5) were obtained for theta frequencies in hippocampal regions of the right hemisphere. Largest effects in terms of event-related desynchronisation (ERD) (see section 2.5) were observed for alpha TSE curves at 400ms in response to pleasant and unpleasant stimuli equally. The observation of preferential increased ERS in hippocampal regions to unpleasant stimuli for theta rhythms is thought to reflect excitatory postsynaptic potentials (Nishitani 2003).

The involvement of the parietal areas, and more precisely, their functional aspects in affective processing were investigated by Schutter, Putman, Hermans & van Honk (2001) using a selective attention paradigm including angry and neutral faces. They reported significant correlations between selective attention to angry faces and right parietal beta, and observed that increases in right-sided baseline beta activity reflected greater avoidant responses to angry faces. Van Honk et al. (1998, 2001) observed that increased levels of cortisol as well as elevated depression were linked to the avoidance responses to angry faces. Reduced depressions scores, elevated mood and vigilant attention to angry faces, on the other hand were linked to approach domains of behaviour Davidson (2000).

1.7. Summary and rationale

As has been shown in this introduction the processing of faces is thought to be regarded as distinct from the processing of objects and other non-face stimuli. Different models have been put forward that link the processing of faces and also variable aspects of faces such as facial expression to distinct structures within the brain (see 5.7. and 1.1.2; see also **Appendix1**). In addition, temporal aspects have been outlined that again attempt to differentiate the neural sequence of activation related to the processing of faces and also that of facial affect.

Therefore, this thesis aims to further elaborate on the issues involved in the processing of faces per se and also in the processing of facial affect. For these reasons,

several experiments are to be carried out, first investigating the processing of faces per se (see chapters 3 and 4, experiments 1 and 2), to establish findings of 'pure face processing module' and to elaborate on neural networks involved in the processing of faces in space, time and frequency. Secondly, the processing of facial affect is to be investigated to see if and how the processing of facial affect differs from that of face perception per se (see chapters 5 and 6, experiments 3 and 4). In doing so the following questions will be addressed: Is there indeed a specialised area within the brain solely responsible for the processing of faces, or can the processing of faces and other objects or indeed the processing of facial affect be linked to the same areas but is differentially processed in time and frequency domains?

The use of magnetoencephalography (see chapter 2) with its precise temporal resolution allows the exploration of the timing of basic neural processes at the level of cell assemblies. Its improved spatial resolution allows sufficient overlap to compare the findings of MEG investigations to those of fMRI. Therefore it is a suitable technique to investigate the detailed and refined processes involved in face perception and the perception of facial affect.

Chapter 2 Magnetoencephalography – an introduction to the methods

This chapter will outline the principles of magnetoencephalography, as this technique, or tool, was chosen to investigate face perception, and the perception of facial emotional expressions in this thesis. The chapter will state, in brief, the methodological aspects and 'physics' of magnetoencephalography, but the main focus will be placed on the ways in which biomagnetic data can be interpreted. The appropriateness and effectiveness of MEG for the investigation of cognitive and emotional processes will in this way be assessed. If the technical aspects go beyond the scope of this chapter, references to relevant readings are provided.

2.1. Introduction: What is Magnetoencephalography (MEG)?

Magnetoencephalography is an entirely non-invasive technique for functional brain mapping that localises and characterises electrical activity of the central nervous system by measuring the associated magnetic fields that derive from the brain. Within the nervous system, neuronal current flows generate associated magnetic fields, and by measuring the intercellular currents of the neurons, information can be obtained about the brain's spontaneous activity or its activity in response to a stimulus. MEG provides excellent temporal resolution in the millisecond time-range and spatial discrimination within 2-5mm. It is therefore able to image neurological function, and to measure the activity of the brain in real time, hence allowing the 'observation of the brain in action'. MEG data can be used to identify function (by using localisation procedures based upon MRI scans) within the healthy and un-healthy brain. Hence, MEG and MRI can be fused into a composite image of function and anatomy, thus allowing considerable clinical potential.

Neuromagnetic investigations aim to identify active brain areas. Two aspects, however, complicate this: (1) there is no unique solution to the inverse problem (see section 2.3.2), thus, appropriate assumptions about the source and volume conductor models need to be made (see section 2.3.2.1); and (2) due to the multitude of simultaneously active brain regions weak signals are usually masked by the strongest signals (e.g. Hari 1991). How these problems can be overcome in order to capitalise utilization of MEG methods will be addressed.

2.1.1. *Physiological source of MEG signals*

Electric and magnetic field changes are due to post-synaptic neuronal currents of a large number of synchronously active, or well-aligned pyramidal cells, which consist of dendrites, cell bodies and axons. The numerous connections between the brain parts are mediated by nerve fibres, which are connected to dendrites and cell bodies via synapses (see **Figure2-1**).

(Illustration by Lidia Kibiuk, taken from http://web.sfn.org/contentPublications/BrainFacts/brainfacts.pdf)

Ionic exchange between the cell and its surroundings produces an equilibrium between diffusion processes, and electrical forces establish a negative potential of approximately −70mV within the cell. Stimulation of cells by means of chemical electrical or mechanical stimulation leads to alterations to the cell's transmembrane potential, finally resulting in cell depolarisation, or hyperpolarisation, at the cell's synapses (Pinel 1997; Wikswo 1989). As a cell is conductive, depolarisation, or hyperpolarisation, cause

current flows within the cell (i.e. intra-cellular current) as well as a return current outside the cell (extracellular current).

Dendritic currents, which arise due to depolarisation and hyperpolarisation, flow roughly perpendicular to the cortex. Due to the convoluted nature of the cortex and the site of cell stimulation, the flow of currents to the scalp surface can either follow a tangential or radial progress (**Figure2-2**). These currents can be measured on the scalp or outside the head, providing they conform to the assumption that the head can be modelled by a spherical conducting medium. Due to symmetry, magnetic fields are produced only by currents generated by tangential cells (**Figure2-3**) (Hämäläinen et al. 1993; Hari 1993; Vrba & Robinson 2001).

(Taken from Vrba & Robinson 2001)

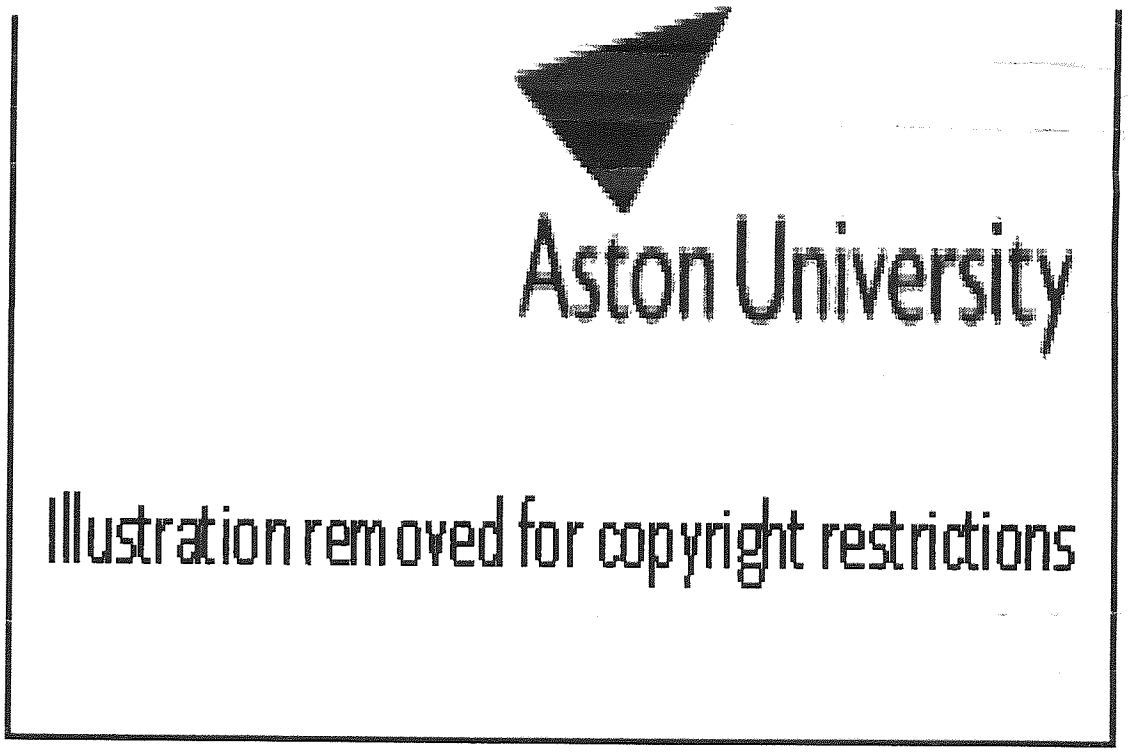
current
(Taken from Vrba & Robinson 2001)

2.1.1.1. Action potentials (AP) and postsynaptic potentials (PSP)

The net current flow in the cortex is as a result of pyramidal cell orientation perpendicular to the cortical surface. MEG signals are thus mainly caused by currents in the walls of the cortical fissures.

Action potentials (AP) and postsynaptic potentials (PSP), excitatory PSP, seem to be possible sources of the recorded MEG signal (see **Figure2-4**). The leading and trailing edges of a propagating AP can be described by two opposite current dipoles that

form a current quadrupole, whereas a PSP produces a dipolar field. Quadrupolar fields diminish more rapidly, as a function of distance, hence AP fields are relatively weaker than PSP fields, and, in duration, are only a fraction of that of a PSP. It is therefore assumed that PSPs not APs are the main contributors to the MEG signal (Hari 1993). The current associated with one PSP produces a dipole moment, and it is possible to calculate its size (for equation and detail refer to e.g. Hämäläinen et al. 1993). For example, a typical dipole moment corresponds to activation of an area of 2-5cm^2. This necessitates concerted activation of tens of thousands of neurons, but during spontaneous rhythmic activity much wider areas may be firing synchronously (Hari 1993).



(Taken from Baillet et al. (2001) IEEE Signal Processing Magazine).

2.2. Data acquisition

2.2.1. Measurements

Magnetic signals can be measured using induction coils that are composed of loops of wire. Spontaneous or evoked magnetic fields generating from the brain induce a current

in these coils and, in turn, a magnetic field in a special device called superconducting interfering device (SQUID) is produced. When a time-varying magnetic flux passes perpendicular to the coil, it induces a time-varying electrical current within the wire (see Hämäläinen et al. 1993). Electric currents within the brain generate weak magnetic fields that are picked up by a superconducting flux transformer. Subsequently, the signal is perceived by a SQUID.

Superconducting coils have little or no electrical resistance; hence the amount of current induced in the coil can track even the smallest changes in the magnitude of the impinging magnetic flux. For simplicity, the SQUID can be thought of as a very low noise device for transducting magnetic fields, or currents, into a voltage. A SQUID acts as a low-noise, high-gain, current-to-voltage converter that provides the system with sufficient sensitivity to detect neuromagnetic signals of only a few femto Tesla in magnitude (Baillet, Mosher & Hari 2001; Hari & Forss 1999). A SQUID can be used as a magnetometer by operating it within a flux-locked loop. The sensitivity of the SQUID to magnetic fields can be enhanced by further coupling it to a superconducting pick-up coil, having greater area and number of turns than the SQUID inductor, alone. This pick-up coil is termed a "flux transformer". The SQUID and induction coils of biomagnetometers are generally maintained in a superconducting state by immersion within a liquid helium bath contained in an insulated cryogenic vessel known as a dewar (for detail see Romani 1987).

Magnetometers and gradiometers, both are detectors used for biomagnetic measurements. SQUID magnetometers (as outlined above) are sufficiently sensitive to detect neuromagnetic signals of only a few femto Tesla in magnitude. In order to allow for an increase in the usage of MEG for clinical purposes, e.g. epileptic surgery, magnetometer based MEG systems have been developed in order to reliably measure from deeper sources (http:/www.4dneuroimaging.com/About4D/Experience.html). Gradiometers allow the measuring of weak signals when the signal source is close to the detection coils (http://www.tristantech.com7prod_biomagnet.html). The usages of axial gradiometers combined with SQUID designs attempts to increase and maximise the signal to noise ratio in order to improve the quality of the recorded signal particularly in demanding urban environments (http://www.ctf.com/products/meg/ctf/overview.html).

2.3. The inverse and forward problems

2.3.1. The forward problem

The forward problem is concerned with the computation of what the output of the gradiometer (see 2.2.1) would be if a certain region of cortex were active. This requires certain simplifications and assumptions, for instance that neural activity is modelled as a set of dipolar current sources, and the head is modelled by a volume conductor. The magnetic field in the sensors can be computed, using volume-conducting theory based on the Biot & Savart Law. The relationship between the magnetic field contributions and its source current element is what is known as the Biot-Savart Law (http://www.aston.ac.u.uk/lhs/research/nri/meg/intro/forward.shtml#volumeconductor) (for more details see the above link).
The calculation of the electrical potential or the magnetic field outside the head, given a particular distribution of current inside the head, is know as the forward problem. The solutions to the forward problem depend on a source model of the properties of the current sources (e.g. location, orientation, and amplitude), and a head model of the electromagnetic properties of the brain, skull and other tissues as electrically conductive media (Kutas, Federmeier & Sereno 1998).

2.3.1.2. Methods of forward solutions

2.3.1.2.1. Head models – spherical head models

The spherical head model is based on the assumptions that the head consists of a set of nested concentric homogenous spherical shells representing brain, skull and scalp.

2.3.1.2.2. Head models – realistic head models

Although the spherical head model works well indeed, the heads of human beings are anisotropic, inhomogeneous and not spherical, thus contradicting the assumptions of the spherical head model approaches. Therefore, the use of anatomical information obtained from method such as MRI or CT allows for improvements. To solve the forward problem, surface boundaries are first extracted for brain, skull and scalp and are

subsequently included in boundary element methods (BEM) in order to calculate the forward field (Kutas et al. 1998). This method, although it indicates an improvement to the methods relying on spherical head models, still assumes homogeneity and isotrophy within the regions of the head, thus assuming that the conductivity within one shell (brain, skull and scalp) are constant. This led to the development of the three dimensional finite element methods (FEM), which appear able to measure the entire head volume at several millimetre resolution, thereby accounting for fluid-filled spaces, local inhomogeneities and anisotropies arising from white matter fibre tracts (George et al. 1995; Kutas et al. 1998). Hence, FEM would provide a rather powerful approach to solving the forward problem.

2.3.2. The inverse problem

The deduction of neuronal currents from measured external electrical potentials or magnetic fields is what is known as the inverse problem. Helmholtz (1853) was amongst the first to show that no unique reconstruction seems to exist for a current density distribution in a volume conductor for a given electrical potential distribution in the surface of a conductor. Consequently, there is no unique solution known to overcome the inverse problem (e.g. Williamson & Kaufman 1990; Hämäläinen et al. 1993; Hari, Levaenen & Raji 2000). Suggestions that would allow limiting the number of potential solutions, thereby forming reasonable estimates of source configuration include imposing anatomical and, or, neurophysiological constraints. Some assumptions about the source have to be made to address the inverse problem. Consequently, the validity of the modelling assumptions determines whether or not a solution to the inverse problem can be regarded as correct, or not. Several techniques have been applied to the inverse problem, and some will be briefly outlined below.

2.3.2.1 Methods of inverse source solution

2.3.2.1.1. Dipole fitting techniques – current dipole model

If a small area of activated cortex is centred at a particular location, and the observation point is some distance away, the primary current distribution can be established or approximated by an equivalent current dipole. However, as brain activity does not really

exist in terms of current dipoles, the dipole model is only a convenient representation for coherent activation of larger numbers of pyramidal cells (Baillet, Mosher & Leahy 2001). The popularity of the dipole model is due to the fact that primary current sources can always be broken down into smaller parts, which then represent equivalent current dipoles. Here, however, the problem arises that too many small regions and thus their dipoles would be required to represent a large region of coherent activation, in which case they would be better represented by a multipolar model (Baillet et al. 2001). In addition, the dipole model presumes that one or a few dipoles are able to describe collected data. The procedure to obtain these dipoles involves varying the position and the moment of a dipole until the squares of differences between the measured data and the forward solution of the assumed dipole are minimal (for detail see Baillet et al. 2001).

Shortcomings of algorithms for the calculation of dipoles, however, may result in the dipole position estimated corresponding to local minima, thus, a different position resulting in smaller minima would have led to a more adequate description of the data. Additionally, the non – uniqueness of the inverse problem would require an a priori estimate of the number of dipoles. This estimate could be based on anatomical or physiological information. Furthermore, decisions would also need to be made regarding the nature of the dipole, i.e. would a moving, a fixed or a rotating dipole describe the data best.

2.3.2.1.2. Deviation scan

The deviation scan method is similar to a dipole fit method, but is repeated for a number of locations. On each location a measure is calculated accounting for the possibility that a single dipole in that location could account for the measured MEG (or EEG) signal. The results for the deviation scan are independent, however, hence adding new information and consequently can be used to verify the dipole fit. The difference between the measured and forward calculated field need to be determined for each location, resulting in the square of the inverse of the lowest deviation in the used time range. The larger this result appears to be, the more likely is it that a dipole at this location describes the measured activity adequately. The deviation scan can offer information about the location and number of successively active centres. An advantage of this method is that a global minimum will always be found, i.e., if a deviation scan

shows a "hot spot" that coincides with the location of a single dipole fit, the assumption that a dipole that a dipole in that location can be measured can be seen as confirmed. Yet, if several sources are generated simultaneously, results of the deviation scan might be misleading, i.e. if a global maximum, and thus a more "smeared", or widespread pattern would be revealed by the deviation scan, one would need to consider that the underlying dipole model may be wrong (see Huiskamp 2001, Hämäläinen et al. 1993). In sum, the deviation scan could be seen as providing a confidence interval for a single equivalent dipole.

2.3.2.1.3. Multiple signal classification (MUSIC)

Multiple Signal Classification (MUSIC) was developed in the array signal processing community and subsequently adopted for EEG and MEG source localisation (Mosher, Lewis & Leahy 1992). In its approach it resembles a dipole fit, or dipole sources, most prominently with fixed orientations, but it can also be extended to moving dipole methods. It works by searching for sources independent of each other in time, i.e. at each location it tests for the presence of a source, and if a source is found present, a generalised 3 by 3 by 3 matrix is generated, sufficient for the computation of the dipole orientation (Mosher et al. 1992; Baillet et al. 2001). Once all the sources are found, time-dynamics are established, i.e. the resulting signal space is used to examine whether the existence of dipoles is plausible at various time–independent locations. If activity cannot be assigned to sources at fixed locations it is considered noise, and thus excluded. If several synchronously active sources are responsible for the recorded signals then the results of the MUSIC procedure may have to be considered misleading, i.e. this approach is limited by the fact that it is likely to fail when source are strongly correlated (Sekihara et al.1994; Mosher et al. 1992). In order to improve the method, the recursively applied and projected (RAP) MUSIC approach was developed (for details see Baillet et al. 2001; Mosher et al. 1992).

2.3.2.1.4. Low-resolution brain electromagnetic tomography (LORETA)

This inverse solution method computes a dense 3-D distribution where electric sources are located at each grid point in the brain in terms of current density values (A/m^2). The

strength and direction of the activity at each of these grid points determine the electric and magnetic field that can be measured (Pascual-Marqui, Michel & Lehman 1994). One characteristic of the LORETA linear solution is the proposition that activity at any voxel must be as similar as possible to the average activity of its neighbouring voxels. This property corresponds to the fact that neighbouring neurons show more highly synchronised activity than neurons that are far apart. The intention of LORETA therefore is to find the smoothes possible solution that can be applied to establish the optimal and unique 3-D distribution that localises the observed electrical activity in the brain. The smoothness constraint, however, results in relatively low spatial resolution; hence in the LORETA method a "blurred-localised image" of neuronal activity is produced (Pascual-Marqui et al. 1994, p.50). Thus, a low-resolution tomography of electrical activity at every moment in time is so generated, with the advantage of high time-resolution of the electric-magnetic signal being maintained. Hence, LORETA contains sufficient information for the approximate (blurred) determination of a 3-D source, without the need for any precise a-prior information or constraints.

Experimental evidence in support of LORETA localising neuronal activity with low errors has been reported by, e.g., Haalman & Vaadia (1998), Menendez et al. (2001), Pascual-Marqui (1997), Pascual-Marqui et al. (2002), Phillips et al. (2002) and Sukov & Barth (1998).

Limitations of LORETA are its spatial resolution, yet this could be improved by combining LORETA and information derived from MRI images. Instead of using a spherical model, real head shape models would be advantageous. A further shortcoming relates to the use of analyses that rely on averaging signals across participants, given the differences in brain and head shapes, and intra-individual functions. This applies to cognitive tasks, or cognitive processing in particular.

2.3.2.1.5. Distributed source models

Distributed source models do not make any assumptions as to the number of sources that could be underlying the electrical, or magnetic signals recorded. The basis of this approach is given by the fact that a volumetric grid of possible locations could first be produced, subsequently analysed and thus result in an estimated configuration of neural activity that matches the observed one. Examples of distributed source approaches are

the minimum norm estimate and beamforming methods such as synthetic aperture magnetometry (Hari & Forss 1999).

2.3.2.1.5.1. Minimum-norm estimations and minimum-norm least-square inverse approaches

Minimum Norm Estimation (MNE) approaches are based upon the assumption that source configurations using the least energy as well as minimising the differences between measured and observed fields are able to account for the measured data. This also implies the assumption, or constraint, that the source configurations lay on the most superficial layer of the source space (Hillebrand et al. 2004).

The MNE is a source reconstruction technique that aims to localise electrical activity on the human cortex for recordings of magnetic fields outside the head. The standard approach minimises the current density distribution of an underlying dipole moment, i.e. a vector field is calculated on a predetermined grid, where each vector represents a current dipole. As there are, generally, more source locations than sensors, a problem is inevitable. The standard minimum norm approach considers the current density distribution with the minimal norm a possible solution. A major disadvantage of this method is that the reconstructions appear rather smeared (Pascual-Marqui 1999).

The minimum-norm least square inverse approach looks for an inverse solution that minimises the residual error, such that the sum of squares of the differences between the measured and predicted field patterns has minimum power among all the least square solutions (Wang 1993). It requires a-priori assumptions for defining the source space in which a set of dipoles approximates the primary current distribution. Additionally, assumptions are also made as to the imaging space being in the same location as the true source space produced by the magnetic field. This, however, is not always possible, due to, for instance, co-registration errors. The MNLS approach requires many sensors in order to obtain an adequately detailed image of the reconstructed source. However, the source reconstruction approach using MNLS is biased towards the solutions that occur nearest to the sensors (due to the minimum norm constraints). Also, for a discrete source the solution appears to be 'spread out' resulting in a blurred image of a point source, and consequently leads to difficulties in interpreting the data (Hari 1991).

2.4. Synthetic Aperture Magnetometry

2.4.1. Why choose SAM?

In the past, the analysis of MEG data has been concerned mainly with averaged evoked response paradigms, assuming that brain activity is time-locked to external events. While the averaging of MEG (and EEG) signals enhances signal-to-noise ratio, thus permitting quantitative measures of specific brain activity to be reproducible, only a small portion of the brain is accessible to this method. The primary and sensory motor areas activate synchronously with external events; yet, areas implicated in the processing of higher cognitive functions have more inconsistent latencies. Therefore, averaged signal of time-variable events would not be able to accurately reproduce the character of their sources (Vrba & Robinson 2001). Partly due to these reasons and because of the development of whole-head MEG sensor arrays, three dimensional source estimation methods have been applied more widely. One such method is Synthetic Aperture Magnetometry (SAM), which is appropriate for the analysis of non-averaged MEG signals and provides exceptional spatial resolution without a-priori specification of the number of active sources (Vrba & Robinson 2001; Cheyne, Barnes Holliday, & Furlong 2000).

SAM attempts to explain only parts of the data that it could explain. SAM is an adaptive, minimum variance beamformer technique, analogue to those used for achieving high selectivity from radio antenna arrays (Vrba 1997). Beamformers construct a spatial filter for a selected point in space (target voxel) such that the filter output is a linear combination of the measurements over time, with a weight vector being represented for each target voxel also. The weight vector is determined by minimising the source strength power. The SAM beamformer is four–dimensional as it is sensitive to both voxel location and source orientation, thus, exhibiting better spatial resolution than conventional beamformers (Vrba & Robinson 2001). Since signal to noise ratio decreases with increasing source depth, the influence of uncorrelated noise projected by the beamformer also increases. Therefore it would be advantageous to use the ratio of the estimated source power to the estimated projected (uncorrelated) noise power for constructing images of source power over large areas of the brain (Van Veen, Van Drongelen, Yuchtman, & Suzuki 1997). Differences in source power are calculated

at target voxels for active and control windows using pseudo – t statistics (Robinson & Vrba 1999). SAM images can be reconstructed for specific frequency bands of interest.

2.4.1.1. How does it work?

The brain is separated into many target locations, or, voxels, with an optimal spatial filter being computed for each target voxel linking the signal at this target location to the signal recorded at the MEG sensor location. Each spatial filter is designed so that the signals from the location of interest are unperturbed, whilst signals from other locations are being attenuated. This beamforming of the spatial filter is achieved by selectively weighting the contribution of each sensor to the overall output of the spatial filter. The output of the spatial filter is an indication of the neuronal activity at that target location. A spatial filter is sequentially constructed for a set of voxels in the brain; hence, a spatial image of the brain activity, known as statistical parametric maps (SPMs) can be formed. Such SPMs show peaks in brain regions involved in the task performed by the volunteers in the scanner (see **Figure2-5**).

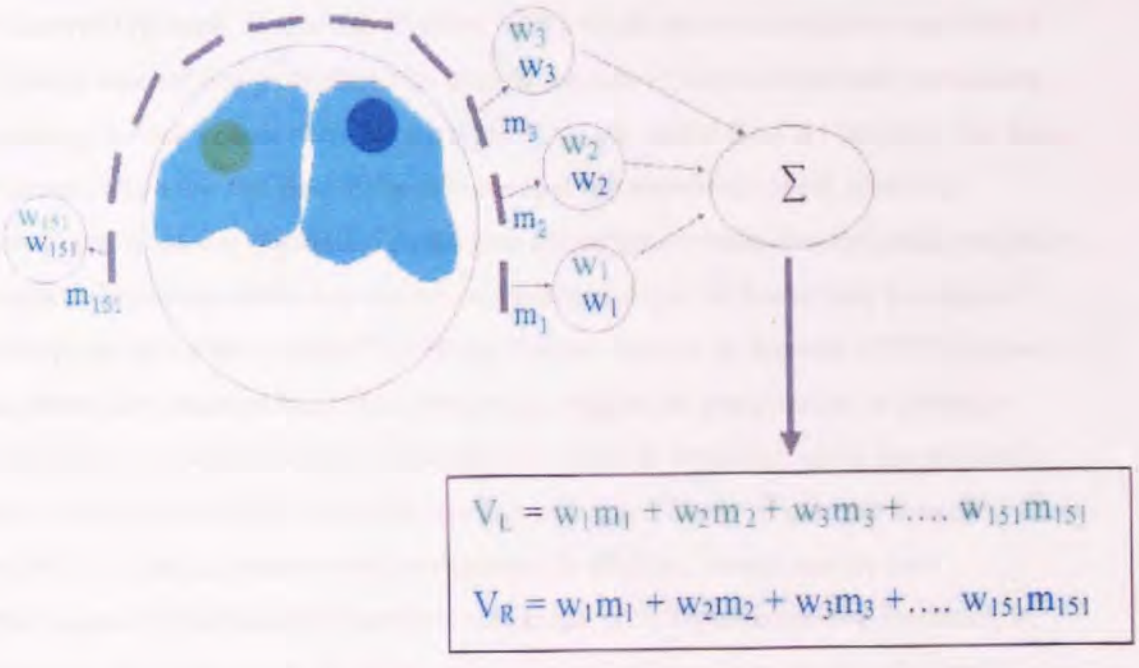


Figure2-5: Theoretical model of the SAM beamformer approach to resolving MEG data. A hypothetical signal distribution is indicated and the outputs of the spatial filter for two target voxels (V_L – green and V_R – blue) are given. Differential weightings (w) are given to signals recorded at each of the 151 sensor locations (m) depending on their distance from the target voxel, and the sum of all weighted signals is calculated.

2.4.2. Advantages of beamforming approaches

Beamformer techniques are performed on the data's co-variance matrix, and can thus be used to localise event-related desynchronisation (ERD) and event-related synchronisation (ERS) (further described in section 2.5). There is no need for averaging, thus, brain responses that are poorly time locked to the stimulus presentation can be studied. This is particularly advantageous for the investigation of higher cognitive functions. The beamformer removes signals that are not from the target location thereby increasing the signal-to-noise ratio for the region of interest.

2.4.3. Group MEG imaging

2.4.4.2. Why do group studies

Group studies are performed when "typical" characteristics of a population are to be investigated in order to establish qualitative aspects of normal functional anatomy or processing, while allowing for the fact that in some volunteers this effect might not be observed (Friston, Holmes & Worsley 1999). Such inference could be regarded as sufficient when trying to characterise generic aspects of human functional processing. Knowing that such characteristics are typical is more useful than not knowing this fact. However, when the aim is to make inferences at the population level, studying participants from that population could give rise to the problem that activation could be assumed significant across a group when, in fact, it might be due to only a couple of participants within the sample. Therefore, Friston, Holmes & Worsley (1999) proposed that inferences about an individual or a group, require the computation of average activation to the within–subject variability. To make an inference about the population from which an individual has come, average activation has to be compared to the variability of that activation over participants. In addition, group studies are advantageous if the research interest is concerned with higher cognitive functions. In such tasks, activation is likely to be more widely distributed across the volunteer's brain, and individual signals could be relatively weak. Hence, to infer some spatial characteristics to a functional task, the results obtained for individual participants need to be considered as part of a group.

2.4.5. Spatial Normalisation

2.4.5.1. What is spatial normalisation and what does it achieve?

Spatial normalisation is the registering of participants' brain images to a template brain image for statistical investigation. Inter-subject averaging to allow determination of group results, using, for instance, statistical parametric mapping (SPM), requires the images to be transformed into some standard stereotactic space (e.g. Friston, Ashburner, Frith, Poline, Heather & Frackowiak 1995). When warping a series of images to match a template, however, it is inevitable that volumetric differences will be introduced into the warped image. For example, if the temporal lobe of a volunteer has half the volume of that of the template, then its volume will be doubled during spatial normalisation. This will provide a potential confound for group studies. In addition, many sulci are common to all brains, but this is not the case for all. Generally, the primary sulci, which are formed earliest and tend to be quite deep, are the ones that are the most consistently present. Later developing ones are much more variable. Hence, parts of some sulci can be objectively matched, whereas others simply cannot (Ashburner & Friston 2001). Classical voxel-based-morphometry (VBM) assumes that the warps were sufficiently smooth hence; these volume changes could be ignored. Advances in normalisation techniques now allow for high-resolution warps.

There is a near infinite number of ways in which the shapes of brains can differ among populations. Thousands of parameters would be required to precisely describe the shape of a brain at the resolution that a typical structural MRI is capable of. Smoothing the data by e.g. 20mm will make the tests more sensitive to regional differences in structures of about 20mm extent. Additionally, smoothing helps to compensate for inexact spatial normalisation (Ashburner & Friston 2001) (for more detail see Friston, Ashburner, Frith, Poline, Heather & Frackowiak 1995).

2.4.5. Group SAM

Using SAM, SPMs are generated for each individual, yet, neither statistical inferences can be inferred nor assumptions be drawn as to how this data relates to groups or samples of population (see Section 2.4.4.2.). Hence group statistics need to be investigated, and this can be achieved using Group SAM.

Once SPMs are obtained for several participants, these can be averaged to reveal shared brain responses to a particular task. This is particularly advantageous when investigating cognitive task as here brain responses might be fairly weak or widely distributed across the cortex (see Section 2.4.4, and Friston, Holmes & Worsley 1999), thus detection might be enhanced when generated across a number of participants. In order to determine group results, the individual SAM images need to be spatially normalised (see above). This can be achieved using SPM99. Once each individuals SAM data is normalised, t images of group averages are created. These can be visualised using mri3dx, using a template brain (Singh, Barnes, Hillebrand, Forde & Williams 2002).

2.4.6. Statistical non-Parametric Mapping

Statistical non-Parametric Testing (SnPM) is a method to provide statistical interference, or support for the interpretation of tomographic data. It is a nonparametric alternative to SPM, based on permutation test theory. Permutation tests quantify those results that have not been expected ("surprise outcomes") in terms of probability, and establish significance levels for these. Permutation tests may require weak distributional assumptions, concerned with degrees of exchangeability. Non-parametric approaches work on the basis of randomisation testing, i.e. group differences can, for instance, be tested against 1500 permutations (randomly chosen group configurations), the multiple comparison problem implicit in the standard voxel-by-voxel hypothesis testing framework is inherently accounted for (for detail see Nichols & Holmes 2002; Holmes et al. 1996).

Using SnPM, analysis can be performed at voxel level using a multiple-subject single condition design. Here, tests can utilize both, the unsmoothed T-statistic and a pseudo-T-statistic. Analyses can also be performed at cluster-level, to assess whether the size of clusters are significant. Using non-parametric permutation testing, cluster-level inferences estimate whether a large connected cluster of moderately high t-values may still reach statistical significance against the null hypothesis due to size, even if no individual voxels reach statistical significance. Spatial resolution however is being traded in against sensitivity.

The cluster–level analysis proceeds in the following way: a t-map is being generated at each permutation iteration and then thresholded at a certain value (primary

threshold). Subsequently, the largest connected clusters, which exceed this threshold, are determined, generating the permutation statistic. At the end of the permutations, a cluster-size threshold can be set to infer the probability of finding a connected cluster greater than the set threshold. By chance this would be less than 0.05. Within the unpermuted t-map, clusters, which appear to be spatially larger than the set threshold, are hence significant at $p < 0.05$. Variance smoothing with a Gaussian kernel width of 20mm is commonly used in our laboratory (for details see Singh, Barnes & Hillebrand 2003).

2.4.7. Time Frequency Representations

To obtain information that cannot readily be seen in the raw signal, mathematical transformation can be applied to extract additional information in time and frequency domains. The most popular used transformation is the Fourier Transform (FT). Other transforms that have successfully been applied are Hilbert Transform, Short-Time Fourier Transform (STFT), Wigner Distributions and Wavelet Transform (WT). Each of these techniques has their own area of application, their advantages and disadvantages. The FT and WT, for instance, can be regarded as reversible transforms. When the time localisation of a spectral component is of interest, and often it is beneficial to know time intervals of particular spectral components, Time Frequency Representations (TFR), such as WT are needed.

2.4.7.1. Fourier Transform

When using FT, signals get decomposed to complex exponential functions of different frequencies. These individual signals still represent the ONE original signal, but now correspond to different frequency bands. In a 3-D representation, the time by frequency by amplitude interactions would be able to show which frequency exits at which time (for detail see http://users.rowan.edu/~polikar/WAVELETS/WTpart1.html).
Here, however, a first drawback has to be mentioned, namely that of Heisenberg's Uncertainty Principle - it seems impossible to accept that something can be at a same time, a particle (an entity confined to a small space) and a wave (spread out over a large region of space (Capra 1983). Thus, strictly speaking, we cannot, know exactly what frequency exists at what time-instance, but only what frequency-bands, or spectral

components, exist at what time-intervals. This represents a problem of resolution (for detail see http://users.rowan.edu/~polikar/WAVELETS/WTpart1.html).

2.4.7.1.1. Short Time Fourier Transforms (STFT)

STFT represents a revised version of FT. The difference between FT and STFT is that in STFT the signal is decomposed into signals so small that they can be assumed to be stationary. Hence instead of a time – function, a window function (w) is chosen. The width of w represents the segment of the signal, which is assumed stationary. In a nutshell, the STFT of a signal is FT of the signal multiplied by the window function (for detail see http://users.rowan.edu/~polikar/WAVELETS/WTpart1.html).

STFT obtains peaks, which correspond to different frequency components, but unlike in FT the peaks are located at different time–intervals. Hence it can be established **what** frequency components are present within the signal and **where** they are located in time. Yet, the problem of resolution remains. As the STFT window is finite, the frequency resolution gets poorer. The time-resolution gets better when the time windows get narrower, yet at the expense of the frequency resolution. An alternative was found in wavelet transforms (WT), which appears able to solve the resolution problem at least to some extent (http://users.rowan.edu/~polikar/WAVELETS/WTpart1.html).).

2.4.7.1.2. Wavelet Analyses: Continuous Wavelet Transform (CWT)

CWT was developed to overcome some of the shortcomings of STFT as outlined above. The transformation procedure is similar to that of STFT, i.e. a signal is multiplied by the function (wavelet). The transform is computed separately for different segments of the time-domain signal.

Wavelet means small wave, and the smallness refers to the condition of the window function being of a finite length. Wave also refers to the condition of the function being oscillatory (for details see http://users.rowan.edu/~polikar/WAVELETS/WTpart1.html).

2.4.8. *Problems of sulcal and gyral sources*

It has often been stated that MEG is insensitive to the detection of activation in deep-seated structures, and also to the detection of sources of radial orientation (e.g. Hari 1993). This has been attested by the observation that magnetic fields tend to drop when the distance to the electrical activity increases. In addition, as mentioned before it has also been observed that when using a spherical head model, currents of radial origin do not produce a magnetic field (Helmholtz 1856). However, it has been demonstrated that deeper sources can be detected (e.g. Tesche 1996) although the accuracy has been traded in. Research by Hillebrand & Barnes (2003), based on realistic cortical structures indicates that the sensitivity of MEG is not limited by source orientation, i.e. radial sources could be detected, and that source depth is not a limiting factor with respect to sensitivity and accurate detection as long as there is sufficient signal to noise ratio. Thus, the recording of longer epochs or more trials would prove advantageous if the regions of interest in a functional imaging study are deeper-seated structures.

2.5. Data Interpretation

2.5.2. *ERS and ERD*

As outlined earlier, SAM can be applied to non-phase-locked data. It therefore renders itself suitable to investigate cognition-related changes in oscillatory power (Basar et al. 2001; Singh et al. 2002).

When performing specific tasks, e.g. sensory, motor or cognitive tasks, task related changes would occur in specific frequency bands, in appropriately localised areas of the brain. These changes in oscillatory power correspond to either decreases of power in a specific frequency band, or increases, and are hence known as Event – Related Desynchronisation (ERD) and Event – Related Synchronisation (ERS), respectively (Pfurtscheller & Lopes da Silva 1999).

These changes can either be phase – locked to the stimulus onset, or time – but not phase – locked to the stimulus. ERD and ERS are generated by changes in one or more parameters that control the oscillations of neuronal networks, and reflect changes in activity of local interactions between main neurons and inter-neurons that control the

frequency component of the ongoing EEG or MEG. Thus, ERD and ERS are highly frequency band specific, and the frequency band of interest needs to be stated when referring to ERD and ERS (Pfurtscheller & Lopes da Silva 1999).

The observation that certain events can block, or desynchronise, ongoing (alpha) activity was first reported by Berger in the 1930s. He noticed that these changes were time – locked to the event, but not phase – locked, hence, linear methods such as averaging would not have been able to detect these changes (Pfurtscheller & Lopes da Silva 1999).

ERD is connected to increased activation in a given cortical area, and is thought to be related to task-related, or transient, uncoupling of this area from a larger cortical network. ERS, on the other hand, seems to be linked to reductions in activation of task-irrelevant areas, possibly associated with inhibition (Neuper & Pfurtscheller 2001).

A disadvantage when describing ERD and ERS within the data is the fact that these phenomena are highly variable between participants (Singh et al. 2002). Studies by Singh et al. (2002) investigating cognitive tasks, such as letter fluency and biological motion have reported significant oscillatory power changes, which can be described as task – related ERD. Here the question may be raised as to why a cortical area is described as being 'active' when in response to a given task oscillatory power decreases? Singh et al. argued that consistency across different functional imaging modalities (e.g. use of metabolic imaging techniques as in fMRI and PET) with respect to the detection of 'active' areas requires the acceptance of increases in local haemodynamic responses might reflect local increases in mean neuronal activation. Hence, a link is suggested to exist between ERD and increases in neuronal activity as indicated by increases in the Blood – Oxygenated Level Dependant (BOLD) response.

Studies that look into neuronal modelling and simulations have suggested that increases in the mean level of neuronal activation in specific areas may result in decreases of oscillatory power, i.e. ERD, in particular at low frequencies, yet, simultaneous increases in oscillatory power, i.e. ERS, may also be observed in high frequencies (Pfurtscheller & Lopes da Silva 1999).

However, increases in cortical power have been observed in for instance gamma frequencies where bursts of increased activity have been reported in response to the successful perception of ambiguous figures (e.g. Tallon-Baudry et al. 1997, Rodriguez et al. 1999). The debate regarding the phenomena of ERD and ERS will be considered throughout and re-visited in the general discussion (see section 7.2.1).

2.5.1.1. Quantification of ERD and ERS in time and space

The signals recorded by EEG and MEG can be quantified and subsequently be displayed relative, as percentage, to the power of the same EEG / MEG derivations recorded during a reference or baseline period (i.e. before the occurrence of the event): ERD % = (A – R) / Rx100 (A is the power in the frequency band after the event, whereas R is the power in the frequency band before the event).
Event – related changes in EEG and MEG signals need time to develop (and recover); this seems particularly true for alpha (Pfurtscheller & Lopes da Silva 1999).

2.6. Relationship to other functional imaging techniques

2.6.1. EEG

2.6.1.1. Relationship to EEG measurements

There appear to be more similarities than difference when comparing EEG to MEG. However, the generated maps in MEG and EEG do differ and it has also been suggested that EEG maps may indeed reveal additional source of cortical activity (Cohen & Cuffin 1983). EEG measures the difference in voltage or potentials between electrode sites across the scalp, using a reference electrode to provide for a comparison point that allows comparison to a potentially electrically silent point.

The differences in conductivity of brain tissue, skull and scalp are thought to significantly influence scalp-recorded electric signals, yet they do not affect the recorded magnetic field as intensely as they disturb EEG pattern. Hence, scalp potentials are untrue reflections of the brain's electrical currents, or events; yet, magnetometers measure the absolute magnitude of the magnetic field without the need for a reference point (e.g. Hämäläinen & Sarvas 1989; Hari 1993). Thus, an advantage of MEG over EEG is the fact that the neuromagnetic signal can penetrate the skull and scalp without distorting the signal. Therefore, the spatial resolution is higher in MEG than it is in EEG.

A further difference lies in the fact that MEG and EEG measure different neuronal population. In EEG, dipoles oriented in any directions can be measured, yet

EEG recordings are more sensitive to radially oriented dipoles (even in the presence of tangentially oriented sources) (Cohen & Cuffin 1983). MEG signals on the other hand are more sensitive to tangentially oriented sources, or dipoles, as in the spherically symmetric volume conductor a radially oriented dipole does not produce a magnetic field outside the volume conductor (DeMunck 1989). When tangential current sources are however located close to the surface of the brain, MEG-based dipole modelling is an adequate tool for locating the sources. Therefore, the simultaneous recording of EEG and MEG would allow for the studying of deep and radial sources as well as the localising of tangential components of brain activity (Huotilainen et al. 1998).

EEG, compared to MEG, has a low spatial resolution, which is thought to be due to activity being recorded at few cortical sites. However, MEG and EEG seem to have comparable temporal resolution. It is difficult to see how EEG could complement the MEG methodology. However, as noted above, the reduced sensitivity observed to radial sourced in MEG does not provide a problem for EEG recordings, where these can be assessed effectively with EEG. In addition, MEG recordings cannot be undertaken on people who have metal implants, who can however take part in EEG investigations. An increased user-friendliness in EEG operations (particularly acquisition) and advances in its transport possibilities allow for a more mobile application for ambulatory (clinical) as well as research purposes (Rippon 2006 in press).

2.6.2. fMRI and PET

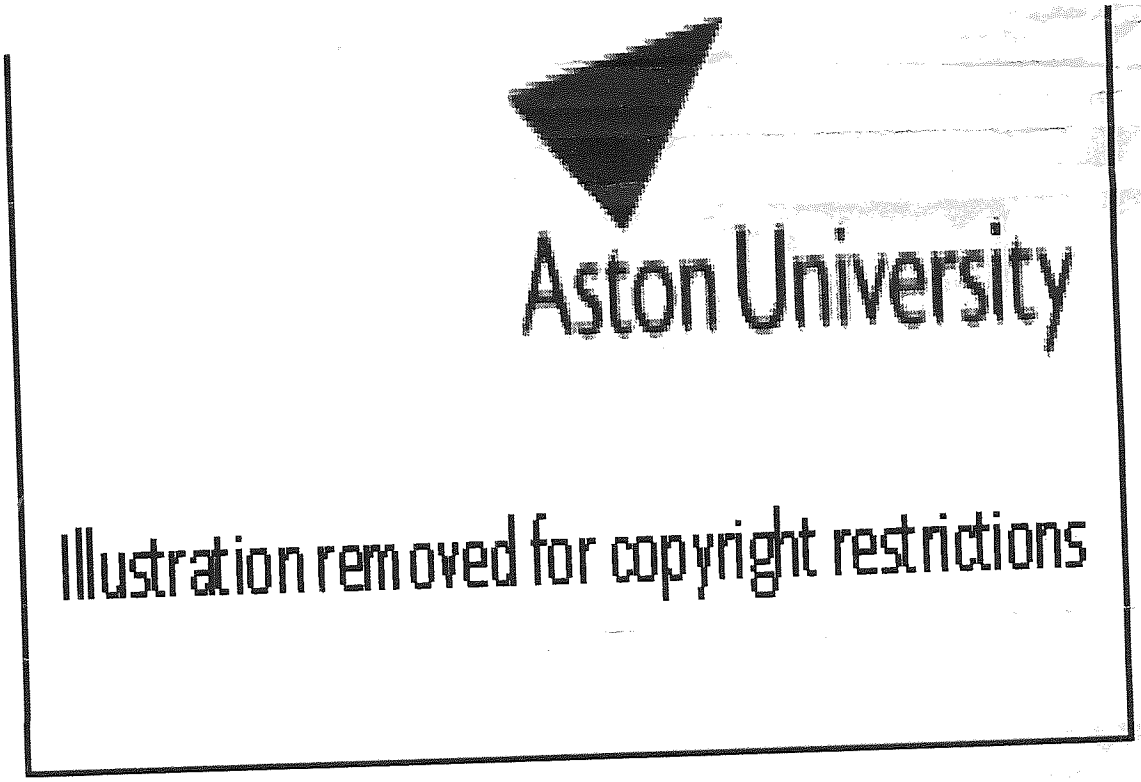
As stated before, MEG provides a direct measure of neuronal activity by estimating the magnitude and direction of the current flow. In contrast, fMRI and PET are based on correlates of neuronal activity such as the haemodynamic or metabolic changes and are thus more secondary consequences to the changes observed in cortical neural activity. This implies the assumption that the local metabolic changes are indirectly related to the increases in neuronal function. Therefore, fMRI and PET are thought to be slow and indirect measures of electrical activity. These techniques are also thought to be somewhat more invasive. FMRI subjects participants to high static magnetic fields and a small alternating radio-frequency field, whilst using a large coil to detect weak radio signals arising from the head. PET, on the other hand, requires the injection of radioactive tracers into the participants' bloodstream. The blood oxygenation level dependant in fMRI is the method for visualising the haemodynamic change, using the

level of blood oxygen as an indicator of increases in activity. The BOLD signal increases when the oxygenation of the blood decreases (Aine 1995).

The spatio-temporal resolution of the fMRI signal needs to establish whether the BOLD signal reflects the changes of blood flow in large vessels or in the finer mesh structures of the vascular network. This is important, as it would have implication for the spatial resolution of fMRI. Oxygenation levels in large veins could reflect activity that originates from large areas of brain. If this is the case, average activity would be represented over these areas, resulting in the neural resolution being relatively poor. Evidence has been reported by Engel et al. (1997) who localised the fMRI signal with a precision of 1.1mm, thereby suggesting that the signal seems to arise from vessels that serve a small region of the brain.

The temporal resolution of the fMRI signal is not ideal for the accurate resolution of neural response in the sub-millimetre range, given that they are secondary phenomena during which many cortical responses take place. The temporal resolution of fMRI compared to MEG is approximately 1s, although fMRI data can be collected at 50ms to 100ms time-intervals. For PET, the temporal resolution is in the tens of seconds range.

Comparing fMRI and PET to MEG again highlights some of the advantages of MEG, such as its non-invasiveness, its direct measurement of electromagnetic responses, its excellent temporal resolution, and its adequate spatial resolution. However, the spatial resolution does not match that of fMRI and PET, but advances in the application of beamformer techniques have lead to improvements in spatial resolutions. Drawbacks, however, are the non-uniqueness of the inverse problem, and the fact that the MEG signal can be easily contaminated by noise. The latter, however, can be overcome by the use of magnetically silent environments.



(from http://www.ctf.com/products/meg/ctf/overview.htm)

2.7. Applications of MEG to face perception research

MEG allows the precise location of neuronal activity. While morphological observation of the brain has progressed with MRI to the point of viewing cerebral changes directly in full detail, the functional observation of brain activity is still incorrect and imprecise. Besides classical EEG, methods of functional observation such as single photon emission CT (SPECT), positron emission CT (PET) and fMRI – only detect neuronal activity indirectly from changes in blood flow, metabolism or synaptic activity. Neuronal activity may correlate generally with those factors but discrepancy is likely. It

has been shown in chapter 1 that models and theories exist that not only link the processing of faces and facial affect to specific regions within the brain (see section 1.4.7 and 1.4.8) but also to latencies (see section 1.5). Less evidence exists which associates the processing of faces to specific frequency bands.

As has been shown in chapter 2, MEG can provide precise temporal resolution that allows the exploration of the timing of basic neural processes at the level of cell assemblies. The application of MEG to (low) sensory processing has shown its usefulness in the investigation of spatial, temporal and frequency specific information. Application of the technique to higher level cognitive processes such as language processing and the processing of visual stimuli such as faces (e.g. Sams et al. 1997; Liu, Harris & Kanwisher 2001) has provided some insight as to the advances that can be drawn from the investigating the temporal characteristics associated with the processing of face.

The detailed processes that characterise face perception and the processing and identification of facial emotions require assessments that allows for the quantification of subtle differences that occur in space, time and specific frequency bands. SAM does not rely on a-priori assumptions about the number of active sources (as do dipole methods), it does not rely on signal averaging and is able to analyse non-phase locked stimuli. Using SAM, task-related changes of spectral power can be obtained in terms of frequency specific increases or decreases of event-related spectral power. Therefore, MEG and SAM were selected to investigate face perception (chapters 3 and 4) and facial affect (chapters 5 and 6).

Chapter 3 Does the processing of faces differ from that of houses?

3.1. Introduction

3.1.1. Is face processing special?

Faces are special visual stimuli and the nature of the neural substrates associated with their processing is the subject of considerable debate. A central issue concerns whether there are domain specific mechanisms dedicated to face processing alone (e.g. Kanwisher, McDermott & Chun 1997) or whether the processing of faces is merely reliant upon more domain-general mechanisms which are also capable of processing non-face objects (e.g. Gauthier et al. 1999; Tarr & Gauthier 2000).

Evidence from neurological patients indicates the existence of a double dissociation for face and object recognition, and functional imaging data from healthy controls augments these claims (Kanwisher et al. 2000). A number of studies have thus sought evidence for the differential processing of faces and control stimuli. Haxby et al (1994) and Sergent, Ohta & McDonald (1992) have found occipito-temporal regions such as the fusiform gyrus are active selectively to faces, and Puce et al. (1996); McCarthy et al. (1996) and Kanwisher, McDermott & Chun (1997) reported activation within the fusiform as being at least twice as large in response to faces than to letter strings or non-face objects. Face-selective responses have been described in ERP studies (Bentin et al. 1996), in MEG studies (Liu et al. 2000), and in studies employing intracranial recordings (Allison et al. 1999; McCarthy et al. 1999; Puce, Allison & McCarthy 1999). This evidence seems on the one hand quite compelling, but it has also been argued that apparently face specific mechanisms are not face specific per se but specific for making fine-grained discrimination between visually similar exemplar categories (e.g. Kanwisher et al. 2000; Gauthier et al. 2000).

Houses can be seen as similarly complex non-face objects, which are encountered with equal regularity as faces. A number of studies have been carried out investigating processing differences related to the processing of these stimulus categories. These will now be considered.

3.1.1.1. Face and house processing

3.1.1.1.1. Spatial correlates of face and house processing

Several neural regions have been implicated in the processing of faces, most importantly the fusiform gyri, the superior temporal gyri, the inferior occipital gyri, inferior frontal gyri, lingual gyri and the amygdala (Joseph 2001; Blonder et al. 2004). The 'Fusiform Face Area' (FFA) (Puce et al. 1995a; Kanwisher, McDermott & Chun 1997) has been identified in numerous studies as responding most strongly to faces (Allison et al. 1994; Courtney et al. 1996; Haxby et al. 1991; 1994; Kanwisher, McDermott & Chun 1997; McCarthy et al. 1997; Puce et al. 1995; 1996). Others, however, have argued that the FFA's role is concerned with expertise in recognising distinctions between *subordinates* in a class (e.g. Gauthier et al. 1999; 2000; Blonder et al. 2004). Another theory argues that the processing of faces is accomplished by a distributed network incorporating the whole ventral temporal cortex and thus cannot be confined to anatomically segregated regions (Ishai et al. 1999). Chao et al. (1999a) who investigated the processing of faces and non-facial control stimuli reported activation to facial stimuli (human and animal) within the lateral fusiform gyrus bilaterally and in the right posterior superior temporal sulcus relative to pictures of houses.

Blonder et al. (2004) conducted a study to investigate further the role of the FFA with respect to the processing of facial stimuli. They presented participants with photographs of human and dogfaces, and of houses, using scrambled images as control conditions. Stronger activation to both face conditions compared to houses was found in lateral fusiform gyri, in BA37 (bilaterally), in middle and inferior occipital gyri, in BA18 and BA19 (bilaterally). Significant responses to human faces only were recorded in parahippocampal / amygdala regions. However, in the medial fusiform gyrus, in BA19, the most significant response was recorded to houses, and then to dogfaces. No significant activation could be found for the human face stimuli. In addition, significant responses to houses but to none of the face stimuli were recorded in the posterior cingulate and in parahippocampal/medial fusiform areas (BA19 and BA37) ("Parahippocampal Place Area" - Epstein & Kanwisher 1999), as well as the lingual / medial fusiform areas (BA19), the superior occipital gyrus (BA19) and the posterior cingulate (BA30).

Thus, the lateral fusiform regions appear to be sensitive to facial stimuli but as activation within this region was also reported to house stimuli, it cannot be ascertained that the lateral fusiform regions are selective to faces only. A further study that used face and house stimuli to differentiate the neural processing mechanisms of face and object recognition reported activation in the right lateral fusiform gyrus in response to faces, but bilateral regions within the medial fusiform gyrus and the parahippocampal gyrus were also activated to a stronger degree in response to houses than faces (Serences et al. 2004). Serences et al. used a perceptual switching paradigm, i.e. participants saw the image either as a face turning into a house or vice versa. When participants noticed the change in the perception of the stimulus, the BOLD response showed an intriguing pattern with regards to its time-course. When a switch occurred from the (non-preferred) house stimuli to the (preferred) face stimuli, the BOLD response within right lateral fusiform areas increased, whereas the BOLD signal decreased within these areas when the switching went into the opposite direction, i.e. when the preferred face stimuli turned into house stimuli. In addition, the shifting of attention between the house and face stimuli was associated with stronger BOLD responses in the right superior frontal sulcus and precentral gyrus, as well as within the medial superior parietal lobule including the cuneus, bilaterally within the precuneus cortex and the intraparietal sulcus, and within the left lingual and fusiform gyri (Serences et al. 2004). These findings are in line with previous research that has associated the processing of house stimuli with increases in activation (BOLD) in parietal and superior frontal regions (e.g. Ishai et al. 2000; Sala et al. 2003).

A further investigation of face and house recognition yielded preferential activation to houses within the collateral sulcus and the transverse occipital sulcus whereas the presentation of faces led to activation within the posterior fusiform gyrus, the inferior occipital gyrus and the superior temporal sulcus (Mukamel et al. 2004). They again used fMRI and conducted a region of interest analysis based on previous findings by e.g. Kanwisher et al. (1997), Ishai et al. (1999), Hasson et al. (2003), Epstein & Kanwisher (1999) and Maguire et al. (2001). Thus, assumptions as to the location of activated sources need to be considered when interpreting their findings, as well as the possibility of activation within areas that have not been included in their analytical approaches.

3.1.1.1.2.Temporal sequence of face and house processing

It is possible that face versus house processing could be differentiated in the temporal domain. Eimer (2000b), using ERP techniques, reported a longer latency response to house than to face stimuli, 200ms as compared to 150ms.

Ishai et al. (1999, 2000) investigated the differential effects of face and non-face (i.e. house and chair) stimuli on patterns of neural activity in occipital and temporal regions. They observed activity across a distributed network including the fusiform gyri, inferior occipital and midoccipital gyri as well as inferior temporal regions. In addition, they reported significantly different responses to houses, faces and chairs. Houses showed greater activation (BOLD responses) in ventral temporal regions such as the medial fusiform, and in dorsal occipital regions, whereas faces revealed significantly larger BOLD responses in lateral fusiform gyri. Using the data collected by Ishai et al. (1999), Mechelli et al. (2004), using dynamic causal modelling (DCM), reported additional activation to face, house and chair stimuli relative to scrambled control images within superior and inferior parietal areas. In addition, they also reported intrinsic connections from V3 to parietal areas as well as to more category-responsive areas (e.g. for faces – lateral fusiform, for houses – medial fusiform); and also from the parietal areas to the category responsive areas (for details see Mechelli et al. 2004).

As evidenced in ERP studies, it is predicted that the main effects of activation, i.e. changes in cortical oscillatory power, will be observed within the first 500ms following stimulus onset, with peaks of amplitude change to faces occurring at approximately 200ms (equivalent to the face-specific N170). Differences in amplitude at the face-specific latencies (e.g. 150-200ms as in Eimer 2000b) for faces compared to houses were reported for temporal sites only; at occipital sites such differences did not reach significance. Thus, the longer time window was included to investigate if such amplitude differences would occur at later stages, due to the lesser salience of house compared to face stimuli. In addition, Pierret, Peronnet & Echallier (1994) reported positive effects at occipito-temporal sites for latencies of 240 to 450ms, as well as negative effects at posterior sites for latencies of 500 to 700ms in response to objects that differed in size.

The differential processing of face and house stimuli has not been widely explored in terms of frequency specificity. The networks involved incorporate relatively widespread cortical areas, so it is predicted that variations could be seen in the beta

waveband (Von Stein and Sarnthein 2000). Rodriguez et al. (1999), however, point out that gamma phase-synchrony might also be involved in such a task which, as the basic process may involve discrete areas of localised activation, but additional task demands may require larger-scale links "gamma-phase synchrony (and desynchrony) which could be viewed as a mechanism that subserves large-scale cognitive integration" (Rodriguez et al. 1999 p433). They first observed an induced-gamma response as showing increased synchrony to (perceived) Mooney faces (compared to non-perception Mooney faces, i.e. those seen as meaningless shapes) at latencies of approximately 200 to 260ms. These findings as well as the observations by Tallon-Baudry et al. (1998) of gamma increases in response to the perception of a gestalt-like stimulus would lead to the prediction of (differential) involvement of gamma frequencies in the perception of face, but also house stimuli.

To investigate whether or not there are specialised regions and mechanisms that are differentially involved in the processing of faces and objects, we carried out a study in which stimuli of faces and houses were used as well as scrambled versions of each to allow comparison. Given previous literature it emerged that the majority of studies favoured Region of Interest (ROI) approaches. To improve on this, i.e. to rule out the non-detection of potentially active areas, the following investigation aimed to explore the contributions, or activation across the whole of the brain. However, the results from previous findings were used to guide our hypotheses. It was predicted that the presentation of faces as well as houses will lead to activation within occipito-temporal regions (e.g. Ishai et al. 1999), including the lateral fusiform and inferior occipital gyri for faces (e.g. Chao et al. 1999a, b; Blonder et al. 2004), whereas for houses compared to faces differential patterns of activation within the temporal but also within parietal areas are anticipated. In addition, differential patterns of oscillatory power are predicted, with face specific processing taking place within 0 to 200ms – as indexed by the face specific N170 – whereas object processing of complex non-face stimuli such as houses would be predicted to occur within a time-window of 0 to 500ms as suggested by the findings of e.g. Pierret et al. 1994.

3.2. Method

3.2.1. Materials and Participants

Stimuli were selected from the Ekman and Friesen (1976) series of *Pictures of Facial Affect*, which contains black and white photographs of facial expressions of 10 actors (six female). The photographs have been digitally altered to depict only the contour of the face, i.e. hair, ears etc. are removed. The images selected for the current investigation comprised neutral expressions only. As ten neutral expressions (six female, four male) were too few to bear sufficient power all ten face stimuli were repeated six times, yielding 60 face stimuli. Fifteen stimuli of houses were chosen, taken from the same set of house stimuli as used by Ishai et al. (1999, 2000). These were repeated four times, also yielding 60 house stimuli. In addition, scrambled versions of each stimulus type were used. To create scrambled control images, pixels were randomly chosen and reassembled using Adobe Photoshop CS. For stimulus display Presentation software (http://nbs.neuro-bs.com/presentation/download) was used.

Nine healthy participants (four female, all right handed) gave consent to take part in the investigation. The average age of the participants was 28.2 years (range 24 to 37). The Aston University Human Sciences Ethics committee approved the study. Participants were seated within a magnetically shielded room, and viewed, through a mirror, a monitor, placed outside the shielded room, on which the stimuli were presented. The distance between the participants and the monitor was approximately 2m.

3.2.2. Experimental Paradigm

On each trial, participants were asked to fixate on a white circle for 1500ms before a target stimulus was presented for 200ms. The fixation point then returned and was followed by a second image also presented for 200ms. Participants were instructed to indicate as soon as they knew whether or not the two stimuli presented were identical or not by pressing the appropriate button on a response box. For stimuli to be regarded identical, the two faces had to be of the same identity, or the two houses had to be exactly the same. The pairs presented contained face and face stimuli, house and house

stimuli, face and house stimuli, face and scrambled stimuli or house and scrambled stimuli. (see **Figure3-1**).

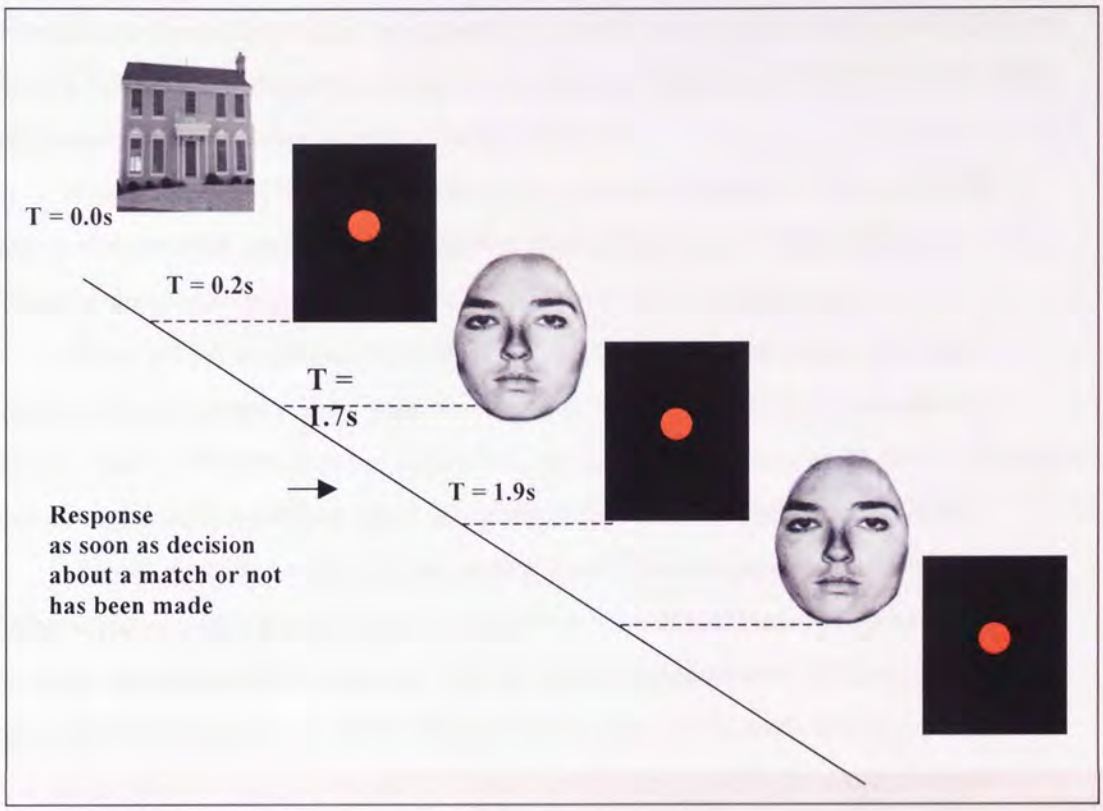


Figure3-1: Representation of experimental design.

3.2.3. Image Acquisition and Analyses

MEG signals were recorded with a third order gradiometer configuration using an Omega 151-channel magnetometer (CTF Systems Inc., Canada).

Head localisation information was acquired by recording the position of head localisation coils before and after the recording session. Following data acquisition, a 3-D digitiser (Polhemus Isotrack) was used to digitise participants' heads and allow co-registration of each participant's MEG and MRI data. This was achieved using Align (www.ece.drexel.edu/ICVC/Align/align11.html), which matches the participant's digitised head-surface to the head-surface extracted from their individual, anatomical MRI (Kozinska 1997).

To analyse the MEG data, Synthetic Aperture Magnetometry (SAM) was used (see section 2.4.1.1.). SPMs were generated for predetermined frequency bands (2-8Hz; 8-13Hz; 13-25Hz; 25-40Hz and 5-40Hz) and time-windows (0 to 200ms; 0 to 500ms)

over the entire brain at 5mm resolution to localise power changes in response to the face stimuli and the control stimuli. Positive values are interpreted as relative increases in power, also referred to as ERS, or increases in event related spectral power (ERSP) and negative values are interpreted as relative decreases in power, also referred to as ERD, or decreases in event related spectral power (ERSP).

Using SPM99 (Friston et al. 1995), the Magnetic Resonance Image (MRI) of each participant was spatially normalised to a template space. The resultant normalisation parameters were applied to the volumetric SAM images.

Thus, all SAM images (nine participants, five frequency bands, two time-windows and six comparisons: face vs. baseline; house vs. baseline; scrambled vs. baseline; face vs. house; face vs. scrambled, house vs. scrambled) were then in the same three-dimensional coordinate space allowing group analyses (Singh et al. 2002).

To test specific predictions regarding the differential activation of face compared to non-face stimuli, direct comparisons are drawn between faces and houses and faces and scrambled images, as well as indirect comparisons of faces to baseline. Using SnPM (Holmes et al. 1996; Nichols & Holmes 2002), analyses of significance were performed at voxel level and at cluster level using a multiple subject single condition design. Variance smoothing was performed using a Gaussian kernel (σ = 20mm). Using non-parametric permutation testing, cluster-level inferences estimate whether a large connected cluster of near significant t-values may reach statistical significance. Voxel level inferences were estimated additionally. Spatial resolution however is being traded in against sensitivity (for details see Nichols & Holmes 2002; Singh, Barnes & Hillebrand 2003).

For the visualisation of the results on a template brain, SPM was used as well as mri3dX (http://www/aston.ac.uk/lhs/staff/singhkd/mri3dX/). In all figures the left side of the brain is displayed on the left side of the image, and coordinates provided are stated in Talairach & Tournoux (1988) version. In the figures presented, increases in cortical power are indicated by colourscale of red – orange – yellow, with yellow regions being the most significantly active areas. Decreases in cortical oscillatory power are indicated by a colourscale of blue – pink – white, with white regions being the most significantly active areas (see colour bar on page 74, **FigureB**).

To investigate the time course and frequency specificity of the obtained activation within significant regions, time-frequency representations (TFRs) were generated using Morlet wavelet analysis (Tallon-Baudry et.al. 1997). The wavelet

method was chosen as it provides a better compromise between time and frequency resolution than Moving Window Fourier Analysis. Once the TFRs for each participant were generated, averages were computed by averaging the TFRs of all participants.

FigureB: Colourbar indicating

ERD or decreases in ERSP indicated by blue – pink – white

ERS or increases in ERSP indicated by red – orange – yellow.

3.3. Results

SAM analyses were performed for two time-windows, 0 to 200ms and 0 to 500ms, across the following frequency bands: theta (2-8Hz), alpha (8-13Hz), beta (13-25Hz), gamma (25-40Hz) and across a wide frequency range of 5-40Hz. Unless otherwise stated the results reported are significant at voxel level. A table of results detailing pseudo-t statistics, coordinates and region showing changes in cortical power are included in **Appendix2**.

3.3.1. 200ms

3.3.1.1. Face versus House – Face Specific Comparisons

When comparing face stimuli to houses, significant changes in oscillatory cortical power could be observed in the following frequency bands: 13-25Hz, 25-40Hz and also across a wide frequency range of 5-40Hz.

For **beta** (13-25Hz), faces compared to houses yielded significant increases in cortical oscillatory power in right parietal regions, namely the postcentral gyrus ($t = +5.54$, $p < 0.01$) and the angular gyrus ($t = +4.97$, $p < 0.05$) (see **Figure3-2**).

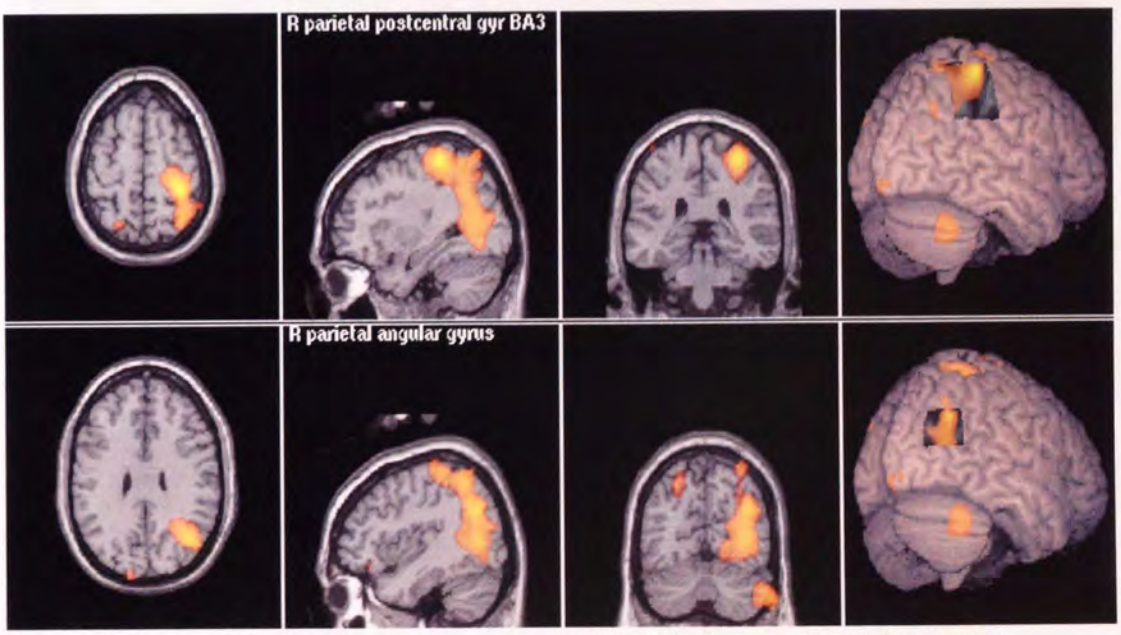


Figure3-2: Responses to faces compared to houses in 13-25Hz frequency band for the 0 to 200ms time-window. SPMs show significant increases in cortical oscillatory power in the right parietal lobe, displayed onto a template brain.

In **gamma** (25-40Hz) significant results could be demonstrated at cluster level. The permutation distribution revealed a maximum cluster size of 870 voxels with a critical threshold being calculated at 4.76. With a primary threshold of 3, a significant cluster (size = 951; $p < 0.05$) was found in the right parieto-occipital areas, including the precuneus and cuneus regions, BA19. In these areas increases in cortical oscillatory power was observed (see **Figure3-3**).

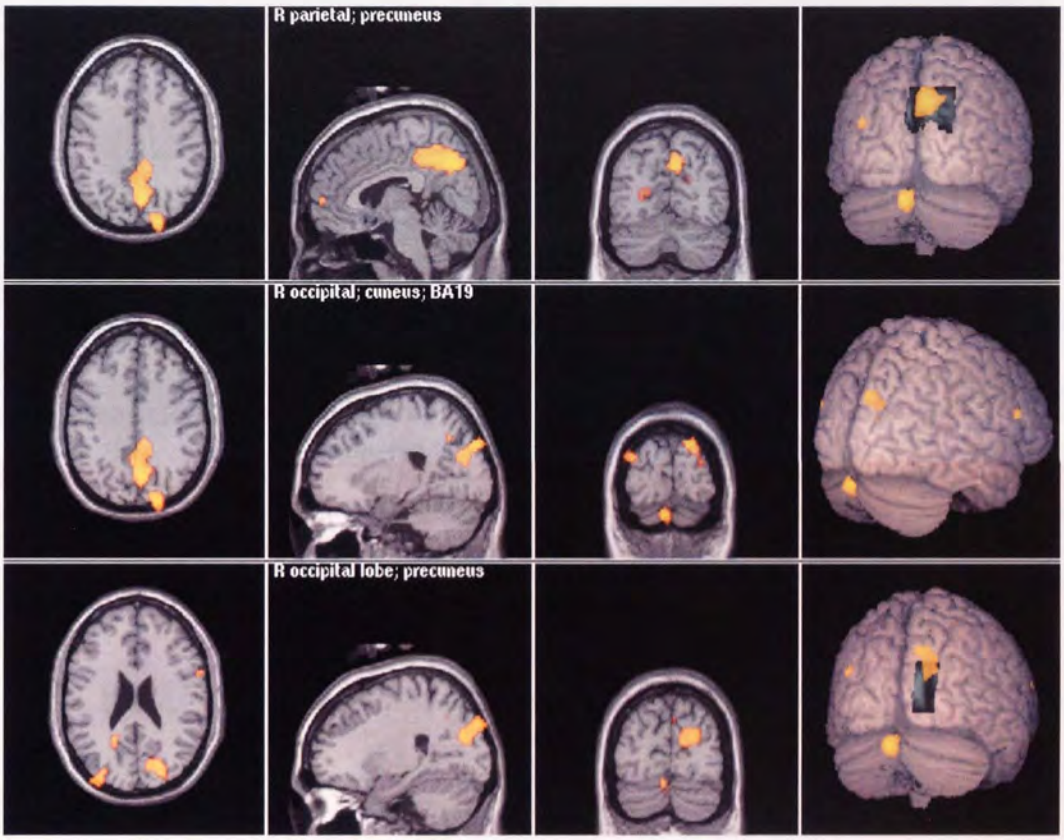


Figure3-3: Responses to faces compared to houses in 25-40Hz frequency band for the 0 to 200ms time-window. SPMs show significant increases in cortical oscillatory power in the right parietal lobe, precuneus (top row) within right occipital areas, cuneus and BA19 (middle row) and in the precuneus area (bottom row). SPMs are displayed onto a template brain.

Across the 5-40Hz frequency range, faces compared to houses showed significant increases in cortical oscillatory power within the right superior temporal gyrus ($t = +5.54$; $p < 0.01$) and within the right inferior frontal gyrus, BA44 ($t = +4.72$; $p < 0.05$) (see **Figure3-4**).

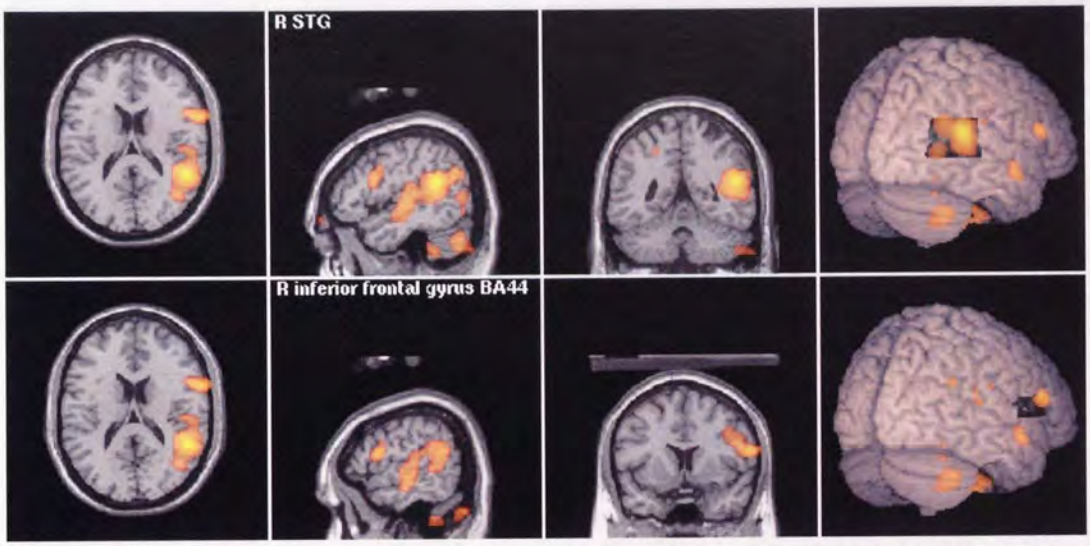


Figure3-4: Responses to faces compared to houses across a 5-40Hz frequency range for the 0 to 200ms time-window. SPMs show significant increases in cortical oscillatory power in the right superior temporal gyrus (top row) and within right inferior frontal gyrus and BA44 (bottom row). SPMs are displayed onto a template brain.

3.3.1.2. Face versus Scrambled – Face Specific Comparisons

When comparing face stimuli to scrambled control stimuli across the 0 to 200ms time-window, significant changes in oscillatory cortical power could be observed in the following frequency bands: 13-25Hz, 25-40Hz and also across a wide frequency range of 5-40Hz.

For **beta**, increases in cortical oscillatory power were also evident within right parietal areas, namely within the right inferior parietal lobule, BA40 ($t = +6.27$, $p < 0.01$), the right postcentral gyrus ($t = +5.35$, $p < 0.05$) and the right angular gyrus ($t = +5.03$, $p < 0.05$). Sub-gyral and cuneus areas also showed increases in cortical power within right occipital regions ($t = +5.83$, $p < 0.01$ and $t = +4.99$, $P < 0.05$, respectively) (see **Figure3-5**).

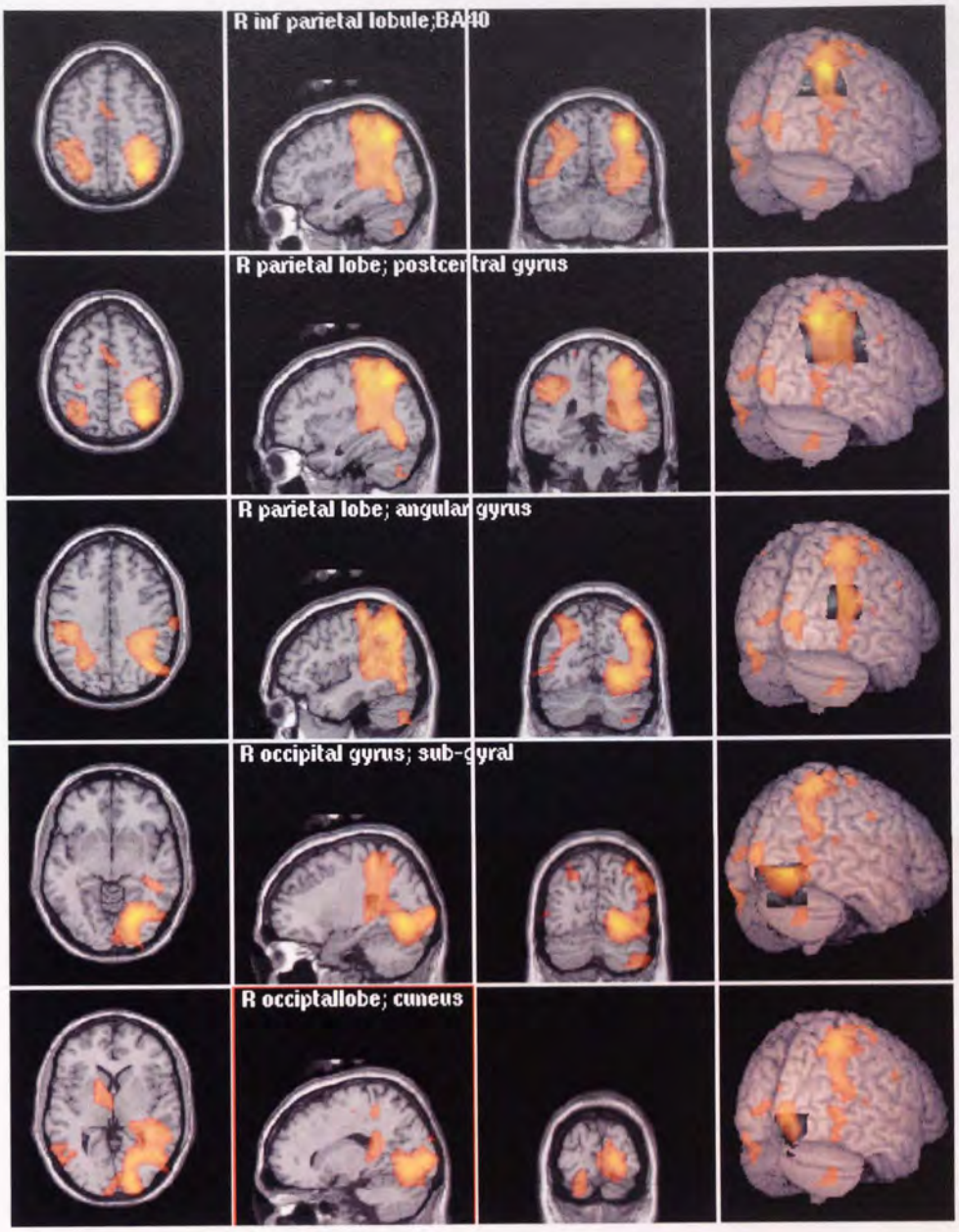


Figure3-5: Responses to faces compared to scrambled control stimuli in 13-25Hz frequency band, for the 0 to 200ms time-window. SPMs show significant increases in cortical oscillatory power in right parietal areas, including inferior parietal lobule (top row), the postcentral gyrus (second row) and the angular gyrus (third row). In addition, right occipital regions were also found to show significant increases in cortical oscillatory power, namely right sub-gyral regions (fourth row) and the cuneus (bottom row). SPMs are displayed onto a template brain.

For **gamma**, significance could be observed at clusters level. The permutation distribution revealed a maximum cluster size of 898 voxels, with the critical threshold being calculated at 4.86. Setting the primary threshold at 2, a significant cluster (size = 5238, $p < 0.05$) could be revealed, including right parietal regions such as the postcentral gyrus ($t = +4.65$, $p = 0.08$) and sub-gyral regions ($t = +4.47$, $p > 0.05$), but also left temporal regions, incorporating left temporal sub-gyral regions ($t = +4.39$, $p > 0.05$). With a primary threshold of 4, a more focused cluster could be observed (cluster size 330, $p < 0.05$), encompassing only the right hemisphere regions (see **Figure3-6**).

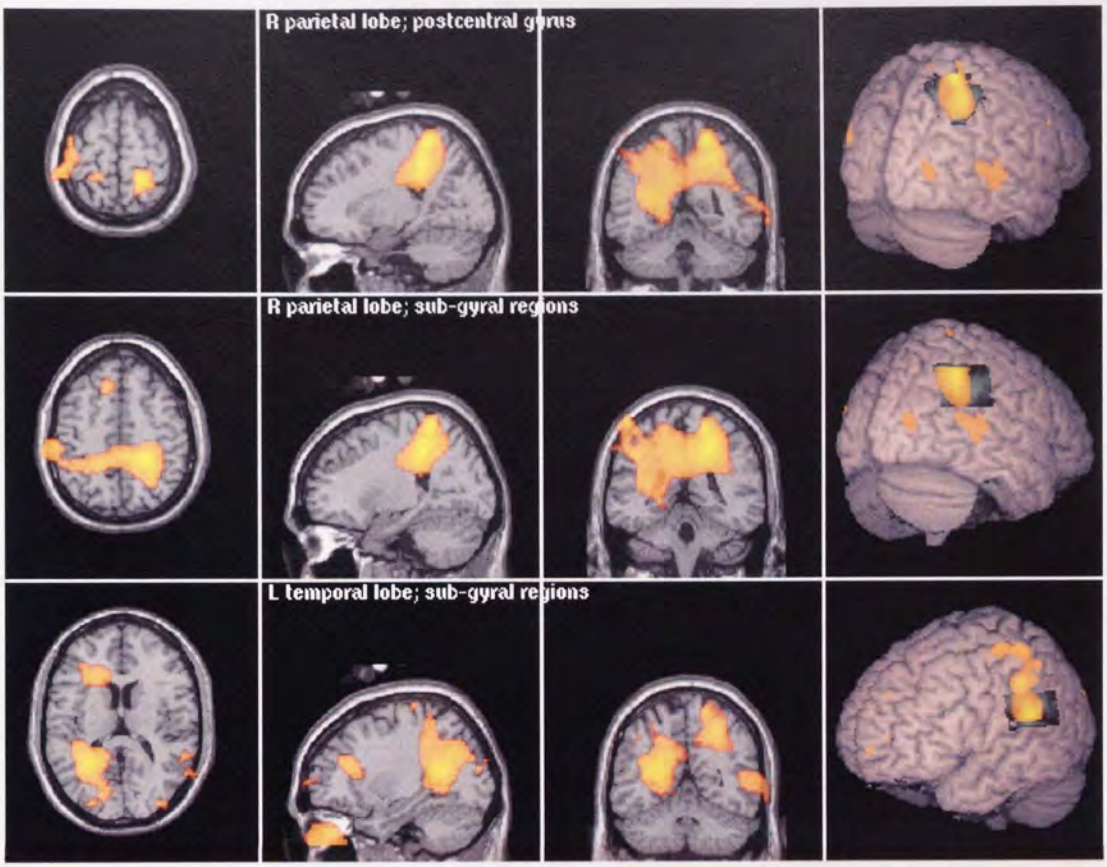


Figure3-6: Responses to faces compared to scrambled images in the 25-40Hz frequency band, for the 0 to 200ms time-window. SPMs show significant increases in cortical oscillatory power in right parietal area, including the right postcentral gyrus (top row) and right sub-gyral regions (middle row). In addition, sub-gyral regions within the left temporal lobe also show increases in cortical oscillatory power (bottom row). SPMs are displayed onto a template brain.

3.3.1.3. Face versus Baseline – Indirect comparisons

To establish whether the differential activation of faces compared to houses and scrambled images is due to different neural networks being recruited by each stimulus category, we also compared face stimuli to a pre-stimulus baseline. Here, significant changes in cortical oscillatory power could be observed for 13-25Hz and 25-40Hz.

For **beta**, significant results could also be observed at cluster level only. The permutation distribution revealed a maximum cluster size of 721, and the critical threshold was calculated at 4.77. Setting a primary threshold of 3, a significant cluster (size = 1371 voxels, $p < 0.01$) was revealed in left temporal regions including the limbic lobe ($t = +4.62$, $p = 0.068$), the posterior lobe ($t = +4.56$, $p = 0.076$) and the inferior temporal gyrus ($t = +4.17$, $p > 0.05$) (see **Figure3-7).** With a primary threshold of 4, the

cluster size decreased to 82 voxels in size, $p < 0.05$. The areas within this cluster are the limbic lobe and the inferior temporal gyrus, as mentioned above.

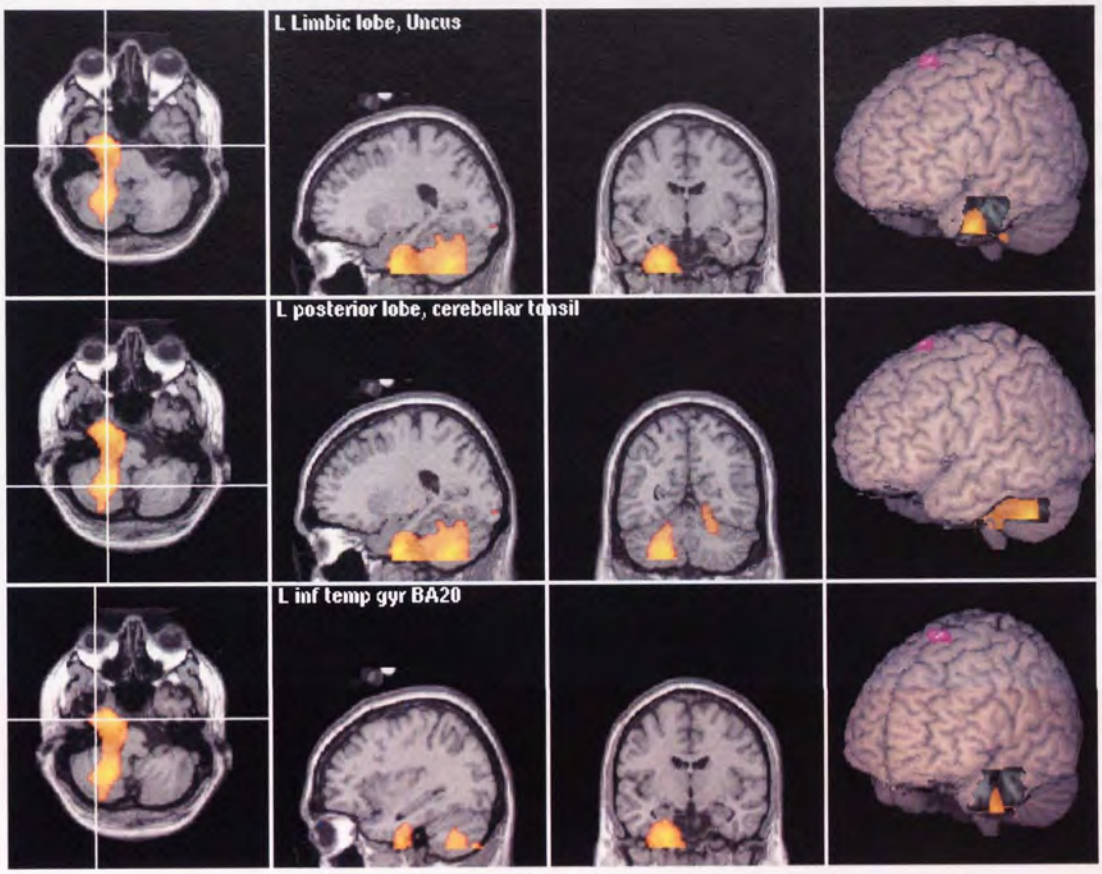


Figure3-7: Responses to faces compared to prestimulus baseline condition in 13-25Hz frequency band, for the 0 to 200ms time-window. SPMs show significant increases in cortical oscillatory power in the left temporal regions, including the limbic lobe (top row), and the left inferior temporal gyrus, BA20 (bottom row). In addition significant ERS was also evident in the left posterior lobe (middle row). SPMs are displayed onto a template brain.

For **gamma**, significant increases in cortical oscillatory power could be observed. Significant voxels were revealed for right and left occipital regions, such as the cuneus, BA18 (right: $t = +7.72$, $p < 0.005$; and left: $t = +6.73$, $p < 0.05$). In addition, the left lingual gyrus also showed significant ERS ($t = +6.36$, $p < 0.005$) (see **Figure3-8**).

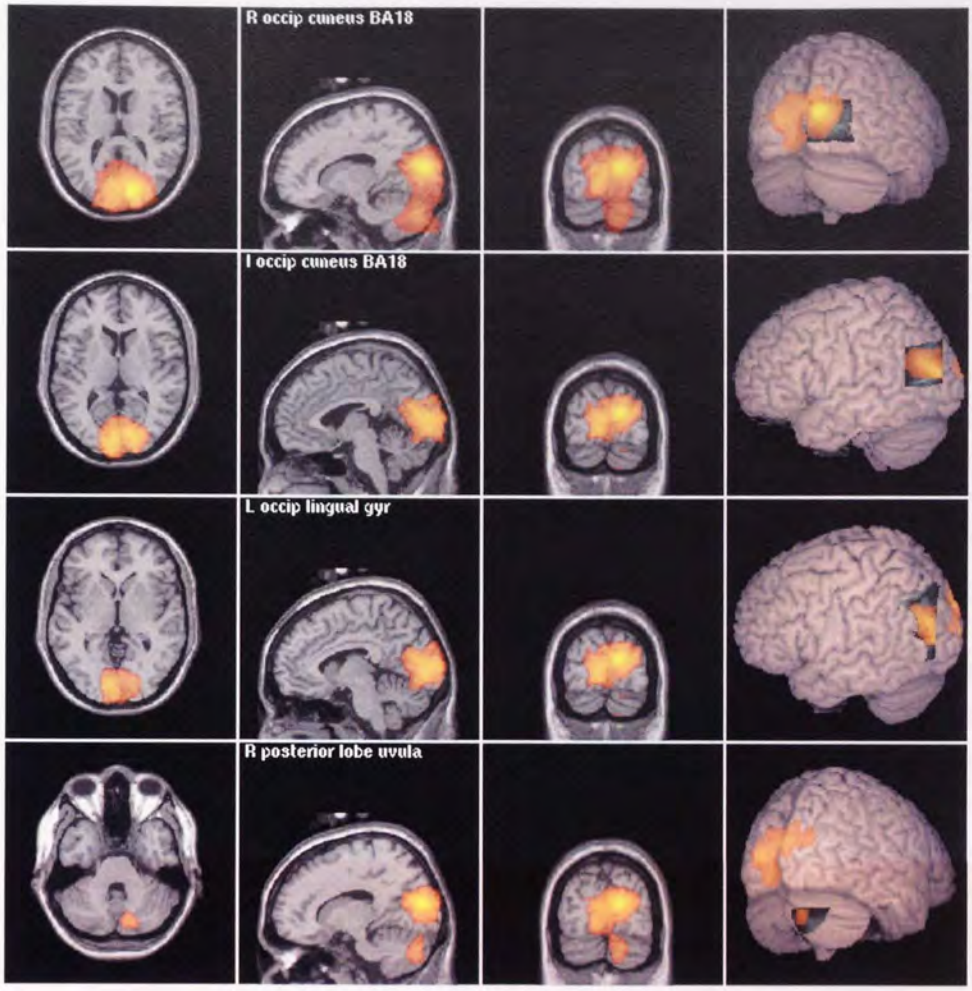


Figure3-8: Responses to faces compared to prestimulus baseline condition in 25-40Hz frequency band, for the 0 to 200ms time-window. SPMs show significant ERS in both occipital areas, including the right cuneus and BA18 (top row), the left cuneus and BA18 (second row) and the left lingual gyrus (third row). In addition, right posterior regions also showed significant ERS (bottom row). SPMs are displayed onto a template brain.

3.3.2. 500m

3.3.2.1. Face versus House – Face Specific Comparisons

When comparing face stimuli to houses, significant changes in oscillatory cortical power could be observed in the following frequency bands: 8-13Hz, 13-25Hz, 25-40Hz and also across a wide frequency range of 5-40Hz.

For **alpha** (8-13Hz), faces compared to houses yielded significant increases in cortical oscillatory power in right posterior areas ($t = +5.44$, $p < 0.05$). At cluster level, significant cortical increases in relative power could be observed. With a maximum cluster size of 904 voxels, and the critical threshold being calculated at 4.85, a primary threshold set at 3 revealed increases in cortical oscillatory power within the right inferior occipital gyrus
($t = +4.19$, $p > 0.05$) as part of the posterior cluster (see **Figure3-9**).

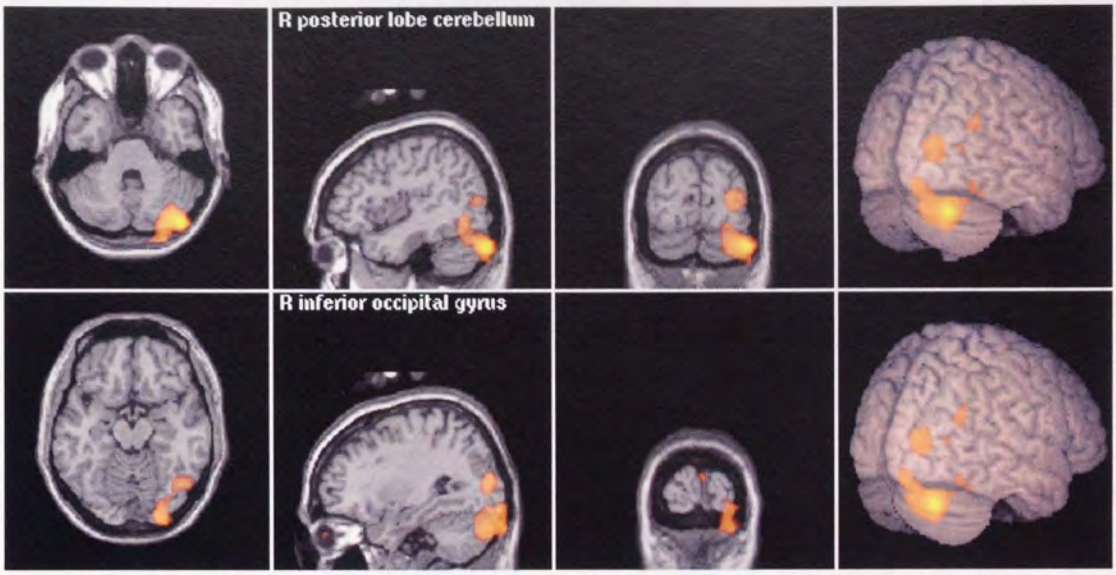


Figure3-9: Responses to faces compared to houses in 8-13Hz frequency band, for the 0 to 500ms time-window. SPMs show significant increases in cortical oscillatory power in the right posterior lobe (top row), as well as within the right inferior occipital gyrus (bottom row). SPMs are displayed onto a template brain.

For **beta**, faces compared to houses yielded significant increases in cortical oscillatory power in sub-gyral regions of the right temporal lobe ($t = +5.61$, $p < 0.005$) and right parietal lobe

($t = +5.56$, $p < 0.005$), but also within the right angular gyrus ($t = +5.49$, $p < 0.01$) and sub-gyral regions within the left parietal lobe ($t = +4.99$, $p < 0.05$) (see **Figure3-10**).

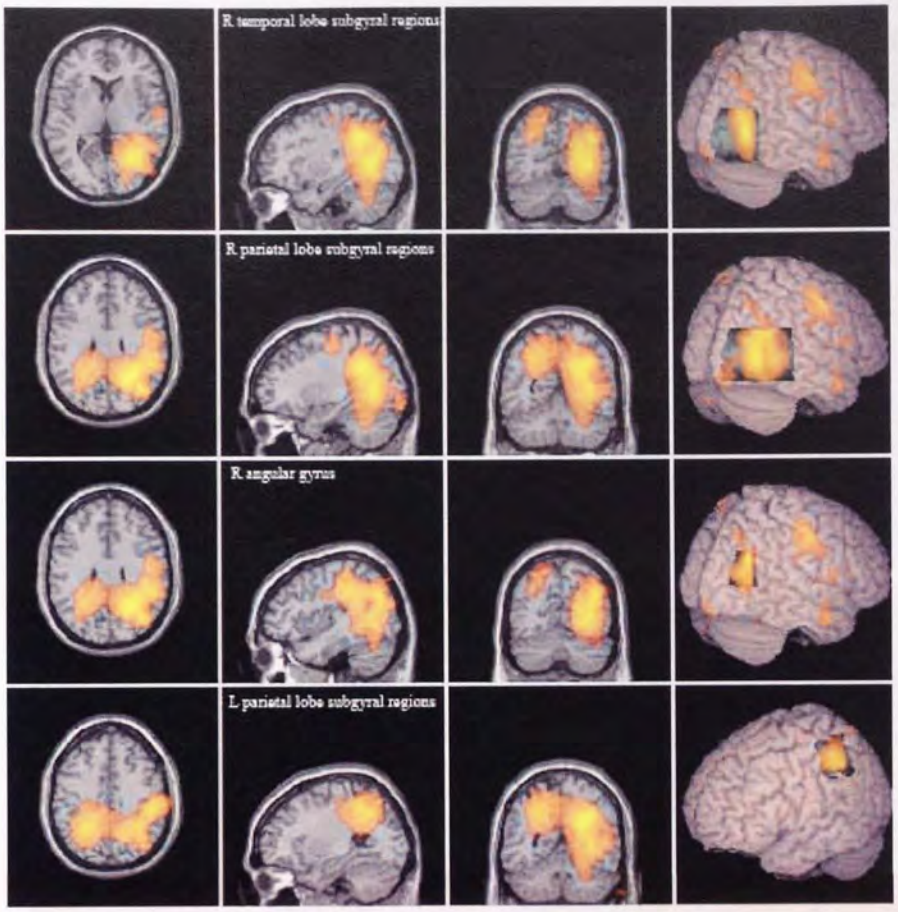


Figure3-10: Responses to faces compared to house stimuli in 13-25Hz frequency band, for the 0 to 500ms time-window. SPMs show significant increases in cortical oscillatory power in sub-gyral regions of the right temporal (top row), and parietal lobes (second row). Increases in relative cortical power are also evident within the right angular gyrus (third row) and within sub-gyral regions of the left parietal lobe (fourth row). SPMs are displayed onto a template brain.

For **gamma**, differential activation for face and house stimuli revealed significant increases in oscillatory cortical power in right parietal areas such as the precuneus ($t = +5.21$, $p < 0.01$, and BA7, $t = +4.77$, $p < 0.05$), and the postcentral gyrus and BA1 ($t = +4.62$, $p < 0.05$). In addition, left parietal areas, i.e. the postcentral gyrus also showed significant increases in cortical power ($t = +4.6$, $p < 0.05$). Sub-gyral regions within the right occipital lobe ($t = +5.33$, $p < 0.01$) and the right cingulated gyrus in the limbic lobe ($t = +4.83$, $p < 0.05$) also showed increases in relative cortical power. Decreases in relative cortical power could be observed within the left inferior frontal gyrus ($t = -5.14$, $p < 0.05$) (see **Figure3-11**).

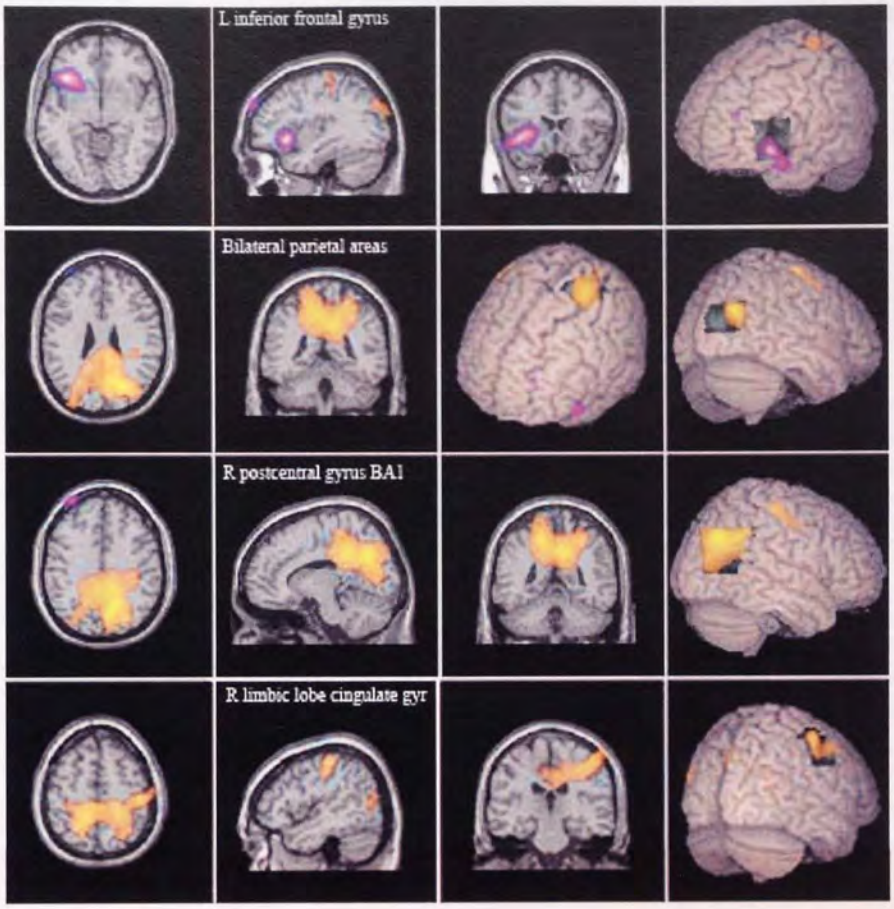


Figure3-11: Responses to faces compared to house stimuli in the 25-40Hz frequency band, for the 0 to 500ms time-window. SPMs show significant decreases in cortical oscillatory power in the left inferior frontal gyrus (top row). Significant increases in cortical oscillatory power were evident within bilateral parietal regions, namely the precuneus and post-central regions (second row), the postcentral gyrus and BA1 (third row) and the limbic lobe, cingulate gyrus (bottom row). SPMs are displayed onto a template brain.

3.3.2.2. Face versus Scrambled – Face Specific comparisons

When comparing face stimuli to scrambled across a longer time window of 0 to 500ms, significant changes in oscillatory cortical power could be observed in the following frequency bands: 8-13Hz, 13-25Hz and 25-40Hz.

For **alpha**, significant increases in cortical oscillatory power are demonstrated in the right middle occipital gyrus ($t = +6.09$, $p < 0.01$) (see **Figure3-12**).

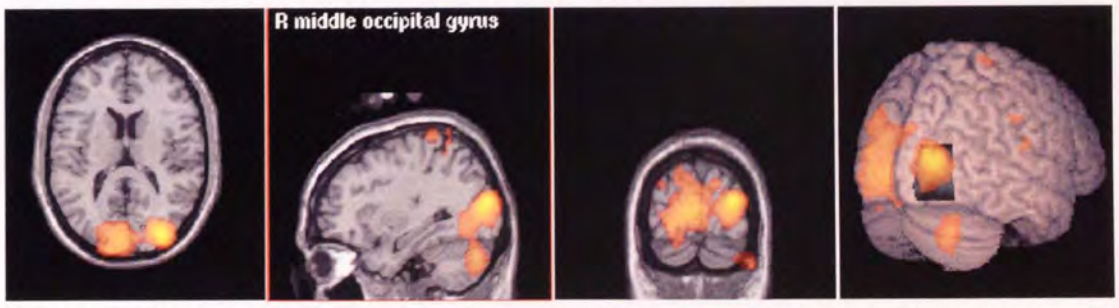


Figure3-12: Responses to faces compared to scrambled control stimuli in 8-13Hz frequency band, for the 0 to 500ms time-window. SPMs show significant increases in cortical oscillatory power in the right middle occipital lobe gyrus. SPMs are displayed onto a template brain.

For **beta**, significant increases in cortical oscillatory power are evident in the right superior temporal gyrus ($t = +6.15$, $p < 0.005$) and within the right and left inferior parietal lobule ($t = +5.21$, $p < 0.05$: $t = +4.33$, $p < 0.05$) (see **Figure3-13**).

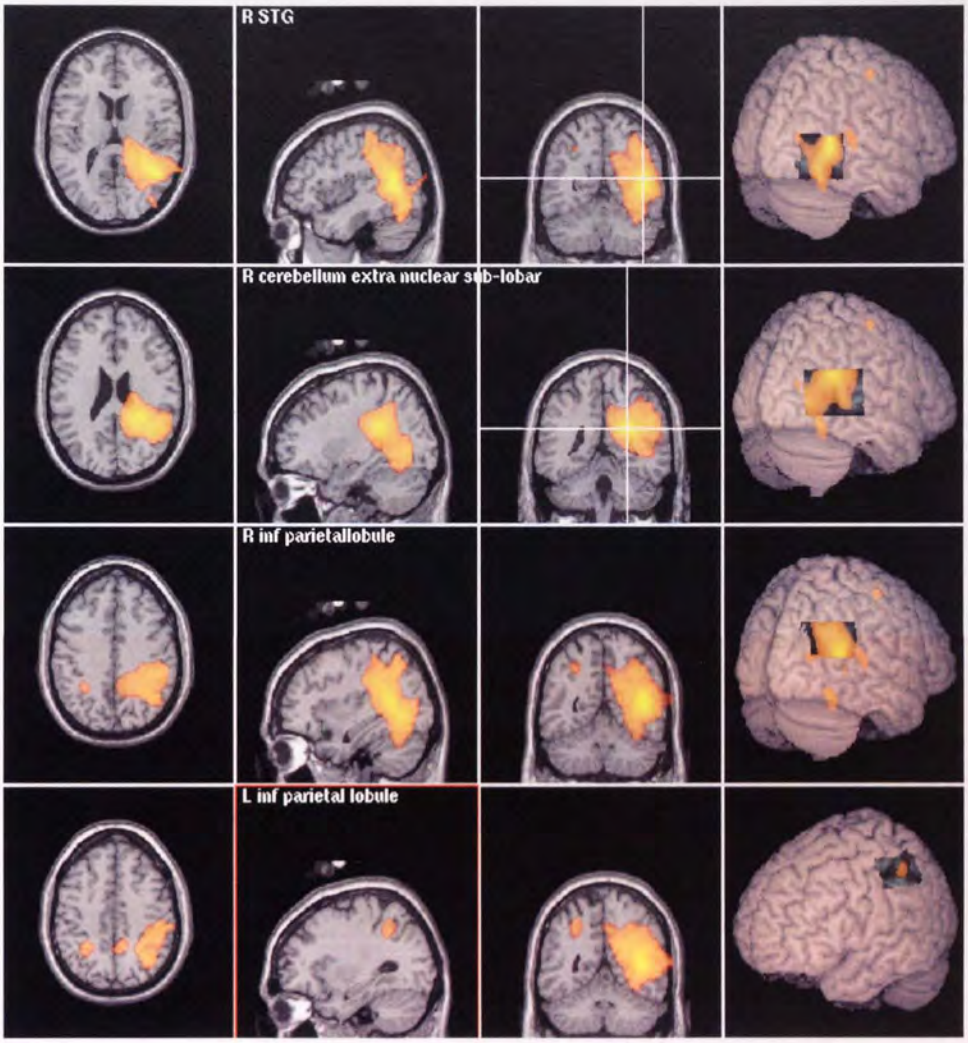


Figure3-13: Responses to faces compared to scrambled control stimuli in the 13-25Hz frequency band, for the 0 to 500ms time-window. SPMs show significant increases in cortical oscillatory power in the right superior temporal gyrus, (top row) and within right sub-lobar regions the right cerebellum (second row). In addition, relative power increases were also evident for the inferior parietal lobule, right hemisphere (third row) and also left hemisphere (bottom row). SPMs are displayed onto a template brain.

For **gamma**, significant increases in cortical oscillatory power are shown in sub-gyral regions of the right parietal lobe ($t = +5.72$, $p < 0.01$) as well as the postcentral gyrus ($t = + 6.52$, $p < 0.005$). In addition, significant increases in relative cortical power are evident within the right superior temporal gyrus ($t = +4.93$, $p < 0.05$) and within sub-gyral regions within the left frontal lobe ($t = +4.8$, $p < 0.05$) (see **Figure3-14**).

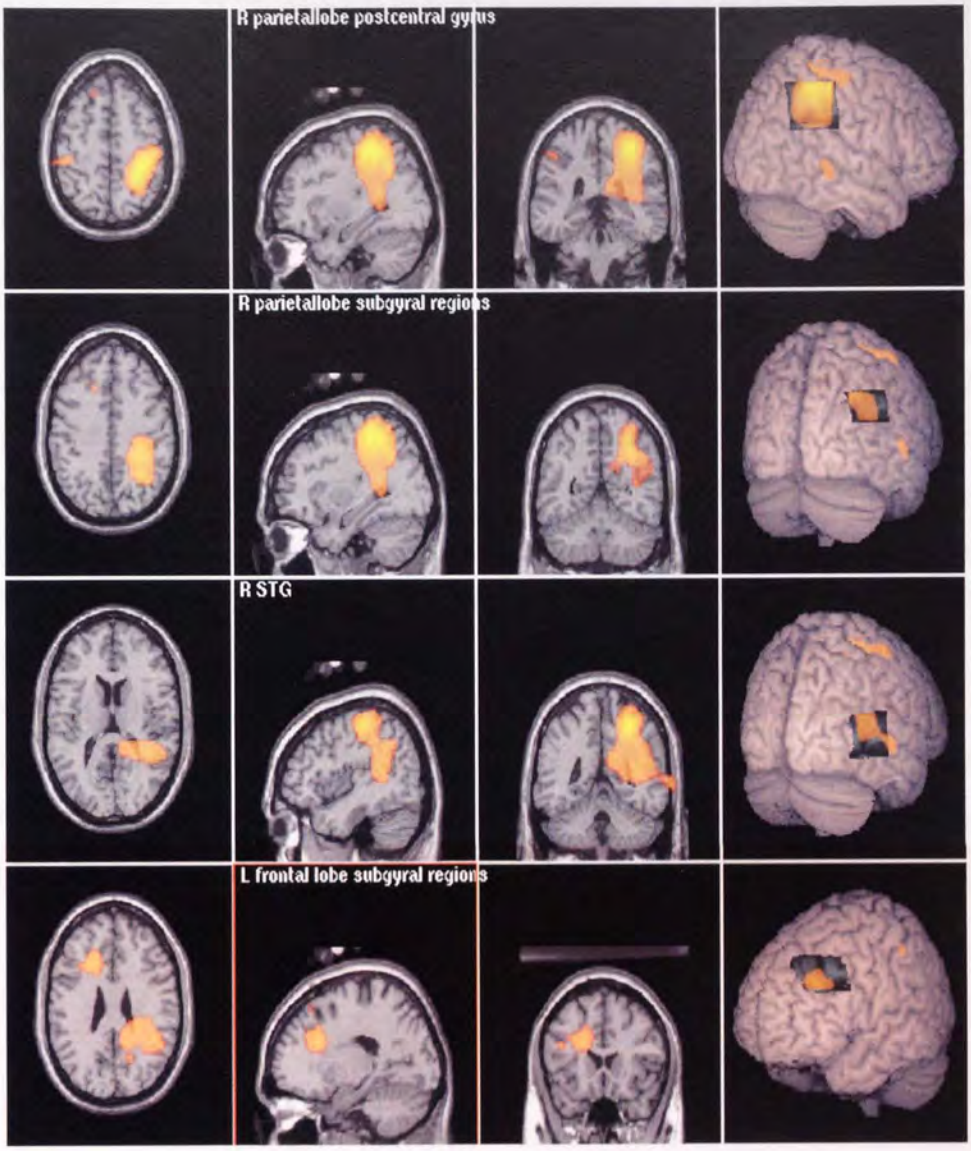


Figure3-14: Responses to faces compared to scrambled control stimuli in the 25-40Hz frequency band, for the 0 to 500ms time-window. SPMs show significant increases in cortical oscillatory power in the right parietal lobe, postcentral gyrus (top row) and within sub-gyral regions of the right parietal lobe (second row). In addition, relative power increases were also evident for the right superior temporal gyrus (third row) and for sub-gyral regions of the left frontal lobe (bottom row). SPMs are displayed onto a template

3.3.3. Time frequency representations

In order to explore the latency and frequency domains of some of the previous findings that directly compared patterns of cortical activation for faces compared to houses we generated Mann Whitney TFRs using Morlet wavelet analysis. The virtual electrodes used to generate these TFRs were based upon the SAM / SnPM coordinates identified by group analysis and individual data were explored to identify individual peaks in those areas. In a Mann Whitney voxel by voxel comparison, faces were included in the analysis as the active condition, and houses as passive condition, hence the spectral power observed in the houses condition was "subtracted" from that observed for the

faces condition. TFRs were generated for each individual and to infer group effects, these were averaged.

Significant increases in cortical power were demonstrated for the right angular gyrus within the right parietal lobe for beta, within the 0 to 500ms time-window (see figure 3-10). The Mann Whitney Group TFRs for a voxel placed within this region revealed prominent increases in cortical oscillatory power at latencies of approximately 150 to 250ms, for frequencies of 14 to 19Hz. A further increase in cortical power was evident between 300 and 400ms for frequencies of 17 to 19Hz. It is also apparent that from approximately 600ms, the most prominent observations are decreases in cortical oscillatory power. **Figure3-15** also shows Mann Whitney TFRs for two participants to illustrate individual differences but also common patterns in time frequency analyses. Participant 1 shows an increase in cortical oscillatory power at almost identical latencies (150 to 250ms) but at somewhat higher frequencies (17 to 23Hz). Participant 2 shows the most prominent increases in cortical power at somewhat earlier latencies, 100 to 200ms, and again at higher frequencies (22 to 26Hz) than is evident in the group representations. In addition, increases in cortical power are also shown (although of less signal strength) at latencies of 300 to 400ms for frequencies of 15 to 18Hz.

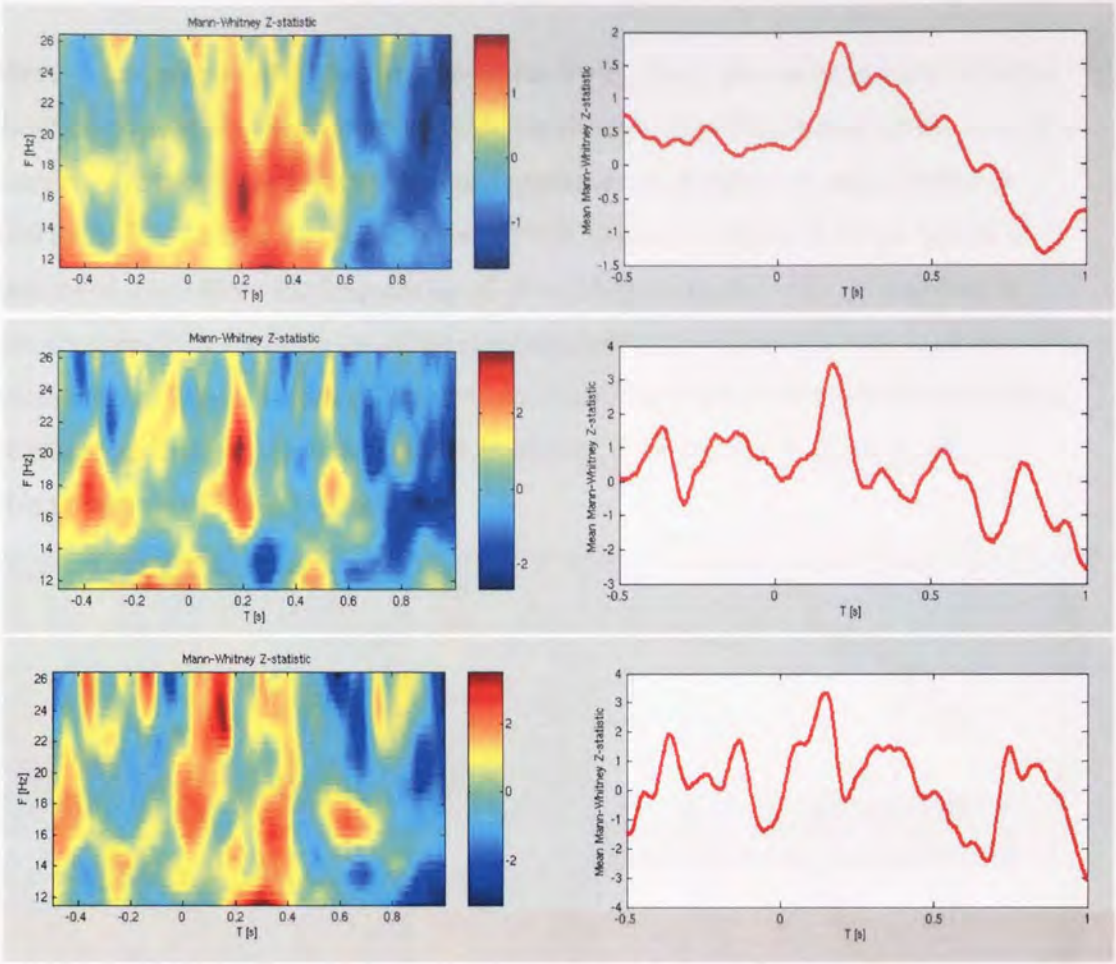


Figure3-15: Group TFRs (top row) for a voxel within the right parietal lobe, angular gyrus. Increases in synchronous power are evident for beta frequencies across the 0 to 500ms time-window as used in the SAM analysis. TFRs for two individuals are represented in middle and bottom rows. Decreases in cortical oscillatory power are also evident within this frequency band, illustrating that synchronous activity can coincide with desynchronous activity. Apart from participant 2 (bottom right), synchronous activity is seen to be followed by desynchronous activity. This observation will be further discussed.

Significant increases in the right STG were observed when contrasting face stimuli to house stimuli for 25 to 40Hz, across the 0 to 500ms time-window (see figure 3-14). Mann Whitney group TFRs indicate that the most prominent increases in cortical power are evident at latencies of approximately 100 to 200ms at frequencies of 5 to 12Hz. At latencies between 200 and 400ms increases in cortical power are also evident at 20 to 25Hz and 25 to 30Hz respectively.

As before, Mann Whitney TFRs for two individuals are included to illustrate patterns of cortical activity that are similar but also differ between the group and individual representations. Participant 1 also shows the most prominent increases in cortical oscillatory power starting at latencies of approximately 20ms, and shows sustained activity across to 400ms, for frequencies of 5 to 12Hz (z-scores = +4). In addition, a further burst of increase in signal power can be seen for latencies of 0 to

200ms, at frequencies of 15 to 23Hz (z-scores = +3). Here, decreases in cortical power follow the pattern of synchronous activity, yet the strength of the signal seems low, as z-scores = –1. Participant 2 shows the most prominent increases in cortical power at latencies of 0 to 150ms, for frequencies of 10 to 13Hz (z-score = +2.5), as well as at latencies of 0 to 180ms for frequencies of 19 to 29Hz (z-score = +2). In addition, at those frequencies a further burst of increases in cortical oscillatory power is evident at a later latency of 300 to 400ms (z-score = +2). Participant 2 also shows notable decreases in cortical oscillatory power sustained between 80 to 400ms, at frequencies of 11 to 15Hz (z-score = -2) (see **Figure3-16**).

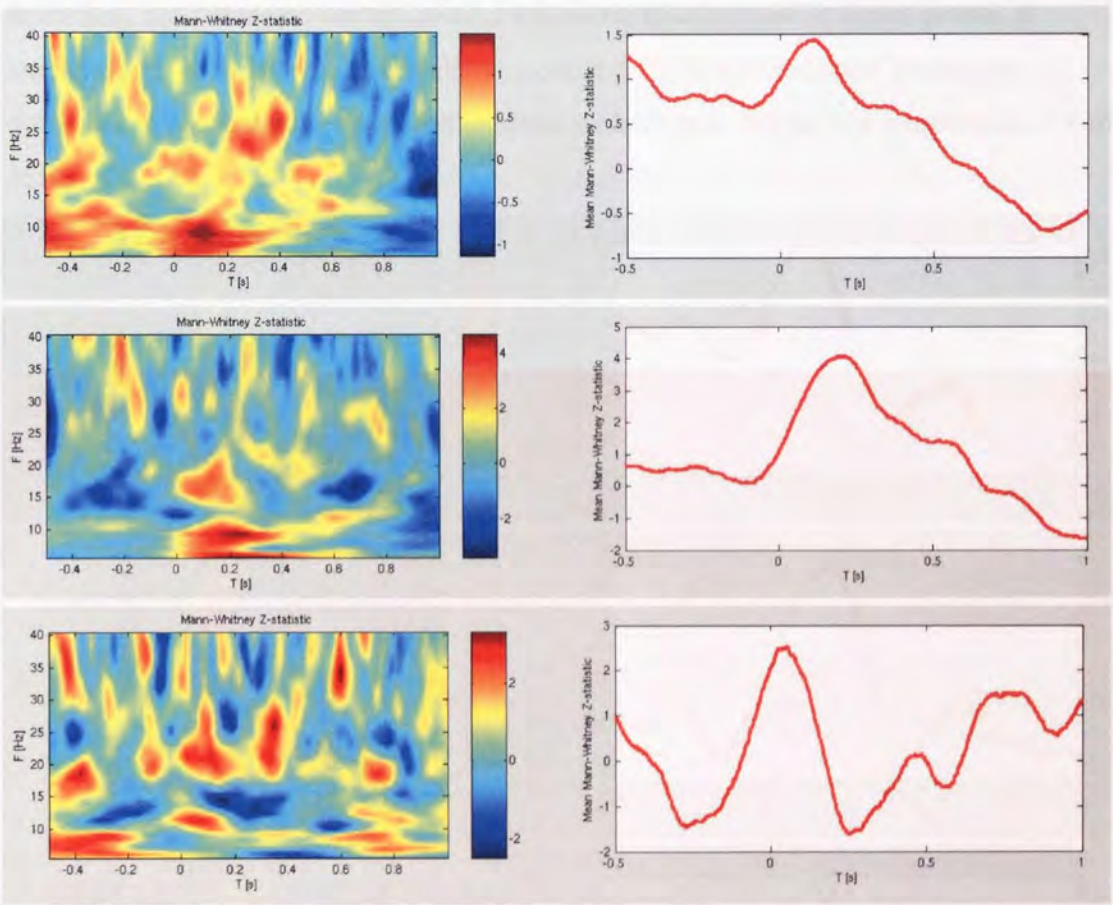


Figure3-16: GroupTFRs (top row) for a voxel within the right superior temporal gyrus. Increases in synchronous power are evident across the 5-40Hz frequency range for the 0 to 500ms time-window as used in the SAM analysis. TFRs for two participants, illustrating inter-subject variability, which would be cancelled out in, group results. As before, there appears to be a co-occurrence of increases in synchronous power and decreases in synchronous power, but here it needs to be considered that frequencies are displayed ranging from theta to gamma.

Significant increases in cortical oscillatory power were also observed in the right inferior occipital gyrus, BA18, for alpha, across the 0 to 500ms time-window (see figure 3-9). Mann Whitney group TFR shows a very prominent increase in cortical oscillatory power at latencies of 100 to 300ms, for frequencies of 7 to 11Hz. This burst of increase

in cortical activity is followed (in time, 300 to 500ms) by decreases in cortical oscillatory power, most prominent at somewhat higher frequencies of 10 to 15Hz.

These patterns of cortical oscillatory power are also present in individual Mann Whitney TFRs, as shown in **Figure3-17.** The TFR for participant A illustrates this burst of power increase at 0 to 350ms, within alpha frequencies (z-score = +5.5). Power decreases are also evident for this participant, at 320 to 420ms; prominent decreases in cortical oscillatory power can be seen at 11 to13Hz (z-score = -2). For participant B a similar pattern of cortical activity could be observed. Prominent increases in cortical oscillatory power at 0 to 100ms, at frequencies of 8.5 to 11Hz (z-score = 4.5). Decreases in cortical oscillatory power are evident following this increase in signal power, at latencies of 300 to 500ms, across alpha (z-score = 0). Somewhat more prominent decreases in cortical power are seen at latencies later than 500ms, for frequencies of 8 to 15Hz.

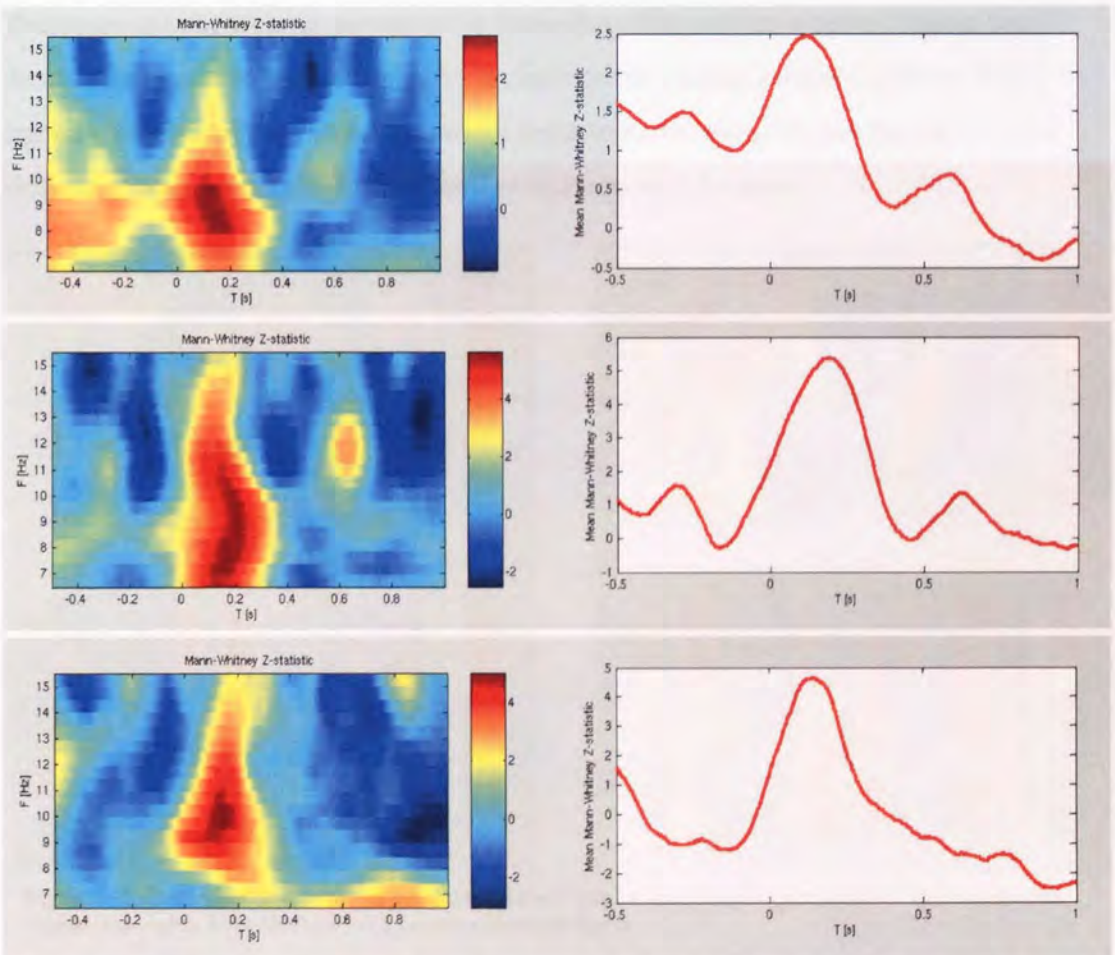


Figure3-17: Group TFRs (top row) for a voxel within the right inferior occipital gyrus, BA18. Increases in synchronous power are evident for alpha frequencies across the 0 to 500ms time-window as used in the SAM analysis. TFRs for two participants are also shown (middle and bottom rows). Prominent increases in cortical oscillatory power are evident in alpha for latencies of approximately 0 to 100ms.

Figure3-18 shows individual frequency representation for a VE placed in the inferior frontal gyrus BA44. Within this area, increases but also decreases in cortical oscillatory power have been demonstrated (using SAM and SnPM). For the 0 to 200ms time-window, for a broad range waveband of 5-40Hz, increases in cortical oscillatory power were observed, whereas for the 0 to 500ms time-window, decreases in cortical oscillatory power are demonstrated for gamma (25 to 40Hz). The TFRs for one participant show that theta (top left) seems to illustrate synchronous activation at about 200ms at 6-7Hz whereas desynchronisation also seems evident at lower frequencies (3-4Hz) sustained over prestimulus trigger time (-200ms) to 400ms post stimulus trigger time. Alpha (top right) seems characterised by increases in synchronous power at pre-stimulus trigger times whereas following stimulus onset low alpha shows decreases in synchronised power (desynchronisation) and some increase in cortical power at higher frequencies (12-13Hz). In beta, increases in synchronous power seem followed by decreases in synchronous power at the lower beta frequencies whereas higher beta frequencies seem to be dominated by an increase in cortical power at 200ms. For gamma, patches of synchronous activity seem to be followed by patches of desynchronous activity in time as well as in frequency domains.

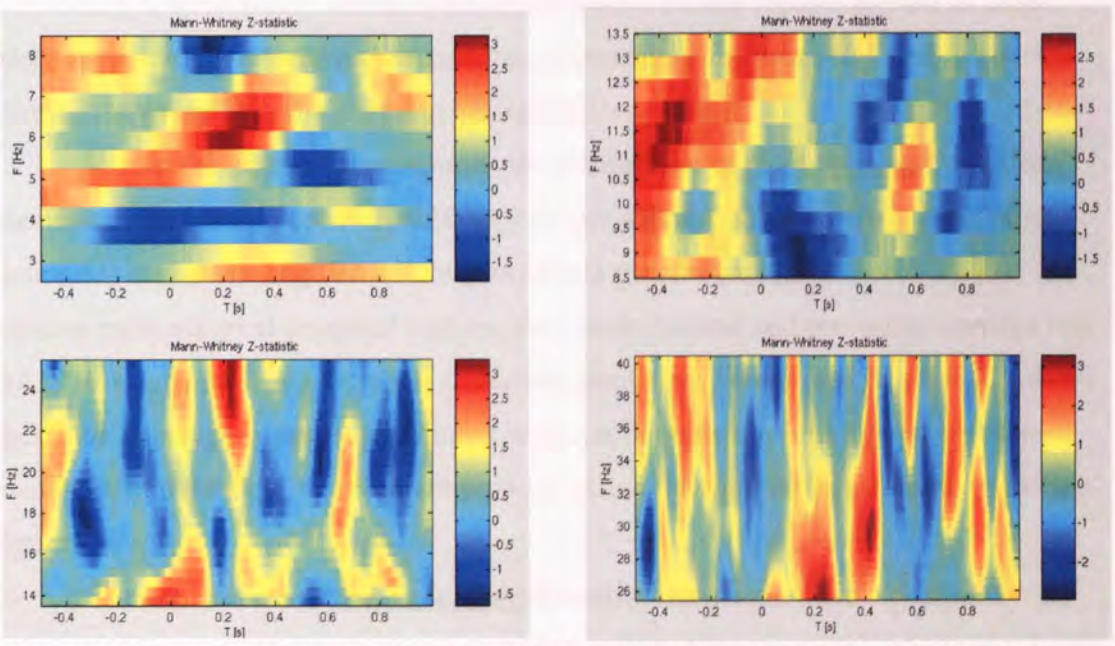


Figure3-18: Individual frequency representation for VE in inferior frontal gyrus BA44. Theta (top left) Alpha (top right), Beta (bottom left), Gamma (bottom right).

3.4. Discussion

The aim of this investigation was to contrast the activation and the relative changes in oscillatory cortical power induced by the presentation of different kinds or categories of perceptual stimuli compared to that of faces. These were houses and faces, and scrambled variations of either to provide for a control condition. Analyses were performed for two time-windows, 0 to 200ms and over a longer time-window of 0 to 500ms. The detailed reporting and discussion of purely house specific findings and patterns of oscillatory power changes related to the processing of houses was considered to be beyond the scope of this thesis.

3.4.1. Summary of results

In summary, the comparison of faces to houses, scrambled control images and a pre-stimulus baseline condition revealed significant increases in cortical power at different frequency bands and across different time-windows. These were shown most markedly in parietal and occipital regions but temporal regions were also involved in the processing of these visual stimuli. To a lesser extent, frontal regions as well as limbic and posterior regions were recruited in the processing of faces as compared to control stimuli. An overall bias for the right hemisphere was evident.

Within the **200ms time-window**, the comparison of faces to houses revealed significant increases in cortical oscillatory power within the right parietal lobe, most noticeably within the angular and the postcentral gyri for beta (see figure3-2). For gamma, right occipital-temporal regions, such as the cuneus and precuneus cortices and BA19 showed significant increases in cortical oscillatory power (see figure3-3). Across the 5-40Hz frequency range, significant increases in cortical oscillatory power were evident within the right superior temporal gyrus and the right inferior frontal gyrus (see figure3-4).

The comparison of face to scrambled control images revealed significant increases in cortical oscillatory power within the right inferior parietal lobule and BA40, the angular gyrus and also for the right occipital lobe and cuneus cortex in beta (see figure3-5). For gamma, significant increases in cortical oscillatory power were evident in the right parietal lobe and the postcentral gyrus as well as within sub-gyral regions of the left temporal lobe (see figure3-6).

To assess the responses evoked to faces per se, comparisons were also drawn between faces and a pre-stimulus baseline period. Here, left limbic and temporal regions (inferior temporal gyrus) showed increases in cortical power in beta (see figure3-7). For gamma, occipital regions of both hemispheres showed increases in occipital areas, notably, the cuneus cortex and BA18 as well as the lingual gyri (see figure3-8).

Within the **500ms time-window**, faces compared to houses revealed increases in cortical oscillatory power in right posterior / occipital regions such as the right inferior occipital gyrus for alpha (see figure3-9), and increases in oscillatory power for parietal areas bilaterally, but also within the right angular gyrus and within sub-gyral regions of the temporal lobe in beta (see figure3-10). For gamma, a network of cortical areas including precuneus cortex and BA7 of the right parietal lobe but also postcentral gyri of both hemispheres as sub-gyral regions of the right occipital lobe, the cingulate gyrus and the limbic lobe showed increases in cortical oscillatory power. In addition, left inferior frontal gyrus revealed decreases in cortical oscillatory power (see figure3-11).

The comparison of faces to scrambled control stimuli revealed increases in cortical oscillatory power within the right middle occipital gyrus for alpha (see figure3-12). For beta, increases in cortical oscillatory power were demonstrated within the right superior temporal gyrus, as well as the left and right inferior parietal lobule (see figure3-13). For gamma, sub-gyral regions of the right parietal lobe, the postcentral gyrus, the right superior temporal gyrus and sub-gyral regions within the left frontal lobe showed increases in cortical oscillatory power (see figure3-14).

3.4.2. Interpretation of Results

3.4.2.1. Differences in the processing of face and house stimuli – Are faces special but houses are not?

This investigation yielded support for the involvement of face specific regions such as the right superior temporal sulcus (figures 3-4 and 3-13), right occipital areas (figures 3-3, 3-5 and 3-9), left and right lingual gyri (figures 3-5 and 3-8) as well as left inferior temporal regions (figure 3-9). This supports other research reporting face specific regions associated with occipito-temporal areas such as the lateral fusiform gyrus, but also with the superior temporal gyrus and frontal areas (Clark et al. 1996; McCarthy et al. 1997; Haxby et al.1999).

Levy et al. (2001) have linked the specialisation in face processing to a central field bias, as, for instance, the identification of facial expression is thought to require a detailed scrutiny of the face to allow for such subtle task. Houses and buildings, on the other hand, are much larger objects, and their low level features (edges, corners) possibly are not centred, and thus occupy more peripheral field locations (Levy et al. 2001). Additionally, the processing of houses has been linked to increases in activation (BOLD) in the more medial regions of the fusiform gyrus, but it has also been claimed that the processing of houses or object categories per se involves the ventral temporal cortex in a much broader sense (e.g. Ishai et al. 1999). 'Building-selective' voxels have also been established in areas adjacent to the PPA (e.g. Aguirre, Zarahn & D'Esposito 1998; Ishai et al.1997).

The processing of faces compared to houses did appear to be related to more specialised and segregated regions and this might be linked to the different recognition goals associated with the categories of houses and faces (see figures 3-7 & 3-13). The recognition of faces at an individual level is learnt from an early age, as it is a crucial aspect of social interactions. Thus, the development of face-specific modules would indeed be plausible. The recognition of houses, on the other hand, could be regarded somewhat different, as spatial information is of prime importance here (see e.g. figures 3-9 & 3-11). How does my house differ from my neighbours may be of importance, but how the other houses in the street differ from one another may not be vital. For objects, however, there is no need to differentiate or discriminate between different categories of e.g. chairs, thus, they are recognised at a "higher entry level" (Gauthier 2000b, p.2).

A lack of object-specific processing areas for both stimulus categories has previously been reported by Farah & Aguirre (1999). They conducted a meta-analysis and looked separately at the activation patterns associated with words, objects and faces. They showed that the maxima of each individual stimulus set yielded activity within wide areas of cortex for each stimulus condition. One reason for such widespread activity, and the lack of specialisation (segregation) can be seen in the tasks that were performed in the studies included in Farah & Aguirre's meta-analysis. The cognitive content of such tasks as well as their complexity might have led to interactions between cognitive processes and thus thwarted the subtraction methods (or direct comparisons) used in these studies (Friston et al. 1996, Zarahn et al. 1997 cf. Farah & Aguirre 1999). This leads to more general methodological issues that have to be addressed in order to make full sense of neuroimaging data.

3.4.3. Methodological considerations in functional neuroimaging research

3.4.3.1. Task demands

The observed dominance of the right hemisphere in the processing of face and house stimuli was also observed by Ishai et al. 1999; 2000 who reported that the processing of visual percepts lead to increased responses in the right hemisphere. Parietal involvement would arise from the visuo-spatial nature of the task, where holistic processing is required to carry out the required comparison.

In addition, the observed frontal involvement could be associated with the 'working memory' type requirements of the task. Participants had to keep in memory a first image and then compare it to a subsequent image to assess whether or not these were identical. In previous functional imaging experiments, one-back memory tasks had been linked to increases in activation in the prefrontal cortices as well as in posterior parietal areas (Braver et al. 1997; Carlson et al. 1998; Cohen et al. 1997 & Jonides et al. 1997). Thus, the differential involvement in frontal areas in this investigation (see figures 3-4 & 3-11) might be linked to the concept of working memory (e.g. Baddeley 1996). Information needs to be kept in the cognitive system (e.g. short-term-memory) to allow the comparison of the second visual percept (i.e. the second face) to the first one (as the first face no longer exists in the immediate visual environment) (Baddeley & Della Salla 1996, Druzgal & D'Esposito 2001).

3.4.3.2. Intersubject variability

One issue that has to be addressed when attempting to interpret group data from functional imaging experiments is that of individual differences and variability in the shape and size of the brains of the individual participants. Patterns of activation in some cytoarchitectonic locations may be mapped differently in the standard brain that is used to infer group effects. Thus, each participant could have their own face and house specific areas, yet these precise locations within the larger visual recognition areas might differ from person to person thus complicating group interpretation (Farah & Aguirre 1999). Hence, inconsistencies observed between previous literature and the

current investigation could be due to the marked individual differences between participants (see figures 3-15 & 3-16).

3.4.3.3. Direct versus indirect comparisons of visual stimuli

The observation drawn from this investigation of the apparent lack of a clear-cut distinction between the areas involved in the processing of face, houses and control stimuli would need further investigation. Here, it might have been useful to include, in more detail, the patterns of cortical activity observed by comparing houses to a pre-stimulus baseline as well as to the scrambled control images. House versus baseline conditions revealed the activation of left and right parietal and occipital areas, i.e. similar areas to those established for face versus house conditions. This again indicates that the processing of houses may not necessarily rely on a distinct neural module responsible for house recognition. Indeed, Ishai et al. (1997) observed that activation patterns to faces, for example, extended into regions also maximally responsive to houses, hence showing a widely distributed network associated with the processing of face and house stimuli. This has led Gauthier (2000b) to suggest that a house-processing module may still exist; yet it may also be involved in processing a face. Thus, it is possible that overlapping patterns of cortical activity exist for different stimulus categories, alongside category specific areas. Ishai et al. (1997) and Haxby et al. (2000b) propose that the extrastriate visual areas are topologically organised into continuous representations for objects, rather than having a number of modules dedicated to a single category.

In addition, it could be argued that the same areas (and extrastriate areas seem a reasonable candidate structures) might be suitable for different processing strategies, e.g. encoding subtle difference between two similar classes of visual stimuli that could then be associated with activation within the same region. Differences, however, might be evident in time and frequency domains. The current investigation showed that increases in cortical activity seem to be present across different frequency bands for a number of neural correlates of face and house processing. Here, frequency-specific increases in cortical oscillatory power were evident for parietal regions, which were associated with beta frequencies, whereas occipito-temporal regions were linked to gamma frequencies.

3.5. Conclusion

Despite the claim of numerous previous researchers of there existing different neural networks for different object categories, this study demonstrates a substantial amount of overlap in cortical regions activated in response to different objects, in this case faces and houses. Therefore, instead of focusing on the strongest responses within one area to a category, relevant weaker responses (in category-related areas or different neural structures) also need to be considered as playing a part in the distribution of cortical representations to objects or categories (Hanson, Matsuka & Haxby 2004). Bartels & Zeki (2004 pp75), providing a similar argument, pointed out that findings from neuroimaging investigations do not "...show the non-involvement of areas and that positive results [obtained] are only of a correlational nature." Faces and houses alike are linked to distinct processing hypotheses. Faces are thought be processed by areas implicated in expert discrimination of visual stimuli, and houses are linked to areas in which the processing of spatial information is associated with houses. Yet, for both category-specific regions experiments have found activation to other stimuli. Thus, it has been suggested that the same voxels might be recruited by a chair, a house, a car or a face as long as they share the same processing requirement.
The debate concerned with the "exact" spatial location of object (house) and face processing might remain a "great puzzle" (Haxby et al. 2000b). Maybe the ventral temporal cortex or the extrastriate visual areas are indeed 'responsible' for the processing of these different stimuli, and how processing is distinguished is not so much to do with the 'location' of activity but with the neural interactions between these different areas. Houses and faces could indeed be processed within the same regions, and maybe the identification of the stimulus as a house or a face is associated with different cortical oscillatory patterns or latencies. If, for instance, a face appears to induce activity within a house-selective region, it might be that inhibitory processes are 'at work', signalling a No-Go or "No need to respond as a face" type of reply. In this investigation, however, it should be noted that increases in cortical oscillatory power were observed almost exclusively, so there is no clear evidence of inhibitory processes as indexed by event related desynchronisation. However, the distinctiveness offered by combining findings in the time, space and frequency domains suggests that this could be a more fruitful approach to attempt to identify the potentially specialised cortical correlates of face processing. It may further the investigation of neurobiological and

neuropsychological issues associated with object processing, and in particular with the processing of faces.

Chapter 4 An MEG investigation of the 'Face Inversion Effect'

4.1. Introduction

Faces are very complex stimuli and it is therefore assumed that, possibly, faces are more difficult to recognise than objects (Farah et al. 1995). It has been suggested that the perception of faces is special as face recognition processes are thought to be qualitatively different from other object recognition processes. It has been proposed that face processing relies upon the processing of 'holistic representations' of face components, whereas object recognition is thought to be based upon the processing of representations that are decomposed into constituent parts (Eimer 2000a; Diamond & Carey 1986; Farah et al. 1991). According to the holistic processing hypothesis, upright faces are encoded as wholes, and not decomposed into individual features, thus they are processed configurally. Inverted faces on the other hand are processed analytically, like objects (Itier & Taylor 2004).

4.1.1. Are faces special? Effects of face inversion on face processing

Face processing is underpinned by a multiple component neural system, which is able to process whole faces as well as face parts. It is thought that the selective activation of face specific neural networks at the earlier stages of the visual processing stream allows for the possibility of increasing the efficiency of face processing by restricting consequent stages to a particular class of internal models i.e. that of faces. A number of face processing models incorporate components that enable early structural face encoding, using physiognomic features as input and gaining an integrated, although not fully identified, output representation (Bruce & Young 1986; Moses, Ullman & Edelman 1993; Rhodes 1995).

In healthy participants, behavioural studies have shown that face recognition appears severely impaired when face stimuli are presented upside-down, i.e. inverted (Diamond & Carey 1986). Numerous behavioural studies have demonstrated such difficulties, and a few functional imaging studies have investigated the neural substrates underlying the face inversion effect. These have suggested that the inversion effect might result from a disruption of configural processing (Leube et al. 2003), as it has previously been assumed that configural cues strongly influence the recognition of

upright, but not inverted, faces (Valentine 1988; Tanaka & Farah 1993; Murray, Young & Rhodes 2000).

4.1.2. Investigations of the neural substrates of face inversion

4.1.2.1. ERP studies

The neural correlates of the face inversion effect, or configural face processing, are associated with a right hemisphere processing dominance, as the right hemisphere shows more pronounced face inversion effects (e.g. Farah et al. 1995; Leehey, Carey, Diamond & Cahn 1978). This has also been indicated in studies on split-brain monkeys (e.g. Vermeire & Hamilton 1998), in investigations on humans using event-related potentials (e.g. Rossion et al.1999) and in functional imaging studies (e.g. Aguirre, Singh & D'Esposito 1999; Haxby et al. 1999; Kanwisher, Tong & Nakayama 1998). Single unit recordings in monkeys (Perrett et al. 1988; Perrett et al. 1998) and scalp recordings from humans (Jeffreys 1989) have revealed comparable response amplitudes for the face specific N170 component to upright and inverted faces. Perrett et al. (1982) observed that in the macaque, cells within the temporal cortex are sensitive to the configuration of face components. Thus, when facial features were rearranged in target stimuli, activity in face specific neurons decreased.

ERP studies on the face inversion effect revealed that the face specific N170 is present for inverted faces too. Thus, rather than being involved in holistic face recognition processes only, it is assumed to reflect the perceptual encoding of face components also (Bentin et al. 1996). However, longer response latencies to inverted faces for the N170 component have been reported when participants were required to perform face discrimination tasks (e.g. Rossion et al. 1999; Rossion et al. 2000, Eimer 2000a). Rossion et al. (1999), for example, reported that in a delayed matching task, the N170 component was delayed and larger to inverted faces. At occipito-temporal areas, significant latency differences were observed with mean latencies for upright faces (156ms for right hemisphere (RH), and 157ms for left hemisphere (LH)) being smaller than mean latencies for inverted faces (167ms for both, right and left hemispheres). With respect to amplitude, significant differences were observed for occipito-temporal sites, with amplitudes for upright faces (-3.53 μV for RH and –2.9μV for LH) being smaller than those observed for inverted faces (-6.03μV for RH and –5.1μV for LH).

Eimer (2000a) also reported a small (approximately 8ms) but robust delay in latencies when processing inverted faces. He quantified the N170 as taking place between 150ms and 200ms post-stimulus. Significant differences were obtained at temporal sites, with latencies to upright faces (170ms for RH and 167ms for LH) being smaller than those for inverted faces (177ms for RH and 175ms for LH).

Eimer (2000b) argued that the delay might in fact indicate a 'difference' face specific component, reflecting the successive stages of face-processing, on the one hand, the perceptual analysis and the structural encoding, on the other and, following on from the previous, the classification and identification of individual face stimuli. Thus, the latency differences are interpreted as due to the involvement of different neural generators.

The observed increases in amplitude and latency have been linked to increases in the level of difficulty when processing inverted faces. George & Hole (1995) have argued that the processing of inverted faces is more difficult, and thus leads to sustained attentional 'processing negativity'. Such delays are thought to be due to insufficient configural information provided by upside down faces (Rossion et al. 1999; Eimer 2000a).

The perception of gestalt-like figures is linked to increases in synchronisation within the gamma band. This has been associated with the rhythmic synchronisation of neuronal firing (within the gamma range) that is necessary for the binding of spatial and temporal sub-processes, which allows the perception of a coherent image (Tallon-Baudry & Bertrand 1999). Rodriguez et al. (1999) showed participants upright and inverted Mooney faces and reported 'induced' gamma responses, i.e. increases in synchronisation, at latencies of approximately 230ms. These were significantly larger to the upright Mooney faces than to the inverted ones, which were reported to be perceived as meaningless percepts. Thus, phase-synchrony seems to differ between the perception of upright (meaningful) and inverted (meaningless) perceptual stimuli.

4.1.2.2. fMRI investigations

Sekuler et al. (2004) observed that similar, i.e. occipito-temporal regions were involved differentially when participants performed a face discrimination task, using both upright and inverted face conditions. The paradigm used by Sekuler et al involved the presentation of a face stimulus embedded in noise followed by two face stimuli, and it had to be guessed which of the two faces was presented previously. Sekuler et al.'s (2004) results showed that processing upright and inverted faces differs quantitatively, not qualitatively, as information is extracted more efficiently from upright faces, perhaps as a by-product of orientation – dependant expertise.

Leube et al. (2003) further investigated the face inversion effect, and, drawing on previous findings of the superior temporal lobe being involved in face processing (Haxby, Hoffman & Gobbini 2000) as well as spatial processing (Karnath, Ferber & Himmelbach 2001), hypothesised the involvement of superior temporal areas in the processing of the more configural properties of faces. Leube et al. (2003) reported stronger signal changes for upright faces (compared to inverted faces) in the right superior temporal gyrus (BA2) and in the right insular cortex (BA21). They also reported activation of a face-specific right hemisphere network comprising right lingual (BA18), right inferior occipital (BA19) and right fusiform (BA37) gyri. Similar results have also been reported by Haxby et al. (1999) who described decreases in neural responses within superior temporal areas in response to inverted (compared to upright) faces. Leube et al. (2003) concluded that the involvement of right temporal gyri and the right insular cortex may reflect the configural (i.e. holistic) processing of faces, as activation within these areas was absent when faces were inverted.

In summary, upright faces are encoded into memory holistically (i.e. without explicitly represented parts), inverted faces are not - they appear to be represented with the same degree of part decomposition as non-face objects such as house. The inversion of faces has been related to the slowing down of facial encoding, as well as to enhanced activity, related to an increase in the level of difficulty of facial processing (Rossion et al. 1999).

As there is some inconsistency regarding the spatial mapping of the face inversion effect, it is aimed to establish if there are functionally and anatomically distinct systems for the perception of upright versus inverted faces, as suggested by neurological studies, or whether similar regions are involved in the processing of

upright and inverted faces as has been shown in functional imaging studies. The processing of faces is predicted to lead to activation within face-specific regions such as the extrastriate visual areas and occipito-temporal regions. The involvement of temporal regions, as observed in previous fMRI investigations, is to be explored.

As previously described, the use of virtual electrodes in those areas indicated by SAM as differentially activated offers the possibility of generating TFRs to investigate timing differences. However, the reported delays of the face specific N170 (see section 4.1.2.1) appear to be quite subtle. SAM analyses are performed on two different time-windows, 0 to 200ms to investigate the face-specific N170, and across a larger time-window of 0 to 400ms to allow for delayed activity to inverted faces.

Additional, frequency specific measures can be obtained. Given the findings by Rodriguez et al. (1998) with upright and inverted Mooney faces, the involvement of gamma frequencies is predicted (see also chapter 3).

4.2. Method

4.2.1. Materials and Participants

Stimuli were selected from the Ekman and Friesen (1976) series of *Pictures of Facial Affect*, which contains black and white photographs of facial expressions of 10 actors (six female). The photographs have been digitally altered to depict only the contour of the face, i.e. hair, ears etc. are removed. The images selected for the current investigation comprised happy and sad expressions for all ten individuals, plus corresponding neutral expressions, generating a total of 30 facial stimuli in the upright condition. As this did not suffice, each of these facial stimuli was repeated three times, yielding a total of 90 upright facial stimuli. Identical photographs were used in the inverted and upright conditions. Using Adobe Photoshop CS the photographs were simply rotated by 180 degrees. Ninety inverted facial stimuli were thus used. A similar paradigm was used by Eimer & Holmes (2002). For stimulus display Presentation software (http://nbs.neuro-bs.com/presentation/) was used.

Nine healthy participants (eight female, one left-handed) gave consent to take part in the investigation. The average age of the participants was 29 years. Due to movement, head localisation failed for two participants resulting in usable data for seven participants (six females; one left handed, average age 27years). The study was approved by the Aston University Human Sciences Ethics committee. Participants were seated within a magnetically shielded room, and viewed, through a mirror, a monitor, placed outside the shielded room, on which the stimuli were presented. The distance between the participants and the monitor was approximately 2m.

4.2.2. Experimental Paradigm

On each trial, participants were asked to fixate on a white circle for 1500ms before a stimulus was presented for 500ms. The stimulus was either an upright face or an inverted face depicting a happy, sad or neutral expression. The fixation point then returned followed by a second image being presented for 500ms, again the stimulus being an upright or an inverted face of the above mentioned valence. Upon a delay a cue (red circle) indicated that the participant should make a button-press response,

indicating whether the two faces presented were identical in facial expression, or not (see **Figure4-1**).

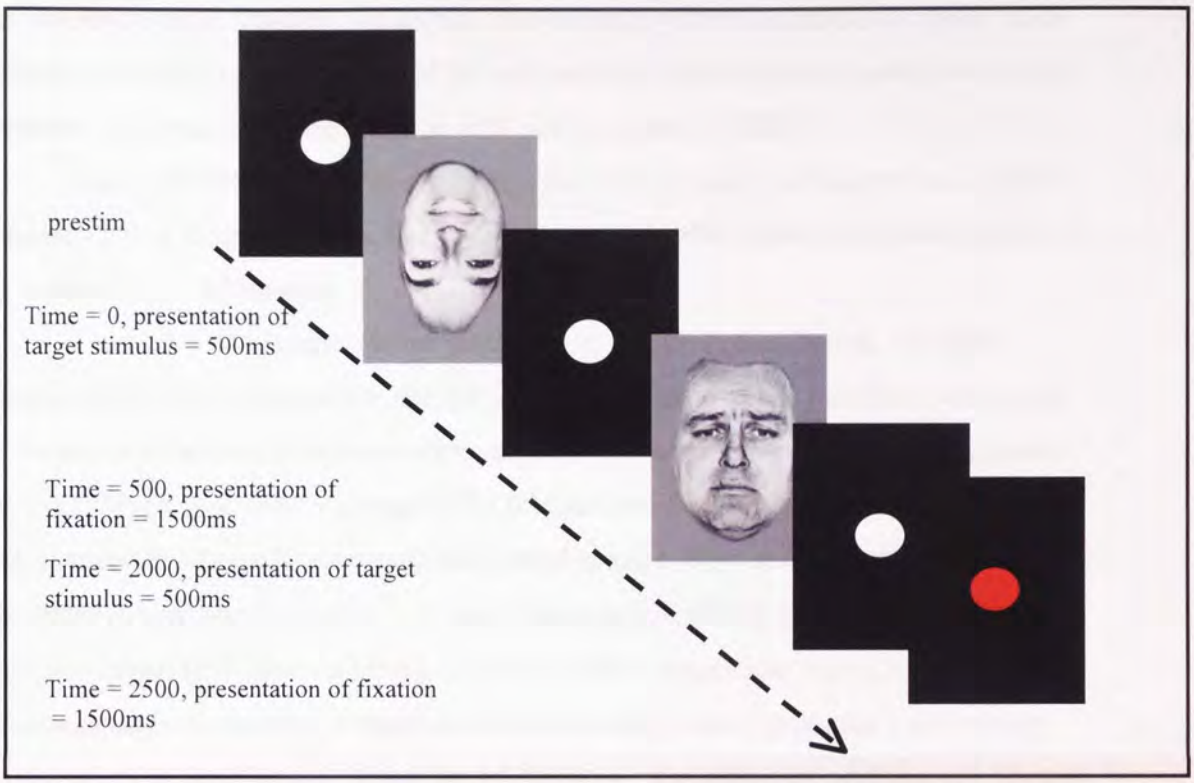


Figure4-1: Experimental paradigm, showing examples of the stimuli and timing used in the experiment. Participants were required to press an appropriate button on the response box as soon as they saw the fixation change from white to red.

4.2.3. Image Acquisition and Analyses

MEG signals were recorded with a third order gradiometer configuration using an Omega 151-channel magnetometer (CTF Systems Inc., Canada).

Head localisation information was acquired by recording the position of head localisation coils before and after the recording session. Following data acquisition, a 3-D digitiser (Polhemus Isotrack) was used to digitise participants' heads and allow co-registration of each participant's MEG and magnetic resonance imaging (MRI) data. This was achieved using Align (www.ece.drexel.edu/ICVC/Align/align11.html), which matches the participant's digitised head-surface to the head-surface extracted from their individual, anatomical MRI (Kozinska 1997).

To analyse the MEG data, Synthetic Aperture Magnetometry (SAM) was used (see section 2.4.1.1.). SPMs were generated for predetermined frequency bands (2-8Hz; 8-

13Hz; 13-25Hz; 25-40Hz and 5-40Hz) and time-windows 0 to 200ms and 0 to 400ms over the entire brain at 5mm resolution to localise power changes in response to upright and inverted stimuli. Positive values are interpreted as relative increases in power, also referred to as ERS, or increases in ERSP and negative values are interpreted as relative decreases in power, also referred to as ERD, or decreases in ERSP.

Using SPM99 (Friston et al. 1995), the MRI of each participant was spatially normalised to a template space. The resultant normalisation parameters were applied to the volumetric SAM images.

Thus, all SAM images (seven participants, five frequency bands, two time-windows and three comparisons: upright vs. baseline; inverted vs. baseline; and upright vs. inverted) were then in the same three-dimensional coordinate space allowing group analyses (Singh et al. 2002). Using SnPM (Holmes et al. 1996; Nichols & Holmes 2002), analyses of significance were performed at voxel level and at cluster level using a multiple subject single condition design. Variance smoothing was performed using a Gaussian kernel (σ = 20mm). Using non-parametric permutation testing, cluster-level inferences estimate whether a large connected cluster of near significant t-values may reach statistical significance. Voxel level inferences were estimated additionally. Spatial resolution however is being traded in against sensitivity (for details see Nichols & Holmes 2002; Singh, Barnes & Hillebrand 2003).

For the visualisation of the results on a template brain, SPM was used as well as mri3dX (http://www/aston.ac.uk/lhs/staff/singhkd/mri3dX/). In all figures the left side of the brain is displayed on the left side of the image, and coordinates provided are stated in Talairach & Tournoux (1988) version. In the figures presented, increases in cortical power are indicated by colourscale of red – orange – yellow, with yellow regions being the most significantly active areas. Decreases in cortical oscillatory power are indicated by a colourscale of blue – pink – white, with white regions being the most significantly active areas (see colourbar page 74, **FigureB**).

To investigate the time course and frequency specificity of the obtained activation within significant regions, time-frequency representations (TFR) were generated using Morlet wavelet analysis (Tallon-Baudry et al. 1997). The wavelet method was chosen as it provides a better compromise between time and frequency resolution than Moving Window Fourier Analysis. Once the TFRs for each participant were generated, averages were computed by averaging the TFRs of all participants.

4.3. Results

SAM analyses were performed for two time-windows, 0 to 200ms and 0 to 400ms, across the following frequency bands: theta (2-8 Hz), alpha (8-13Hz), beta (13-25Hz), gamma (25-40Hz) and across a wide frequency range of 5-40Hz. Unless otherwise stated the results reported are significant at voxel level. A table of results detailing pseudo-t statistics, coordinates and region showing changes in cortical power are included in **Appendix3**.

4.3.1. Direct comparisons: upright versus inverted facial stimuli

To investigate the differences between the processing of upright and inverted faces, group analysis were performed using GroupSAM.

These revealed changes in oscillatory power within occipital and temporal regions (e.g. right middle occipital gyrus, cuneus, BA7 as well as middle and superior temporal gyri) predominately within the 0 to 200ms time-window and within the right hemisphere. For occipital regions, power changes could be observed for alpha frequencies (8-13Hz) and across a wide frequency rage of 5-40Hz. Within temporal regions, theta (2-8Hz) and beta (13-25Hz) frequencies were engaged. Left and right frontal as well as parietal areas also showed increased involvement in the processing of upright versus inverted faces. For the 200ms time window, power changes could be observed predominately in left frontal areas, whereas this pattern seems more bilateral across a longer time-window of 400ms. Left parietal areas, particularly, were engaged during the longer time-window of 0 to 400ms, whereas right parietal areas seemed more engaged for the 0 to 200ms time-window.

Subsequent statistical inferences using SnPM did not yield significant results. However, to explore processing for upright versus inverted faces further, time-frequency representations were generated, using Mann-Whitney wavelets. A virtual electrode was placed within the right middle occipital gyrus, and TFRs generated for each individual. For Mann Whitney TFRs upright faces were included in the analyses as active stimuli and inverted faces as passive stimuli, i.e. the activity for inverted faces was "subtracted" from that of upright faces. These were then averaged to allow inferences about group data (**Figure4-2**).

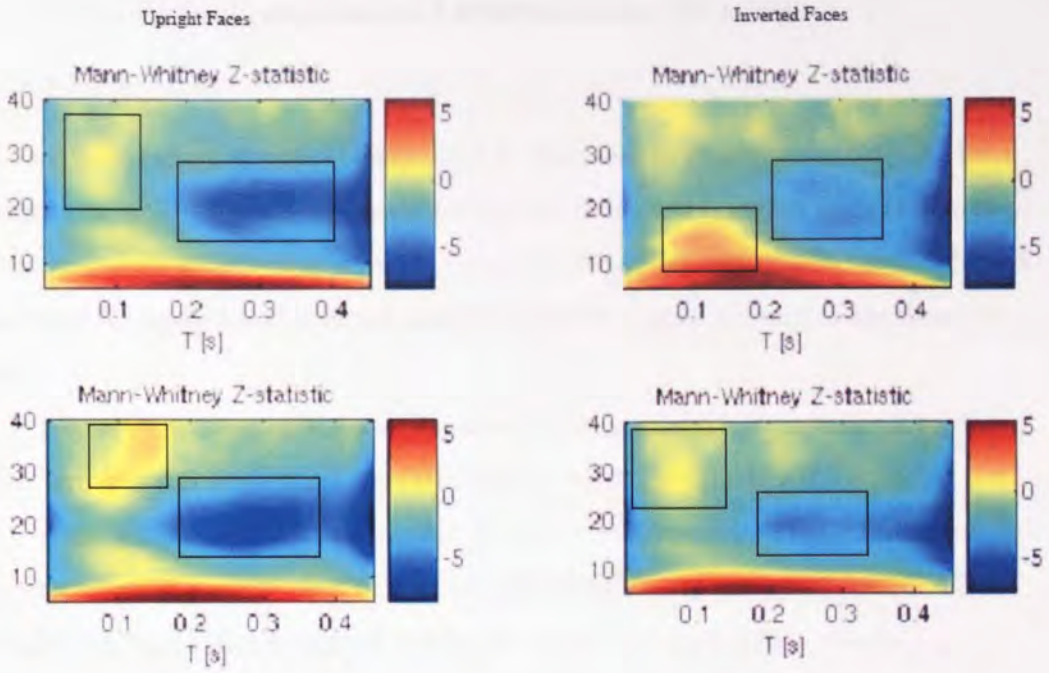


Figure4-2: Mann Whitney TFRs showing the differences in cortical power for upright (left) and inverted (right) faces.
Top row: shows oscillatory power changes for a VE within the middle occipital gyrus. Initial increases in cortical oscillatory power are followed by decreases in cortical power (see boxes).
Bottom row: shows oscillatory power changes a VE within the right parietal lobe, precuneus area. Initial increases in cortical oscillatory power are followed by decreases in cortical power.

The time-frequency representations in figure4-2 illustrate the changes in oscillatory power with increases in cortical oscillatory power being evident at 0 to 200ms across the whole frequency range shown and decreases in spectral power at 200 to 400ms. Within the first 200ms, somewhat more prominent increases in cortical oscillatory power appear at the high beta / low gamma frequencies at 25-30Hz, both for the middle occipital gyrus (top row) and for the right parietal lobe (bottom row).

Differences between the upright (left) and inverted (right) conditions seem present at the frequency level, with lower frequencies (8 to 18Hz) being implicated in the processing of inverted faces. Decreases in cortical oscillatory power seem to be more dominant at later latencies, 200 to 400ms. These seem particularly prominent at the beta range between 15 and 25Hz, for both middle occipital and parietal areas and are more prominent for upright than inverted faces.

Therefore, the change in cortical activation from increases at early latencies to decreases in cortical power at later latencies was investigated further by drawing comparisons between the 0 to 200ms time-window and the 200 to 400ms time-window.

4.3.2. Indirect comparisons: 0 to 200ms versus 200 to 400ms

4.3.2.1. Alpha

SAM analyses were computed, using the 0 to 200ms-time window as a baseline to compare changes in oscillatory power for upright faces and inverted faces (separately) during the 200 to 400ms time window. Using SnPM, significant results were obtained at voxel level for upright and inverted faces (compared to their respective baseline) for alpha.

For **upright faces**, ERS was revealed in the right and left posterior lobe, the cerebellum (inferior semi-lunar lobule (right: $t = +7.41$, $p < 0.01$; left: $t = +5.79$; $p < 0.05$), in the left parietal lobe, precuneus, BA7 ($t = +7.07$; $p < 0.01$), the right occipital lobe, precuneus ($t = + 5.84$; $p < 0.05$), the right middle temporal gyrus ($t = +5.66$, $p < 0.05$) and the right inferior parietal lobule ($t = +5.42$, $p < 0.05$) (**Figure4-3**).

For **inverted faces**, ERS was demonstrated in the right occipital lobe, middle temporal gyrus ($t = +7.56$, $p < 0.05$), the right middle occipital gyrus ($t = +7.14$, $p < 0.01$) and within the right posterior lobe, cerebellum (uvula) ($t = +5.26$, $p < 0.05$) (**Figure4-4**).

This shows that somewhat different networks of cortical activity are recruited for the processing of upright compared to inverted faces. Upright faces recruited cortical networks within both hemispheres, as well as involving parietal areas. Right middle temporal and occipital areas are implicated in both conditions.

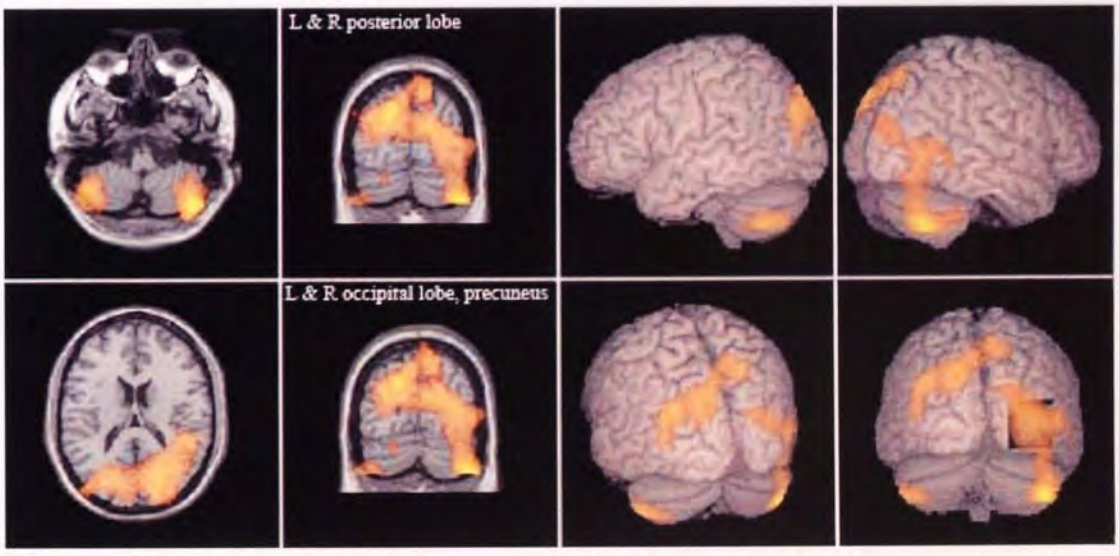


Figure4-3: Responses to upright faces compared to baseline in the 8-13Hz frequency band, for 0 to 200ms versus 200 to 400ms. SPMs show significant ERS in the right and left posterior lobe (top row), within the left occipital lobe, precuneus, within the right occipital lobe, precuneus (bottom row) displayed onto a template brain.

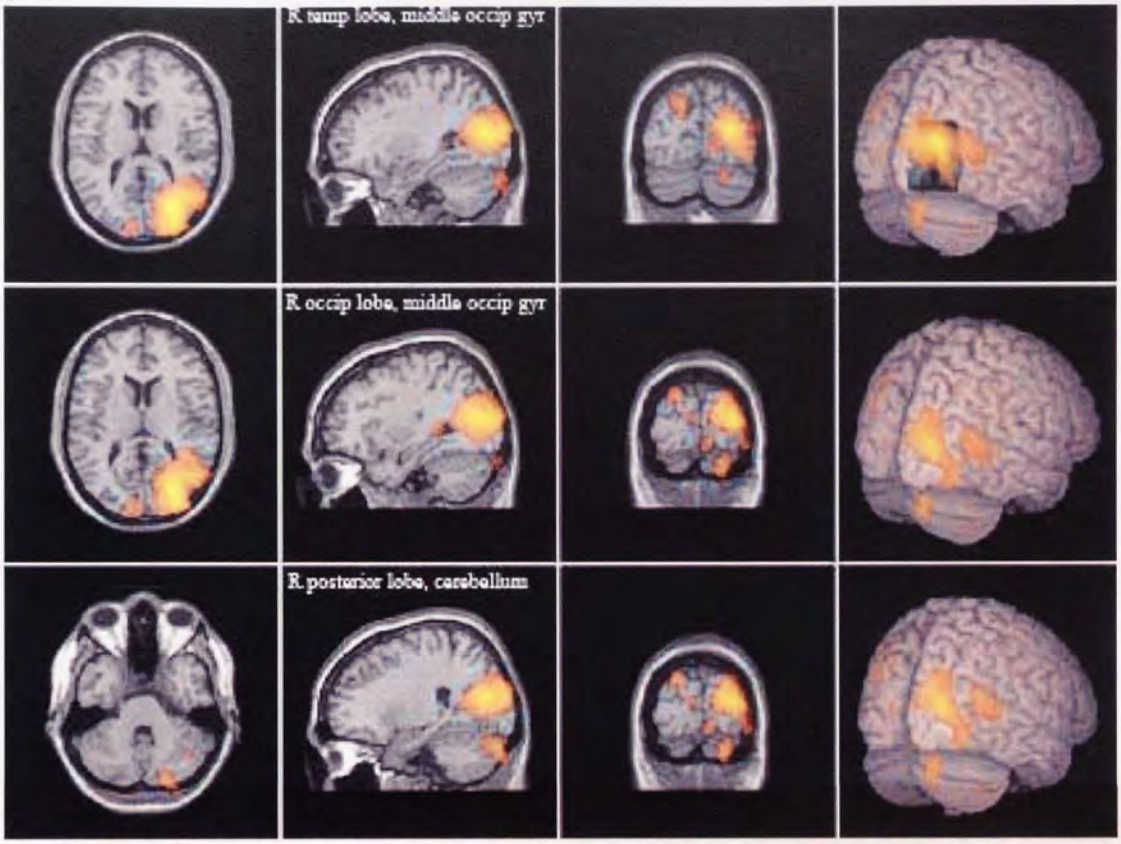


Figure4-4: Responses to inverted faces compared to baseline in the 8-13Hz frequency band, for 0 to 200ms versus 200 to 400ms. SPMs show significant ERS in the right temporal lobe, middle occipital gyrus (top row), within the right occipital lobe, middle occipital gyrus (second row), within the right posterior lobe, cerebellum (third row), displayed onto a template brain.

4.3.2.2. 5 to 40Hz

SAM analyses were computed, using the 0 to 200ms-time window as a baseline to compare changes in oscillatory power changes for upright faces and inverted faces (separately) during the 200 to 400ms time window. Using SnPM, significant results were obtained at voxel level for upright and inverted faces (compared to their respective baseline) across a wide frequency range of 5-40Hz.

For **upright faces**, ERS was demonstrated within the left parietal lobe, the precuneus ($t = +6.63$, $p < 0.01$), the right middle occipital ($t = +5.30$, $p < 0.05$) and temporal gyri ($t = +5.04$, $p < 0.05$), and within the right parietal lobe, superior parietal lobule ($t = +4.91$, $p < 0.05$) (**Figure4-5**).

For **inverted** faces, ERS was shown in the right middle occipital gyrus ($t = +6.12$, $p < 0.01$), the right temporal lobe in sub-gyral regions ($t = +5.60$, $p < 0.01$) and within the right posterior lobe and the cerebellum, $t = +5.33$, $p < 0.01$). In addition,

ERD was also observed, within the middle frontal gyrus ($t = -4.69$, $p < 0.05$) (**Figure4-6**).

As before, upright faces recruited networks within both hemispheres, whereas the processing of inverted faces is confined to areas within the right hemisphere. Upright faces involve parietal areas and only inverted faces showed ERD in right frontal areas.

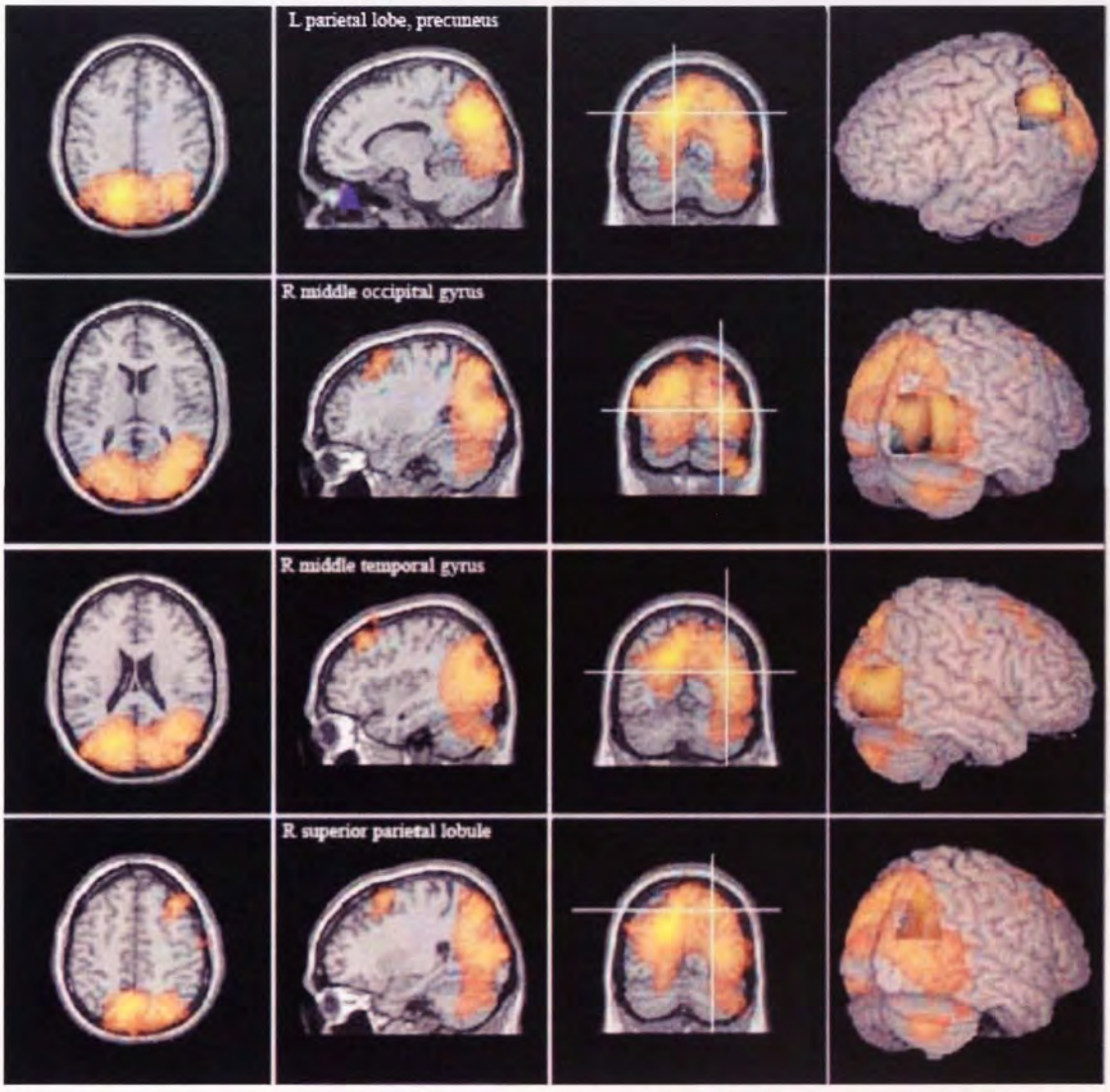


Figure4-5: Responses to upright faces compared to baseline in the 5-40Hz frequency range, for 0 to 200ms versus 200 to 400ms. SPMs show significant ERS in the right parietal lobe, precuneus (top row), within the right middle occipital gyrus (second row), within the right middle temporal lobe (third row), and within the right superior parietal lobule (bottom row), displayed onto a template brain.

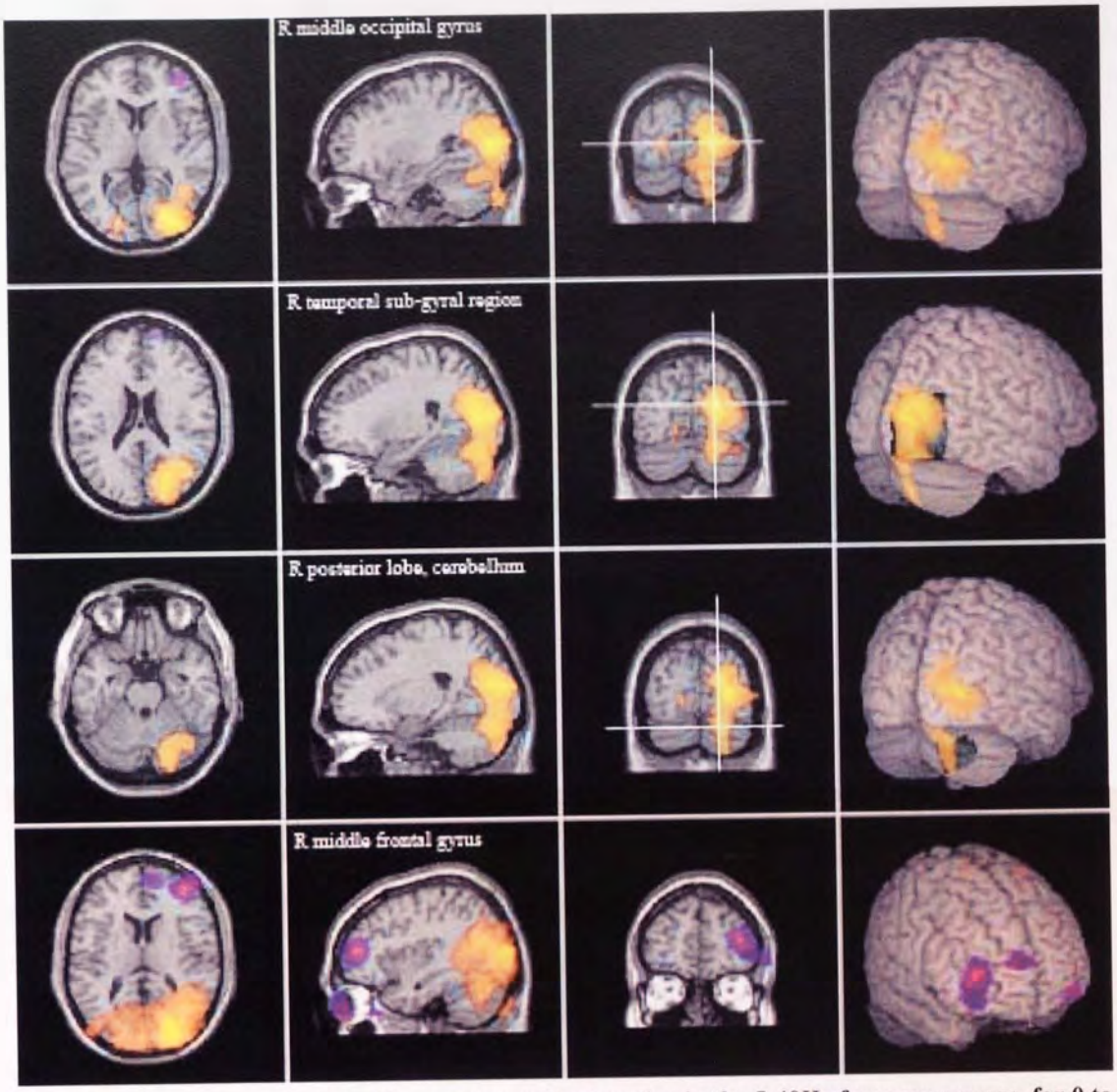


Figure4-6: Responses to inverted faces compared to baseline in the 5-40Hz frequency range, for 0 to 200ms versus 200 to 400ms. SPMs show significant ERS in the right middle occipital gyrus (top row), within the right temporal lobe, sub-gyral regions (second row), within the right posterior lobe, cerebellum (third row). ERD is demonstrated within the right middle frontal gyrus (bottom row), displayed onto a template brain.

Having established the differences for the processing of upright and inverted faces for time-windows of 0-200ms and 200-400ms, additional analyses were performed to assess the difference between upright and inverted faces at latencies of 0 to 400ms compared to their prestimulus trigger time.

4.3.3. Indirect comparisons: Upright versus baseline and Inverted versus baseline for 0 to 400ms time-window

Within this time-window both conditions compared to their respective baselines yielded significant results for beta (13-25Hz) and gamma (25-40Hz) frequencies.

4.3.3.1. Beta

For **upright faces**, for a critical threshold of $t = 5.08$, $p < 0.05$, significant voxels were observed within the right parietal lobe, precuneus regions BA7 ($t = 5.44$, $p < 0.05$), and within the left parietal lobe, precuneus ($t = 5.3$, $p < 0.05$). In these areas ERD was observed (see **Figure4-7**).

For **inverted faces**, with a critical threshold of $t = 5.15$, $p < 0.05$, significant voxels were observed within the left occipital lobe, cuneus ($t = 7.16$, $p < 0.01$), within the right superior parietal lobule ($t = 6.95$, $p < 0.01$), within the right parietal lobe, precuneus area ($t = 6.64$, $p < 0.05$) and within the right middle occipital gyrus ($t = 5.34$, $p < 0.05$). In these areas ERD was observed (**Figure4-8**).

These findings confirm the differential involvement of parietal and occipital areas in the processing of upright and inverted faces. Left parietal areas were implicated in the processing of upright faces, but not of inverted faces and bilateral occipital areas were observed when processing inverted but not upright faces. This observation, however, differs to those made in direct comparison.

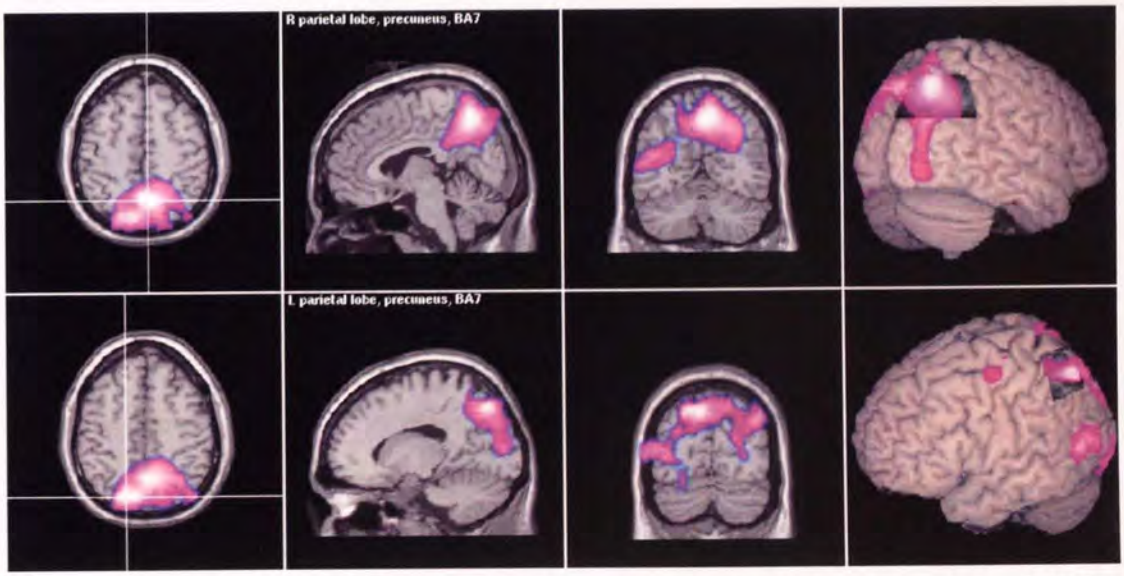


Figure4-7: Responses to upright faces compared to baseline across 13-25Hz frequency band, for 0 to 400ms. SPMs show significant ERD in right (top) and left (bottom) parietal lobe, precuneus areas, displayed onto a template brain.

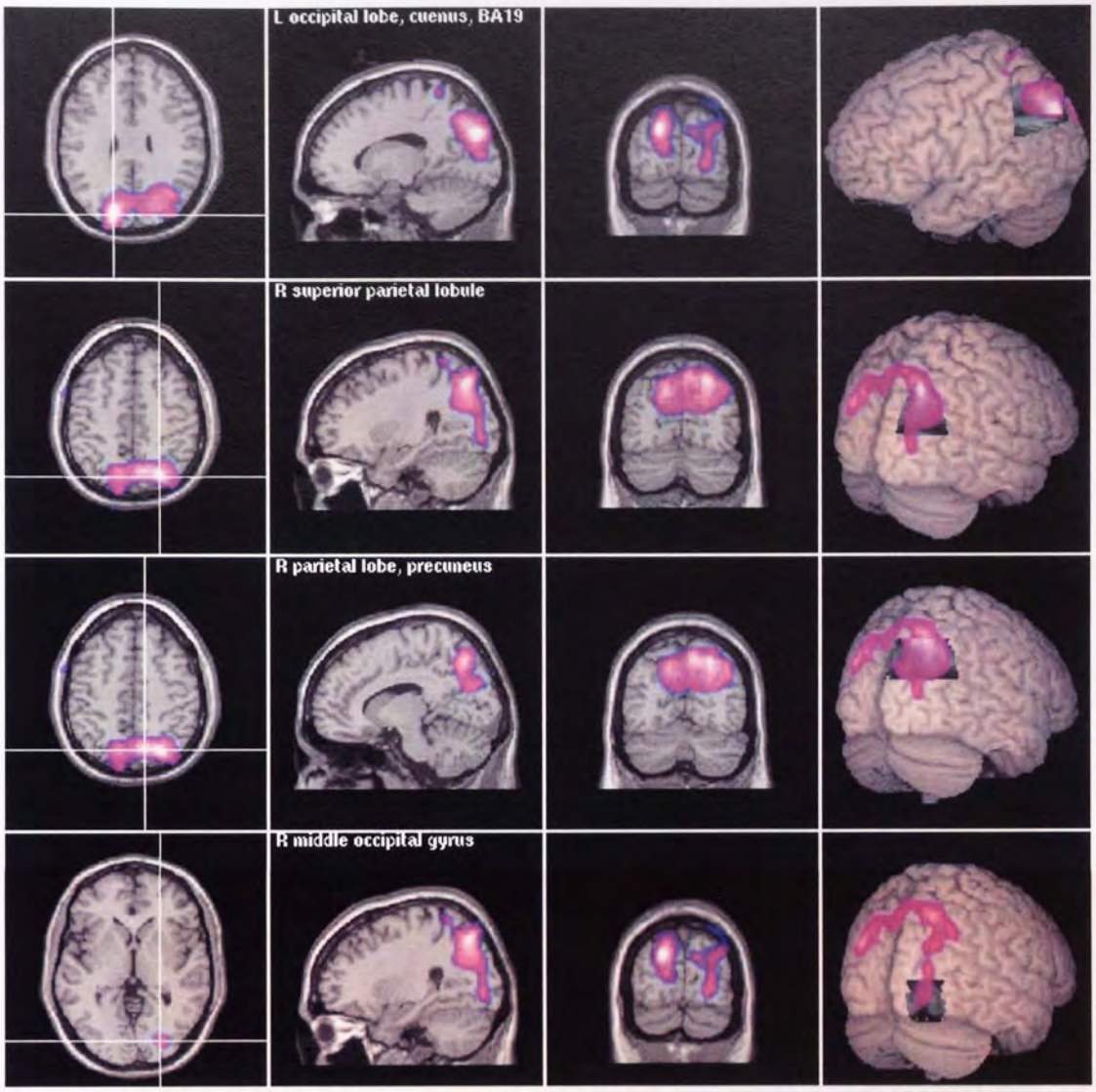
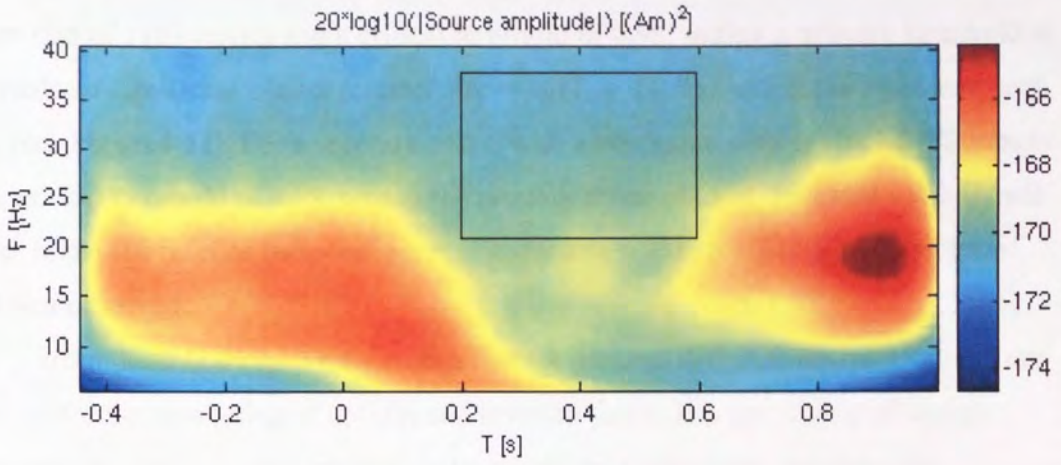


Figure4-8: Responses to inverted faces compared to baseline in the 13-25Hz frequency band, for 0 to 400ms. SPMs show significant ERD in the left occipital lobe, cuneus, BA19 (top) and within the right superior parietal lobule (second row), the right parietal lobe, precuneus, (third row) and within the right middle occipital gyrus (bottom row), displayed onto a template brain.

These findings were further investigated with TFRs generated using Morlet wavelet analysis. For virtual electrodes (VE) placed within the right parietal lobe, precuneus, and postcentral gyrus (see **Figure4-9**) TFRs revealed the desynchronisation, i.e. a decrease in cortical oscillatory power at latencies of 200 to 600ms, as had been observed in the SAM results.

Upright Faces: Right parietal lobe, precuneus



Inverted Faces: Right parietal lobe, precuneus

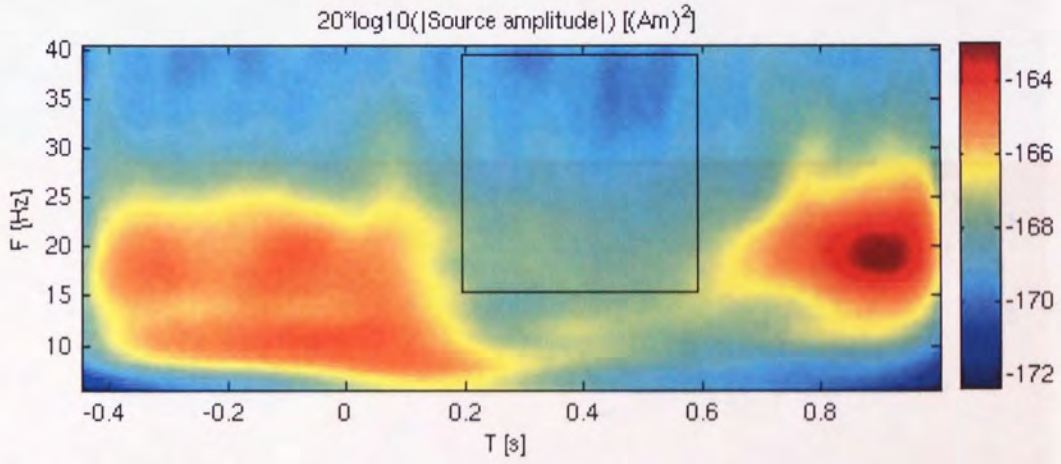


Figure4-9: TFR representing decreases in oscillatory power for a voxel within the right parietal lobe, precuneus regions, at latencies of approximately 200ms sustained over 400ms, within beta and gamma frequencies (see box).

4.3.3.2. Gamma

For **upright faces**, with a critical threshold of 5.09, $p < 0.05$, significant voxels were observed within the right middle occipital gyrus, ($t = 5.75$, $p < 0.05$), and within the right parietal postcentral gyrus, BA2 ($t = 5.41$, $p < 0.05$). In these areas ERD was observed

(see **Figure4-10**).

For **inverted faces**, significant results were obtained at cluster level. The permutation distribution of the cluster analysis revealed two clusters. With a maximum cluster size of 1103 voxels and a critical threshold of 4.98, setting a primary threshold at 3, revealed a significant cluster (cluster size = 1611, $p < 0.05$) within the right temporal lobe, (see **Figure4-11**). For a second cluster, with a maximum cluster size of 152 voxels and a critical threshold of 4.98, setting the primary threshold at 4, revealed a significant cluster in the left inferior temporal gyrus (cluster size = 216, $p < 0.05$). In these areas ERD was observed.

From these findings it can be seen that for gamma, different neural networks are recruited for the processing of upright and inverted faces. The processing of upright faces is associated with right parietal and right occipital structures, whereas the processing of inverted faces is linked to bilateral temporal regions.

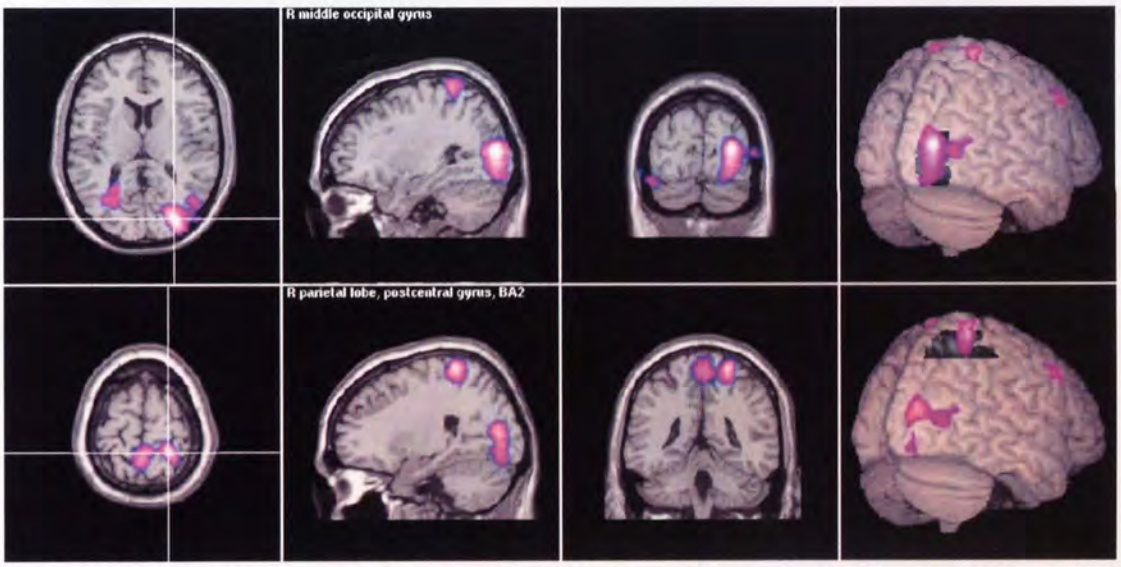


Figure4-10: Responses to upright faces compared to baseline across 25-40Hz frequency band, for 0 to 400ms. SPMs show significant ERD in right middle occipital gyrus (top) and right parietal lobe, postcentral gyrus BA2 (bottom), displayed onto a template brain.

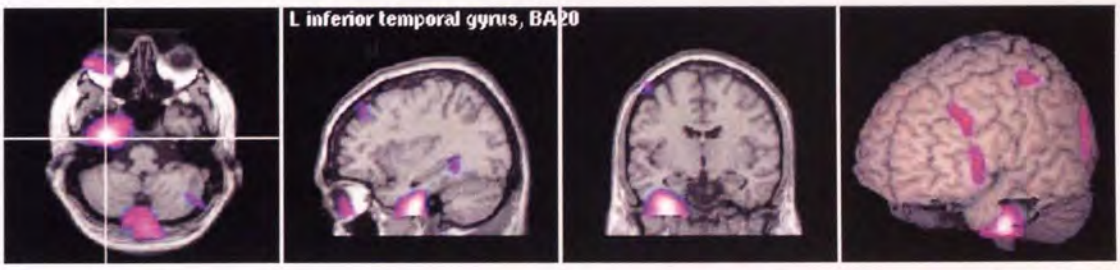
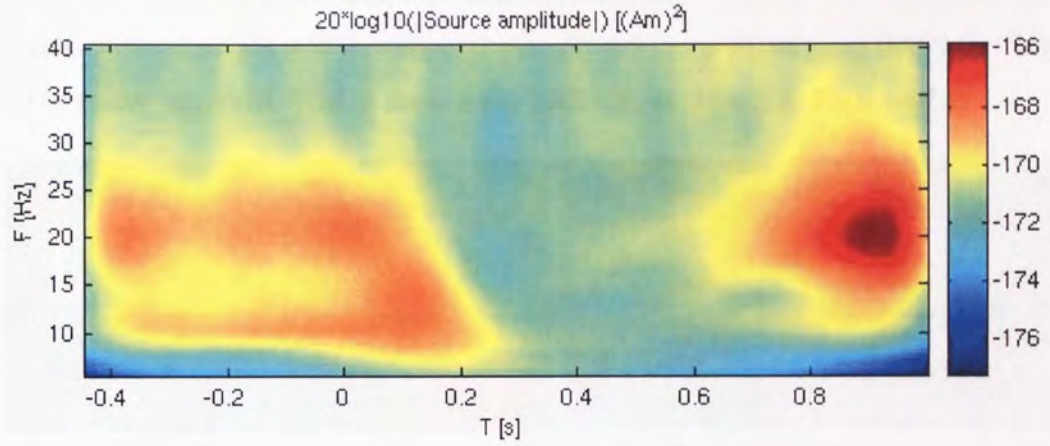


Figure4-11: Responses to inverted faces compared to baseline in the 25-40Hz frequency band, for 0 to 400ms. SPMs show significant ERD in the left inferior temporal gyrus, BA20.

As before, these results were further explored using wavelet analysis to generate TFRs, for VEs placed within the right middle occipital gyrus (see **Figures4-12**).

Upright Faces: Right middle occipital gyrus



Inverted Faces: Right middle occipital gyrus

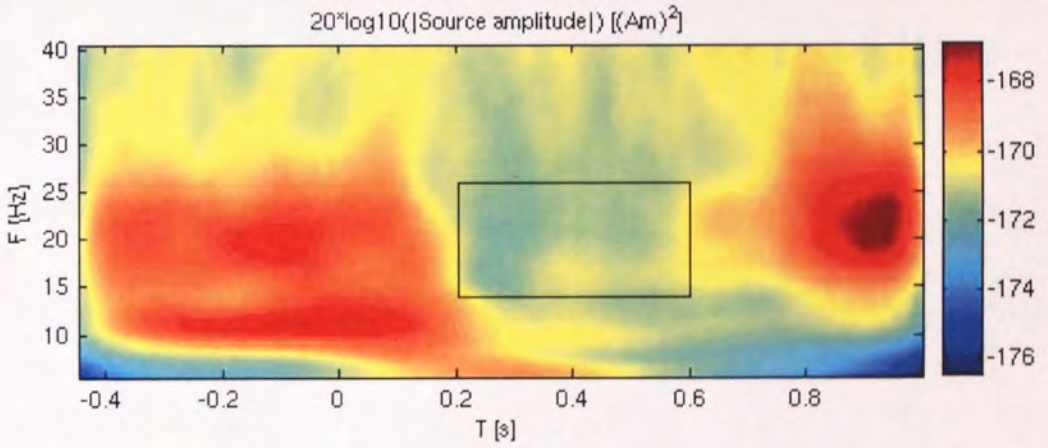


Figure4-12: TFR representing changes in oscillatory power for a voxel within the right middle occipital gyrus. Decreases in cortical oscillatory power are evident for latencies of 200ms sustained over 400ms, at beta and gamma frequencies.

4.3.3.3. Indirect comparisons: upright versus baseline 0 to 200ms and inverted versus baseline 0 to 200ms

Significant results were obtained for the alpha frequency band and for a wide frequency band of 5-40Hz.

4.3.3.3.1. Alpha

For **upright faces**, with a critical threshold of 4.93, significant results were revealed within the left posterior lobe, $t = -5.17$, $p < 0.05$. In these areas ERS was observed (see **Figure4-13**).

For **inverted faces**, with a critical threshold of $t = 5.07$, $p < 0.05$, significant voxels within the right middle temporal gyrus ($t = 5.26$, $p < 0.05$) and BA39 ($t = 5.41$, $p < 0.05$) were observed. Within these areas ERS was evident (see **Figure4-14**).

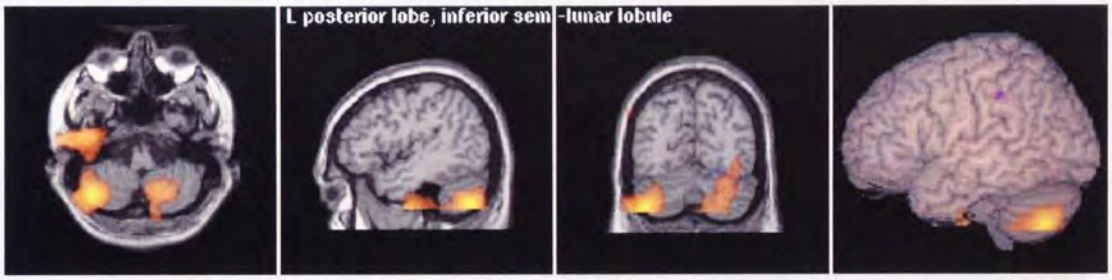


Figure4-13: Responses to upright faces compared to baseline in 8-13Hz frequency band for 0 to 200ms. SPMs show significant ERS in left posterior lobe, displayed onto a template brain.

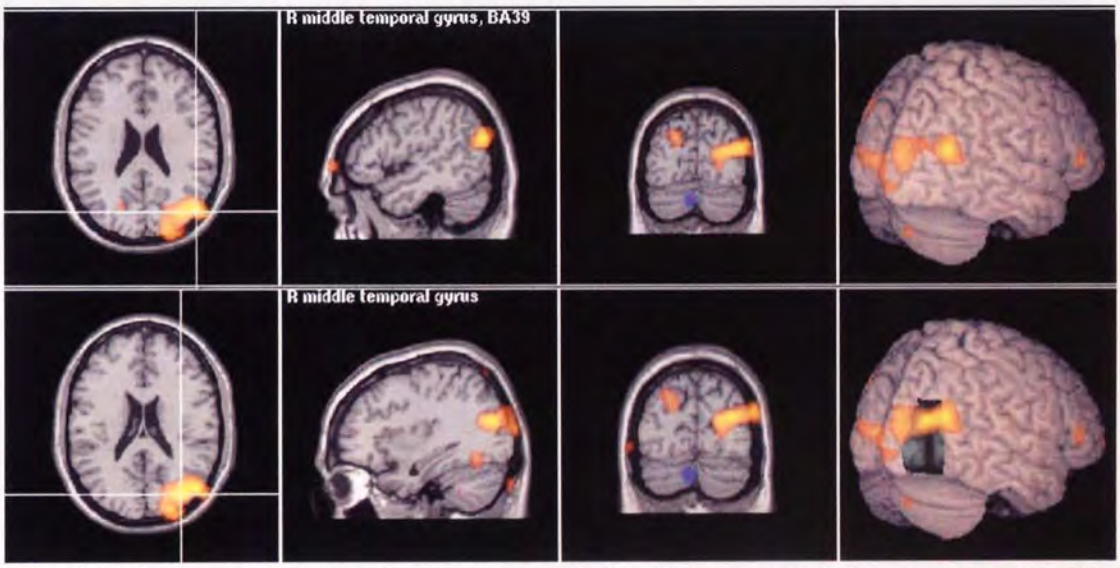


Figure4-14: Responses to inverted faces compared to baseline across 8-13z frequency band for 0 to 200ms. SPMs show significant ERS in right middle temporal gyrus, displayed onto a template brain.

4.3.3.3.2 5 to 40Hz

For **upright faces**, significant results were obtained at voxel as well as cluster level. A significant cluster was observed within the right occipital lobe, the lingual gyrus, BA18 ($t = 4.83$, $p < 0.05$; voxel level). The permutation distribution of the cluster analysis revealed a maximum cluster size of 820 voxels, with a critical threshold of 4.81. Setting

a primary threshold at 3, a significant cluster of ERS (cluster size = 515, $p < 0.05$) was reported within the right occipital lobe, lingual gyrus (see **Figure4-15**).

For **inverted faces**, significant results were obtained at voxel level. With a critical threshold of $t = 5.07$, $p < 0.05$, significant voxels were observed within the right middle temporal gyrus ($t = 6.77$, $p < 0.01$), within the right occipital lobe and sub-gyral regions ($t = 6.3$, $p < 0.01$), within the right occipital lobe, cuneus area ($t = 6.2$, $p < 0.01$) and within the right occipital lobe, lingual gyrus ($t = 5.42$, $p < 0.05$). In these areas ERS was observed (see **Figure4-16**). In addition, ERD was observed at voxel level within the left superior frontal gyrus ($t = 5.38$, $p < 0.05$) (see **Figure4-17**).

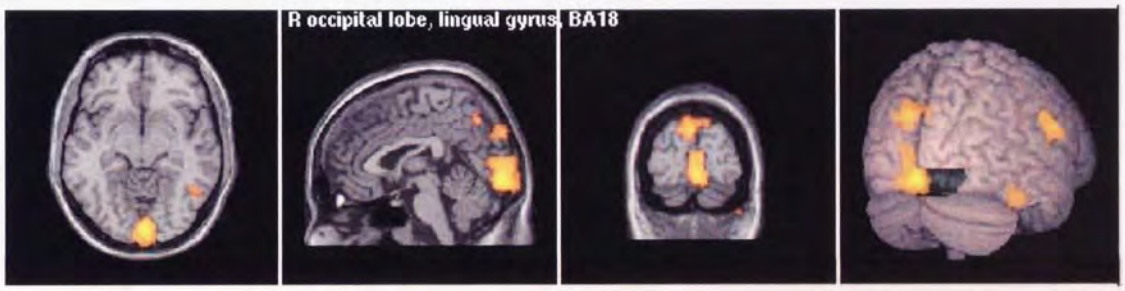


Figure4-15: Responses to upright faces compared to baseline across 5-40Hz frequency range, for 0 to 200ms. SPMs show significant ERS in right occipital lobe, lingual gyrus, BA18 displayed onto a template brain.

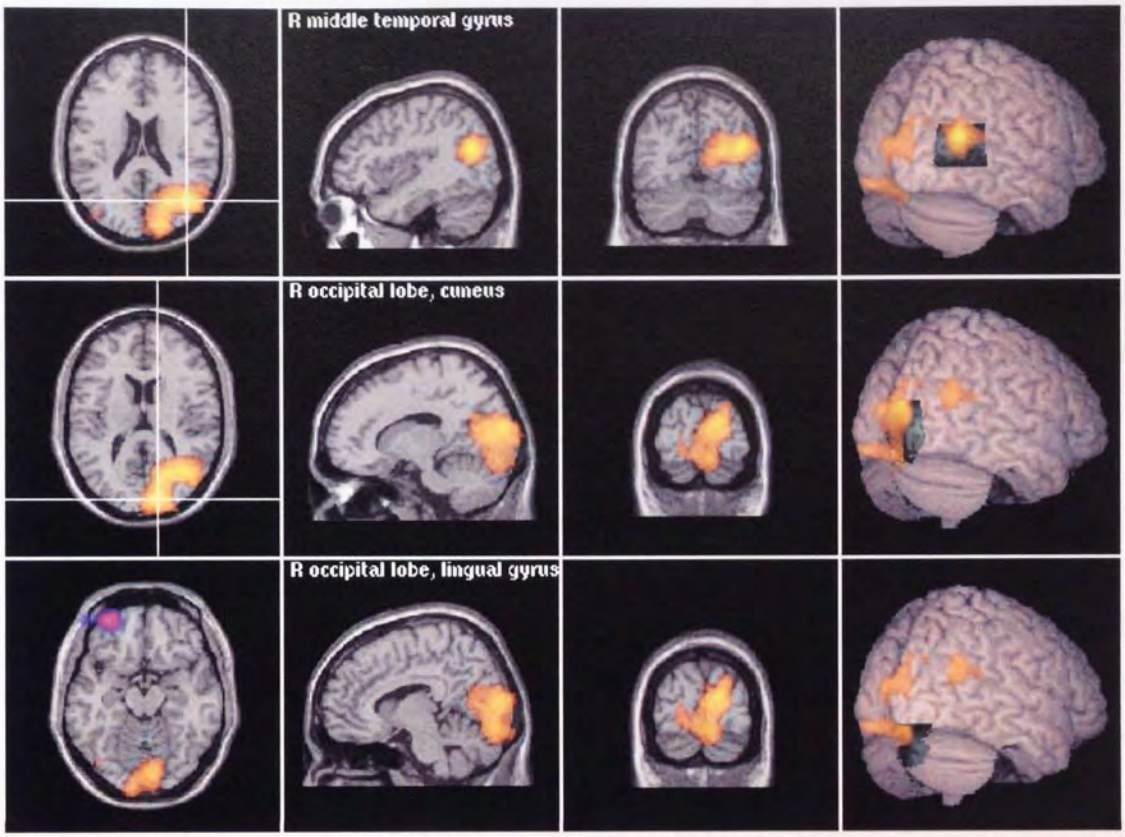


Figure4-16: Responses to inverted faces compared to baseline across 5-40Hz frequency range, for 0 to 200ms. SPMs show significant ERS in right middle temporal gyrus (top), and in right occipital regions, cuneus regions (middle row) and lingual gyrus (bottom row) displayed onto a template brain.

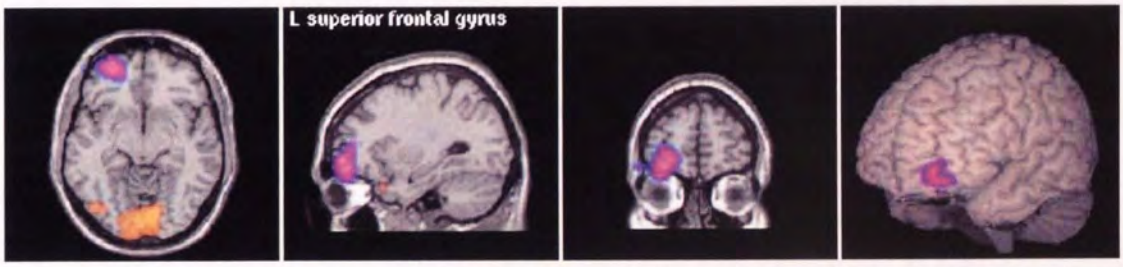


Figure4-17: Responses to inverted faces compared to baseline across 5-40Hz frequency range, for 0 to 200ms. SPMs show significant ERD in left superior frontal gyrus, displayed onto a template brain.

4.4. Discussion

4.4.1. Summary of Results

This study aimed to investigate the face inversion effect in terms of its spatio-temporal and potentially frequency-specific dynamics. Latency delays, particularly at occipito-temporal sites were predicted in response to inverted faces and it was explored whether oscillatory patterns would show differential involvement to upright and inverted facial stimuli.

4.4.1.1. Direct comparisons: upright faces versus inverted faces

Direct comparisons of cortical oscillatory power to upright versus inverse faces, revealed no significant signal changes using non-parametric permutation testing (SnPM). TFRs using Mann Whitney wavelets were generated based on results obtained from group SAM analyses, and revealed changes in cortical oscillatory power within right occipital and right parietal areas. The Mann Whitney TFRs indicated a change in synchronous activity from increases in cortical power, or synchrony, within the first 200ms to decreases in cortical power at later latencies, 200 to 400ms (see figure4-2).

These observations were investigated further and significant patterns in cortical oscillatory power were established. For upright and inverted faces, comparisons were made between the 0 to 200ms and a 200 to 400ms time-window, for alpha frequencies and across a broad frequency band of 5 to 40Hz. At alpha frequencies differential increases in cortical oscillatory power were evident at the hemispheric level, with networks in both hemispheres showing increases in synchrony for the processing of upright faces (see figure 4-3), whereas inverted faces were associated with changes only within the right hemisphere (see figure 4-4). Occipital and temporal regions are implicated in the processing of upright as well as inverted faces; yet parietal areas are recruited in addition, when processing upright faces (see figures 4-3 & 4-4).

A similar pattern in terms of hemispheric asymmetry was observed for 5-40Hz. Temporal and occipital regions show increases in cortical power when processing upright and inverted faces, but in addition, increases in synchrony in parietal areas is observed when processing upright faces (see figure 4-5 & 4-6). Furthermore, the

processing of inverted faces revealed decreases in cortical oscillatory power in right frontal areas (see figure 4-6).

Thus, similar patterns and dynamics of cortical oscillatory power could be established for the processing of upright and inverted faces, with the exception of desynchronisation observed for right frontal areas in the inverted condition only. To investigate the potential differences in cortical oscillatory power for upright and inverted faces further, indirect comparisons were also explored.

4.4.1.2. Indirect comparisons

Comparing upright faces to baseline within a short 0-200ms time window, ERS could be observed in two different frequency bands. For alpha (8-13Hz), significant voxels were demonstrated in the left posterior lobe, and the cerebellum (see figure4-13), whereas across a wider frequency range of 5-40Hz power increases were evident within right occipital regions e.g. lingual gyrus and BA18 (see figure 4-15). For the same comparison over a longer time window, 0 to 400ms, however, ERD could be observed in different frequency bands. For beta (13-25Hz), event-related decreases were evident in left and right parietal areas, precuneus regions (see figure 4-7), whereas for gamma (25-40Hz) power decreases could be seen in the right middle occipital gyrus and the postcentral gyrus (see figure 4-10). Hence, processing upright faces leads to increases in event-related spectral power in posterior areas at alpha frequencies and in occipital areas at 5-40Hz at early latencies (0 to 200ms), but to decreases in event-related spectral power at beta frequencies in bilateral parietal areas and at gamma frequencies in right occipital and parietal areas at longer latencies (0 to 400ms).

When comparing inverted faces to baseline, a similar pattern in terms of power changes could be established. For the 200ms time window, ERS could be observed in alpha in the right middle temporal gyrus, BA39 (see figure 4-14). Across a wider frequency range of 5-40Hz, ERS was evident in the right middle temporal gyrus as well as within right occipital regions, e.g. lingual gyrus (see figure 4-16). In addition, ERD was shown in the left superior frontal gyrus (see figure 4-17). Across the 400ms time window, ERD was observed for beta and gamma frequencies. For beta, left and right occipital as well as right parietal areas showed decreases in cortical oscillatory power (see figure 4-8), whereas in gamma significant decreases in cortical synchrony could be observed within left and right temporal regions (see figure 4-11). Hence, the processing

of inverted faces shows a similar pattern of cortical power changes, with increases in cortical power being evident at early latencies (0 to 200ms) for alpha frequencies in right temporal areas and for 5 to 40Hz in temporal as well as occipital areas, and additionally, ERD was revealed for the left superior frontal gyrus. At later latencies (0 to 400ms) decreases in cortical oscillatory power were evident for beta in temporal, parietal and occipital areas, and for gamma in bilateral temporal regions.

In summary, the processing of upright and inverted faces showed increases in spectral power at alpha and broad range frequencies and decreases in event-related spectral power at beta and gamma frequencies. However, in addition to occipital and parietal areas, which are recruited in both conditions the processing of inverted faces also relies upon temporal structures and revealed decreases in cortical oscillatory power within left frontal areas.

4.4.2. Interpretation of Results

4.4.2.1. Overall differences between upright and inverted faces

Similar brain regions are involved in the processing of upright and inverted faces, yet inverted faces have been shown to evoke larger activity (Linkenkaer-Hansen et al. 1998; Rossion et al. 1999). Given the observation that t-values were generally larger in the inverted face condition (with the exception of the 0 to 400ms time-window at the 25-40Hz frequency band) (see tables1 and 2 in **Appendix3**), it could be argued that enhanced activation i.e. enhanced changes in cortical oscillatory power in response to inverted faces could be found in this investigation also.

4.4.2.2. Lateralisation effect and spatial considerations

The observation of a right hemisphere bias, as well as the involvement of the aforementioned face-specific regions and of temporal areas (see figures 4-5, 4-6, 4-10, 4-14, 4-15, 4-16) has also been reported in studies investigating the face inversion effect, e.g. Aguirre, Singh & D'Esposito (1999); Haxby et al. (1999) and Kanwisher, Tong & Nakayama (1998). Leube et al. (2003) stated that the neural correlates of the face inversion effect are likely to be located in the right hemisphere. In addition, Haxby et al. (1999) reported small decreases in neural activity for inverted faces in the superior temporal areas. Decreases in cortical synchrony within temporal regions were reported

within the longer time-window (see figure 4-11), therefore corresponding to the observation from fMRI. The involvement of right parietal areas (precuneus areas and postcentral gyri) (see figures 4-7 & 4-8) has also been reported by Itier & Taylor (2004) who found ERP face inversion effects largest for parietal and temporal sites, in children as well as in adults (Taylor et al. 1999; 2001a). Thus, the current investigation was able to replicate some of the spatial correlates of upright and inverted face processing as established using fMRI and EEG. This investigation also revealed significant decreases in cortical oscillatory power within the left superior frontal gyrus in the inverted face condition. Decreases in the left middle frontal gyrus were also reported in the previous investigation on differential processing of faces and houses and was thought to be related to task demands (see section 2.5.1).

4.4.2.3. Temporal considerations

In ERP studies (e.g. Rossion et al. 1999; Eimer 2000a) it is argued that the face-specific N170 is delayed when faces are presented upside down. In this investigation, ERS was observed for upright faces, as well as inverted faces, in occipito-temporal areas within the 0 to 200ms time-window. The evidence, however, for delayed responses to inverted faces is less conclusive in the current investigation. Activation in face-specific regions, which are expected to be implicated in the processing of upright, though not necessarily inverted faces (Haxby et al. 1999), is evident in both conditions (compared to baseline) within the shorter time window of 0 – 200ms. Average TFRs indicated similar patterns of activation for upright and inverse conditions. Thus, Mann Whitney wavelets were generated to further assess differential patterns of oscillatory power changes with more precise emphasis on timing information (see figures 4-2, 4-9 & 4-12). However, the patterns of cortical power changes were similar for upright and inverted faces.

The ERS in occipito-temporal regions observed for the 0 to 200ms time-window, could be reasoned to be due to visual processing which categorises the stimuli as faces per se, taking place within 200ms. This appears to be common to the processing of upright as well as inverted faces. Therefore, it is consistent with the observation that inversion does not modify the low-level features of a face (e.g. Kanwisher et al. 1998; Rossion et al. 1999). Studies by Allison et al. (1999), McCarthy et al. (1999) and Puce, Allison & McCarthy (1999), investigating intra-cortical ERPs to upright and inverted faces, revealed a face-specific component in ventral occipito-temporal areas at latencies

of 200ms (N200), which they thought reflects the pre-categorical perceptual analysis of faces. Thus the results of the current investigation seem in line with findings linked to the categorical analysis of faces being identified at latencies below 200ms.

4.4.2.4. Theoretical assumptions and potential implications for models of face processing

4.4.2.4.1. Face-specific processing modules

Rossion et al. (1999) stated the processing of inverted faces would proceed more slowly and would require more neural activity – in particular within the right occipito-temporal regions. The delayed and, to some extent, the larger amplitude of the N170 in, for instance Rossion et al.'s study, as well as enhanced ERS to inverted faces in this investigation, appear to be linked to an increase in processing resources. Therefore, explanations have been put forward, proposing that the altering of processing strategies might be due to a loss of configural face information when processing inverted faces. This is also assumed to be associated with an increase in difficulty of the task or in recognising and categorising an inverted face as a face. An alternative explanation for the observation of amplitude increase when processing inverted faces has been put forward by Haxby et al. (1999). They stated that face inversion might not significantly decrease neural activity within face-selective regions, but increases the responses in ventral extrastriate regions that would also respond to other visual categories such as houses. And indeed, similarities between the patterns of cortical oscillatory changes observed in the present and in the previous study (see chapter 3) are to be noted. Thus, the larger amplitude observed for inverted faces may be due to recruiting additional processing resources in object perception systems. If this is the case, then maybe the processing of upright and inverted faces does indeed involve, maybe not necessarily two distinct processing systems, but complementary ones. Therefore, in order to process inverted faces, neural networks or areas are involved in addition to the ones recruited for (upright) face processing. In this case, then, faces can be regarded as being processed by a somewhat specialized, face-specific module, whereas inverted faces may seem to be processed more in terms of object-recognition modules (see also Haxby et al. 1999, Moscovitch & Melo 1997). Thus, faces are indeed a special source of visual

stimuli recruiting their own face-specific neural networks, as long, it seems, as they remain upright and thus can be perceived holistically and categorically.

4.4.2.4.2 Face Expertise

Similar neural mechanisms seem involved in the processing of inverted and upright faces. Although it is possible that different populations of neurons lead to these responses for upright and inverted faces, it is equally possible that both types of stimuli lead to activation of the same, expertise related mechanisms (Tarr & Gauthier 2000; Gauthier et al. 2003). According to Perrett, Oram & Ashbridge (1998) it is probable that due to the levels of expertise in the processing of upright faces, more neurons in the temporal cortex would respond more selectively to upright (compared to inverted) faces.

Furthermore, Perrett et al. (1998), investigating the effects of orientation on perception in monkeys, proposed that different numbers of cells would code for the various face views of face parts, thus leading to differential timing of activity in cell populations when processing upright and inverted faces. A normal, i.e. upright face would therefore recruit a larger amount of cells than those faces whose configurations had been altered. The recruitment of neural networks bilaterally in upright compared to unilateral activation when processing inverted faces could be a demonstration of this (see figures 4-3 & 4-4). The advantage for processing upright faces may, hence, simply be a by-product of relative expertise. In support, researchers have shown that perceptual learning can be quite specific (e.g. Gauthier et al.1998). Greater expertise in the processing of upright than inverted faces would thus lead to greater processing efficiency.

4.4.2.5. Methodological considerations in functional imaging research

4.4.2.5.1. Stimuli and task demands

By presenting identical stimuli in two different orientations, the observation of differential activation is assumed to be due to orientation, or face perception per se rather than differences in the low-level features present in the stimuli (Kanwisher et al. 1998). Farah et al. (1995b) pointed out that inverted faces are an ideal (non-face)

control stimulus, as it keeps constant virtually all physical stimulus parameters (e.g. spatial frequency, complexity, inter-item similarity). Yet, a large body of evidence suggests the existence of a face inversion effect. No significant changes in cortical oscillatory power were observed for the fusiform gyri in this investigation at group level inferences; yet, it was reported at individual level. This might have been due to the fact that the task involved here was a facial expression discrimination task, rather than a pure face detection task. Similar observations have also been made by Kanwisher et al. (1998).

Rossion et al. (1999) compared patterns of activation when performing a one-back memory task and a passive-viewing condition, using inverted and upright faces. They noted that in a passive viewing condition, the observed inversion effects were large and evident in all participants whereas in the one back memory task these effects were rather small and evident only in six out of ten participants. Thus, the apparent 'lack' of an inversion effect observed in this investigation might have been due to the task demands as participants performed a one back memory task where the task-specific feature was in fact the emotional expression. Thus, configural processing mechanisms may have been used to process upright as well as inverted faces, as the focus of the task was not the orientation but the emotional content of the stimulus (i.e. the perception of emotional expression may be dependent upon configural or feature encoding, regardless of orientation?).

The investigation of inversion on the categorization and the processing of facial expressions, however, were not pursued in this thesis for several reasons. There is conflicting evidence regarding the effects of face inversion on the recognition and judgment of facial expression. McKelvie (1995), for instance, observed that expressions are more difficult to identify on inverted faces when they are based on configurational information. Behavioural data showed that the identification of happy faces was equally good for faces in upright and inverted orientation; yet, the recognition accuracy for sad faces was reduced following the inversion of the face stimuli. Other studies, using, for instance, the Thatcherised faces, have revealed that participants failed to recognize the grotesque facial expressions (Thompson 1980). This has been put down to the fact that there may be a reduction in the ability to detect, or extract, relevant emotional information from inverted faces, i.e. the decoding of emotional information seems to be working best when faces are in their upright orientation, presented in the way that they are most commonly encountered. In addition, there would not have been sufficient

statistical power as indexed by the amount of trials to warrant the investigation of separate facial expressions in an inverted orientation. This, however, could be addressed in a further experiment, with increased numbers of trials in each emotional condition.

In addition, the stimulus set chosen necessitated the repeated use of the stimuli available, and in previous studies using ERPs a greater positivity to repeated items than to items presented for the first time had been observed (Taylor et al. 2001a). Thus, the increases in synchronous activity observed, might also be due to the repetition of the stimulus material. Itier & Taylor (2004) have observed the involvement of prefrontal areas during short (but not long) lags in continuous recognition tasks. In their study orbital-frontal areas at latencies of approximately 250ms to 400ms best modelled these effects. Thus, the involvement of frontal regions for inverted faces (200ms window, see figure 4-17, or figure 4-6) might have been due to the engagement of working memory systems in order to perform the task. The observed delay in the inverted face condition may, however, be taken as further evidence for the increase in task difficulty related to the processing of inverted faces. Here, behavioural measures such as reaction time (RT) would have been useful in elucidating the effects of inversion on RT. In a future study, the experimental design would not rely on a cued response paradigm but a RT paradigm instead.

4.4.2.5.2. Analyses protocols

Given that the 'difference' in patterns of cortical changes between upright faces and inverted faces are very subtle indeed, it may need to be considered that the way in which the data has been analysed may not have been the most appropriate. The majority of previous studies have looked at ERP measures and obtained fairly reliable and consistent latency differences for the processing of upright versus inverted faces, with inverted faces showing significant delays in processing latencies (Eimer 2000b; Rossion et al. 1999; Schweinberger et al.1997; see introduction). However, the delays in latencies reported have also been quite subtle, and as the analysis window investigated here comprised 0 to 200ms (given the times mentioned for inverted and upright face processing lie within this window) it is possible that latency differences in cortical oscillations have been missed. Here it would have been advantageous to look at overlapping time windows and chose very wide frequency bands to allow sufficiently short time windows, e.g. 0 to 50ms, 25 to75ms, 50 to 100ms, 75 to 125ms etc.

Therefore, perhaps it was not viable to expect confirmation of such results using SAM, and as the TFRs that were generated to allow the inspection to temporal evolution of cortical signals as well as frequency specific components, are guided by the findings from the SAM analysis, it could be argued that the lack of differentiation in the TFRs is to be traced back to the possibility of SAM being an unsuitable method of analysis in this case.

4.5. Conclusion

Evidence from ERP studies proposed that there are different ERP components involved in the structural encoding of face components, the timing of which are affected by stimulus properties (such as inversion) and attention.

The current investigation allowed the replication of some face-specific patterns of cortical activity being localized to extrastriate visual areas such as the lingual gyri, middle occipital gyri and temporal areas. Thus, MEG and SAM seem indeed able to substantiate findings from fMRI in terms of spatial characteristics of face processing and face inversion. In addition, the processing of inverted faces also yielded some findings that have been reported for the processing of objects in published studies (and of houses in a previous study in this series of investigations). Hence, the processing of upright and inverted faces may involve separate, yet not entirely exclusive and distinct 'mechanisms', but potentially involves complementary networks. The increased involvement of temporal regions for the processing of inverted faces compared to the processing of upright faces might hint at such differential engagement, and at the additional recruitment of specialized areas in order to allow sufficient processing of components when encountered in inverted orientation.

The observation of signal changes in cortical oscillatory power in a short time window of 0 to 200ms for upright and for inverted faces can be seen as partially supporting findings from ERP studies. Reasons for probable discrepancies between the current investigation and previous studies for delayed peak activations in the inverted faces condition are considered to be due to the differences in methodology as well as analyses techniques and protocols. This study also investigated the frequency specific dynamics in a novel and therefore hypothesis-generating manner. Similar frequency bands were engaged in the processing of upright as well as inverted face condition, notably, alpha, beta, gamma and a 5 to 40 frequency range. Frequency-specific

processing patterns were associated with response latency differences, as alpha and broadband (5 to 40Hz) frequencies were linked to short time-windows and beta and gamma frequencies to longer time-windows. The observation of a larger involvement of increases in synchronous power in the shorter time-windows might be due to the coupling of networks, as the desynchronisation observed for the latter time windows could thus be regarded as the active decoupling of neural assemblies.

In summary, this study substantiated some previous findings particularly in the spatio-temporal domains of face processing and specifically the face inversion effect. It has been possible to add some insight into the frequency-specific components that are involved in the face inversion effect. It was shown that the face inversion phenomenon might indeed have neural correlates that can be mapped in space, in time and in frequency domains.

Chapter 5 Investigation of the processing of facial emotional expressions using MEG

5.1. Introduction

5.1.1. Spatial correlates of facial affect

It is now accepted that there are regions of the brain, which are relatively specialised in the processing of facial stimuli. Foremost are regions within the extrastriate visual cortex (e.g. fusiform gyri) and the superior temporal gyri (e.g. Allison, Puce & McCarthy 2000; Haxby, Hoffman & Gobbini 2000), and the amygdala (e.g. Adolphs 2002) has also been implicated in face processing. In addition, psychological investigations with brain-damaged patients (e.g. Hornak, Rolls & Wade 1996; Young et al. 1993b) have provided some insight into the neural processing of affective expressions, and support has been gained from functional imaging methodologies, such as PET (e.g. Morris et al. 1996) and fMRI (e.g. Kanwisher, McDermott & Chun 1997).

Additionally, studies with non-human primates revealed that neuronal firing in inferior frontal areas (e.g. Wilson et al. 1994), extrastriate visual areas (e.g. Hasselmo et al. 1989) and the amygdala is modulated when stimuli depicting facial expressions of emotions or conveying emotionally significant information are presented (e.g. Brothers, Ring & Kling 1990; Nishijo et al. 1988).

5.1.1.1. Amygdala

The role of the amygdala in emotional processing has been investigated widely (see LeDoux 1996). In humans, activation within the amygdala has mostly been reported in response to the processing of emotions related to fear or threat (e.g. Adolphs et al. 1994; Breiter et al. 1996), and Aggleton (1992) observed a general reduction of emotional responses following amygdalar lesions. It is now known that the amygdala acquires low-level inputs from sensory specific areas of the thalamus, higher-level information from sensory-specific cortical areas, and sensory independent information from the hippocampal formation. These connections enable the amygdala to process the emotional significance of information, as well as complex situations. The wide-ranging

anatomical connections including re-entrant projections to visual cortices suggest that the amygdala might be involved in neuro-modulation of sensory processing and response coordination (Morris, Ohman & Dolan 1998). Hence, the amygdala appears to play an important role in the appraisal of emotional meaning, and in controlling behavioural responses (LeDoux 1996, Amaral et al. 1992).

In contrast to previous reports of preferential involvement of the amygdala in the processing of emotions related to fear and threat, it is now assumed that the amygdala may play a more generalised role in the processing of emotionally valenced stimuli, and in particular to emotionally valenced faces (Breiter et al. 1996). Their study revealed preferential amygdala activation in response to rapid presentation of fearful compared to neutral faces in a fixed order, as well as in a counterbalanced experimental condition. In the counterbalanced condition, however, there was also amygdala activation in response to happy versus neutral faces.

Gur et al. (2002a) showed that the cognitive processing of facial expressions led to an attenuation of the amygdala response, which seemed to be associated with the engagement of the right prefrontal cortex (BA47). They considered whether the amygdala response would be triggered by any presentation of emotional stimuli or whether it only appears when the emotion conveyed is task relevant as Sprengelmeyer et al. (1998) did not report amygdala activation in a task involving gender discrimination. Gur et al. concluded that limbic responses to displays of facial emotion did indeed appear to be modulated by the relevance of the emotional content of the stimulus, in this case a face. In particular, the amygdala and the hippocampus were activated when the participants' task involved the discrimination of emotional valence from faces. Wild et al. (2003), investigating the effects of emotional expression presentation on facial mimicry, reported activation of the basotemporal lobes, hippocampus and amygdala regions, in response to the presentation of happy faces. Such response, however, seemed to be correlated with a priming effect caused by the act of perception (and performance of assigned (congruent) facial movements) as opposed to the valence of the stimulus. Hence, it is unclear whether the mere perception of a face depicting a happy expression was indicative of involvement of limbic areas like the amygdala.

Kesler-West et al. (2001) demonstrated activation within the right and left amygdala and entorhinal cortices when comparing passive viewing of blocks of scrambled to blocks of neutral faces. Gur et al. (2002b) also reported that the lateralised

responses in the amygdala shifted from greater right-sided activity within the first block to greater left-sided for the second block containing emotionally valenced stimuli. This shift may reflect hemispheric differences in the time course of the amygdala response to facial emotional expressions. Phillips et al. (2001) reported differences in the timing of left and right amygdala responses to neutral and fearful stimuli, which were also linked to a greater number of active voxels within the right hemisphere to neutral expression whereas equal numbers of voxels were active in response to neutral and fearful expressions in the left hemisphere.

5.1.2. Temporal correlates of facial affect

With respect to the *timing* of emotional face processing, combining information from neuroimaging studies with the high temporal resolution offered by ERP studies, Pizzagalli et al. (2002) noted that the cholinergic-mediated basal forebrain regions (e.g. nucleus accumbens, sublenticular extended to amygdala) may become activated very quickly and tune subsequent activity in visual cortices subserving face processing through a mechanism of increased vigilance and (or) attention (Heimer 2000; Sarter & Bruno 2000, LeDoux 2000). In their study Pizzagalli et al. demonstrated that affective features conveyed by faces can influence structural face encoding, which occurs within the fusiform gyrus within approximately 160ms post-stimulus.

Halgren et al. (1994a) conducted a study in which implanted electrodes were used to obtain recordings from occipital, temporal and parietal regions as well as from the limbic system (amygdala, hippocampal formation ad posterior cingulate gyrus) of patients who were awaiting epilepsy elective surgery. They performed a declarative memory task in which patients were presented with unfamiliar faces. In addition to early components, N75-P105, most probably generated in visual cortical areas 17 and 18 (located in and around the lingual gyrus), and components N130-P180-N240 generated in the basal occipito-temporal cortex (fusiform gyrus, areas 19 and 37), Halgren et al. also demonstrated a N310-N430-P630 sequence of responses to faces, which was largest in the hippocampal formation and the amygdala, but was probably locally generated in many sites including the lingual gyri, lateral occipito-temporal cortex, middle and superior temporal gyri, temporal pole, supramarginal gyrus, and posterior cingulate gyrus. They proposed that during the N310, faces might be multiply encoded for form and identity (inferotemporal), emotional (amygdala), recent

declarative mnestic (hippocampal formation) and semantic (supramarginal and superior temporal sulcal supramodal cortices) properties. These multiple characteristics may be contextually integrated across inferotemporal, supramodal associations, and limbic cortices during the N430, with cognitive closure following during the P630.

Streit et al. (1999), using MEG, investigated which neural substrates correlate with the recognition of facial emotions and revealed (selective) activation within the right amygdala at a latency of about 220ms in a facial expression judgement task in two (out of four) participants.

5.1.3. Frequency specific considerations regarding facial affect

With respect to the frequency specific processing of emotional information it has been suggested from animal literature that amygdala oscillations show a unique pattern. During wakefulness fast activities of low amplitude (delta) are evident, and during emotional arousal, regardless of a positive or negative valence, theta oscillations have been observed (Pare, Collins & Pelletier 2002). Ponomarenko et al. (2003) showed that amygdala oscillations also include fast gamma frequencies (30 to 100Hz). In human participants, frequency-specific assumptions regarding emotional information have revealed asymmetries for frontal alpha (e.g. Davidson 2001).

5.1.4. Summary and hypotheses

The MEG investigation presented here aims to explore further the nature of activation patterns involved in facial expression recognition. It is predicted that the presentation of faces per se in comparison to scrambled control images will lead to relative changes in cortical oscillatory power within face-specific regions like the occipito-temporal areas, e.g. the fusiform and lingual gyri, and middle and superior temporal gyri. These changes in event-related spectral power are predicted to occur within an earlier time-window (0 to 200ms) as indexed in the face-specific N170 component established in ERP studies and as has been shown in the previous investigation in this thesis. In addition, frontal and limbic structures are hypothesised to be implicated in the processing of facial expressions. Here, differential involvement of left and right hemispheres is to be explored within frontal and limbic structures.

Previous investigations within this thesis (see chapter3 section 3.4.2.1and 3.4.3.1. and chapter 4 section 4.4.2.2.) showed a rather marked right hemisphere

dominance for face (and object) processing, yet, emotion-specific patterns of oscillatory changes might be more distinct within left hemispheres. In addition, the processing of facial affect is predicted to occur after initial face categorisation processes, i.e. within the later, 0 to 400ms time-window. To obtain additional information about the time-course of activation for the processing affective information from faces, time-frequency representations will be explored.

5.2. Method

5.2.1. Materials and Participants

Stimuli were selected from the Yale Face Database (http://cvc.edu/projects/yalefaces/yalefaces.html.), which contains 165 greyscale images of facial expressions of 15 individuals. The stimulus set for the current investigation comprised 12 images, six depicting happy and six depicting sad expressions, plus 12 scrambled versions of these images. Scrambling was performed using Delphi programming software. The presentation of stimuli was conducted in a block design. Block A consisted of the six happy facial expressions and their corresponding scrambled images (Block As), block B consisted of the six sad facial expressions and their respective scrambled images (Block Bs). Each block was repeated five times to provide a sufficient amount of trials for each condition, in an AAs-BBs-AAs-BBs- ... design. Thus the total amount of happy, sad or scrambled images participants were presented with was 30. Stimulus presentation was enabled through a VSG system (Cambridge Research Systems Ltd., England).

Six healthy participants (all female, one left-handed) gave consent to take part in the investigation. The average age of the participants was 23.8 years. The study was approved by the Aston University Human Sciences Ethics committee. Participants were seated within a magnetically shielded room, and viewed, through a mirror, a monitor, placed outside the shielded room, on which the stimuli were presented. The distance between the participants and the monitor was approximately 2m.

5.2.2. Experimental Paradigm

Participants were instructed to fixate on a central fixation cross on the screen for the stimulus – a face – to appear, and then to concentrate on the emotional content of the picture, i.e. the facial expression displayed. The stimulus presentation occurred in emotion-specific blocks consisting of six images, displayed for six seconds, each followed by a blank period of six seconds. During this blank period participants were asked to rate the emotional content to ensure attention was being paid to these characteristics of the face. Blocks contained emotional stimuli of either happiness or

sadness, which were alternated with blocks containing their respective scrambled images of the same mean luminance. The presentation of each scrambled image again was followed by a blank period (See **Figure5-1**).

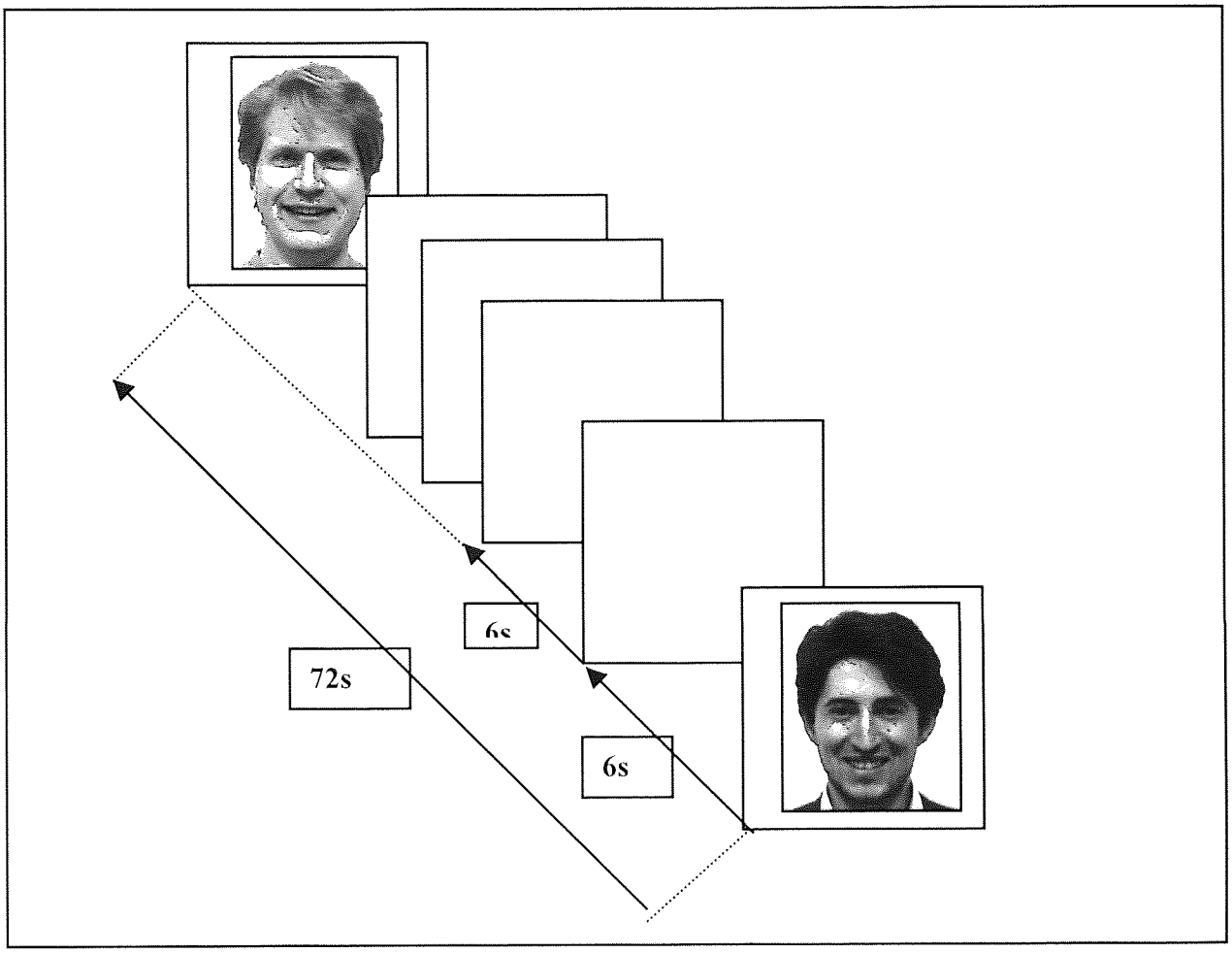


Figure5-1: Schematic representation of the experimental design. Participants were presented with a photograph showing an emotional expression, displayed for 6s. During the 6s blank period that followed, participants were asked to rate the emotional state of the person displayed in the photographs.

5.2.3. Image Acquisition and Analyses

MEG signals were recorded with a third order gradiometer configuration using an Omega 151-channel magnetometer (CTF Systems Inc., Canada). Activity was sampled at 625Hz with an Anti-Aliasing Filter of 200Hz. Data were recorded in a single un-averaged run, divided into 20 blocks of 72 seconds each, giving a total of 120 trials. Following acquisition, raw data were passed through a 1Hz high and 100Hz low pass

filter. DC corrections were performed by removing the DC offset, and trials containing eyeblinks contaminating the signal were excluded.

Head localisation information was acquired by recording the position of head localisation coils before and after the recording session. Following data acquisition, a 3-D digitiser (Polhemus Isotrack) was used to digitise participants' heads and allow co-registration of each participant's MEG and MRI data. This was achieved using Align (www.ece.drexel.edu/ICVC/Align/align11.html), which matches the participant's digitised head-surface to the head-surface extracted from their individual, anatomical MRI (Kozinska 1997).

To analyse the MEG data, Synthetic Aperture Magnetometry (SAM) was used (see section 2.4.1.1.). SPMs were generated for predetermined frequency bands (2-8Hz; 8-13Hz; 13-25Hz; 25-40Hz and 5-40Hz) and time-windows 0 to 200ms; 0 to 400ms over the entire brain at 5mm resolution to localise power changes in response to the stimuli of differing emotional content and the control stimuli. Positive values are interpreted as relative increases in power, also referred to as ERS, or increases in ERSP, and negative values are interpreted as relative decreases in power, also referred to as ERD, or decreases in ERSP.

Using SPM99 (Friston et al. 1995), the Magnetic Resonance Image (MRI) of each participant was spatially normalised to a template space. The resultant normalisation parameters were applied to the volumetric SAM images. Thus, all of the SAM images (six participants, five frequency bands, two time-windows and four comparisons: happy versus sad; happy versus scrambled images; sad versus scrambled images and all faces regardless of emotional expression versus scrambled images) were then in the same three-dimensional coordinate space allowing group analyses (Singh et al. 2002). Using SnPM (Holmes et al. 1996; Nichols & Holmes 2002), analyses of significance were performed at voxel level and at cluster level using a multiple subject single condition design. Variance smoothing was performed using a Gaussian kernel (σ = 20mm). Using non-parametric permutation testing, cluster-level inferences estimate whether a large connected cluster of near significant t-values may reach statistical significance. Spatial resolution however is being traded in against sensitivity (for details see Nichols & Holmes 2002; Singh, Barnes & Hillebrand 2003).

For the visualisation of the results on a template brain, SPM was used as well as mri3dX (http://www/aston.ac.uk/lhs/staff/singhkd/mri3dX/). In all figures the left side of the brain is displayed on the left side of the image, and coordinates provided are

stated in Talairach & Tournoux (1988) version. In the figures presented, increases in cortical power are indicated by colourscale of red – orange – yellow, with yellow regions being the most significantly active areas. Decreases in cortical oscillatory power are indicated by a colourscale of blue – pink – white, with white regions being the most significantly active areas (see colourbar on page 74, **FigureB**).

To further investigate the time-course and frequency specificity of obtained activation within the limbic lobe cluster, time-frequency representations (TFRs) were generated using Morlet wavelet analysis (Tallon-Baudry et al. 1997). The wavelet method was chosen as it provides a better compromise between time and frequency resolution than Moving Window Fourier Analysis. Once the TFRs for each participant were generated, mean TFRs were computed by averaging the TFRs of all participants.

5.3. Results

SAM analyses were performed for two time-windows, 0 to 200ms and 0 to 400ms, across the following frequency bands: theta (2-8Hz), alpha (8-13Hz), beta (13-25Hz), gamma (25-40Hz) and across a wide frequency range of 5-40Hz. A cluster analysis, using SnPM, demonstrated significant power changes for three frequency bands, alpha (8-13Hz), beta (13-25 Hz) and gamma (25-40Hz), in time windows, 200ms and 400ms. A table of results detailing pseudo-t statistics, coordinates and region showing changes in cortical power are included in **Appendix4**.

5.3.1. Face versus Control Images – Face specific comparisons

Within the 0 to 200ms time-window, SnPM revealed significant results at cluster level for the 13-25Hz (beta) and for the 25-40Hz (gamma) frequency band for the comparison of facial stimuli to scrambled images. For **beta**, the permutation distribution revealed a maximum cluster size of 5159 voxels, with a critical threshold being calculated at 5.07. With a primary threshold of 2, a significant cluster (cluster size = 1823; $p<0.05$) was found within the left middle frontal gyrus (pseudo-t = -5.74; $p < 0.05$, thus significant at voxel level also). Here, decreases in event-related spectral power were observed (see **Figure5-2** top). For **gamma**, the permutation distribution revealed a maximum cluster size at 4175 voxels, with a critical threshold being calculated at 4.93. With a primary threshold of 2, a significant cluster (cluster size = 5619; $p<0.05$) was found encompassing the left temporal regions including fusiform gyrus, and BA37 (pseudo-t = -4.17), the left culmen (pseudo-t = -3.85) as well as the left middle temporal gyrus (pseudo-t = -3.78). In these areas decreases in event-related cortical power were observed, and assumed to be reduced in the face relative to the scrambled images (see **Figure5-2** bottom). The culmen is the anterior prominent portion of the vermis of the cerebellum, rostral to the primary fissure. TFRs were generated to explore theses power changes further, see section 5.3.3.

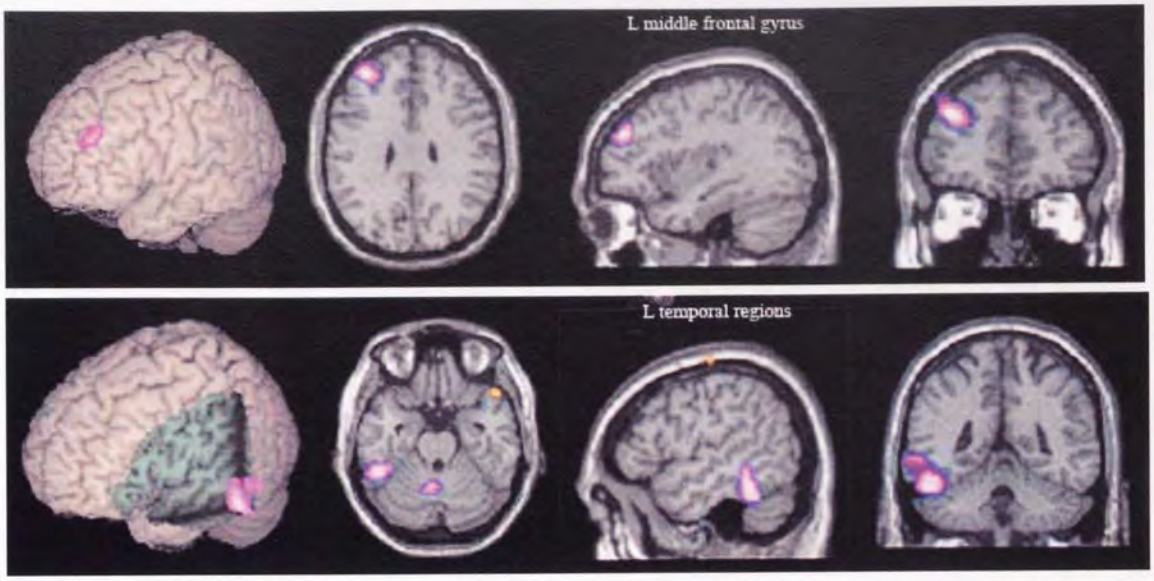


Figure5-2: SnPM showing significant decreases in cortical oscillatory power for all faces compared to scrambled control images during 0 to 200ms-time window.
Top – 13 to 25Hz: cluster showing significant decreases in cortical power ($p<0.05$; corrected) within left middle frontal regions, displayed onto a template brain.
Bottom - 25 to 40Hz: cluster showing significant power decreases ($p<0.05$; corrected) within left temporal regions, including fusiform gyrus and culmen, displayed onto a template brain.

Within the 0 to 400ms time-window, SnPM revealed significant clusters of activation for **beta** when comparing all facial stimuli to scrambled images. The permutation distribution revealed a maximum cluster size of 4790, with a critical corrected threshold calculated as 4.977. With a primary threshold of 2, a significant cluster (cluster size = 6770, $p < 0.05$) was found in the left superior frontal gyrus (pseudo-t = +5.43). Here, an increase in event-related spectral power was observed, indicating that more synchronised oscillatory power was observed in that region in the all faces condition compared to the scrambled images condition (see **Figure5-3**).

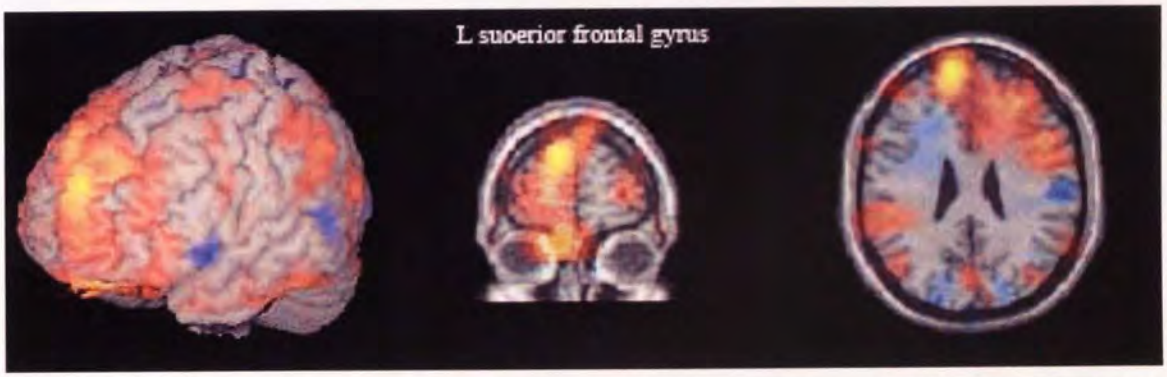


Figure5-3: SnPM results for all faces compared to scrambled control images for 0 to 400ms in the beta band. The cluster shows significant increases in cortical oscillatory power ($p<0.05$; corrected) within the left superior frontal gyrus.

5.3.2. Facial expressions of emotions versus control images – emotion specific comparisons

For the comparison of emotional faces to control stimuli, significant results were obtained for the longer time-window of 0 to 400ms, for the comparison of happy to scrambled images. There were no significant changes in cortical oscillatory power when comparing sad faces to scrambled images.

The comparison of happy faces to scrambled images revealed significant changes in cortical power within the alpha, beta and gamma wavebands.

For **alpha**, the permutation distribution revealed a maximum cluster size at 446 with the critical value calculated at $t = 5.02$. With a primary threshold of 2, a significant cluster (cluster size = 619, $p < 0.05$) was found within the left middle frontal gyrus (pseudo-t = +5.39). In this area an increase in relative power was observed (see **Figure5-4** top). For **beta**, the permutation distribution revealed a critical value calculated at $t = 4.81$. With a primary threshold of 2, a significant cluster (cluster size = 4, $p < 0.05$) was found within the left superior frontal gyrus (pseudo-t = +4.94). In this area increases in cortical power were observed (see **Figure5-4** bottom). In **gamma**, the permutation distribution revealed a maximum cluster size at 960, with a critical value calculated at $t = 5.2$. With a primary threshold of $t = 4$, a significant cluster (cluster size = 1394, $p < 0.05$) was found within the right limbic lobe, including the parahippocampal gyrus and the amygdala (pseudo- t = +4.54). In these areas increases in relative power changes were observed (see **Figure5-5**).

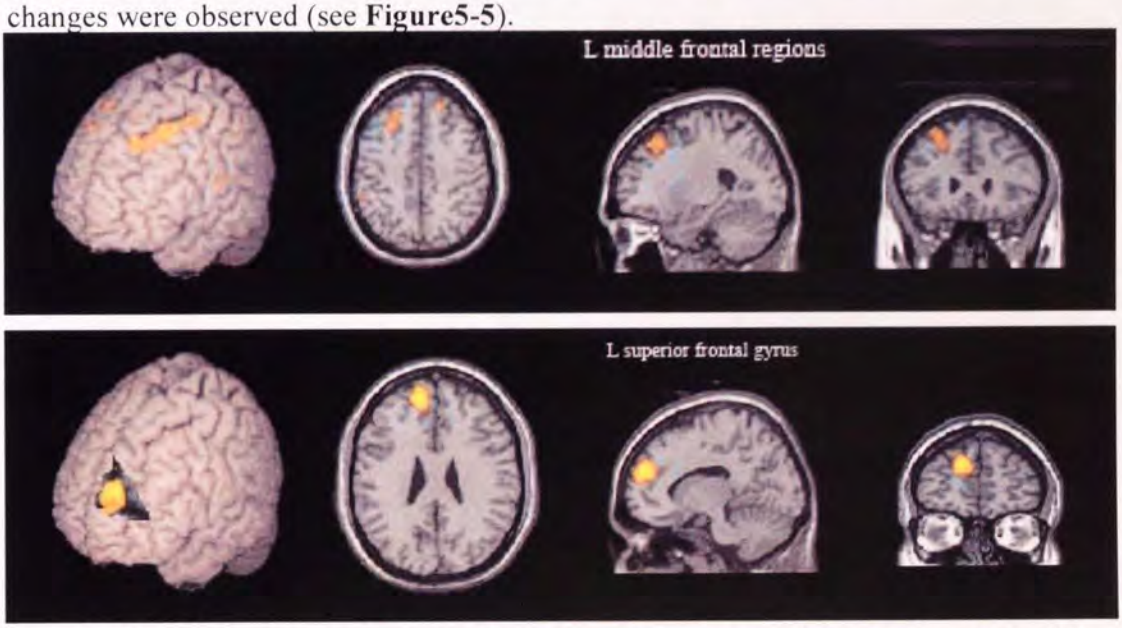


Figure5-4: SnPM group results for happy faces compared and scrambled control images for 0 to 400ms. Event-related increases in cortical oscillatory power are shown:
Top - 8-13Hz: a cluster within left middle frontal regions.
Bottom - 13-25Hz: a cluster within left superior frontal gyrus.

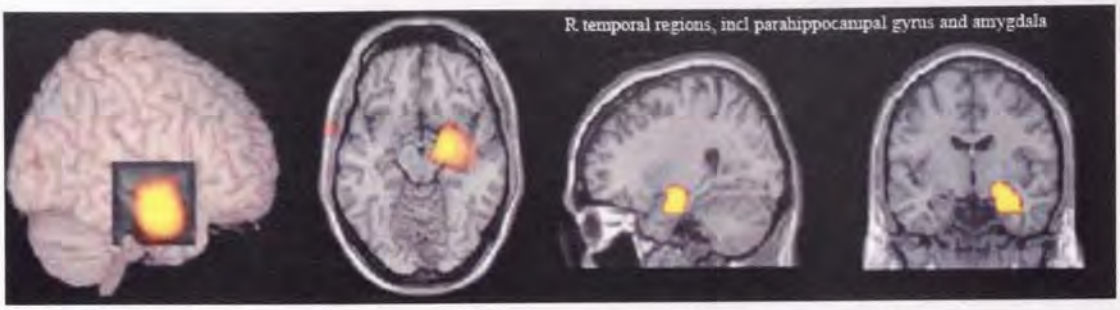


Figure5-5: SnPM group results for happy faces compared to scrambled control images for 0 to 400ms in gamma. The cluster shows significant event-related power increases within right temporal regions, including the parahippocampal gyrus and the amygdala, displayed on a template brain.

To further characterise the event-related changes in the amygdala, time-frequency representations using Mann Whitney wavelet analysis for coordinates within each participant's amygdala were produced and then averaged to generate a group spectrogram. In a Mann Whitney voxel by voxel comparison happy faces were included in the analysis as the active phase, scrambled images as the passive phase. Thus, the spectral power of the passive phase, here the scrambled images, was subtracted from the spectral power of the active phase, i.e. the happy face condition. (The resultant wavelet TFR thus displays the remaining changes in cortical oscillatory power that are stronger in the active than the passive phase). Distinct increases in cortical oscillatory power can be seen at two different frequencies, at lower frequencies between 26 to 28Hz, and at higher frequencies, between 36 to 38Hz. At these frequencies, 'peaks' in cortical oscillatory power are evident at latencies of approximately 200ms (from 150ms to about 320ms) for the right amygdala (see **Figure5-6,** left panel). Although the z-scores are low for the group averages, z-score of individuals indicate significant increases in cortical oscillatory power (for z-scores see individual TFRs in **Figure5-7**). TFRs were also generated for the corresponding voxel within the left amygdala. Here, decreases in oscillatory power at the 36 to 38Hz frequency band are evident, with 'peaks' in signal power changes occurring at approximately 180ms (see **Figure5-6**, right panel). This reversal in cortical power changes, i.e. increases in cortical oscillatory power within the right hemisphere, and decreases in cortical power changes in the left hemisphere, prompted additional SAM analyses for a time-window spanning 150 to 300ms for a frequency band of 32 to 40Hz. In contrast to the increases in cortical power revealed for the right amygdala for 25 to 40Hz, decreases in cortical power were revealed in the left hemisphere for a cluster in the temporal gyrus, including the parahippocampal gyrus, the amygdala, BA36 as well as the fusiform gyrus and BA37. The cluster failed to reach statistical significance (see **Figure5-8**). As before, TFRs were generated for voxels

within the left and right parahippocampal gyrus to explore the frequency and temporal domains further. Group TFR are displayed in **Figure5-9,** individual TFR for illustrative purposes are shown in **Figure5-10.**

Right Amygdala **Left Amygdala**

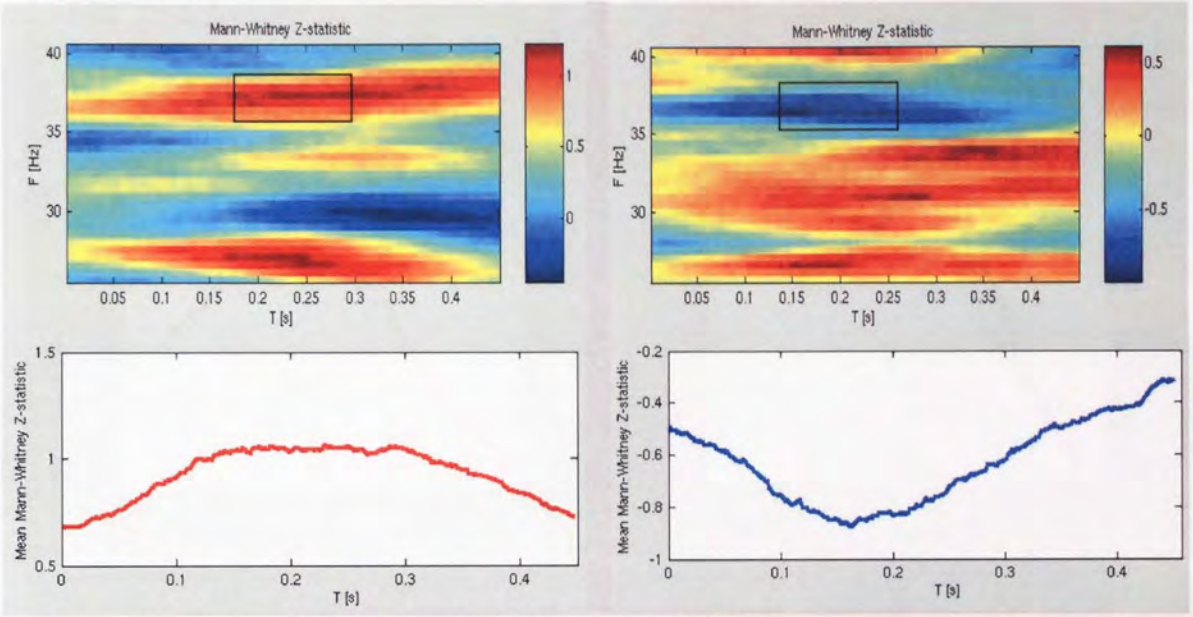


Figure5-6: Mann-Whitney TFRs using Morlet wavelets generated for a voxel in the right amygdala, which showed significant increases in cortical oscillatory power in the SAM/SnPM analysis for 400ms time-window. The group TFR show the differences between the passive (= scrambled) condition and the active (= happy) condition assessed on a voxel by voxel comparison. Increases in signal power can be seen in the right hemisphere between 150 to 300ms for 36 to 38Hz. For a corresponding voxel within the left hemisphere, at the same frequencies, decreases in cortical power are evident at somewhat earlier latencies, approximately 180ms.

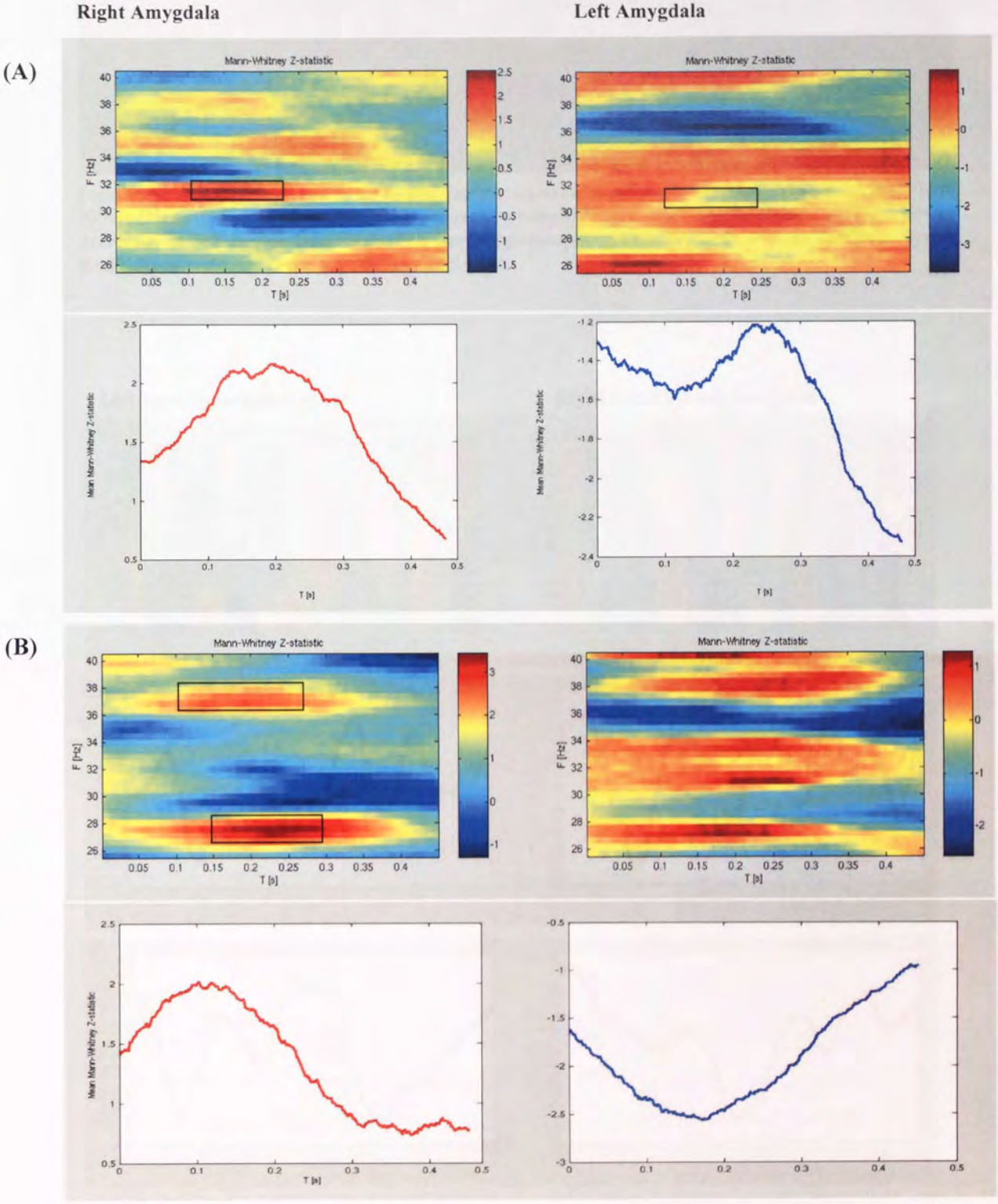


Figure5-7: Mann Whitney TFR for two participants (a & b). Increases in relative signal power for the right amygdala and decreases in spectral power for the left amygdala are evident. The traces in the lower part of the figure represent latency information and z-statistics at 30 to 40Hz.
(A): At around 32Hz increases in cortical oscillatory power are evident, with 'peaks' in power signals at latencies of 150ms to 200ms (somewhat earlier than seen in the group spectrograms).
(B): At around 26 to 28Hz, and at 36 to 38Hz, increases in cortical oscillatory power are evident, at latencies for 150 to 300ms.
The y-axis represents the individual (and group) z-scores, hence differs between participants and groups but also between left and right hemisphere findings.

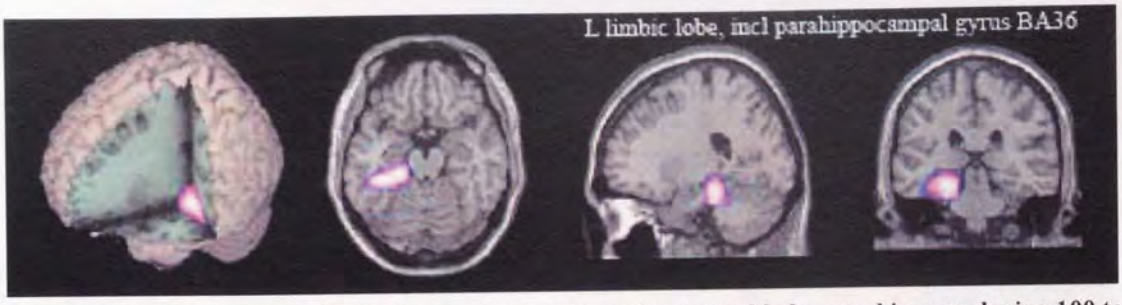


Figure5-8: SnPM group results for happy faces compared to scrambled control images during 100 to 300ms-time window in the 32 to 40Hz frequency range. Figure illustrates a cluster showing power decreases in left limbic lobe, including parahippocampal gyrus, BA36 as well as fusiform gyrus, BA37. Results do not reach significance in SnPM.

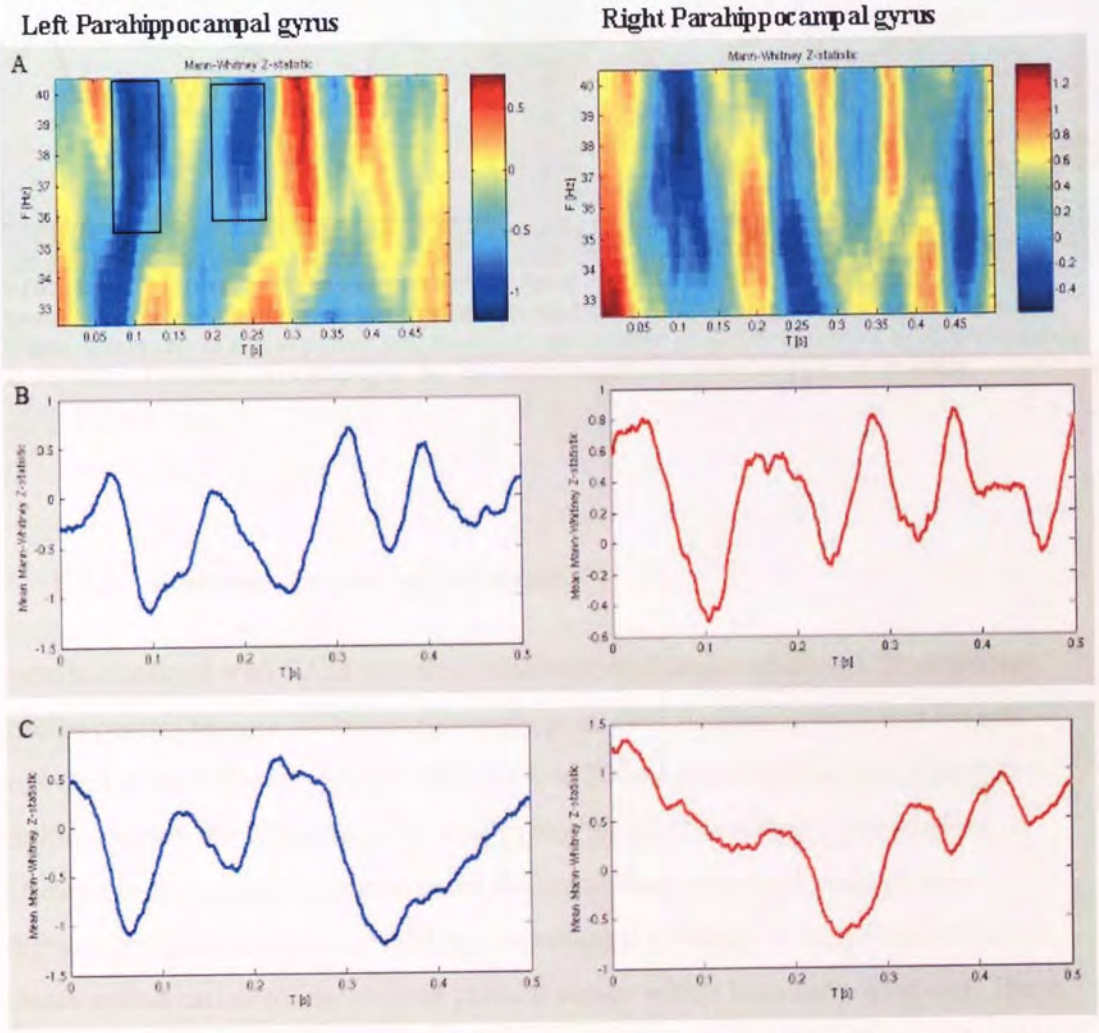


Figure5-9: Group Mann Whitney TFR to show decreases in event-related power observed for a voxel within the left parahippocampal gyrus. The TFR demonstrates event-related decreases in signal power particularly at 32 to 38Hz, at approximately 100ms and 250ms. TFRs are also shown for a corresponding voxel within the right hemisphere. Here, the z-scores indicate a less prominent decrease in cortical oscillatory power. The power traces show cortical power changes at frequencies 36 to 38Hz (B) and 29 to 31 Hz (C). The y-axes indicate Mann Whitney z-scores hence the scales (y-axes) are different for the power traces presented.

Left parahippocampal gyrus **Right parahippocampal gyrus**

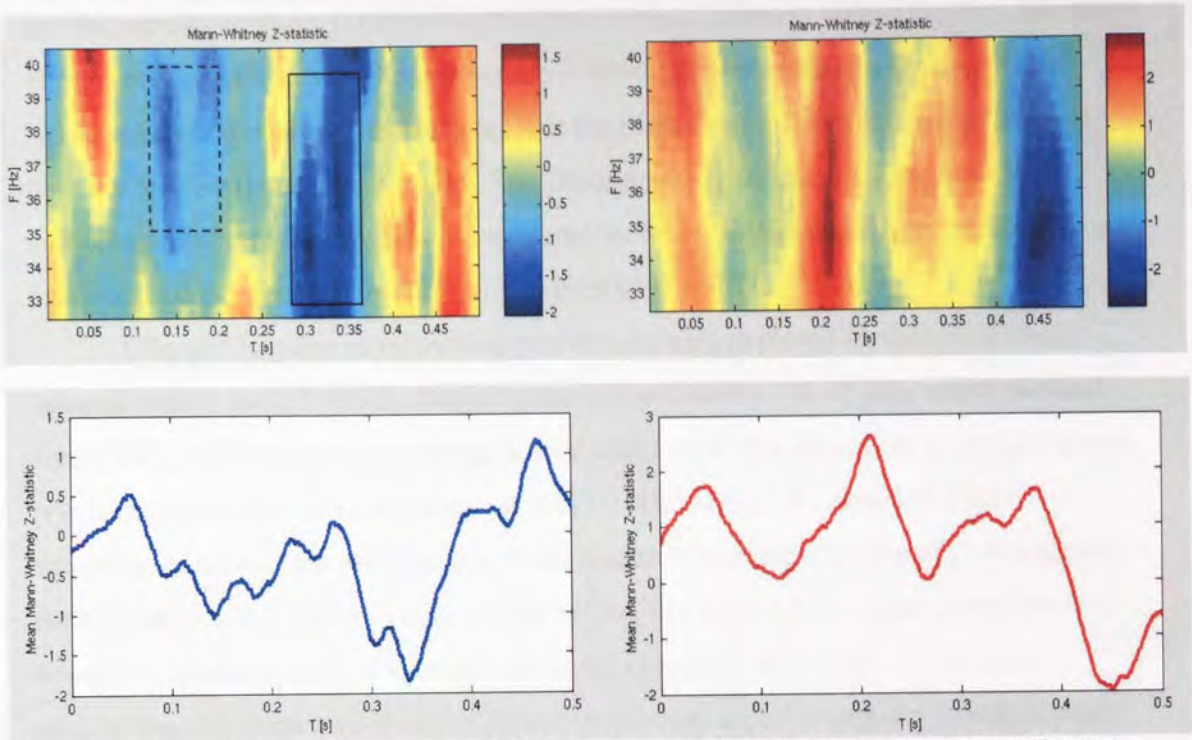


Figure5-10: Mann Whitney TFR for one participant, for a voxel within the parahippocampal gyrus. Most prominent decreases in signal power are later in time than in the group data, at approximately 300 to 350ms. Decreases in signal power are, however, also evident at earlier latencies, at approximately 150ms at 35-40Hz. The traces are displayed for the same frequency range as TFR, 32 to 40Hz.

5.3.3. Temporal sequence of activation

The results obtained with SAM revealed relative power decreases for all faces versus scrambled control images, within occipito-temporal (left fusiform gyrus) and frontal regions (left middle frontal gyrus) within the 0 to 200ms time-window (see figure5-2). In addition, within the left superior frontal gyrus, for the 0 to 400ms time-window, significant power increases were revealed for the all faces versus scrambled face condition (see figure5-3). Thus, SAM results revealed a change in relative power from decreases within earlier to increases in cortical power within later time-windows. These were investigated further by generating time frequency representations for voxels within the occipito-temporal complex, the middle frontal gyrus and the superior frontal gyrus.

Figure 5-11 illustrates the relative decreases in power changes in the occipito-temporal area for a voxel placed within the fusiform gyrus (coordinates=-51 -45 -24). From the TFRs it seems evident that the decreases in cortical oscillatory power shown in the SAM images are due to the decreases in relative power in the scrambled face

condition. The TFRs for the scrambled condition indicate decreases in cortical power for frequencies of 36 to 38Hz within the first 200ms. Contrary, within the first 200ms of the all faces condition signal increases are evident. However, the percentage signal change observed in the TFRs indicates that the increases in power are less prominent than the relative decreases in power. The percentage signal change shown in the colourbars, indicate that the maximum signal increase for the all faces condition = 2, the maximum power decrease in the all faces condition = -6).

Changes in patterns of cortical power were also explored further for a voxel selected within the left middle frontal gyrus (coordinates = -36 45 30), which showed significant decreases in event-related power with SAM. The reduction in cortical power is evident in the low beta frequency band (13-16Hz) within the scrambled faces condition. Contrary, the all faces condition revealed increases in cortical power across the beta band at 0 to 200ms latencies. As before, the increases in signal power are less strong, as the percentage of increases in signal change in the all face condition is smaller than the decreases in signal power (maximum signal increase = 2, maximum power decrease = -8) (**Figure5-12**). Thus, the decreases in cortical power observed in SAM could be due to the decreases in cortical power observed in both conditions. Mann Whitney TFRs or bootstrapping would have allowed a more effective interpretation.

Power changes are also explored for a selected voxel within the left superior frontal gyrus (coordinates = 48 39 -27) for which SAM analysis revealed increases in cortical power for the longer time-window of 0 to 400ms. Here, increases in cortical oscillatory power are evident, and more prominent, in the all faces condition relative to the scrambled images. Increases in cortical activity being most pronounced in the 16 to 20Hz band across 300ms, but also between 12 to 15Hz and 22 to 25Hz for 0 to 200ms. Increases in cortical power are also evident in the scrambled condition although less intense (see **Figure5-13**). As before, the percentage of signal change would indicate a more prominent change in terms of decreases of cortical power. Here, however, they appear within the scrambled faces condition, at somewhat later latencies (400 to 500ms).

Scrambled Images

All Faces

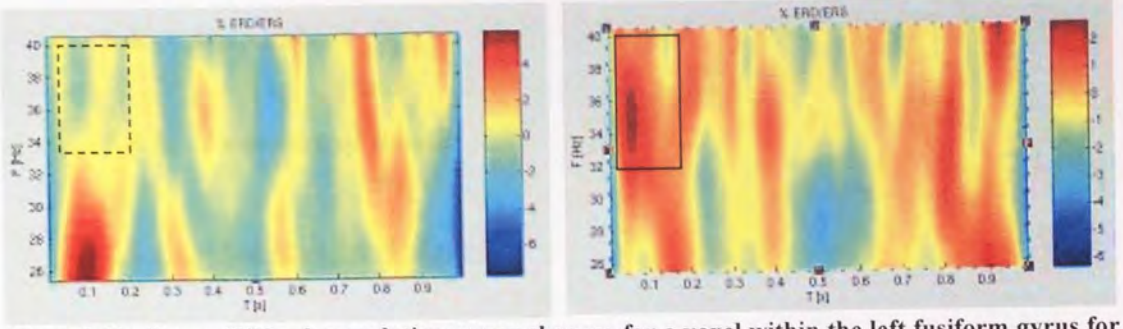


Figure5-11: Group-TFRs show relative power changes for a voxel within the left fusiform gyrus for scrambled images (left panel) and all faces (right panel). Decreases in cortical oscillatory power are shown in the all faces conditions at latencies of 80 to 100ms at 25 to 28Hz, and at 180ms at 36 to 40Hz. Decreases in signal power are evident in the scrambled faces condition at frequencies of 36 to 40Hz.

Scrambled Images

All Faces

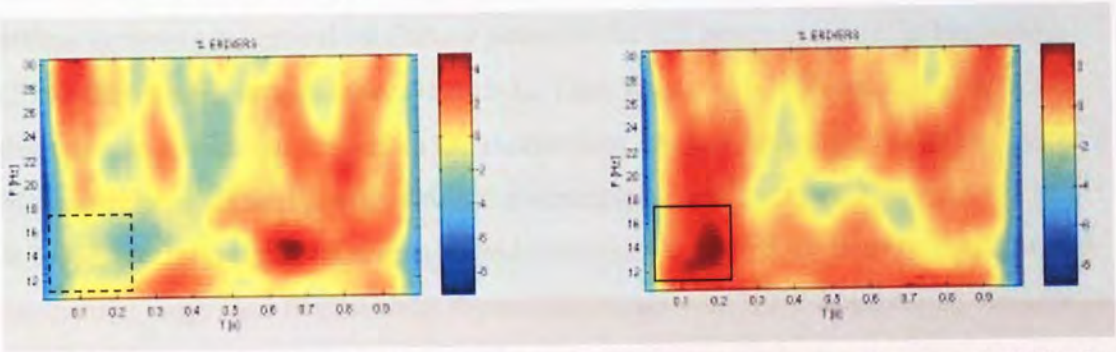


Figure5-12: Group TFRs indicating the differences in relative cortical power for a voxel within the left middle frontal gyrus, for the scrambled faces condition (left panel) and for the all faces condition (right panel). Power decreases are evident in the scrambled face condition within the first 200ms at 12 to 18Hz. These appear absent within the all face condition, where instead, power increases appear evident at those frequencies.

Scrambled Images

All Faces

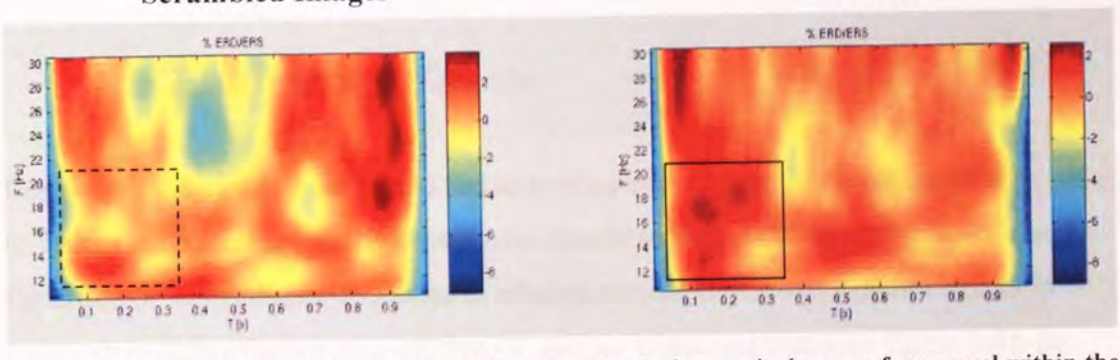


Figure5-13: Group TFRs indicating the differences in relative cortical power for a voxel within the superior frontal gyrus for the scrambled face condition (left panel) and for the all faces condition (right panel). Increases in cortical oscillatory power are evident in the all faces condition across two different latencies. For 400ms, signal increases appear most prominent at 16 to 20Hz frequencies, whereas at 200ms there seem to be power increases at 12 to 15Hz and at 20 to 24Hz.

5.4. Discussion

5.4.1. Summary of Results

5.4.1.1. Face-specific findings

In summary, the current investigation revealed a decrease in cortical oscillatory power when comparing face stimuli to scrambled images in left frontal regions for beta (13 to 25 Hz), as well as in left temporal regions including the fusiform gyrus, BA37, culmen and the middle temporal gyrus for gamma (25 to 40Hz) within a time-window of 200ms (see figure5-2). For the same comparison over a slightly longer time-window of 0 to 400ms increases in cortical oscillatory power in the left superior frontal gyrus in beta (25 to 40Hz) were revealed (see figure5-3). Time frequency representations show that decreases in cortical power within the shorter time window would be due to the changes in event-related cortical power within the scrambled conditions (see figures 5-11, 5-12 & 5-13). Occipito-temporal areas showed decreases in cortical oscillatory power within the gamma range, and frontal areas showed decreases within the shorter time-window in beta, but increases in cortical power within a longer time-window.

The involvement of gamma frequencies for occipito-temporal regions was also observed in chapter 3 and it was proposed that this was associated with the integration of sub-processes to build coherent percepts (e.g. Tallon-Baudry & Bertrand 1999; Rodriguez et al. 1999). This explanation can also be applied to the processing of scrambled faces.

5.4.1.2. Emotion-specific findings

Comparing individual emotions to the scrambled control images for a time-window of 0 to 400ms, emotion-specific processes were demonstrated at different frequencies and for different hemispheres. Increases in relative cortical power were demonstrated in response to happy faces in the left frontal gyri for alpha and beta (see figure 5-4). In addition, power increases were also detected in the right limbic lobe, including the hippocampus and the amygdala, for gamma (25 to 40Hz) (see figure5-5). No significant results were obtained for the shorter time-window, suggesting that the perception of a face per se precedes the processing of emotional information. Frontal areas showed

increases in cortical power at alpha and beta frequencies within the left hemisphere, whereas the right limbic region revealed increases in cortical power at gamma frequencies.

5.4.1.3. Temporal and frequency information differs in individuals

5.4.1.3.1. Amygdala

As mentioned previously, the recognition of facial expressions, in addition to being mapped spatially, can also be mapped in terms of latency and frequency information. Group TFRs (which are averaged individual TFRs) for the *right amygdala* revealed *increases* in cortical power at distinct frequency bands, e.g. 36 to 38Hz (see figure 5-6). The individual TFRs presented showed increases in cortical power at frequencies of 30 to 32Hz for participant A and at frequencies of 26 to 28Hz for participant B (see figure 5-7). Latency differences are less distinct. The group TFR shows a period of 'sustained' increases in cortical activity (from approximately 150ms to 300ms) whereas individual representations show increases in cortical power that are less sustained, occurring between 120 and 180ms for participant A, and at latencies of approximately 100 to 150ms for participant B. Thus, individual differences will need to be considered when trying to make inferences about cortical networks involved in emotional processing. Within the *left amygdala*, *decreases* in cortical power were observed, although they were not statistically significant (see figure 5-6). Group TFRs show the most prominent decreases in cortical oscillatory power at 35 to 38Hz, and similarities are seen in individual participants' data (see figure 5-7). However, the latencies at which the most obvious power decreases occur differ slightly between the group data and the individual representations. Group TFRs indicate peak latencies at approximately 150 to 180ms, whereas the most pronounced signal decreases occur at about 110 to 120ms for participant A and at 120 to 180ms for participant B. It is possible that the lack of statistically significant findings was related to the individual variability in this response.

5.4.1.3.2. Parahippocampal gyrus

Group TFRs for the *left parahippocampal gyrus* showed *decreases* in cortical oscillatory power to 'peak' at latencies of approximately 150 to 250ms, for frequencies

of 34 to 40Hz. This is mirrored in the data presented for one participant. Prominent decreases in cortical activity occur at latencies of approximately 150 to 320ms, at frequencies of 34 to 40 Hz, as in the group data. For the *right parahippocampal gyrus,* the patterns of cortical activity seem to differ more notably between the group's representations and individual data. Group TFRs show decreases in cortical oscillatory power at about 100ms and 250ms at frequencies of 34 to 37Hz. In addition, increases in cortical oscillatory power are also observed, at about 50ms at 32 to 35Hz and at about 200ms at 33 to 37Hz. The most obvious observation within the individual's TFR is an increase in cortical activity at about 200ms for frequencies of 33 to 37Hz. This seems to be almost the opposite of the group representation, yet could possibly be explained in terms of signal strength. Although a more prominent decrease in cortical oscillatory power is evident within the right parahippocampal gyrus, the z – statistics are smaller (z = -0.5 group, z = 0 individual) than those for the observed increases in cortical power (z = 0.8 group, z = 2.5 individual).

In summary, the processing of happy facial expressions is characterised by asymmetrical activation in the amygdala and the parahippocampal gyri. Increases in cortical power are observed in the right amygdala, and the left hippocampus and decreases in cortical power are evident within the left amygdala and the right parahippocampal gyrus. These asymmetries are within the gamma frequency band. The amygdala and parahippocampal findings indicate latency differences, with parahippocampal activity occurring somewhat later.

5.4.2. Interpretation of results

5.4.2.1. Activation for happy but not sad faces

Although significant power changes could be reported for the presentation of happy faces, no detectable power changes were observed when presenting sad faces. This finding, on the one hand, seems to stand in contrast to previous studies, which have reported activation in response to negative emotional expressions, although it is notable that these investigations were concerned mainly with fear or anger. No increase in activation in response to sad faces, on the other hand, was also reported by Phillips et al. (1998) using fMRI. They concluded that the lack of detectable signal increase in

response to facial expressions of sadness might be due to the relatively complex nature of sadness as an emotion (Power & Dalgleish 1997). In support, Morita et al. (2001) stated that positive emotions such as happiness are recognised more easily than negative emotions, and that differences in the detection of activation may be due to emotion intensity rather than valence. Empirical evidence also exists claiming a processing advantage of happy over other facial expressions (Kirita & Endo 1995; Ekman et al. 1982; Kirouac & Dore 1983).

5.4.2.2. Occipito-temporal regions including fusiform gyrus

The role of the occipito-temporal regions and in particular the role of the fusiform gyrus in the processing of faces is well established.

The current study revealed decreases in oscillatory power in response to faces (regardless of emotional expression) and scrambled control images, and hence illustrates the involvement of these regions in the structural processing of faces regardless of any social information that may be conveyed. The involvement of the occipito-temporal areas is also evident in the processing of scrambled faces. The decreases in cortical oscillatory power observed for the scrambled images are thought to be due to the increased difficulty implicated in the processing of scrambled faces. Increases in BOLD signal within occipito-temporal regions and the fusiform gyri in response to face stimuli have been reported (e.g. Kanwisher, McDermott & Chun 1997; Phillips et al. 1997; Kesler-West et al. 2004) and Singh et al. (2002) observed a correspondence between increases in BOLD response and decreases in event-related cortical power in a biological motion task. It is thus assumed that the decreases in cortical power observed here are indicative of the processing of facial as well as scrambled stimuli occurring within occipito-temporal regions.

6.1.1.2.1. Latency considerations

The significant power changes revealed here during a time-window of 0 to 200ms are in line with results from evoked-response paradigms in which a face-specific response at about 170ms post-stimulus onset has been reported (N170, see Eimer et al. 2000c; Schweinberger, Sommer & Stiller 1994). Face specific responses were evident within the 0 to 200ms time-window, and TFRs illustrate some decreases in cortical oscillatory

power in the all faces condition. Here, decreases in cortical oscillatory power could be observed at approximately 150ms for 25 to 27Hz frequencies, and at somewhat later latencies of 180ms at higher frequencies of 36 to 40Hz. At the higher frequencies, particularly, the signal decreases observed are, however, more prominent in the scrambled faces condition, thus, the possibility of decreases in cortical oscillatory power revealed by SAM, being indeed due to the signal power changes in the scrambled rather than the all faces condition, needs to be considered. Here it would have been advantageous to compare indirectly, the patterns of cortical oscillatory power changes to all faces and scrambled images, by looking at each separately compared to their respective prestimulus baselines.

5.4.2.3. Frontal areas

5.4.2.3.1. All faces versus scrambled control images

The findings in respect to the frontal areas need to be considered carefully. When comparing all faces to scrambled control images over the 0 to 200ms time-window, event-related decreases in cortical oscillatory activity were established in the beta waveband (13 to 25Hz) in the left middle frontal gyrus. Using a somewhat longer time-window of 0 to 400ms for the analysis, within the same waveband, event-related increases in cortical oscillatory power were revealed in the left superior frontal gyrus.

These findings indicate that there seems to be a shift in the change of oscillatory power from greater decreases in relative power in the shorter (200ms) time-window to an increase in relative power changes in the longer (400ms) time-window. These oscillatory changes are illustrated in the TFRs in Figures 5-11 to 5-13. In the 200ms time window there is evidence of relative power reductions in the low beta band of 13 to 16Hz. These are, however, more prominent in the scrambled face condition than in the all faces condition, in which increases in cortical oscillatory power seem to be demonstrated at those frequencies.

The TFR generated for the left superior frontal gyrus, on the other hand, shows increases in signal power, and these are more pronounced in the all faces, compared to the scrambled faces conditions. Particularly notable are the power increases at 16 to 18Hz, at latencies of approximately 100 to 300ms, but also at higher frequencies, 26 to 30Hz, at approximately 100ms. This could indicate that the processing of scrambled

images is seen as the more complex component of the perceptual process, initially associated with decreases in cortical oscillatory power. However, it could also be linked to the uncoupling of these neuronal networks to allow synchronisation in later time-windows.

5.4.2.3.2. Emotional expressions versus scrambled control images

In the emotion versus control condition involvement of the left middle and the left superior frontal gyrus was observed in the 400ms time-window only. The association of left frontal areas in the processing of emotional expressions has been documented (e.g. Davidson's model of approach / avoidance behaviour). In addition, Sergent, MacDonald & Zuck (1994) and George et al. (1995), using fMRI and PET have pointed out that the overt processing of facial emotions involves, amongst other structures, the inferior frontal gyri. In support, a study by Dolan et al. (1996) using fMRI revealed activation within the left inferior frontal gyrus in response to happy versus neutral faces. However, activation within the left inferior frontal gyrus was also obtained when all faces (regardless of emotional content) were compared to a control condition. The involvement of medial frontal regions to presentations of happy faces was also reported by Phillips et al. (1998).

The findings obtained in the current study substantiate Streit et al.'s (2000) claim of a time-delay between the functions of structural decoding of faces per se and the decoding of the somewhat more complex facial information that is conveyed in facial expressions. Streit et al. (1999) reported neuromagnetic responses to facial expressions between 180 and 300ms, and, furthermore, stated that little evidence existed indicating that decoding of facial expressions would reliably begin earlier than 180ms post-stimulus presentation. As no significant changes in oscillatory power could be observed for the shorter time window of 200ms in the emotion versus control condition, yet significant power changes occurred in the later, 400ms, time-window, this data supports the notion of structural encoding occurring separately, and earlier, than the decoding of facial expressions of emotions.

5.4.2.4. Limbic Lobe including Amygdala and Parahippocampal Gyrus

Power increases were observed for the comparison of happy and scrambled images in limbic regions including the amygdala and the parahippocampal gyrus. This finding seems to be due to the emotional content of the stimuli presented, as it was not found in the all faces versus scrambled condition. As before, indirect comparisons looking at changes in cortical oscillatory power for happy and scrambled faces and their respective baselines separately could have provided further insight into the conditions yielding the patterns of cortical activity obtained. Different response patterns can be observed as face-responsive neurons in the amygdala receive inputs from different groups of neurons in the temporal cortex that respond to faces on the basis of features such as hair, eyes or mouth. Hence face-selective neurons in the amygdala can respond differentially according to facial emotional expressions.

5.4.2.4.1. Lateralisation effects in amygdalar activation

With humans, Gur et al. (2002a) reported activation within the amygdala and the hippocampus when participants were asked to discriminate facial emotions. Gur et al. (2002a) reported a shift from activation within the right amygdala in the first experimental block to greater left sided activation in the second block. They explained such shift in terms of hemispheric differences in the time course of the amygdalar response to facial emotions (Phillips et al. 2001). A shift in terms of hemispheres could also be observed in this current investigation, yet rather than being solely due to different time courses it was associated with different frequency bands. The significant power increase in the right hemisphere observed over the first 400ms for the gamma waveband of 25 to 40Hz was further investigated by generating time-frequency representations. In addition to increases in cortical oscillatory power in the right hemisphere in two frequency bands, 26 to 28Hz and 36 to 38Hz, TFRs generated for a corresponding voxel in the left hemisphere revealed a prominent reduction in oscillatory power in a narrower frequency range of 35 to 38 Hz. The latency information, on the other hand, revealed some similarities. Within the right hemisphere, changes in cortical oscillatory power seemed present over a period from about 150 to300ms, whereas decreases in cortical power were most prominent at about 150ms within the left hemisphere. Further SAM analysis to investigate this switch of cortical activity showed

a decrease in oscillatory power in comparable areas for the left hemisphere (limbic lobe, parahippocampal gyrus), yet it failed to reach statistical significance.

5.4.2.4.2. Amygdala involvement in facial expressions recognition

Streit et al. (1999) stated that obtaining activation within the amygdala confirmed reports about the role of the amygdala in the processing and evaluation of social and emotional significance of incoming sensory information. Wild et al. (2003) found the involvement of hippocampal and amygdalar regions in response to the presentation of happy faces when also performing congruent mouth movements. In the present investigation, only 'viewing' of the presented expressions was required, hence the perception and potential experience of the emotion might suffice to recruit limbic areas including the amygdala. Amygdala activity has also been observed in studies on facial attractiveness (e.g. Aharon et al. 2001). Happy faces are considered to be more attractive (Bartels & Zeki 2000; Senior 2003) thus the involvement of the amygdala in response to happy faces might be due to its role in the appraisal of facial characteristics. In addition, the amygdala is thought to be part of the neural system integrating emotion and memory (LeDoux 1993b), a function of certain importance in facial expression recognition. The middle region of the temporal cortex as well as the amygdala have numerous anatomical connections to the areas involving the visual streams, thus, the fact that the amygdala plays a noticeable role in the analysis of complex social stimuli – such as complex facial configurations – can only be expected.

5.4.3. Theoretical Implications

Physiological findings revealing information regarding where and how processes in the brain unfold in time have valuable implications for models of face processing, e.g. that of Bruce & Young (1986). The Bruce and Young model indicates that the first stage in the face processing sequence is concerned with the identification of the stimulus as a face. In fact, Ellis et al. (1990) has argued that only an initial classification of a stimulus as being a face would enable the activation of the face – processing system. The structural encoding provides data for the next stage, the face recognition units (FRUs), in which descriptions of familiar faces are contained. Within the Bruce and Young model there are three structures associated with face identification. These are concerned

with the interpretation of emotional expression, facial speech analysis and directed visual processing. According to the model, this seems to imply that affective features of a face seem to be extracted from faces only *after* completion of structural encoding, which has been reported to take place at approximately 170ms post-stimulus onset (Bentin et al. 1996; Sams et al. 1997; Eimer & McCarthy 1999; Streit et al. 1999). Pizzagalli et al. (1999; 2002) claim that there exists evidence of face – specific activity being modulated by affective information before 170ms, e.g. as early as 80 to 116ms, i.e. preceding full face processing. In the current study, activation associated with face processing occurred within the first 200ms post-stimulus onset, prior to processing associated with emotional expressions, in concordance with the former group of researchers.

The importance of the involvement of the amygdala in the perception and recognition of emotions from faces has also been shown in a study by Schmolck & Squire (2001) who studied patients with amygdala damage due to Urbach-Wiethe disease. The impairment they observed in their patient sample led to the suggestion of there being at least two factors involved in the processing of facial emotion. One, which requires the ability to discriminate between facial emotions (measured by e.g. a labelling task), and a second one, which relates to the ability to recognise the intensity of facial emotions (as measured by assigning a rating of intensity to displayed emotions). Thus, the ability to characterise amygdala activity during emotional processing as demonstrated in this study has significance for an understanding of its role in normal and abnormal affective functions.

5.5. Summary

MEG data and SAM as an analysis technique can contribute to the investigation of the mechanisms involved in face perception per se but also in the processing of emotional expressions from faces. Spatial correlates for the perception of faces and facial expressions as established in fMRI were found using MEG and SAM. Face specific latency responses could be determined which would substantiate claims of the N170 component, and it has been shown that the perception of facial affect follows an initial face categorisation process. Induced gamma oscillations in response to complex facial configurations have been reported, and validate findings from previous investigations (see chapters 3 and 4). In addition, this investigation has been able to demonstrate that

limbic responses, in particular the amygdala, were detectable when processing facial expressions of emotions, using MEG and SAM. Here differential involvement of the left and right hemispheres was observed.

These intriguing findings prompted further investigations of facial affect incorporating the more widely used and validated set of facial stimuli (i.e. the Ekman & Friesen's stimulus set of facial affect). The subsequent investigation included neutral faces as control stimuli to overcome the potential confound that might be associated with scrambled images being more ambiguous and thus difficult stimuli to process.

Chapter 6 Effects of a discrimination task on facial processing

6.1. Introduction

6.1.1. Neural correlates of facial emotional processing

The viewing of faces and of photographs of faces can elicit emotions in the observer (Wild et al. 2001). Dolan et al. (2000) pointed out that facial emotional expressions supposedly possess innate salience – determined by evolution – thus are able to elicit automatic spontaneous emotional responses.

6.1.1.1. fMRI investigations

Using fMRI, bilateral activation within the fusiform gyrus was reported by Breiter et al. (1996) in response to happy and fearful faces. The involvement of temporal areas in the processing of emotional information has been reported by e.g. Blair et al. (1999), Breiter et al. (1996) and Dolan et al. (1996). In addition, Rapcsak, Comer & Rubens (1993) stated that the right middle temporal gyrus seems to play an essential functional role in the verbal labelling of emotional facial expressions. In response to facial expressions, Sergent (1994) observed activation within the cingulate cortex, and George et al. (1993) reported signal increases in anterior cingulate gyri. The presentation of happy facial expressions has been associated with signal increases in posterior cingulate areas (e.g. Kilts et al. 1995, 2003). The involvement of subcortical structures such as the amygdala has been widely demonstrated in studies of emotional processing (e.g. Gur et al. 2002a; Dolan 2002; Hyman 1998). Blair et al. (1999) reported activation within the amygdala also in response to the presentation of sad faces.

Phillips et al. (1998) reported activation within both cingulate gyri (anterior cingulate gyrus, BA24 on the left; and posterior cingulate gyri BA23, BA30 and BA31 bilaterally) in response to happy facial expression, and also within medial frontal regions bilaterally, the left supramarginal gyrus (BA40), the right putamen and dorsolateral prefrontal cortex (BA46) and the left caudate nucleus. Contrasting sad facial expressions with neutral ones revealed activation within the left supramarginal (BA40), the right dorsolateral prefrontal cortex (BA45) and the left middle occipital cortex (BA18). The observed signal increase however appeared to be due to the

presentation of neutral rather than sad faces (Phillips et al. 1998). Thus, Phillips et al. (1998) concluded that there are dissociable neural substrates underlying the presentation of facial expressions of happiness and sadness.

6.1.1.2. EEG and ERP studies

EEG investigations into positive and negative emotion processing have persistently reported ERPs at left hemisphere electrodes in response to happiness or positive emotions in general, and at right hemisphere electrodes in response to negative emotions like sadness, anger, fear and disgust (e.g. Davidson et al. 1990b; Graham & Cabeza 2001; Jones & Fox 1992). Ahern & Schwartz (1985) investigated lateralisation effects for emotional processing using EEG, and observed differential involvement of the hemispheres for positive and negative emotion. Left-hemispheric activation as measured by decreases in alpha was observed for positive, right-hemispheric activation for negative emotions.

Using LORETA, Pizzagalli et al. (2000) reported the involvement of bilateral occipito-temporal regions (including lingual and fusiform gyri) extending into inferior temporal gyri in response to emotion – eliciting faces. A study by Esslen et al. (2004) reported findings of significant left hemisphere activation in response to different emotional conditions (such as disgust, fear, anger, sadness, surprise and happiness), and concluded that the processing of these basic emotions proceeds via both hemispheres.

Further EEG investigations using global analysis approaches such as LORETA - e.g. Gianotti et al. (2003); Esslen et al. (2004) or Global Field Power - e.g. Eger et al. (2003) have found emotion–related ERPs to peak at around 100ms followed by a later component at approximately 140ms to 200ms. The ability to localise emotion – relevant activity during time segments that discriminate between affective and neutral faces has revealed dynamic patterns of neuronal activity for individual emotions. Esslen et al. (2004) could thus demonstrate that each emotion indeed involved a limited number of brain areas. All emotion conditions investigated engaged the orbital and lateral prefrontal cortex (PFC). In addition, during happiness and sadness activation appeared rather prominent in the temporal cortex, and in all conditions except fear, the cingulate cortex was found active.

6.1.1.2.1. Time course of emotion specific processing

Face specific ERPs and MEG waveforms with latencies of 155ms to 190ms have been reported by Jeffreys (1996), Bentin et al. (1996), Allison et al. (1994), Sams et al. (1997) and Schendan, Ganis & Kutas (1998). More recently however, Liu, Harris & Kanwisher (2002) reported findings of M100 and M170 components, which they associated with successful face categorisation. The latter component was also found to correlate with successful face identification. Aiming to map the time course of emotional processing, Esslen et al. (2004) reported distinct latencies at which areas implicated in emotional processing were active. For happy faces, an early time segment of approximately 138ms to 205ms activation was found within left and right frontal areas, and left and right temporal areas were found to be active at latencies of approximately 240ms to 290ms. For sad faces, first effects were reported for approximately 100ms to 125ms within left postcentral regions, the orbital and lateral prefrontal cortices were active at latencies of approximately 140ms to 200ms, and 220ms to 260ms, respectively. In addition, activity was reported for bilateral ventro-medial and orbito-frontal regions, right PFC, bilateral temporal areas, and the right occipital cortex, bilateral frontal regions and the posterior cingulate gyrus for latencies within 400ms. Davidson & Irwin (1999) assigned the PFC a crucial role in affective working memory, thus the cognitive demand of the task may have elicited the later bout of activation in Esslen et al.'s study.

In an emotion discrimination task in which the target emotion was surprise, Krolak-Salmon et al. (2001) reported evoked potentials to faces at temporal sites (bilaterally) at latencies of 150ms post-stimulus. At later latencies, 250ms to 500ms, differential activation to emotional compared to neutral facial expressions was observed. During an expression discrimination task, ERPs to the different facial expressions were observed even later still, between 550 and 750 ms.

Nelson & Kestenbaum (1991) however, revealed a N400 and a late P700 component that varied as a function of target emotional expression. In a further study by Kestenbaum & Nelson (1992) a P300 component was observed at parietal and left and right temporal sites, which was greater to happy than to angry faces in adults (but greater to angry faces than to happy ones in children).

6.1.1.2.2. Frequency specific processing of emotion relevant information

The functional significance of individual frequency bands in relation to the processing of emotional expressions has not been widely explored. The frontal asymmetry model proposed by Davidson incorporates differential involvement of frontal alpha in the processing of, for instance, expressions of happiness and disgust. Facial expressions of disgust were associated with less alpha power at right frontal areas compared to happiness expressions, which in turn were linked to less alpha power in left frontal areas (Davidson 2001). Furthermore, Davidson, Ekman & Friesen (1990a) found that the "Duchenne Smile" was related to greater left hemisphere activation in frontal and anterior brain regions (at alpha frequencies). Greater right frontal activation (i.e. less alpha power) was also reported during punishment conditions in a punishment versus reward related task (Sobotka, Davidson & Senulis 1992). These decreases in alpha power have since been taken as an indication of alpha activation, and reduced levels of alpha activity have become known also as alpha blocking or desynchronisation, in relation to tasks of behavioural and, or, emotional arousal or active task engagement. They reported greater negativity within the right hemisphere (i.e. relative to left hemispheric activation) in response to 'happiness' compared to 'fear' questions. An investigation by Tomarken, Davidson & Henriques (1990) demonstrated that alpha activity in frontal regions was associated with self-reported negative affect in response to emotional stimuli (video-clips).

Ahern & Schwartz (1985) stated that other frequency bands are also functionally related to emotional stimulation, and that increases in cortical power (usually linked to increased emotional arousal) have been reported.

Delta frequencies, for instance, have been observed in situations of hostile confrontation (e.g. Hoagland, Cameron & Rubin 1938; Hoagland, Cameron, Rubin & Tegelberg 1938 – cf. Ahern & Schwartz 1985), ***theta frequencies*** have been reported in response to hedonic stimulation of infants (e.g. Maulsby 1971 – cf. Ahern & Schwartz 1985) and ***beta frequencies*** have been linked to increased stress responses and apprehension (e.g. Berkhout 1969 – cf. Ahern & Schwartz 1985). In addition, Rusalova & Kostiunina (2003), using EEG to study the simulation of joy in a goal-achievement situation, reported that beta activity correlated with emotional levels but also with motivation, which also implicated alpha frequencies bilaterally. Ponomarenko et al.

(2003) observed that, in rats, emotional arousal was associated with beta and gamma oscillations within the pre-piriform cortex. Ahern & Schwartz (1985) also reported of a "total power" frequency range (1 to 31Hz), which was associated with greater involvement in tasks of emotional memory.

Ray & Cole (1985a, b) investigated attentional and emotional aspects in order to map attentional, cognitive and emotional factors in terms of EEG frequency representations. They asked participants to remember sad and happy events from the past and to imagine future ones, but also showed pictures of positive and negative emotional contents. They reported that parietal areas, for 'middle' frequency bands, including alpha, reflected the difficulty of the task. Furthermore, a significant main effect was observed for emotional valence in temporal and parietal areas with greater beta activation for positive than negative conditions. They concluded that the investigation of beta frequencies might prove useful in further studies of cognitive and emotional processing.

Drawing comparisons between the patterns of cortical activation for the different frequency bands, it has been noted that delta and total band power showed an activation pattern opposing the one for alpha in response to positively and negatively valenced questions, i.e. increases in power were observed. For theta and beta, increases in relative as well as in absolute right hemisphere activation could be observed for the 'excitement' and 'fear' questions but not for 'happiness', 'neutral' or 'sadness' ones. It has therefore been argued that theta and beta frequencies might be associated more with general arousal levels of particular emotions, rather than their positive or negative valence (Ray & Cole 1985a, b).

6.1.2. Summary and hypotheses

Thus, the following investigation aimed to further characterise the temporal sequence of cognitive and neural processes underlying the perception of facial expressions, and to explore the functional specificity of the conventional EEG frequencies as well as for a total band power (5-40Hz). Facial expressions of happiness and sadness were chosen, as exemplars of positive and negative emotions. Sadness has been ascribed a role of a regulator of emotional and social interactions since the display of sadness expressions has been linked to inhibition of aggression and the elicitation of altruistic behaviour (Eisenberg et al. 1989). In a PET study, Blair et al. (1999) presented

neutral, sad and angry facial expressions of morphed intensity levels, and recorded activation within left amygdala, right temporal pole BA38, right inferior temporal gyrus BA20, and right middle temporal gyrus BA39, ACC BA38 in response to sad expressions. Happiness on the other hand provided an interesting emotion to study due to the observations of a happy face advantage in behavioural investigations. It has been suggested that happy faces are more likely to be recognised by a different processing strategy (Kirita & Endo 1995). In addition, the observation that young infants are known to first discriminate happy faces from all other facial expressions (Barrera & Maurer 1981) adds to the proposition that happy faces may be recognised in a different way. Functional imaging studies that have included facial expressions of happiness have reported the involvement of subcortical structures like the amygdala, but also the anterior cingulate cortex and frontal regions. Thus, investigating happy and sad facial expressions and using neutral expression as a comparison stimulus might reveal dissociable neural substrates, responding differentially to these distinct emotions.

In this investigation, facial stimuli were chosen from the Ekman & Friesen series of pictures of facial affect as they are the most widely used and most validated set of facial expressions to date. Instead of employing a paradigm in which the rating of emotional content was emphasised – as was the case in the previous experiment – a one back memory task was chosen, allowing for the investigation of more explicit facial emotional processing. Participants were asked to indicate whether the two facial expressions presented were identical or not. Explicit processing of facial emotions has been linked to increases in BOLD signal in temporal areas. The changes in methodology are due to the discussion of the findings from the previous investigation (see chapter 5, section 5.4).

It is hypothesised that face-specific areas such as occipito-temporal and occipital areas including lingual and fusiform gyri are activated, in addition to emotion - specific regions, in particular frontal and temporal regions as well as the cingulate gyri. Left and right frontal areas are predicted to show differential patterns of activation. It is also expected that face specific ERPs and MEG waveforms will be observed at latencies of 150 to 190ms (these have been used by Eimer 2000a-c to quantify the face-specific N170) and that emotional, compared to, neutral expressions will be differentiated by latencies as has been found by Esslen et al. (2004) and Krolak-Salmon et al. (2001). Emotion specific EEG frequencies are to be explored, with frontal alpha frequencies predicted to show differential involvement in the processing of happy and sad facial

expressions. Gamma responses are predicted due to the complexity of the face stimuli and the observations of Rodriguez et al. (1999) and Tallon-Baudry et al. (1997) (see also chapter4), but also because they have been implicated in the previous studies of face processing, with differential effects of gamma for the processing of faces and houses in occipito-temporal regions (see chapter3).

6.2. Method

6.2.1. Materials and Participants

Stimuli were selected from the Ekman and Friesen (1976) series of *Pictures of Facial Affect*, which contains black and white photographs of facial expressions of 10 actors (six female). The photographs have been digitally altered to depict only the contour of the face, i.e. hair, ears etc. are removed. The images selected for the current investigation comprised happy and sad expressions for all ten individuals, plus corresponding neutral expressions (as control stimuli). To obtain adequate amounts of stimulus presentations and trials, each face was repeated three times, yielding a total of 90 facial stimuli, 30 in each expression condition. For stimulus display Presentation software (http://nbs.neuro-bs.com/presentation/download) was used. The presentation of the stimuli proceeded in a randomised order.

Nine healthy participants (eight female, one left-handed) gave consent to take part in the investigation. Due to movement, head localisation failed for two participants resulting in usable data for seven participants (six females; one left handed, average age 27years). The study was approved by the Aston University Human Sciences Ethics committee. Participants were seated within a magnetically shielded room, and viewed, through a mirror, a monitor, placed outside the shielded room, on which the stimuli were presented. The distance between the participants and the monitor was approximately 2m.

6.2.2. Experimental Paradigm

On each trial, participants were asked to fixate on a white circle for 1500ms before a target stimulus was presented for 500ms. The fixation point then returned followed by a second image being presented for 500ms and a delay before a cue (red circle) indicated that the participant should make a button-press response, indicating whether the two facial expressions presented were the same or different. The pairs presented contained faces of same or different emotional expressions (see **Figure6-1**).

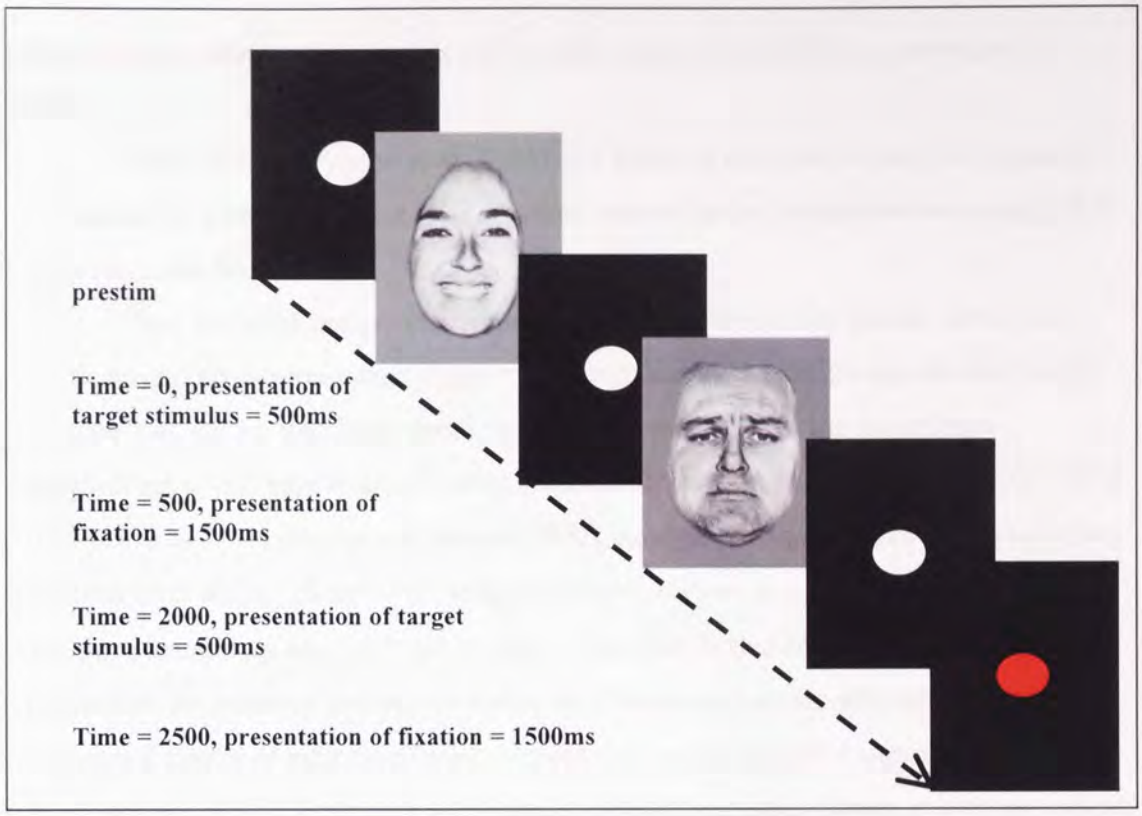


Figure6-1: Experimental paradigm

6.2.3. Image acquisition and analyses

MEG signals were recorded with a third order gradiometer configuration using an Omega 151-channel magnetometer (CTF Systems Inc., Canada).
Head localisation information was acquired by recording the position of head localisation coils before and after the recording session. Following data acquisition, a 3-D digitiser (Polhemus Isotrack) was used to digitise participants' heads and allow co-registration of each participant's MEG and MRI data. This was achieved using Align (www.ece.drexel.edu/ICVC/Align/align11.html), which matches the participant's digitised head-surface to the head-surface extracted from their individual, anatomical MRI (Kozinska 1997).

To analyse the MEG data, Synthetic Aperture Magnetometry (SAM) was used. SPMs were generated for predetermined frequency bands (8-13Hz; 13-25Hz; 25-40Hz and 5-40Hz) and time-windows 0 to 200ms; 0 to 400ms over the entire brain at 5mm resolution to localise power changes in response to the stimuli of differing emotional content and the control stimuli. Positive values are interpreted as relative increases in power, also referred to as ERS, or increases in ERSP, and negative values are

interpreted as relative decreases in power, also referred to as ERD, or decreases in ERSP.

Using SPM99 (Friston et al. 1995), the MRIs of each participant was spatially normalised to a template space. The resultant normalisation parameters were applied to the volumetric SAM images.

Thus, all SAM images (seven participants, four frequency bands, three time-windows and six comparisons: happy vs. neutral; sad vs. neutral; happy vs. sad; happy vs. baseline; sad vs. baseline, neural vs. baseline) were then in the same three-dimensional coordinate space allowing group analyses (Singh et al. 2002). Using SnPM (Holmes et al. 1996; Nichols & Holmes 2002), analyses of significance were performed at voxel level and at cluster level using a multiple subject single condition design. Variance smoothing was performed using a Gaussian kernel (σ = 20mm). Using non-parametric permutation testing, cluster-level inferences estimate whether a large connected cluster of near significant t-values may reach statistical significance. Voxel level inferences were estimated additionally. Spatial resolution however is being traded in against sensitivity (for details see Nichols & Holmes 2002; Singh, Barnes & Hillebrand 2003).

For the visualisation of the results on a template brain, SPM was used as well as mri3dX (http://www/aston.ac.uk/lhs/staff/singhkd/mri3dX/). In all figures the left side of the brain is displayed on the left side of the image, and coordinates provided are stated in Talairach & Tournoux (1988) version. In the figures presented, increases in cortical power are indicated by colourscale of red – orange – yellow, with yellow regions being the most significantly active areas. Decreases in cortical oscillatory power are indicated by a colourscale of blue – pink – white, with white regions being the most significantly active areas (see colourbar on page 74, **FigureB**).

To investigate the time course and frequency specificity of the obtained activation within significant regions, time-frequency representations were generated using Morlet wavelet analysis (Tallon-Baudry et.al. 1997). The wavelet method was chosen as it provides a better compromise between time and frequency resolution than Moving Window Fourier Analysis. Time-Frequency Representations (TFRs) were generated. Once the TFRs for each participant were generated, averages were computed by averaging the TFRs of all participants.

6.3. Results

Analyses were performed across two time-windows, 0 to 200ms to investigate whether 'categorical' face perception processes are performed at shorter latencies than face or emotional discriminations, which were thought to reveal significant power changes within a longer time-window of 0 to 400ms. To explore the functional significance of EEG frequency bands with respect to face and emotional processing, conventional EEG frequency bands were chosen (alpha 8-13Hz, beta 13-25Hz and gamma 25-25Hz. In accordance with Ahern & Schwartz (1985) a broad range waveband was included (5-40Hz). All faces regardless of emotional expression were compared to a prestimulus baseline to explore the face specific-findings from preceding studies. A table of results detailing pseudo-t statistics, coordinates and region showing changes in cortical power are included in **Appendix5**.

6.3.1. All faces versus baseline

In order to investigate the involvement of face specific regions, all facial stimuli were combined and SAM and SnPM analyses performed against a prestimulus baseline condition. Within the 0 to 200ms time-window, significant increases in cortical power, i.e. ERS were obtained for alpha and also for a broad range waveband of 5 to 40Hz.

6.3.1.1. Alpha

Significant results were obtained with a maximum observed pseudo-t value of 4.9, $p < 0.05$, within the left occipital lobe and within cuneus regions, BA19 a trend towards significance was observed (pseudo-t = +4.2; $p > 0.05$) (see **Figure6-2**).

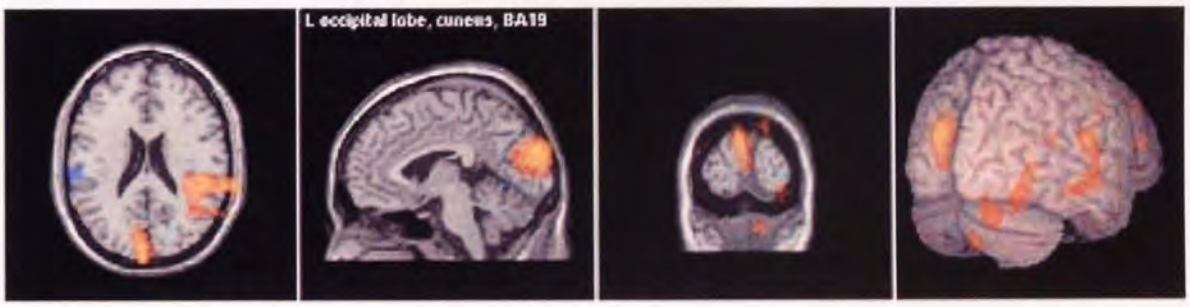


Figure6-2: Responses to all faces regardless of their expression to a prestimulus baseline for 8-13Hz, 0 to 200ms. SPMs show ERS within the left occipital lobe, cuneus, BA19, displayed onto a template brain.

6.3.1.2. 5-40Hz

Significant results were obtained with the critical calculated threshold estimated to be 3.9, the maximum observed value was pseudo-t = +4.8, $p < 0.05$, within the right occipital lobe, lingual gyrus, BA18 (see **Figure6-3**).

The involvement of face specific areas such as the left lingual and fusiform gyri at subthreshold level is illustrated in **Figure6-4**.

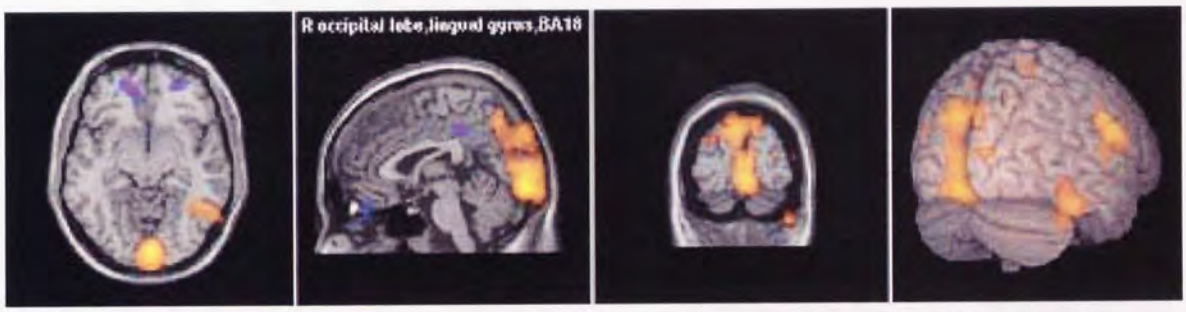


Figure6-3: Responses to all faces regardless of their expression to a prestimulus baseline for 5-40Hz, 0 to 200ms. SPMs show significant ERS within the right occipital lobe, lingual gyrus, BA18, displayed onto a template brain.

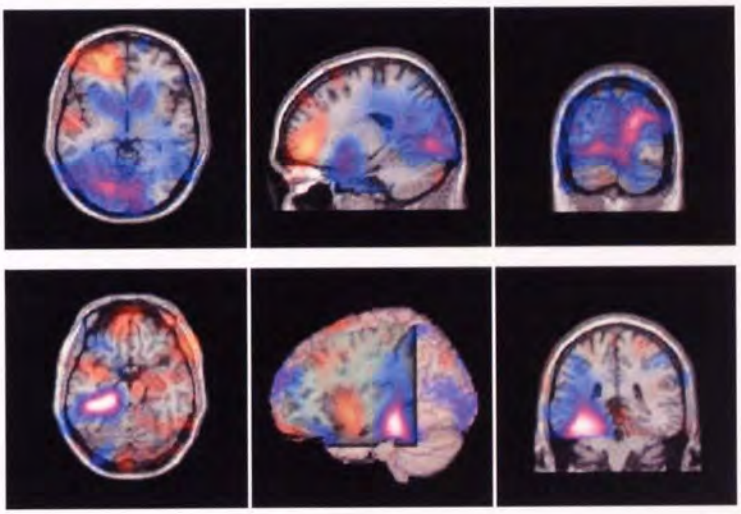


Figure6-4: GroupSAM indicating the involvement of face-specific areas for 25-40Hz. ERD is demonstrated in the left occipital lobe, lingual gyrus, t = -4.75, p > 0.05 (top row) and in left fusiform gyrus, BA37, t = -4.17, p > 0.05; (bottom row).

6.3.2. Neutral facial expressions versus baseline

Within a 200ms time-window, significant decreases in cortical oscillatory power were observed across the broad range waveband of 5-40Hz. SnPM indicate significant ERS effects within the right superior parietal lobule. The critical calculated threshold was estimated to be 5.79, the maximum observed value was pseudo-t = +6.37, $p<0.05$ (see **Figure6-5**).

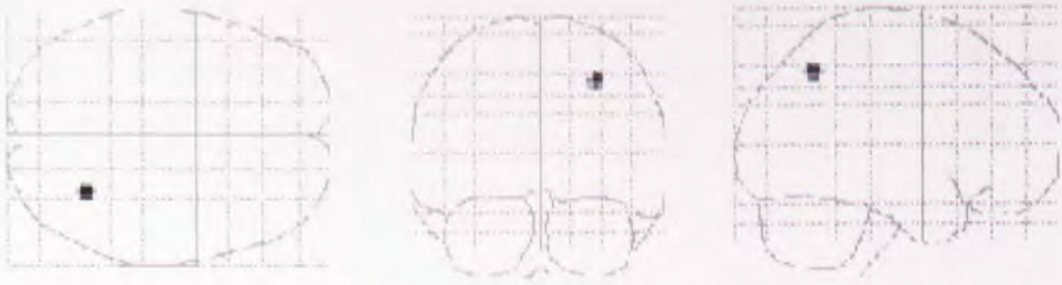


Figure6-5a: Illustration of significant voxels in superior parietal lobule across frequency range of 5-40Hz when comparing neutral facial expressions to baseline. Activation is shown in glass-brain format, dark values represent significant effects.

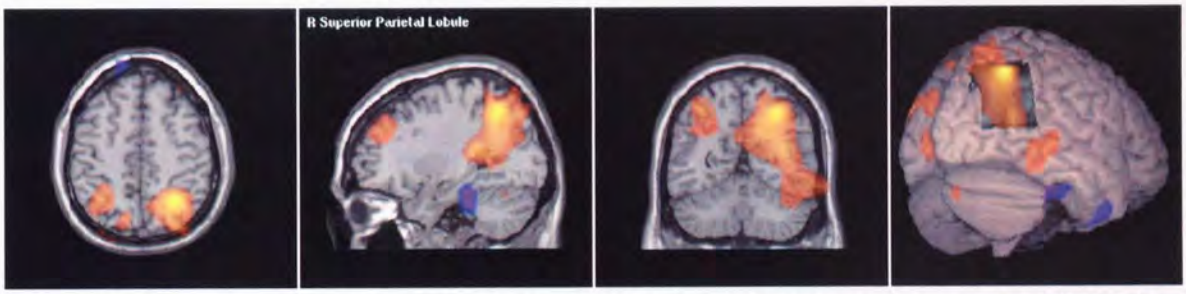


Figure6-5b: Responses to neutral expressions compared to baseline in frequency range of 5-40Hz for 0 to 200ms. SPMs show significant ERS in the right superior parietal lobule, displayed onto a template brain.

6.3.3. Sad versus neutral facial expressions and sad expressions versus baseline

The comparison of sad facial expressions to neutral control stimuli and to a prestimulus baseline did not yield significant results. The reasons for this are explored in the discussion.

6.3.4. Happy versus neutral facial expressions

Across the 0 to 200ms time-window significant results could be demonstrated for gamma (25-40Hz) frequencies at cluster level inferences. With a primary threshold of pseudo-t = 3.0, the permutation distribution for the maximum cluster size revealed the critical cluster size of 839 voxels. A cluster of 1126 voxels was found in the unpermuted volume (pseudo-t = +4.97, $p < 0.05$) in sub-gyral regions of the right frontal lobe, demonstrating increases in cortical oscillatory power (see **Figure6-6**). A voxel within this cluster showed a trend towards significance [at voxel level, $p = 0.065$]

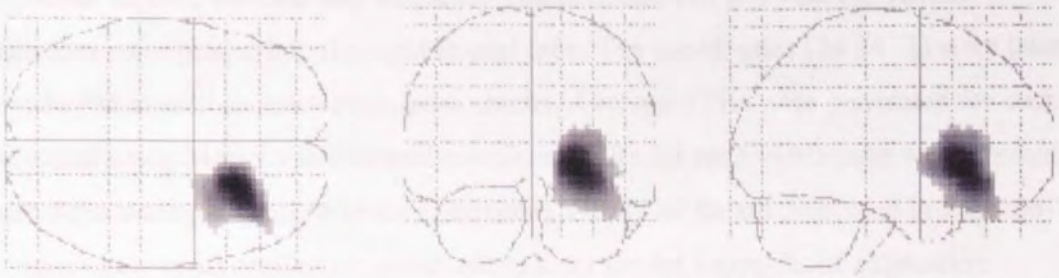


Figure6-6a: Illustration of significant cluster in right frontal lobe for 25-40Hz, 0 to 200ms, when comparing happy facial expressions to neutral ones. Activation is shown in glass-brain format, dark values represent highly significant increases in cortical oscillatory power changes.

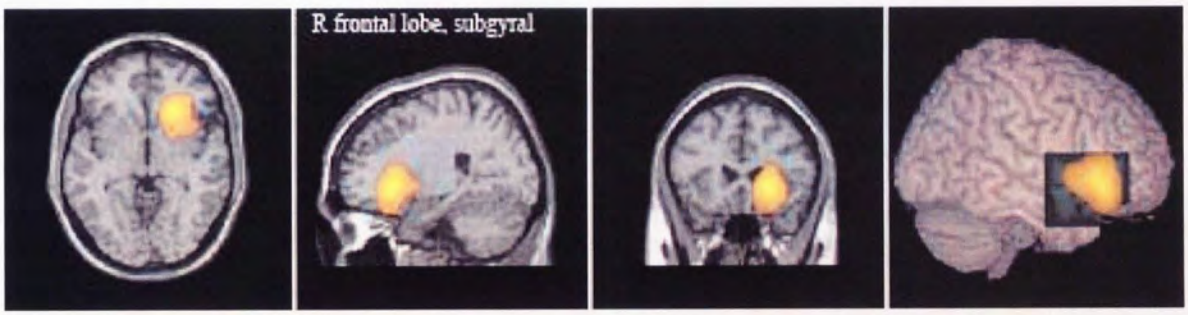


Figure6-6b: SPMs show significant increases in cortical oscillatory power changes in the right frontal lobe, displayed onto a template brain.

To further explore the time and frequency characteristics of this finding, virtual electrodes were placed into the right frontal lobe. The coordinates (24 24 -3) were taken from SnPM as well as individuals peak results. Average TFRs were generated for each individual using Morlet wavelet analysis. Once TFRs for each participant were created, these were averaged to allow group inferences. Group TFRs are displayed in **Figure6-7**. Increases in cortical oscillatory power are evident for the happy facial expression condition (right panel) and the most prominent increase in cortical oscillatory power can be observed at latencies of approximately 180ms for a 30 to 36Hz frequency band, as compared to decreases in neutral expression conditions at similar latencies and frequencies. The increases in cortical oscillatory power observed in the SAM comparison are presumably due to the signal increases observed in the TFRs of the happy face condition.

Neutral Expression **Happy Expression**

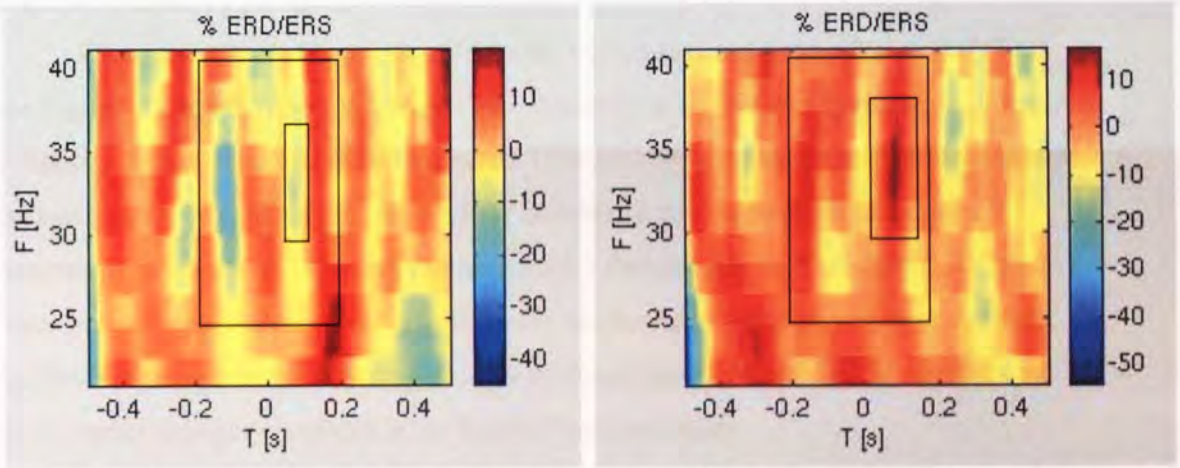


Figure6-7: TFRs for VE placed in the right frontal lobe. Left: changes in cortical oscillatory power associated with the neutral facial expressions. Right: changes in cortical oscillatory power associated with happy facial expressions. The boxes represent SAM results where significant changes were observed.

Average TFRs indicated increases in signal power in the happy face condition. From these TFRs it could only be assumed that the increases in cortical oscillatory power were due to the signal increases observed in the happy face condition. Thus, Mann Whitney time frequency representations were generated for the same voxel within the right frontal areas, to investigate if the observed synchrony observed in the group SAM and SnPM analyses was indeed due to the happy faces condition. In a Mann Whitney voxel by voxel comparison, happy faces were included in the analysis as the active condition, and neutral faces as passive condition, hence the spectral power observed in

the neutral faces condition was "subtracted" from that observed for the happy faces condition. The Mann Whitney TFRs generated for each individual were then averaged to obtain group TFRs (see **Figure6-8,** top row).

For the group Mann Whitney TFRs increases in signal power are evident across the whole 25 to 40Hz waveband. The most prominent increases in cortical oscillatory power, however, can be seen at latencies of approximately 100ms to 200ms, for frequencies of 26 to 28Hz (z-score = +2.5). The middle and bottom row of Figure6-8 show individual TFRs. For participant 1, the most prominent increase in cortical oscillatory power can be seen in the later time windows, 100ms to 200ms, at frequencies of 36 to 40Hz (z-score = +2.5). For participant 2, prominent increases in cortical oscillatory power can be seen at latencies of approximately 20ms to 80ms, for frequencies of 28 to 36Hz (z-score = +1), and a second burst of increases in cortical synchronies is evident at 180ms to 220ms, for frequencies of 32 to 38Hz (z-score = +2.4).

When comparing the average TFRs for the neutral and happy faces conditions (see Figue6-7), to the Mann Whitney TFRs, it can be seen that the increases in cortical oscillatory power observed in the averaged TFR for happy faces are also evident in the averaged Mann Whitney TFR. Particularly notable is this increase in participant 2, however, at latencies of 180ms to 200ms, and for frequencies of 32 to 38Hz. As the z-scores indicate the increases in cortical power are the more prominent power changes, thus the increases in cortical power evident in the group SAM and SnPM analyses are due to power changes observed in the happy faces condition.

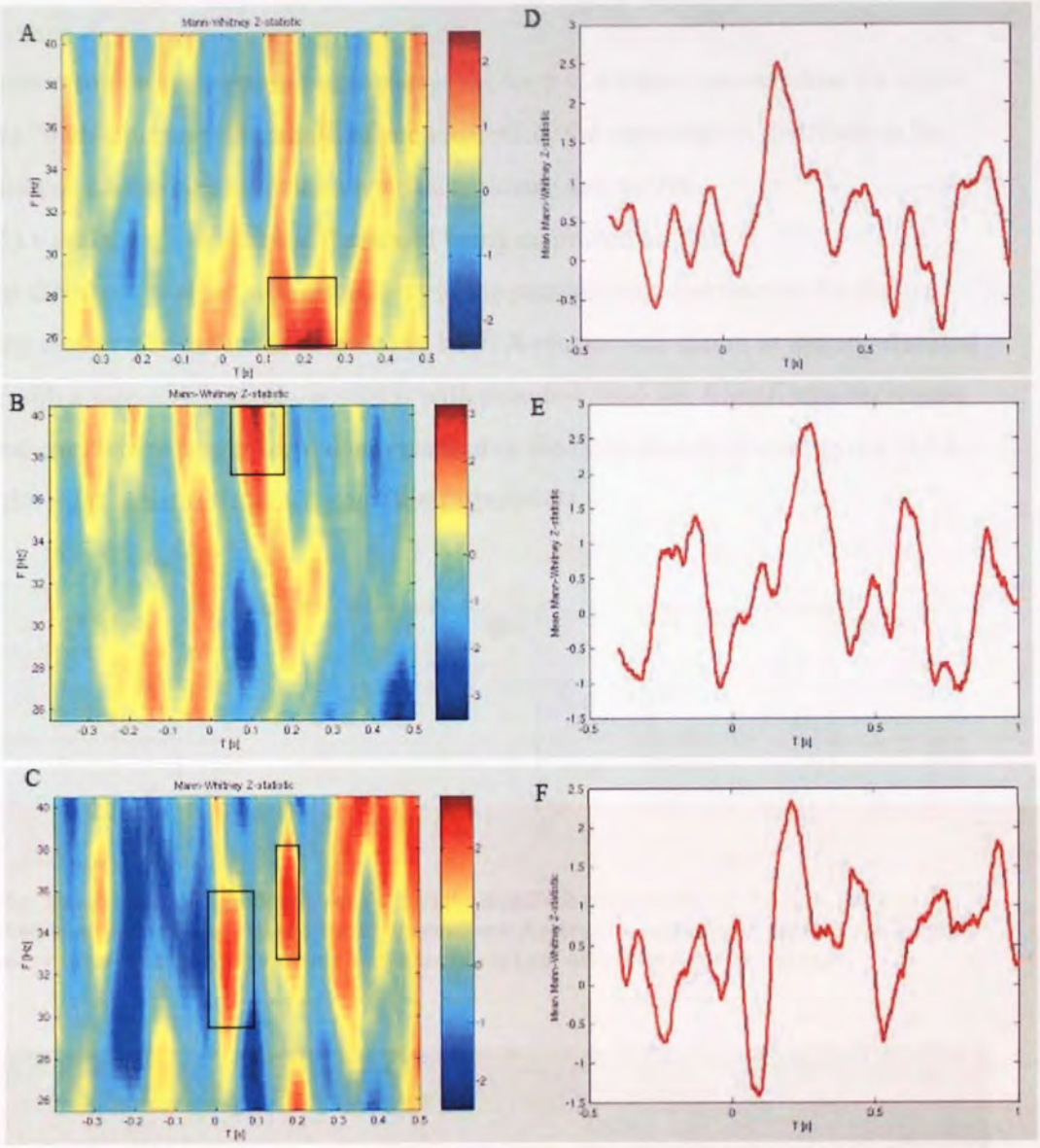


Figure6-8: Mann Whitney TFRs demonstrating increases in cortical oscillatory power for happy compared to neutral faces for a voxel within the right frontal areas.

<u>Top Row</u>: Group TFRs. Increases evident across the whole 25 to 40Hz wave band, signals are strongest at latencies of 100 to 200ms (sustained) at 26 to 28Hz frequencies.

<u>Middle and bottom rows:</u> TFRs for individual participants.

For participant 1, the most prominent increase in cortical oscillatory power can be seen at 100 to 200ms for frequencies of 36 to 40Hz.

For participant 2, prominent increases in cortical oscillatory power are evident at latencies of approximately 20 to 80ms, for frequencies of 28 to 36Hz. A second burst of increase in cortical oscillatory power is evident at around 180 to 220ms, for frequencies of 32 to 38Hz.

The power traces (D-F) demonstrate signal changes at 30 to 40Hz. They show individual Mann Whitney z-scores on y-axis, and time on the x-axis, hence the scaling is different on each part of the figure for each participant and the group average.

6.3.5. Happy versus sad facial expressions

Significant results were obtained at cluster level for 0 to 400ms time-window for alpha (8-13Hz). With a primary threshold of pseudo-t =3.0, the permutation distribution for the maximum cluster size revealed the critical cluster size as 996 ($p < 0.05$) voxels, with the critical threshold being estimated at 5.25.

A further threshold was set with pseudo-t =5, the permutation distribution for the maximum cluster size here was revealed to be 7. A cluster was found in the unpermuted volume with a size of 17 voxels, $p < 0.05$, with pseudo-t = -5.66, Significant decreases in cortical oscillatory power were demonstrated in the right middle frontal gyrus, BA9 as well the right superior frontal gyrus (see **Figure6-9**).

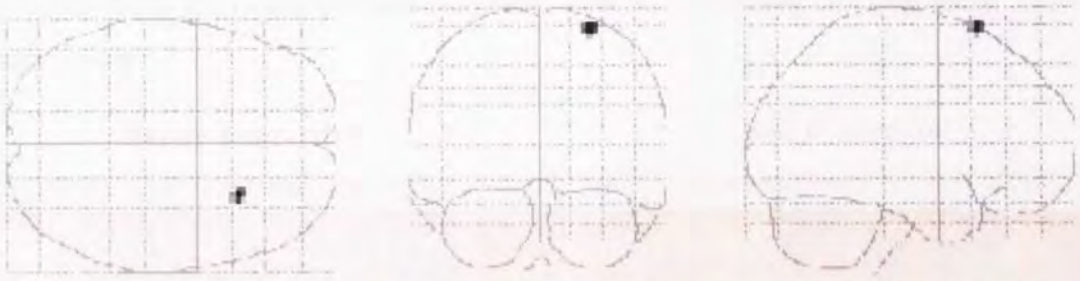


Figure6-9a: Illustration of significant voxels in right middle frontal gyrus for 8-13Hz, for 0 to 400ms when comparing happy to sad facial expressions. Activation is shown in glass-brain format, dark values represent highly significant increases in cortical oscillatory power changes.

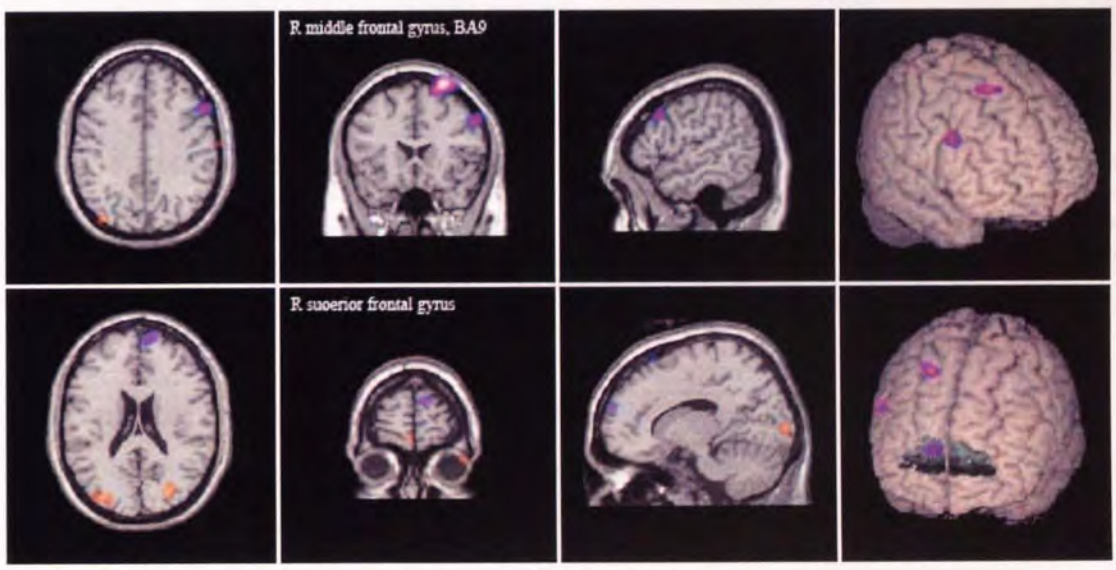


Figure6-9b: Responses to happy compared to sad facial expressions. SPMs show significant decreases in cortical oscillatory power in the right frontal lobe, displayed onto a template brain.
Top: decreases in ERSP shown within the right middle frontal gyrus, BA9.
Bottom: decreases in ERSP shown within the right superior frontal gyrus.

To further explore the time and frequency characteristics of this finding, virtual electrodes were placed into the right superior frontal gyrus (coordinates: 57 18 36). As before, the coordinates to generate TFRs were taken from SnPM as well as individuals peak results. Average TFRs were generated for each individual using Morlet wavelet analysis. Once TFRs for each participant were created, these were averaged to allow group inferences. These group TFRs are displayed in **Figure6-10**. The TFRs show percentage of signal change associated with the presentation of happy faces (left panel) and sad faces (right panel). Within the 8 to 13Hz frequency band decreases in cortical oscillatory power are more pronounced in the happy face condition than in the sad face condition, which in fact seems to show more prominent increases in signal power particularly in the 0 to 400ms and in lower alpha frequencies (see box in figure 6-10). Thus, the decreases in cortical oscillatory power observed in the SAM and SnPM are possibly due to the power changes associated with the processing of happy facial expressions.

Happy Expression **Sad Expression**

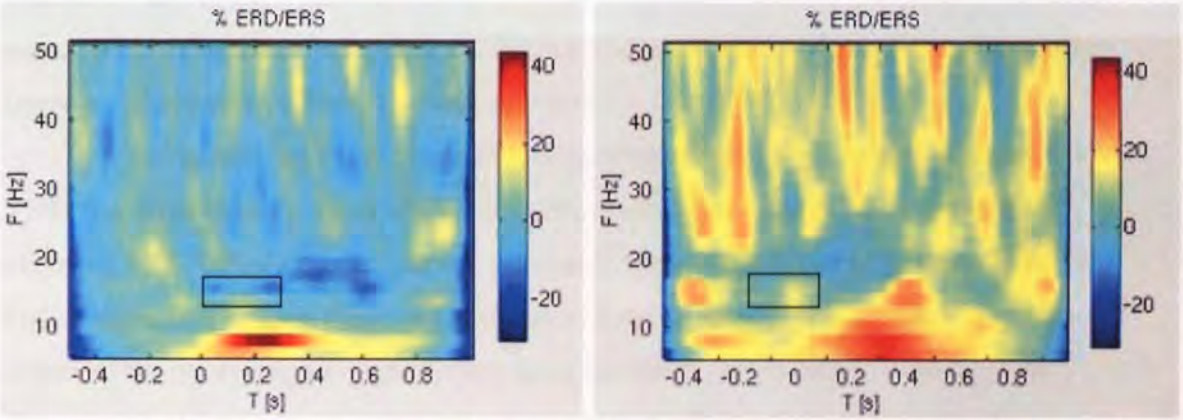


Figure6-10: TFRs for VE placed in the right superior frontal gyrus. Decreases in spectral power evident in happy face condition, at frequencies from alpha to gamma. Decreases are less prominent for sad expressions. Boxes illustrate SAM findings. Thus, the decrease in cortical oscillatory power evident in SPMs are possibly due to the more prominent decreases in synchronized power in the happy face condition

The average TFRs indicated decreases in cortical oscillatory power in the happy face condition, which are less prominent for the sad faces condition. As before, Mann Whitney time frequency representations were generated for the same voxel within the right superior frontal gyrus, to investigate if the observed power decreases observed in the group SAM and SnPM analyses were indeed due to the happy faces condition, as indicated by average TFRs. In a Mann Whitney voxel by voxel comparison, happy faces

were included in the analysis as the active condition, and sad faces as passive condition, hence the spectral power observed in the sad faces condition was "subtracted" from that observed for the happy faces condition. The Mann Whitney TFRs generated for each individual were then averaged to obtain group TFRs (see **Figure6-11,** top row).

For the group TFR, the decreases in cortical oscillatory power are rather marked for the 0 to 400ms across the whole alpha range. For latencies of approximately 200ms to 380ms, power decreases are evident for 8 to10Hz frequencies; at latencies of approximately 50ms to 180ms decreases are more marked at somewhat higher frequencies, 10.5 to 12.5Hz. Between 200ms and 300ms decreases in cortical oscillatory power are also shown at frequencies of 11 to 13.5Hz. Although averaged (group) z-scores are low, individual z-scores indicate significant differences. TFR for two participants are illustrated **in Figure6-11**, see middle and bottom rows. For participant 1, the most prominent decreases in cortical oscillatory power are shown for latencies between 180ms and 400ms,with peak decreases evident at around 250ms, for frequencies of 8 to 11Hz (z-score = -2.0). For participant 2, decreases in cortical oscillatory power are seen at latencies of 50ms to 250ms, at frequencies of 9 to 11Hz (z-score = -2.5). Decreases in cortical oscillatory power are also evident at somewhat later latencies of 300ms to 400ms, for frequencies of 11 to 12.5Hz.

When comparing the average TFRs (see **Figure6-10**) to the Mann Whitney TFRs (see **Figure6-11**), the decreases in cortical oscillatory power observed in the averaged TFR for happy faces are also evident in the averaged Mann Whitney TFR. For higher alpha frequencies, 12 to 16Hz, the most notable decreases in signal power were observed for the average TFR for happy faces condition. In the Mann Whitney TFR these prominent decreases in cortical power can also be observed at somewhat lower frequencies from 11 to 14Hz.

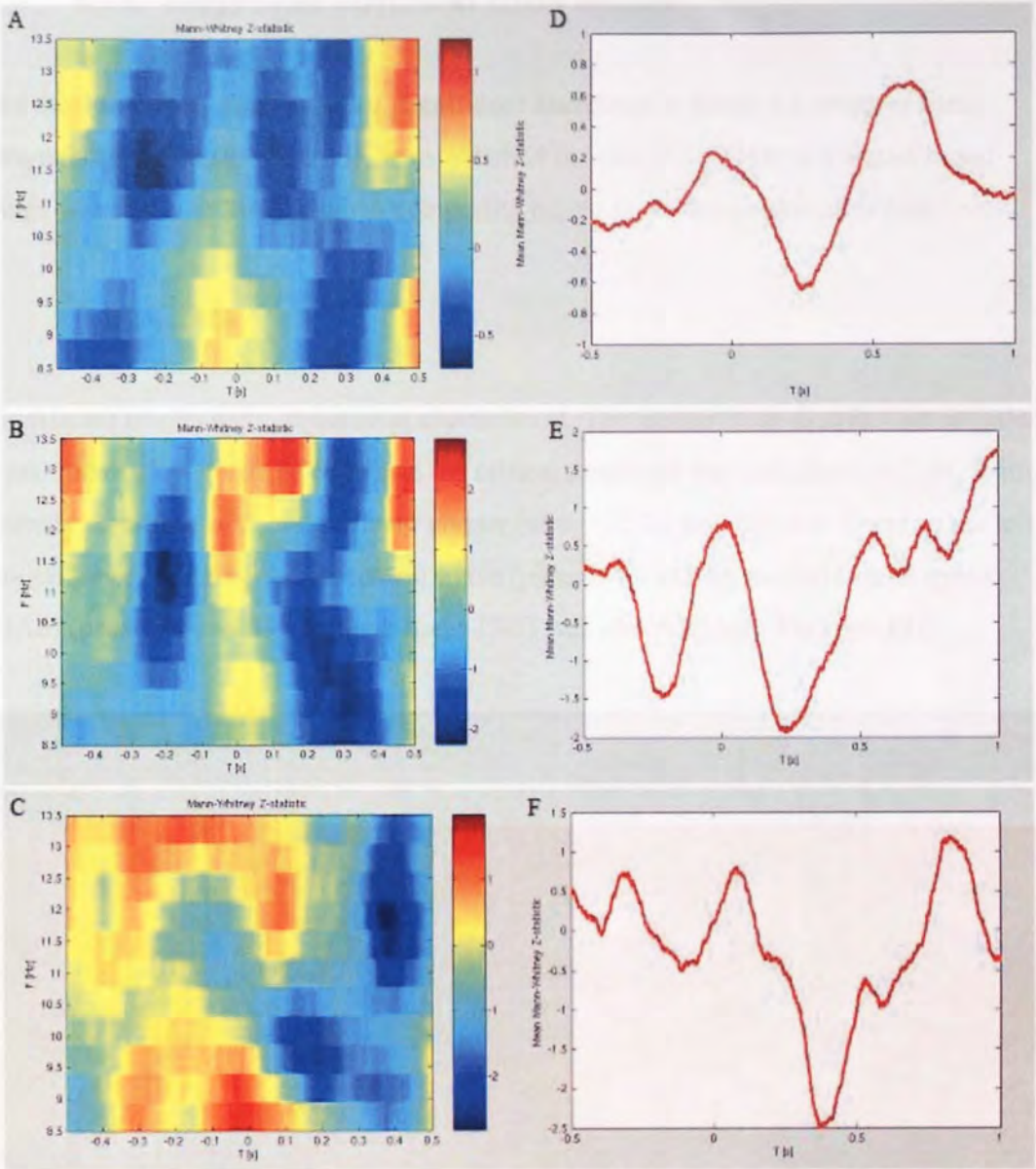


Figure6-11: Mann Whitney TFRs demonstrating differences for happy and sad face conditions. Figure shows the decreases in cortical oscillatory power for a voxel in the right superior frontal gyrus.

<u>Top Row:</u> group TFRs (*A*). Decreases evident at latencies of 100 to 300ms for 10-12Hz, and at 200 to 400ms for 8 to 10Hz.

<u>Middle and bottom row</u>: TFRs for individual participants (B, C).

***B*: the most prominent decreases in cortical oscillatory power can be seen in the later time-windows, 200 to 400ms, at frequencies of 9 to 11Hz.**

***C*: prominent decreases in cortical oscillatory power can be seen for two latencies of approximately 150ms and 400ms, at frequencies of 9 to 11Hz, and 11 to 13Hz, respectively.**

***D-E:* show power traces for 8-13Hz range. Time shown on x-axis, Mann Whitney z-scores on y-axis thus scale is not the same for each power trace.**

6.3.6. Happy facial expressions versus baseline

For the 0 to 200ms time-window, significant decreases in power i.e. event-related desynchronisation (ERD) could be established for beta (13-25Hz) and across broad range waveband of 5-40Hz when comparing happy faces to a prestimulus baseline.

6.3.6.1. Beta

Significant results were obtained at cluster level. The permutation distribution revealed a maximum cluster size of 6403 and the critical threshold was calculated at 5.04. With a primary threshold of 2, a significant cluster (size = 7242, $p<0.05$) was found in the left frontal lobe, including the precentral gyrus (pseudo-t = -4.66), medial frontal gyrus (BA6) (pseudo-t = -4.59). In these areas ERD was observed (see **Figure6-12**).

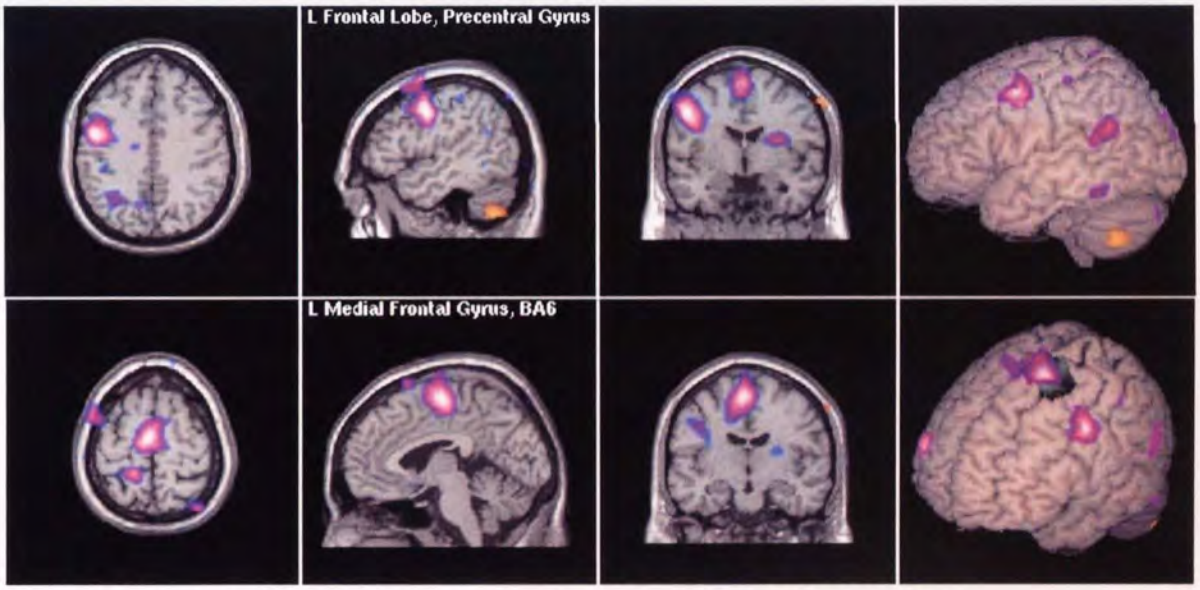


Figure6-12: Responses to happy expressions compared to baseline in 13-25Hz frequency band, for 0 to 200ms. SPMs show significant ERD in left frontal areas, left and precentral gyrus (top) and medial frontal gyrus, BA6 (bottom), displayed onto a template brain.

6.3.6.2. 5 to 40Hz

As before, significant ERD was obtained at cluster level. The permutation distribution revealed a maximum cluster size of 5054, and a critical calculated threshold of 4.99.

With a primary threshold of 2, a significant cluster (size = 5713, $p < 0.05$) was found in the right middle frontal gyrus (pseudo-t = -4.81) and in the left superior frontal gyrus (pseudo-t = -3.9) (see **Figure6-13**).

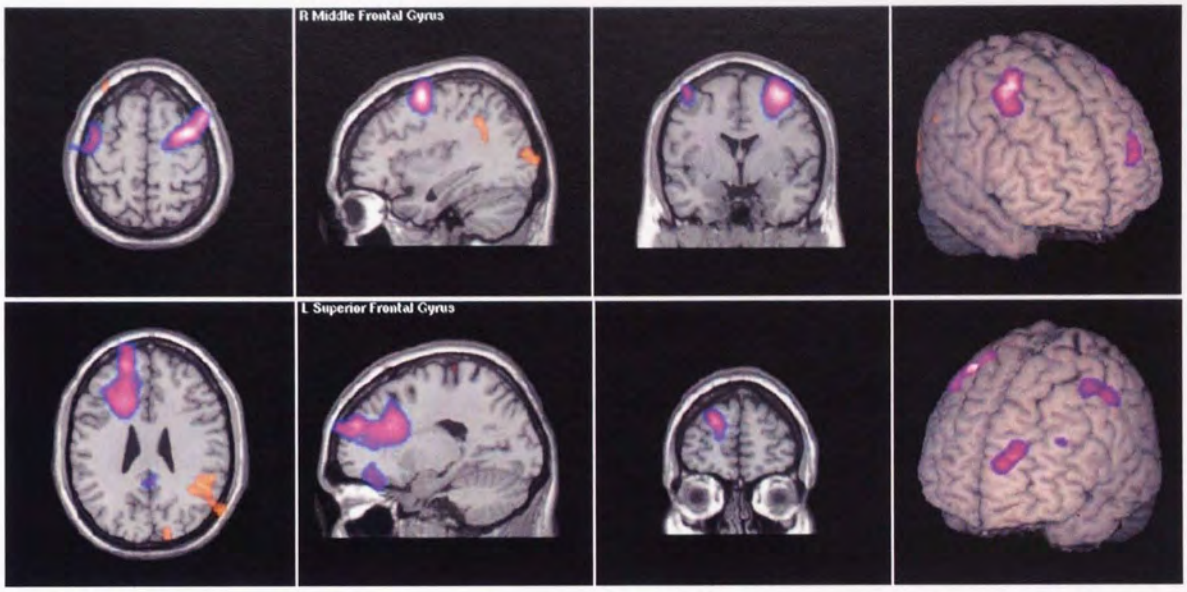


Figure6-13: Responses to happy expressions compared to baseline in frequency range of 5-40Hz, for 0 to 200ms. SPMs show significant ERD in the right middle frontal gyrus (top) and in the left superior frontal gyrus (bottom), displayed onto a template brain.

6.4. Discussion

6.4.1. Summary of results

Increases in cortical power were revealed within the 0 to 200ms time-window for bilateral occipital and right parietal areas for the processing of faces per se (see figures 6-2, 6-3 & 6-5). As before, changes in cortical oscillatory power within the shorter time window could be linked to alpha and broadband frequencies (5-40Hz). This substantiates the observations from the previous face processing chapters (see chapter 3 and 4).

In addition, the current investigation yielded results, which support the notion of the involvement of frontal areas in the processing of emotional facial expressions. Differential patterns of cortical oscillatory power were found for happy compared to sad faces within the longer 0 to 400ms time-window, at alpha frequency. Decreases in cortical oscillatory power within right frontal areas were observed (see figure 6-9). TFRs indicated that the decreases in event-related spectral power are due to the processing of happy (rather than sad faces) and most prominent decreases in cortical power were observed within 100 to 300ms at higher alpha frequencies (10-12Hz) and within 200 to 400ms for 8-13Hz. Hence, the processing of happy and sad faces is differentiable at latencies that are longer than those that categorise faces per se.

Comparing happy facial expressions to neutral ones revealed increases in cortical synchrony in the gamma frequency in right frontal areas (see figure 6-6), and the comparison of happy faces to a prestimulus baseline showed decreases in cortical oscillatory power in left frontal regions in beta and in right and left frontal regions across a wide frequency band of 5 to 40Hz (see figures 6-12 & 6-13), all within the 0 to 200ms time-window. No significant activation could be reported to the presentation of sad faces versus baseline, nor when comparing sad faces to neutral faces. This was also shown in the previous investigation (see chapter 5).

6.4.2. Interpretation of results

Findings from neuroimaging as well as neuropsychological studies repeatedly show that there is a right hemisphere bias, or dominance, for face processing (e.g. Gur, Skolnick & Gur 1994; Adolphs et al. 1996), which has also been shown in the previous investigations in this thesis. Additionally, the recognition of facial expressions is also

thought to rely on the right hemisphere more so than the left hemisphere (Suberi & McKeever 1977). In this study the right hemisphere was engaged to a greater extent, indicating its involvement extends to the processing of emotional expressions, regardless of their valence.

Damasio et al. (2000) stated that the orbital (frontal) cortex, mainly B11, is involved in so called "as-if-body loop" mechanisms, i.e. in situations during which emotions are (self) generated in the absence of a natural emotion-inducing event. This relates to the emotional contagion phenomenon (Wild et al. 2001). They reported activation within the frontal operculum (including inferior frontal gyrus and BA47), bilateral occipito-temporal areas and somatosensory cortex in response to happy faces. Thus, the presence of emotive faces might, to a similar extent, evoke a transient emotional state in the observer without the conscious attempt of inducing mood. Frontal differences were also observed in this study. Left frontal regions demonstrated greater ERD for happy versus baseline comparisons (see Fig. 6-12), and right frontal areas were involved in the processing of happy faces compared to neutral as well as sad ones. Differential involvement of occipito-temporal areas was not clearly demonstrated in this study. Neutral faces compared to baseline revealed activation within occipito-temporal areas only; yet, when contrasts between emotional expressions were assessed (e.g. happy versus neutral) no statistical differences could be reported.

6.4.2.1. Task demands

A memory component has to be considered when interpreting the current results. Participants were asked to indicate if the second face in a sequence was identical to the previously seen one. In order to do this, information regarding gender and facial expressions of the first face would need to be encoded (verbally) for subsequent retrieval. Hence, the engagement of numerous cognitive processes, e.g. knowledge retrieval, declarative memory, would indicate a test of higher cognitive functions rather than (low level) emotion processing. Thus, the involvement of the frontal areas might need to be considered also in relation to their role in tasks of working memory. In the previous studies, frontal involvement was observed in response to the presentations of faces (and control stimuli). Decreases in cortical power within left frontal regions were reported in chapter 3 (see figure 3-11) and chapter 4 (see figure 4-17) and have been linked to the performance of a working memory task. In response to facial expressions

in a passive viewing paradigm, left frontal areas showed decreases as well as increases in synchronous power for different comparisons (see chapter 5 figures 5-2 & 5-4). This observation at this stage leaves open the question of the frontal activation being primarily due to the emotional content of the stimulus or due to the task demands, and will be revisited in the general discussion.

Activation within the precentral areas including premotor areas and BA6 have been reported to unfamiliar versus familiar faces (e.g. Phillips et al. 1998b) and also to fearful and happy faces (e.g. Morris et al. 1996; Morris, Ohman & Dolan 1998). Wild et al. (2003) have argued that activation within precentral regions, which could also be regarded as premotor areas, might be interpreted in terms of preparation stages for facial reactions (to the facial expressions presented). In line with the "social display rules" (e.g. Ekman & Friesen 1969) it is established that in social situations or settings, a smiling face would be responded to with a smile and a sad face would be reciprocated by lowering the corners of ones mouth. Thus, Ekman & Friesen (1969) argued that these social display rules might have led to the recruitment of highly effective neural networks that initiate socially appropriate reactions. As it seems to be easier to reciprocate a smile than to sympathise with a sad face, these mechanisms might have evolved more distinctively for responding to happy facial expressions which could be a further reason for why it might be that cortical activity seems to be showing significant changes more readily in response to happy facial expressions than to sad ones.

Emotional processing is not a function per se; it is an integration of several sub-functions (Esslen et al. 2004), leading to what is known as an emotion (which can be seen as an evaluation strategy, therefore making it likely that several diverse and diffuse cortical and subcortical areas would be implicated in emotional processing). Results by Schweinberger et al. (2003) indicate that seeing a face during a learning task simultaneously activates many neurons in many different cortical areas, possibly representing different features of the face, such as gender or expression.

An association of parietal areas to motivational and emotional factors might explain parietal activation in response to neutral faces compared to baseline. Superior parietal areas have also been linked to spatial attention and feature binding (e.g. Wild et al. 2001) and Tovee (1998a) has claimed that it could be within this region that ambiguous images are assembled into coherent concepts. Thus, drawing together the information within the face to establish the emotional expression but also to allow keeping its representation in memory or comparing it to a stored representation of the

previous face could thus be related to the observed parietal activation. Schutter et al. (2001) showed a significant relationship between parietal EEG (beta) activity and attentional responses to angry faces. They linked their findings to the behavioural dimensions of approach and withdrawal, first established by Davidson (1992). A study by Lang, Bradley & Cuthbert 1998) also obtained activation within the parietal lobules when comparing emotional to neutral stimuli.

Amygdala activation was not demonstrated in this investigation. A possible reason for this could lie in the fact that the task employed involved an explicit face-processing task. Critchley et al. (2000) observed that explicit processing of facial expressions evoked increased BOLD signal in temporal regions, whereas amygdala activation was observed in response to an implicit processing task, such as gender discrimination. Thus, neuroanatomical dissociation between conscious and non-conscious processing of emotional facial expressions was suggested, with explicit processing evoking activity within the visual cortical areas (representing faces) and in posterior (hippocampal) regions, which are associated with declarative memory.

However, facial expression may be processed in an attention-independent implicit way, which does not rely on the detailed cortical representation of the face but implies limbic structures such as the amygdala and insula regions, or prefrontal cortex (Critchley et al. 2000). In addition, Gur, Skolnick & Gur (1994) stated that the involvement of the amygdala depends on the saliency of the affective component, and it is possible that the cognitive nature of the task has restricted the recruitment of subcortical structures implicated in emotional processing. In the previous task participants engaged more directly with the emotional content of the stimuli presented, which might have resulted in the observed activation of limbic structures.

6.4.2.2. Temporal considerations

Significant results in this study were reported for the shorter time-window of 200ms to a greater extent than for the longer time-window of 400ms for which significant cortical power changes could be observed in the happy versus sad face comparison.

As previously described (see section 6.1.1.2, also chapter 3), differential effects for the processing of happy and sad facial expressions have been reported at latencies shorter than 200ms. In this investigation, differential patterns of cortical oscillatory

power were observed at such latencies for happy compared to neutral faces and a prestimulus baseline (see figures 6-6 & 6-12). Differential changes in event-related spectral power for happy and sad facial expressions, however, were observed at latencies of 0 to 400ms (see figures 6-9 & 6-11).

It can therefore be substantiated that the categorization of a face takes place prior to the discrimination of internal facial features such as emotional expression. Hence this study seems to provide evidence for the Bruce & Young model, and is in line with EEG and ERP (e.g. Eimer 2000c; Schweinberger et al. 1999).

The differential processing of facial expressions of happiness and sadness was shown to take place at latencies between 100 and 400ms (see figure 6-11). This coincides with the observations by Esslen and colleagues who reported bilateral ventro-medial and orbito-frontal regions to be implicated in the processing of sad and happy faces at latencies of 240 to 400ms (Esslen et al 2004).

The processing of happy faces compared to neutral ones or baseline revealed significant changes in event-relates spectral power within the 0 to 200ms time-window, which was previously found also by e.g. Krolak-Salmon et al. (2001).

Thus, it seems that the processing of facial emotions is linked to a number of temporal components. The emergence of functional imaging studies with high temporal resolution and improved spatial resolution as in MEG will help in teasing apart the spatial and temporal dynamics associated with the processing of facial emotional expressions.

6.4.2.3. Frequency considerations

The extended frontal oscillations observed in the current investigation ranged across different frequency bands. Decreases in cortical synchrony were observed for alpha when contrasting happy and sad facial expressions. This can be regarded as providing support for the Davidson model of frontal asymmetry, as differential involvement of alpha was observed for happy versus sad facial expressions. The TFRs (see figure 6-11) indicate that greater decreases were observed for the happy face conditions in the right hemisphere, which again can be linked to the asymmetry model as no frontal alpha was reported for the left hemisphere. Additionally, the observation of decreased cortical power for a broadband frequency of 5-40Hz (thus incorporating alpha) in right frontal areas for happy versus baseline comparisons can be taken as

further support for the Davidson model. Here, TFRs would have been helpful to assess the role of frequencies. Furthermore, alpha blocking has been observed previously in tasks of behavioural or emotional arousal or during active task engagement (see Davidson 2001). Ray & Cole (1985a,b) linked task complexity to the involvement of alpha frequencies in parietal areas, which were reported in this investigation also (see figure 6-5). Therefore it remains to be seen whether the frontal involvements in this investigation are due to the emotional content of the stimuli or to the task that participants had to perform.

When comparing happy faces to a baseline, left frontal regions showed decreases in oscillatory power for beta (see figure 6-12). Beta increases in frontal areas were also shown in the previous investigation (see chapter 5) when contrasting happy to scrambled control images. Previous reports have linked beta frequencies to more general (rather than emotion-specific) arousal levels as right hemisphere beta failed to reach significance for emotions of happiness (Ahern & Schwartz 1985). However, as significant cortical power changes were observed in this investigation (and the previous one) for beta frequencies in response to happy faces, a possible role for beta in the processing of positive emotions (or particularly facial expression of happiness) is suggested.

As mentioned previously, activation in parietal areas was established for a rather wide frequency band of 5 to 40Hz for neutral faces versus baseline. This would lend support to the fact that parietal beta activation might be linked to task demand rather than emotion-specific processing. Schutter et al. (2001) obtained EEG beta activation within the parietal lobe. Therefore, the findings reported here could be linked to Schutter et al.'s investigation in terms of frequency specificity, as the beta frequencies (13 to 25 Hz) fall into the frequency range of 5 to 40Hz.

6.4.3. Methodological considerations

The stimulus presentation in this investigation was randomised in order to avoid carry-over effects. Presenting a whole block of facial expressions of sadness, or happiness, as was done in the previous experiment, might have lead to habituation. A study by Breiter et al. (1996), however, concluded that significant carry-over effects are rarely found in emotional experiments that involve the presentation of facial expressions (only).

In future investigations, however, slight changes to the methodology could ascertain that carry-over effects can be ruled out by increasing the delay between presentations of faces (increase ISI), including runs of neutral faces prior to presentation with emotional faces, using as control the average response to all neutral faces thus balancing out carry-over effects into the neutral condition (similar to what was done here).

In an investigation by Wild et al. (2003) the presentation of sad faces also did not yield any emotion-related activity. They argued that the stimuli they had used might not have been strong enough. As this is a second study which has failed to produce significant changes in response to sad (compared to baseline or neutral expressions) using two different stimuli set it is arguable whether a lack of activation is merely due to an inappropriate stimulus set, or whether there is something more inherent in the actual experience or recognition of facial expressions of sadness that leads to dissociation or to differential patterns of cortical activity associated with it (compared to the patterns of neural activity established in response to e.g. facial expressions of happiness). It has previously been argued (see chapter5) that the complexity associated with the emotion of sadness might have resulted in the lack of cortical power changes. Only within a longer time-window of 400ms could significant activation be reported when comparing happy to sad facial expressions. These were observed for the alpha frequency band, within right frontal regions, and might reflect the activation pattern of the happiness expression observed in the other comparisons. This possibility seems substantiated by the findings from TFRs.

The lack of significant findings to facial expression of sadness and the observation of Krolak–Salmon et al. (2001) regarding ERPs to emotional stimuli at latencies post 500ms might have rendered the stimulus presentation time as too short. However, findings of object recognition being remarkably fast and conscious awareness of visual stimuli taking place at 200 – 300ms (Treisman & Kanwisher 1998) suggests that a presentation duration of 500ms is long enough to allow assessment beyond that of feature identification. In addition, there are numerous studies that have identified that face recognition, and the recognition of facial expressions of emotions can take place within 500ms (e.g. Esslen et al. 2004; Pizzagalli et al. 2000; Werheid, Alpay, Jentzsch & Sommer 2005; Schutter, de Haan & van Honk 2004).

6.5. Conclusion

This investigation revealed a right hemisphere bias for face processing as has been established in previous face processing studies (e.g. Adolphs et al. 1996; Gur et al. 2002a), as well as in the previous investigations within this thesis. When comparisons were drawn between all faces regardless of their facial expressions, significant changes in ERS were revealed in the right and left hemispheres. However, the processing of emotional expressions also revealed a greater engagement of the right hemisphere. Thus, the current findings can be spatially related to those observed in investigations looking at the fMRI BOLD response, but do not necessarily confirm the observed left hemisphere bias for emotional processing (see section 6.1.1.1.).

In terms of temporal characteristics of facial emotional processing, the current investigation could substantiate some of the previous observations drawn mostly from EEG / ERP studies. The face specific ERP / MEG waveforms that have been observed to take place at latencies of approximately 155ms to 190ms (e.g. Jeffreys 1996; Liu et al. 2002) could be confirmed, as the perception of faces regardless of emotional expression yielded significant results in the 0 to 200ms time-window, indicating that within this latency window the processing of a stimulus as being a face can indeed be achieved. ERP studies investigating the processing of emotional expressions have associated early time segments also with the processing of facial expressions. Esslen et al. (2004), for instance, reported latencies of 138ms to 205ms for the processing of happy facial expressions. In this current investigation, contrasting happy with neutral expressions led to significant increases in cortical power associated with the processing of happy face within the 0 to 200ms time-window. Some discrepancies that have been observed for the processing of emotional versus neutral expressions, however, might be due to differences in the methodologies used, as here comparisons are made between evoked (ERP) and induced (MEG) responses.

The functional significance of frequency specific activation was also explored in this study. It was found that decreases in right frontal alpha could be observed when contrasting happy facial expressions to those of sadness. In previous investigations (e.g. Davidson 2001) happiness conditions were linked to less alpha power within left frontal regions. Comparing happy faces to baseline, however, revealed ERD within the left and right frontal regions, thus, bearing resemblance to the observations by Davidson 2001. Differences in the methodology, as well as the stimulus material used – verbal stimuli in the Davidson study – might have led to the greater engagement of left hemispheres,

whereas in this investigation the right hemisphere dominance for face processing needs to be taken into consideration.

Alternatively, Tomarken, Davidson & Henriques (1990) linked increase in frontal alpha to negative affective responses to emotional stimuli, thus the decrease in frontal alpha might hence be linked to positive affective responses to emotional stimuli, and the TFR (Figure6-5) indicated that the decreases in cortical oscillatory power were due to the pattern of activation in the happy face condition. Beta frequencies were engaged when processing happy faces compared to baseline, thus it could be assumed that the emotional expressions in this comparison can be seen as the more attention-arousing stimulus (see Rusovala & Kostiunina 2003).

In sum, the processing of facial emotional expressions can indeed be mapped in terms of spatial, temporal and frequency specific information, as this study was able to add temporal information as seen in EEG/ERP studies to the findings of similar neural correlates as were established in functional neuroimaging studies, and in addition explore the functional significance of specific frequency bands in relation to facial emotional expression.

Chapter 7 General Discussion

7.1. What do findings from MEG and SAM add to research on the processing of faces and facial affect?

In this thesis, the suitability of MEG in the processing of faces (chapter 3 and chapter 4) and for the processing of facial expressions of emotions (chapter 5 and chapter 6) was assessed. It was shown that MEG and indeed SAM are able to reproduce findings established with functional imaging techniques such as fMRI in the spatial domain, and, additionally, confirmed the findings from EEG and ERP studies regarding the temporal evolution of face processing and the processing of facial affect. Furthermore, insights were gained regarding the roles of specific frequency bands in the processing of faces and facial expressions. The findings reported are described in terms of either ERD or ERS. These are stimulus- or task-related changes in the ongoing cerebral rhythms (see also section 2.5). Their interpretation is influenced by the ongoing debate as to what ERD, ERS, increases or decreases in ERSP actually represent. According to the traditional belief, (increase in) alpha synchronisation is thought to reflect cortical "idling" (Pfurtscheller et al. 1996a). However, event-related changes in alpha band power have been associated with active information processing (see Klimesch et al. 1999), and Klimesch et al. (2000) showed that in a recognition memory task alpha synchronisation within parieto-occipital areas co-occurred with induced alpha activity showing widespread desynchronisation. Hence, we cannot assign either of these phenomena to being associated with only inhibition or only (active) processing (see also section 7.2.1).

In order to compare findings from fMRI to those derived in MEG studies, the focus so far, has been on fMRI BOLD responses and MEG 'evoked responses'. Singh et al. (2002) demonstrated the correspondence of ERD & positive BOLD effects for cognitive paradigms, and it is suggested that if oscillatory effects correspond to changes in the overall level of activity altered metabolic needs and therefore BOLD responses would be shown (Brookes et al. 2005). If, however, ERD and ERS primarily represent desynchronisation & synchronisation without changes in neuronal firing rates, then they could be fMRI silent. In either case, these neuronal responses would, and should alter the metabolic state thus giving rise to BOLD effects. Using the same simple visual paradigm in an MEG and an fMRI investigation, Brookes et al. (2005) reported alpha ERD, gamma ERS and BOLD signals within the same areas of the visual cortex. Given

that observed increases and decreases in ERSP represent deviations from the natural resting state of the cortex, it could be assumed that the neuromagnetic effects indeed present potential contributors to / for the BOLD effect.

7.1.1. Spatial correlates of face processing

7.1.1.1. Activation of face-specific areas and implication for models and theories of face processing

This thesis showed that face-specific region i.e. temporo-occipitial areas, including the fusiform and lingual gyri, middle occipital gyri as well as superior and middle temporal gyri are implicated in the processing of faces (chapters 3 & 4) and facial expressions (see chapter 5). Although activation within the fusiform gyrus was not observed in every single experiment in this thesis to significance at group level, it was found at individual levels, and also in group analyses at sub-threshold level. This might have been due to the type of task employed. It has been shown that the involvement of the fusiform gyri is found more consistently in tasks involving face identity, rather than in studies incorporating the processing of facial affect. The paradigms in this thesis required additional cognitive processes, and therefore the involvement of the fusiform face areas might have been overridden by structures more involved in cognitive processes, such as memory.

Despite the apparent lack of fusiform involvement in the responses to face processing paradigms, the somewhat differential involvement of extrastriate visual areas for faces compared to houses, inverted faces and other control images would none the less suggest that there are indeed neural substrates that selectively process faces. These might not necessarily be located within one particular area; hence the concept of a fusiform face area being selectively responsive to faces was not fully supported by the studies in this thesis. Direct replication of studies that have identified the FFA in fMRI and MEG however, were not included.

Support for face-specific regions has led to the confirmation of there being more specialised but also more segregated areas, which are thought to be due to the different recognition goals associated with the processing of faces (rather than the processing of houses, scrambled images or inverted faces). The additional recruitment of, for instance, temporal and frontal areas, however, might also be linked to the increase in complexity when processing, for instance, inverted faces.

The observation of the involvement of middle and inferior occipital gyri seem to be in line with the distributed neural system model proposed by Haxby et al. (2000a). Spectral power changes within these regions within the 0 to 200ms time-window would correspond to the proposed role of the occipital gyri in the initial or early perceptual processes. The proposed subsequent involvement of the STS for the processing of facial affect, and the apparent lack of cortical power changes observed within this area in studies 3 & 4 (see chapter 5 & 6) might have been due to stimulus characteristics, as was predicted that the intensity of the emotion presented would impact on the level of cortical power changes observed. The emotional expressions used in these investigations were of moderate intensity.

7.1.1.2. Activation of parietal and frontal areas

The extended involvement of parietal areas and of frontal regions in this series of investigations would substantiate the claim that parietal areas are implicated in memory processes, as their involvement has been reported in studies using N-back memory tasks (Jansma et al. 2000; Krause et al 2000; Rämä et al. 2001; Zurowski et al. 2002). In order to store, retrieve and subsequently match two images, working memory and short-term memory processes needed to be recruited, and therefore the involvement of purely face-specific areas might have been diminished. Alternatively, the decisions as to whether the image presented matched the previous one might have been reached by considering features other than the face-specific aspects of the stimuli, such as general shape.

Parietal areas have been implicated in the processing of emotional and motivational aspects, as well as in spatial feature binding, i.e. in turning an ambiguous figure into a coherent concept (e.g. Tovee 1998a). This is confirmed by evidence of the recruitment of parietal areas observed in studies 1 & 2 (see chapter 3 & 4).

7.1.2. Spatial correlates of facial affect – findings and implications

7.1.2.1. Frontal areas

The processing of facial expressions of emotions was associated with increases in event-related spectral power in left and right frontal areas as well as with parietal areas and limbic regions, e.g. parahippocampal gyrus and the amygdala (see chapter 5

and 6). The involvement of frontal regions has been linked to emotional contagion phenomena (Wild et al. 2001) as well as to the possibility of transient emotional states, whereas premotor and parietal areas have been linked to preparatory processes for 'facial reactions'. According to the social display rules (Ekman & Friesen 1969), it would be regarded as much easier to reciprocate a smile than to react sympathetically to a sad face. Therefore, it could be assumed that the evolution of mechanisms processing happy faces might be somewhat more advanced than the mechanisms processing emotions like sadness. This is in line with the suggestion that the survival relevant functions of emotions like fear and disgust seem to possess a higher salience, and structures like the amygdala are proposed to implement a rapid response 'fear-module'.

Maybe the processing of positive emotions such as facial expressions of happiness could be linked to a mood enhancing status, and, therefore, the evolution of relevant processing mechanisms have become more adaptive than mechanisms involved in the processing of sadness, or negative emotions more generally. In fact, differences in the processing of facial expressions in patients with major depressive disorders (who would be assumed to have a less well-adapted neural system for the processing of negative (facial) emotions) and healthy controls have been observed (e.g. Lawrence et al. 2004; Surguladze et al. 2004; Phillips et al. 2003a, 2003b). Differential processing patterns for healthy and patient populations have been reported within the dorsal and ventral prefrontal cortices with increases in activity in ventrolateral prefrontal cortex being linked to the experience of major depressive episodes, and decreases in activity within the dorsolateral prefrontal cortex which is associated with emotion regulation (Phillips et al. 2003a, 2003b) (see also Chapter 1, section 1.4.3.1.).

Such differential 'adaptation' of brain systems involved in the processing of positive and negative emotions might also be linked to the lack of activation observed when processing facial expressions of sadness in this investigation (as well as in studies showing such lack of significant activity with healthy populations (e.g. Wild et al. 2001, Phillips et al. 1998a). This aspect could be further investigated by looking at the differences in the processing of emotive stimuli related to happiness and sadness, yet avoiding complex cognitive components, such as the memory tasks might have provided here. It would be possible to include physiological measurements such as heart rate or galvanic skin response, as well as measures of psychological well being (e.g. Hospital Anxiety & Depression Scale (HADS) (Zigmond & Snaith 1983), Beck Depression Inventory (BDI), Beck et al. 1961).

7.1.2.2. Limbic structures

The differential involvement of left and right limbic structures (i.e. amygdala and parahippocampal gyrus) provided an interesting and intriguing finding. Asymmetric signal changes in amygdala activity have been observed (e.g. Gur, Skolnick & Gur 1994). The observation of increases in event-related spectral power within one hemisphere, but decreases in event-related power (at similar latencies and frequencies) in the other hemisphere warrants further investigations, as well as highlights the issue as to what exactly phenomena such as ERS and ERD can tell us about neural dynamics.

The failure to replicate this finding in experiment 4 (see chapter 6) has been explained in terms of methodological differences between the two studies. In experiment 3 (chapter 5) emotional stimuli were presented and viewed in a block-design, emotional stimuli were presented for six seconds and participants had to actively engage in the emotional content of the picture by providing (silent) ratings. Experiment 4 (chapter 6), however, employed a random display of emotional and neutral faces presented for 200ms, and a one-back memory task. Thus, it could be argued that the lack of subcortical (limbic) activation in chapter 6 was due to the task demand.

In sum, spatial correlates for the processing of faces, houses, inverted faces and scrambled control images as well as facial expressions of emotions yielded findings similar to those established with fMRI and in EEG studies using source localisation techniques.

7.1.3. Temporal characteristics of face processing and facial affect

The investigation of the temporal dynamics for the processing of faces and facial affect has aimed to confirm the occurrence of the face specific N170, as well as the effects of facial affect upon it. Face-specific ERP and MEG waveforms have been identified at latencies of 155 to 190ms (e.g. Eimer 2000a, 2000b, Schweinberger et al. 2002). In an MEG investigation, the successful categorisation of faces has been linked to a M110 component, whereas the successful identification of a face has yielded the specific M170 component (Liu, Harris & Kanwisher 2002). Face-specific changes in cortical oscillatory power could be reported within the 0 to 200ms time-window (see chapters 3

to 6), hence confirming above findings. TFRs indicate face-specific increases in event-related spectral powers occurring at 150ms to 250ms (e.g. chapter 3).

The processing of facial expressions of emotions has mostly been linked to somewhat longer latencies between 250ms and 550ms (e.g. Krolak-Salmon et al. 2001) and 300ms to 700ms (e.g. Kestenbaum & Nelson 1992). The processing of facial affect in the current series could to some extent confirm these previous findings. The processing of happy faces was associated with changes in cortical oscillatory power within the 0 to 200ms time-window, whereas the processing of happy compared to sad faces yielded significant results in the 0 to 400ms time-window. It could thus be established that the processing of facial affect is linked to numerous temporal components, and it was shown that MEG and SAM prove useful techniques indeed for teasing apart the spatial and temporal dynamics of face processing as well as for the processing of facial emotions.

The observation of face-specific processing taking part within a shorter time window than the processing of facial affect seems to confirm the functional model of face recognition by Bruce & Young (1986). This states that the face needs to be identified as such first, before (other) face relevant information, e.g. gender, age, facial expression, can be derived. Thus, only subsequent to the initial face classification at latencies of 150ms to 200/250ms (see chapter 3 and 6) (or as indexed by face-specific N170 in ERPs) can the processing of facial emotion take place, e.g. at latencies of 300 to 400ms (see chapter 5 and 6).

As mentioned before, Haxby et al. (2000a) ascribed the inferior occipital gyrus the role of an initial processing module. Involvement of occipital areas (inferior and lingual gyri) has been observed, within 0 to 200ms. This could possibly be regarded as some indication for the role of the occipital areas in the initial stages of face categorisation.

7.1.4. Frequency-specific changes in event-related spectral power for faces and facial affect

There is relatively little evidence of frequency-specific characteristics of face processing and for the processing of facial expressions. The perception of ambiguous figures, such as Mooney faces has revealed fronto-parietal gamma synchronisation at latencies of 200 to 350ms (Rodriguez et al. 1999). Tallon-Baudry et al. (1995, 1996) have shown that

the perception of coherence in stimulus arrangements is associated with increased synchronisation of the visual cortices, and Engel et al. (1997) concluded that synchronisation phenomena relevant for neural processing seem to occur particularly in gamma frequencies. Evidence linking emotional processing to alpha (Ray & Cole 1985a, 1985b) and beta (Rusalova & Kostiunina 2003) frequencies had been reported.

The ability of MEG (and SAM) to measure stimulus-specific changes in event-related spectral power for different frequency bands allowed further investigation of these observations. Face processing per se was linked to changes in cortical power within frontal areas for beta, and within more face-specific areas for gamma (see chapter 3 and 4). The processing of facial affect, on the other hand, revealed activation for alpha, beta and gamma frequencies (see chapter 5 and 6).

Extended frontal oscillations were observed for alpha and beta frequencies, and alpha frequencies were also noticed for parietal areas. Alpha frequencies have been linked to specific cognitive processes, such as memory functions (e.g. Klimesch 1997). For alpha, increases in cortical oscillatory power were observed when contrasting happy faces with scrambled control images, whereas decreases in cortical oscillatory power were observed when contrasting happy and sad facial expressions. The former could be linked to the observation of increased synchrony for alpha frequencies in successful task performances, the latter to attentional efforts or arousal. Decreases in event-related spectral power have been associated with increases in the BOLD signal (e.g. Singh et al. 2002), whereas increases in alpha synchrony have previously been linked to 'cortical idling' (Pfurtscheller et al. 1996a) (see also section 7.2.1 this chapter; section 2.5.1 chapter 2).

Beta frequencies have been linked to specific task related processing, and increases in beta band activity within parietal areas have been observed when processing angry compared to neutral emotions (Schutter et al. 2001). Schutter et al. linked their observation of parietal beta in response to angry facial expressions to the approach-avoidance domains established by Davidson (1992). Anger would be regarded as approach behaviour and therefore the involvement of beta frequencies might be linked to approach behaviours in general. In the current investigation, parietal beta activation was reported in response to neutral faces, thus leaving open the association of approach-related emotions and beta involvement.

Gamma has been associated with the integration of functionally discrete activations as well as with internal representations in perception and memory (Tallon-

Baudry et al. 1997). This "binding" phenomenon (i.e. the merging of separate features into a single percept) is associated with coherent gamma band activity across the cortical areas involved, and 'bursts' of gamma increases have been reported in response to successful perception of ambiguous percepts (e.g. Tallon-Baudry et al 1997; Rodriguez et al. 1999; Singer et al. 1990).

7.2. Suitability of MEG for the processing of face and facial affect

As outlined above, the application of MEG and SAM revealed the involvement of distinct cortical areas and networks in the processing of faces and facial affect, their temporal characteristics and frequency specificities.

The observation of different cortical power changes (i.e. increases and decreases occurring simultaneously, or within one frequency band for different comparisons) in relation to the processing of faces and emotional expressions compared to control stimuli is intriguing.

7.2.1. Debate surrounding ERD and ERS

The debate as to what precisely the increases and decreases in event-related spectral power changes represent, and how they can be linked, or contrasted, to the BOLD response remains. Initially (as previously mentioned, see 7.1.4.) increases in the BOLD signal were linked to decreases in event-related spectral power, whereas increases in even-related synchronisation at, for instance, alpha frequencies, were related to cortical idling. As shown in this thesis, increases and decreases in event-related spectral power can co-occur, and given the findings in chapter 3, increases in cortical power can dominate the signal changes. Assuming that throughout the whole experiment the brain had been idling, however, would prove nonsensical. Neuper & Pfurtscheller (2001) observed increases in cortical oscillatory power as well as decreases within the same frequency band. They concluded that the simultaneous observation of ERD and ERS for specific frequency components reflects the activation as well as deactivation (or inhibition) of cortical neuronal networks under certain circumstances. Thus, changes in cortical oscillatory power not only reflect cortical activation related to increases in energy demands (also expressed in enhanced blood flow or enhanced glucose metabolism), but also processes of selective inhibition of

those networks not specifically involved in the associated neural processes (Neuper & Pfurtscheller 2001).

Alternatively, the concurrent observation of ERS and ERD has also been observed by Rodriguez et al. (1999). Here, increases in cortical synchronisation in response to the perception of an ambiguous figure were followed by a period of desynchronisation thought to reflect the generation of a new dynamic neuronal ensemble and thus a new cognitive state. In terms of temporal characteristics this observation seems able to provide an explanation as the increases in synchrony, for instance, for happy expressions were observed within the earlier time-window, and the decreases in spectral power within the later time-window (see chapter 6, sections 6.3.4. and 6.3.5.). However, the current investigations and those by Rodriguez et al. (1999) still represent different stimulus comparisons, and were observed at different frequencies. Here alpha instead of gamma frequencies as in the Rodriguez et al. (1999) study were observed.

Therefore, in order to complement information that can be obtained (or has already been obtained) separately in fMRI and MEG studies, it is important to look at how MEG responses, i.e. increases and decreases in event-related spectral power can be compared to the BOLD signal. Direct comparative studies using the same experimental paradigms and populations should be conducted with fMRI and MEG to highlight the nature of the relationship between the BOLD response and event-related spectral power changes. In addition, the use of spatial information from fMRI investigations can validate the spatial assumptions that have been used to solve the inverse solution in MEG investigations.

In sum, the debate surrounding the relationship between the event-related spectral power changes, ERD or ERS and the BOLD signal highlights the need to establish and investigate brain dynamics in a four-dimensional fashion, rather than looking at spatial, temporal and frequency correlates in isolation. As has been shown here, MEG and SAM are able to integrate space, frequency and time, thus allowing the research into the processing of faces and facial affect to be taken beyond the localisation of areas associated with it.

7.2.2 *Methodological considerations when comparing findings from different functional methodologies*

The discrepancies observed between spatial correlates as established in fMRI and EEG / ERP to those reported here are thought to be due to differences in methodology as well as analyses procedures. In fMRI results are often based on region of interest approaches and the involvement of brain areas other than those specified can be overlooked. EEG methodologies have so far been associated with relatively low spatial resolution, which is due to the recording of fewer electrode sites and the use of less precise source localisation techniques. In addition, in EEG studies, signal averaging is used and approaches such as MNLS approaches (see section 2.3.2.1 and 2.4.1) differ from the beamforming approaches in their reliance upon phase-locked stimuli, the use of a priori assumptions and signal source projections.

7.3. Conclusions

Cognitive and emotional processes are characterised by the functional integration of many specialised brain areas, and the studying of event-related brain dynamics would therefore offer a more refined picture of the brain processes underlying such processes. Advanced imaging techniques such as MEG and analyses methods such as SAM begin to show the underlying neural correlates of such integrations. Changes in event-related spectral power will have to be considered as the critical link between the haemodynamic response (fMRI) and temporal dynamics underlying neuronal activity (e.g. Murray et al. 2002). Additionally, growing evidence exists regarding the interactions between event-related neural responses (as indexed by the ERPs) and ongoing brain oscillations (e.g. Fries et al. 2001). Thus, the investigation of neural correlates of face processing and the processing of facial affect using different methodologies (as indicated above, section 7. 2.1) would enhance our understanding of these processes. Several issues have arisen when considering the findings within this thesis - such as the effects of varying the cognitive load in tasks on face perception- and these would need to be addressed in further studies of face processing. Incorporating stimulus materials that have shown to evoke responses persistently within specific areas and using identical paradigms in fMRI (for spatial domain), EEG (temporal domain) and MEG to verify space, time and

frequency would allow an even more precise prediction of neural correlates for face perception and the perception of facial affect.

References

Adolphs, R. 1999a, "Social cognition and the human brain.", *Trends in Cognitive Sciences*, vol. 3, no. 12, pp. 469-479.

Adolphs, R. 1999b, "The human amygdala and emotion.", *Neuroscientist*, vol. 5, no. 2, pp. 125-137.

Adolphs, R. 2001, "The neurobiology of social cognition.", Current *Opinion in Neurobiology*, vol. 11, no. 2, pp. 231-239.

Adolphs, R. 2002, "Neural systems for recognizing emotion.", *Current Opinion in Neurobiology*, vol. 12, no. 2, pp. 169-177.

Adolphs, R. 2003, "Is the human amygdala specialized for processing social information?", *Amygdala in Brain Function: Basic and Clinical Approaches*, vol. 985, pp. 326-340.

Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. R. 1994, "Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala.", *Nature*, vol. 372, no. 6507, pp. 669-672.

Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. R. 1995, "Fear and the human amygdala.", *Journal of Neuroscience*, vol. 15, no. 9, pp. 5879-5891.

Adolphs, R., Damasio, H., Tranel, D., & Damasio, A. R. 1996, "Cortical systems for the recognition of emotion in facial expressions.", *Journal of Neuroscience*, vol. 16, no. 23, pp. 7678-7687.

Adolphs, R., Tranel, D., & Damasio, A. R. 1998, "The human amygdala in social judgment.", *Nature*, vol. 393, no. 6684, pp. 470-474.

Adolphs, R. & Tranel, D. 1999, "Preferences for visual stimuli following amygdala damage.", *Journal of Cognitive Neuroscience*, vol. 11, no. 6, pp. 610-616.

Adolphs, R., Russell, J. A., & Tranel, D. 1999, "A role for the human amygdala in recognizing emotional arousal from unpleasant stimuli." *Psychological Science*, vol. 10, no. 2, pp. 167-171.

Adolphs, R., Tranel, D., Hamann, S., Young, A. W., Calder, A. J., Phelps, E. A., Anderson, A., Lee, G. P., & Damasio, A. R. 1999, "Recognition of facial emotion in nine individuals with bilateral amygdala damage." *Neuropsychologia*, vol. 37, no. 10, pp. 1111-1117.

Adolphs, R., Damasio, H., Tranel, D., Cooper, G., & Damasio, A. R. 2000, "A role for somatosensory cortices in the visual recognition of emotion as revealed by three-dimensional lesion mapping." *Journal of Neuroscience*, vol. 20, no. 7, pp. 2683-2690.

Adolphs, R., Jansari, A., & Tranel, D. 2001, "Hemispheric Perception of Emotional Valence From Facial Expressions." *Neuropsychology*, vol. 15, no. 4, pp. 516-524.

Adolphs, R., Tranel, D., & Damasio, A. R. 2003, "Dissociable neural systems for recognizing emotions." *Brain and Cognition*, vol. 52, no. 1, pp. 61-69.

Aggleton, J. P. 1992, "The functional effects of amygdala lesion in humans, a comparison with findings in monkeys." in *The amygdala.*, J.P. Aggleton, ed., Wiley-Liss, New York, pp. 485-503.

Aguirre, G. K. 1999, "Face Recognition Turned Upside-Down.", *Neuron*, vol. 22, no. 1, pp. 5-6

Aguirre, G. K., Zarahn, E., & D'Esposito, M. 1998, "An Area within Human Ventral Cortex Sensitive to "Building" Stimuli: Evidence and Implications.", *Neuron*, vol. 21, no. 2, pp. 373-383.

Aguirre, G. K., Singh, R., & D'Esposito, M. 1999, "Stimulus inversion and the responses of face and object-sensitive cortical areas.", *Neuroreport*, vol. 10, no. 1, pp. 189-194.

Aharon, I., Etcoff, N., Ariely, D., Chabris, C. F., O'Connor, E., & Breiter, H. C. 2001, "Beautiful Faces Have Variable Reward Value: fMRI and Behavioural Evidence.", *Neuron*, vol. 32, no. 3, pp. 537-551.

Ahern, G.L. & Schwartz, G.E. 1985, "Differential lateralisation for positive and negative emotion in the brain: EEG spectral analysis." *Neuropsychologia*, vol. 23, no. 6, pp. 745-755

Aine, C. J., George, J., Medvick, P., Supek, S., Flynn, E., & Bodis-Wollner, I. 1989, "Identification of multiple sources in transient visual evoked neuromagnetic responses." in *Advances in Biomagnetism*, S. J. Williamson et al., eds., Plenum Press, New York.

Aine, C. J. 1995, "A conceptual overview and critique of functional neuroimaging techniques in humans: I. MRI/fMRI and PET.", *Critical Review of Neurobiology*, vol. 9, no. 2-3, pp. 229-309.

Allison, T., McCarthy, G., & Spencer, D. D. 1993, "Localization of the face area of human sensorimotor cortex by intracranial recording of somatosensory evoked potentials.", *Electroencephalography and Clinical Neurophysiology*, vol. 87, no. 2, p. S88-S89.

Allison, T., McCarthy, G., Nobre, A., Puce, A., & Belger, A. 1994, "Human extrastriate visual cortex and the perception of faces, words, numbers, and colours.", *Cerebral Cortex*, vol. 4, no. 5, pp. 544-554.

Allison, T., Puce, A., Spencer, D. D., & McCarthy, G. 1999, "Electrophysiological studies of human face perception. I: Potentials generated in occipitotemporal cortex by face and non-face stimuli.", *Cerebral Cortex*, vol. 9, no. 5, pp. 415-430.

Allison, T., Puce, A., & McCarthy, G. 2000, "Social perception from visual cues: role of the STS region.", *Trends in Cognitive Sciences*, vol. 4, no. 7, pp. 267-278.

Amaral, D. G., Price, J. L., Pitkanen, A., & Carmichael, S. T. 1992, "Anatomical organisation of the primate amygdaloid complex." in *The amygdala.*, J.P. Aggleton, ed., Wiley-Liss, New York, pp. 1-66.

Amaral, D. G. 2002, "The primate amygdala and the neurobiology of social behaviour: Implications for understanding social anxiety.", *Biological Psychiatry*, vol. 51, no. 1, pp. 11-17.

Anderson, A. K., Spencer, D. D., Fulbright, R. K., & Phelps, E. A. 2000a, "Contribution of the anteromedial temporal lobes to the evaluation of facial emotion.", *Neuropsychology*, vol. 14, no. 4, pp. 526-536.

Anderson, A. K. & Phelps, E. A. 2000b, "Expression without recognition: contributions of the human amygdala to emotional communication.", *Psychological Science: a Journal Of The American Psychological Society / APS*, vol. 11, no. 2, pp. 106-111.

Ashburner, J. & Friston, K.J. 2001, "Why voxel-based morphometry should be used." *Neuroimage*, vol. 14 no. 6 pp. 1238-43.

Baddeley, A. 1988, "Cognitive psychology and human memory.", *Trends in Neurosciences*, vol. 11, no. 4, pp. 176-181.

Baddeley, A. 1996 "The fractionation of working memory." *Proceedings of the National Academy of Sciences of the United States of America,* vol. 93, no. 24, pp. 13468-13472

Baddeley, A. 1998, "Recent developments in working memory.", *Current Opinion in Neurobiology*, vol. 8, no. 2, pp. 234-238.

Baddeley, A. & Wilson, B. 1988, "Comprehension and working memory: A single case neuropsychological study.", *Journal of Memory and Language*, vol. 27, no. 5, pp. 479-498.

Baddeley, A. & Della Salla, S. 1996 "Working memory and executive control." *Philosophical Transactions of the Royal Society of London. Series B - Biological Sciences*, vol. 351, no. 1346, pp. 1397-1403

Baillet, S., Mosher, J. C., & Leahy, R. M. 2001, "Electromagnetic Brain Mapping.", *IEEE Signal Processing Magazine* pp. 14-30.

Bar, M., Dale, A. M., Tootell, R. B. H., Schacter, D., Rabbel, C., & Halgren, E. 2000, "Cortical mechanisms and dynamics specific to conscious object recognition.", *NeuroImage*, vol. 11, no. 5, Supplement 1, p. S685.

Barrera, M. E. & Maurer, D. 1981, "The perception of facial expressions by the three-month-old.", *Child Development*, vol. 52, no. 1, pp. 203-206.

Bartels, A. & Zeki, S. 2004, "The chronoarchitecture of the human brain--natural viewing conditions reveal a time-based anatomy of the brain.", *NeuroImage*, vol. 22, no. 1, pp. 419-433.

Basar E, Basar-Erogul C, Karakas S, Schürmann M. 2001, "Gamma, alpha, delta, and theta oscillations govern cognitive processes." *International Journal of Psychophysiology*, vol. 39 no. 2-3 pp. 241-8.

Bauer, R. M. 1984, "Autonomic recognition of names and faces in prosopagnosia: a neuropsychological application of the Guilty Knowledge Test.", *Neuropsychologia*, vol. 22, no. 4, pp. 457-469.

Bauer, R. M. & Verfaellie, M. 1988, "Electrodermal discrimination of familiar but not unfamiliar faces in prosopagnosia.", *Brain and Cognition*, vol. 8, no. 2, pp. 240-252.

Baylis, G. C., Rolls, E. T., & Leonard, C. M. 1987, "Functional subdivision of temporal lobe neocortex.", *Journal of Neuroscience*, vol. 7, pp. 330-342.

Bear, D.M. 1983, "Hemispheric specialisation and the neurology of emotion." *Archives of Neurology*, vol. 40, pp. 195-202

Beck, A.T., Ward, C.H., Mendelson, M., Mock, J. & Erbaugh, J. 1961, "An inventory for measuring depression. *Archives of General Psychiatry*, vol. 4, pp. 561-571

Bentin, S. & McCarthy, G. 1994, "The Effects of Immediate Stimulus Repetition on Reaction Time and Event-Related Potentials in Tasks of Different Complexity.", *Journal of Experimental Psychology: Learning, Memory, and Cognition*, vol. 20, no. 1, pp. 130-149.

Bentin, S. & Ibrahim, R. 1996, "New evidence for phonological processing during visual word recognition: the case of Arabic.", *Journal of Experimental Psychology: Learning, Memory, and Cognition*, vol. 22, no. 2, pp. 309-323.

Bentin, S. & Deouell, L. 2000, "Face detection and face identification: ERP evidence for separate mechanisms." *Journal of Cognitive Neuropsychology*, vol. 17, pp. 35-54

Bentin, S. & Golland, Y. 2002, "Meaningful processing of meaningless stimuli: The influence of perceptual experience on early visual processing of faces.", *Cognition*, vol. 86, no. 1, p. B1-B14.

Bentin, S. & Carmel, D. 2002, "Accounts for the N170 face-effect: a reply to Rossion, Curran, & Gauthier.", *Cognition*, vol. 85, no. 2, pp. 197-202.

Bentin, S., Moscovitch, M., & Nirhod, O. 1998, "Levels of processing and selective attention effects on encoding in memory.", *Acta Psychologica*, vol. 98, no. 2-3, pp. 311-341.

Berkhout, J., Walter, D.O. & Adey, W.R. 1969, "Alterations of the human electroencephalogram induced by stressful verbal activity.", *Electroencephalography and Clinical Neurophysiology*, vol. 31, no.2, pp. 157-165

Blair, R. J., Jones, L., Clark, F., & Smith, M. 1997, "The psychopathic individual: a lack of responsiveness to distress cues?", *Psychophysiology*, vol. 34, no. 2, pp. 192-198.

Blair, R. J., Morris, J. S., Frith, C. D., Perrett, D. I., & Dolan, R. J. 1999, "Dissociable neural responses to facial expressions of sadness and anger.", *Brain*, vol. 122, no. 5, pp. 883-893.

Blair, R. J. R., Mitchell, D. G. V., Peschardt, K. S., Colledge, E., Leonard, R. A., Shine, J. H., Murray, L. K., & Perrett, D. I. 2004, "Reduced sensitivity to others' fearful

expressions in psychopathic individuals.", *Personality and Individual Differences*, vol. 37, no. 6, pp. 1111-1122.

Blonder, L. X., Smith, C. D., Davis, C. E., West, M. L., Garrity, T. F., Avison, M. J., & Andersen, A. H. 2004, "Regional brain response to faces of humans and dogs.", *Cognitive Brain Research*, vol. 20, no. 3, pp. 384-394.

Bodamer, J. 1947, "Die Prosopagnosie.", *Archiv fuer Psychiatrie und Nervenkrakheiten*, vol. 179, pp. 6-53.

Borod, J. C., Koff, E., Perlman Lorch, M., & Nicholas, M. 1986, "The expression and perception of facial emotion in brain-damaged patients.", *Neuropsychologia*, vol. 24, no. 2, pp. 169-180.

Bowers, D., Blonder, L. X., Feinberg, T., & Heilman, K. M. 1991, "Differential impact of right and left hemisphere lesions on facial emotion and object imagery.", *Brain*, vol. 114, no. 6, pp. 2593-2609.

Bowers, D., Bauer, R. M., Coslett, H. B., & Heilman, K. M. 1985, "Processing of faces by patients with unilateral hemisphere lesions: I. Dissociation between judgments of facial affect and facial identity.", *Brain and Cognition*, vol. 4, no. 3, pp. 258-272.

Bowers, D., Bauer, R. M., & Heilman, K. M. 1993, "The nonverbal affect lexicon: theoretical perspectives from neuropsychological studies of affect perception.", *Neuropsychology*, vol. 7, no. 4, pp. 433-444.

Braver, T. S., Cohen, J. D., Nystrom, L. E., Jonides, J., Smith, E. E., & Noll, D. C. 1997, "A parametric study of prefrontal cortex involvement in human working memory.", *NeuroImage*, vol. 5, no. 1, pp. 49-62.

Breen, N., Caine, D., & Coltheart, M. 2003, "Models of face recognition and delusional misidentification: a critical review.", *Cognitive Neuropsychology*, vol. 17, no. 1, pp. 55-71.

Breiter, H. C. & Rauch, S. L. 1996, "Functional MRI and the study of OCD: from symptom provocation to cognitive-behavioural probes of cortico-striatal systems and the amygdala.", *NeuroImage*, vol. 4, no. 3, p. S127-S138.

Breiter, H. C., Etcoff, N. L., Whalen, P. J., Kennedy, W. A., Rauch, S. L., Buckner, R. L., Strauss, M. M., Hyman, S. E., & Rosen, B. R. 1996, "Response and habituation of the human amygdala during visual processing of facial expression.", *Neuron*, vol. 17, no. 5, pp. 875-887.

Brierley, B., Shaw, P., & David, A. S. 2002, "The human amygdala: a systematic review and meta-analysis of volumetric magnetic resonance imaging.", *Brain Research Reviews*, vol. 39, no. 1, pp. 84-105.

Broks, P., Young, A. W., Maratos, E. J., Coffey, P. J., Calder, A. J., Isaac, C. L., Mayes, A. R., Hodges, J. R., Montaldi, D., Cezayirli, E., Roberts, N., & Hadley, D. 1998, "Face processing impairments after encephalitis: amygdala damage and recognition of fear.", *Neuropsychologia*, vol. 36, no. 1, pp. 59-70.

Brookes, M.J., Gibson, A.M., Hall, S.D., Furlong, P.L., Barnes, G.R., Hillebrand, A., Singh, K.D., Holliday, I.E., Francis, S.T. & Morris, P.G. 2005, "GLM-beamformer method demonstrates stationary field, alpha ERD and gamma ERS co-localisation with fMRI BOLD response in visual cortex", *NeuroImage*, vol. 26, pp. 302-308

Brothers, L. 1996, "Brain mechanisms of social cognition.", *Journal of Psychopharmacology*, vol. 10, no. 1, pp. 2-8.

Brothers, L., Ring, B., & Kling, A. 1990, "Response of neurons in the macaque amygdala to complex social stimuli.", *Behavioural Brain Research*, vol. 41, no. 3, pp. 199-213.

Bruce, V. & Young, A. W. 1986, "Understanding face recognition.", *British Journal of Psychology*, vol. 77, pp. 305-327.

Bruyer, R., Laterre, C., Seron, X., Feyereisen, P., Strypstein, E., Pierrard, E., & Rectem, D. 1983, "A case of prosopagnosia with some preserved covert remembrance of familiar faces.", *Brain and Cognition*, vol. 2, no. 257, p. 284.

Burgess, A. P. & Gruzelier, J. H. 2000, "Short duration power changes in the EEG during recognition memory for words and faces.", *Psychophysiology*, vol. 37, pp. 596-606.

Bush, G., Luu, P., & Posner, M. I. 2000, "Cognitive and emotional influences in anterior cingulate cortex.", *Trends in Cognitive Sciences*, vol. 4, no. 6, pp. 215-222.

Cahill, L., Babinsky, R., Markowitsch, H. J., & McGaugh, J. L. 1995, "The amygdale and emotional memory.", *Nature*, vol. 377, no. 6547, pp. 295-296.

Calder, A. J., Young, A. W., Rowland, D., Perrett, D. I., Hodges, J. R., & Etcoff, N. L. 1996, "Facial emotion recognition after bilateral amygdala damage: Differentially severe impairment of fear.", *Cognitive Neuropsychology*, vol. 13, no. 5, pp. 699-745.

Calder, A. J., Young, A. W., Karnat, A., Sprengelmeyer, R., Perrett, D. I., & Rowland, D. 1997, "Selective deficits in emotional expression recognition following brain damage.", *International Journal of Psychophysiology*, vol. 25, no. 1, p. 69.

Calder, A. J., Young, A. W., Karnat, A., Sprengelmeyer, R., Perrett, D. I., & Rowland, D. 1997, "Selective deficits in emotional expression recognition following brain damage.", *International Journal of Psychophysiology*, vol. 25, no. 1, p. 69.

Calder, A.J., Young, A.W., Rowland, D., Perrett, D.I. 1997, "Computer-enhanced emotion in facial expressions.", *Proceedings of the Royal Society of London Series B-Biological Sciences*, vol. 264 no. 1383 pp. 919-25.

Campbell, R. 1978, "Asymmetries in interpreting and expressing a posed facial expression.", *Cortex*, vol. 19, pp. 327-342.

Canli, T., Zhao, Z., Brewer, J., Gabrieli, J. D. E., & CAHILL, L. 2000, "Event-related activation in the human amygdala associates with later memory for individual emotional experience.", *Journal of Neuroscience*, vol. 20, no. 19, p. RC99.

Canli, T., Zhao, Z., Desmond, J. E., Kang, E., Gross, J., & Gabrieli, J. D. E. 2001, "An fMRI study of personality influences on brain reactivity to emotional stimuli.", *Behavioural Neuroscience*, vol. 115, no. 1, pp. 33-42.

Canli, T., Sivers, H., Whitfield, S. L., Gotlib, I. H., & Gabrieli, J. D. E. 2002, "Amygdala response to happy faces as a function of extraversion.", *Science*, vol. 296, no. 5576, p. 2191.

Canli, T. & Amin, Z. 2002, "Neuroimaging of emotion and personality: Scientific evidence and ethical considerations.", *Brain and Cognition*, vol. 50, no. 3, pp. 414-431.

Canli, T., Amin, Z., Haas, B., Omura, K., & Constable, R. T. 2004, "A double dissociation between mood states and personality traits in the anterior cingulate.", *Behavioural Neuroscience*, vol. 118, no. 5, pp. 897-904.

Capra, F. (1983) *The turning point*. Flamingo

Carlson, S., Martinkauppi, S., Rami, P., Salli, E., Korvenoja, A., & Aronen, H. J. 1998, "Distribution of cortical activation during visuospatial n-back tasks as revealed by functional magnetic resonance imaging.", *Cerebral Cortex*, vol. 8, no. 8, pp. 743-752.

Chao, L. L., Martin, A., & Haxby, J. V. 1999a, "Are face-responsive regions selective only for faces?", *Neuroreport*, vol. 10, no. 14, pp. 2945-2950.

Chao, L. L., Haxby, J. V., & Martin, A. 1999b, "Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects.", *Nature Neuroscience*, vol. 2, no. 10, pp. 913-919.

Chaplin, T. C., Rice, M. E., & Harris, G. T. 1995, "Salient victim suffering and the sexual responses of child molesters.", *Journal of Consulting and Clinical Psychology*, vol. 63, no. 2, pp. 249-255.

Cheyne, D.O., Barnes, G.R., Holliday, I.E. & Furlong, P.L. 2000, "Localisation of brain activity associated with non-time locked tactile stimulation using SAM." *Conference Proceedings*, 12th International Conference on BioMagnetism, August 13th to 17th, Helsinki University of Technology, Espoo, Finland

Cicone, M., Wapner, W., & Gardner, H. 1980, "Sensitivity to emotional expressions and situations in organic patients.", *Cortex*, vol. 16, pp. 145-158.

Clark, V. P., Keil, K., Maisog, J. M., Courtney, S. M., Ungerleider, L. G., & Haxby, J. V. 1996, "Functional magnetic resonance imaging of human visual cortex during face matching: a comparison with positron emission tomography.", *NeuroImage*, vol. 4, no. 1, pp. 1-15.

Cohen, D. 1968, "Magnetoencephalography: Evidence of magnetic fields produced by alpha-rhythm currents.", *Science*, vol. 161, pp. 784-786.

Cohen, D. & Cuffin, B. N. 1983, "Demonstration of useful differences between magnetoencephalogram and electroencephalogram.", *Electroencephalography and Clinical Neurophysiology*, vol. 56, no. 1, pp. 38-51.

Cohen, J. D., Dunbar, K. O., Barch, D. M., & Braver, T. S. 1997, "Issues concerning relative speed of processing hypotheses, schizophrenic performance deficits, and prefrontal Function: Comment on Schooler et al. (1997).", *Journal of Experimental Psychology: General*, vol. 126, no. 1, pp. 37-41.

Collins, D. R., Lang, E. J., & Pare, D. 1999, "Spontaneous activity of the perirhinal cortex in behaving cats.", *Neuroscience*, vol. 89, no. 4, pp. 1025-1039.

Compton, R.J., Banich, M.T., Mohanty, A., Milham, M.P., Herrington, J., Miller, G.A., Scalf, P.E., Webb, A. & Heller, W. 2003, "paying attention to emotion: an fMRI investigation of cognitive and emotional Stroop tasks." *Cognitive, Affective and Behavioural Neuroscience*, vol. 3, no. 12, pp. 81-96

Corkin, S., Twitschel, T.E. & Sullivan, E.V. 1979, "Safety and efficacy of cingulotomy for pain and psychiatric disorders. " In E.R. Hitchcock (Ed) *Modern concepts in psychiatric surgery*, pp. 253-272. Elsevier

Courtney, S. M., Ungerleider, L. G., Keil, K., & Haxby, J. V. 1996, "Object and spatial visual working memory activate separate neural systems in human cortex.", *Cerebral Cortex*, vol. 6, no. 1, pp. 39-49.

Critchley, H. D., Simmons, A., Daly, E. M., Russell, A., van Amelsvoort, T., Robertson, D. M., Glover, A., & Murphy, D. G. M. 2000, "Prefrontal and medial temporal correlates of repetitive violence to self and others.", *Biological Psychiatry*, vol. 47, no. 10, pp. 928-934.

Critchley, H. D., Mathias, C. J., & Dolan, R. J. 2001, "Neural activity in the human brain relating to uncertainty and arousal during anticipation.", *NeuroImage*, vol. 13, no. 6, Supplement 1, p. 392.

Critchley, H. D., Mathias, C. J., & Dolan, R. J. 2002, "Fear conditioning in humans: The influence of awareness and autonomic arousal on functional neuroanatomy.", *Neuron*, vol. 33, no. 4, pp. 653-663.

Critchley, H. D., Melmed, R. N., Featherstone, E., Mathias, C. J., & Dolan, R. J. 2002, "Volitional control of autonomic arousal: a functional magnetic resonance study.", *NeuroImage*, vol. 16, no. 4, pp. 909-919.

Critchley, H.D., Mathias, C.J., Josephs, O., O'Doherty, J., Zanini, S., Dewar, B.-K., Cipolotti, L., Shallice, T. & Dolan, R.J. 2003, "Human cingulate cortex and autonomic control: converging neuroimaging and clinical evidence.", *Brain*, vol. 126, pp. 2139-2152

D'Esposito, M., Detre, J. A., Aguirre, G. K., Stallcup, M., Alsop, D. C., Tippet, L. J., & Farah, M. J. 1997, "A functional MRI study of mental image generation.", *Neuropsychologia*, vol. 35, no. 5, pp. 725-730.

D'Esposito, M., Zarahn, E., & Aguirre, G. K. 1999, "Event-related functional MRI: implications for cognitive psychology.", *Psychological Bulletin*, vol. 125, no. 1, pp. 155-164.

Damasio, A. R., Damasio, H., & VanHoesen, G. W. 1982, "Prosopagnosia: anatomical basis and behavioural mechanisms.", *Neurology*, vol. 32, pp. 331-341.

Damasio, A.R., Grabowski, T.J., Bechara, A., Damasio, H., Ponto, L.L., Parvizi, J., Hichwa, R.D. 2000, "Subcortical and cortical brain activity during the feeling of self-generated emotions.", *Nature Neuroscience*, vol. 3, no. 10, pp. 1049-1956

Davatzikos, C., Genc, A., Xu, D., & Resnick, S. M. 2001, "Voxel-based morphometry using the RAVENS maps: methods and validation using simulated longitudinal atrophy.", *NeuroImage*, vol. 14, no. 6, pp. 1361-1369.

Davatzikos, C., Li, H. H., Herskovits, E., & Resnick, S. M. 2001, "Accuracy and sensitivity of detection of activation foci in the brain via statistical parametric mapping: a study using a PET simulator.", *NeuroImage*, vol. 13, no. 1, pp. 176-184.

Davatzikos, C. 2004, "Why voxel-based morphometric analysis should be used with great caution when characterizing group differences.", *NeuroImage*, vol. 23, no. 1, pp. 17-20.

Davidson, R. J. 1992, "Anterior cerebral asymmetry and the nature of emotion.", *Brain and Cognition*, vol. 20, no. 1, pp. 125-151.

Davidson, R. J. 1993, "Parsing affective space: perspectives from neuropsychology and psychophysiology.", *Neuropsychology*, vol. 7, pp. 464-475.

Davidson, R.J. 2000, "Affective style, psychopathology, and resilience: brain mechanisms and plasticity". American Psychologist, vol. 55, no. 11 pp. 1196-214.

Davidson, R.J. 2001, "Toward a biology of personality and emotion.", *Annals of the New York Academy of Science*, vol. 935, pp. 191-207

Davidson, R.J. & Irwin, W. 1999, "The functional neuroanatomy of emotion and affective style.", *Trends in Cognitive Science*, vol. 3, no.1, pp. 11-21

Davidson, R. J., Ekman, P., & Friesen, W. V. 1990a, "The Duchenne smile: emotional expression and brain physiology.", *Journal of Personality and Social Psychology*, vol. 58, no. 2, pp. 342-353.

Davidson, R. J., Ekman, P., Saron, C. D., Senulis, J. A., & Friesen, W. V. 1990b, "Approach-withdrawal and cerebral asymmetry: emotional expression and brain physiology.", *Journal of Personality and Social Psychology*, vol. 58, no. 2, pp. 330-341.

Davidson, R. J., Leslie, S. C., & Saron, C. 1990c, "Reaction time measures of interhemispheric transfer time in reading disabled and normal children.", *Neuropsychologia*, vol. 28, no. 5, pp. 471-485.

Davis, M. 1986, "Pharmacological and anatomical analysis of fear conditioning using the fear-potentiated startle paradigm." *Behavioural Neuroscience*, vol. 100, no.6, pp. 814-24.

Davis, M. 1997, "Neurobiology of fear responses: The role of the amygdala.", *Journal of Neuropsychiatry and Clinical Neurosciences*, vol. 9, no. 3, pp. 382-402.

Davis, M. & Whalen, P. J. 2001, "The amygdala: vigilance and emotion.", *Molecular Psychiatry*, vol. 6, no. 1, pp. 13-34.

Deouell, L.Y., Bentin, S., Soroker, N. 2000, "Electrophysiological evidence for an early (pre-attentive) information processing deficit in patients with right hemisphere damage and unilateral neglect." *Brain*, vol. 123 no. 2, pp. 353-65.

Devinsky, O., Morrell, M.J., Vogt, B.A. 1995, "Contributions of anterior cingulate cortex to behaviour.", *Brain*, vol. 118 no. 1 pp. 279-306.

DeKosky, S. T., Heilman, G. E., Bowers, D., & Valenstein, I. 1980, "Recognition and discrimination of emotional faces and pictures.", *Brain and Language*, vol. 9, pp. 206-214.

DeMunck, J.C. 1989, "The estimation of time-varying dipoles on the basis of evoked potentials." *Electroencephalography and Clinical Neurophysiology*, vol.77, no. 2, pp. 156-160

Diamond, R. & Carey, S. 1986, "Why faces are and are not special: An effect of expertise.", *Journal of Experimental Psychology: General*, vol. 115, pp. 107-117.

Dimberg, U. 1986, "Facial expressions as excitatory and inhibitory stimuli for conditioned autonomic responses.", *Biological Psychology*, vol. 22, no. 1, pp. 37-57.

Dimberg, U. & Lundquist, L. O. 1990, "Gender differences in facial reactions to facial expressions.", *Biological Psychology*, vol. 30, no. 2, pp. 151-159.

Dolan, R. J. 1997, "Conceptual and methodological approaches in functional activation studies illustrated by studies of emotion.", *European Psychiatry*, vol. 12, no. Supplement 2, p. 107s.

Dolan, R. 1998, "A cognitive affective role for the cerebellum.", *Brain*, vol. 121, no. 4, pp. 545-546.

Dolan, R. J. 2002, "Emotion, cognition, and behaviour.", *Science*, vol. 298, no. 5596, pp. 1191-1194.

Dolan, R. J., Fletcher, P., Morris, J., Kapur, N., Deakin, J. F. W., & Frith, C. D. 1996, "Neural activation during covert processing of positive emotional facial expressions.", *NeuroImage*, vol. 4, no. 3, pp. 194-200.

Dolan, R.J, Fink, G.R., Rolls, E., Booth, M., Holmes, A., Frackowiak, R.S. & Friston, K.J. 1997, "How the brain learns to see objects and faces in an impoverished context.", *Nature*, vol. 389, no. 6651, pp. 596-599

Dolan, R. J., Lane, R., Chua, P., & Fletcher, P. 2000, "Dissociable temporal lobe activations during emotional episodic memory retrieval.", *NeuroImage*, vol. 11, no. 3, pp. 203-209.

Doppelmayr, M. & Klimesch, W. 1997, "Event-related desynchronisation (ERD), absolute power and the selection of frequency bands: methodological aspects.", *Electroencephalography and Clinical Neurophysiology*, vol. 103, no. 1, p. 154.

Drevets, W.C., Raichle, M.E. 1992, "Neuroanatomical circuits in depression: implications for treatment mechanisms.", *Psychopharmacological Bulletin*, vol. 28 no.3 pp. 261-74.

Druzgal, T. J. & D'Esposito, M. 2001, "A neural network reflecting decisions about human faces.", *Neuron*, vol. 32, no. 5, pp. 947-955.

Eger, E., Jedynak, A., Iwaki, T., & Skrandies, W. 2003, "Rapid extraction of emotional expression: evidence from evoked potential fields during brief presentation of face stimuli.", *Neuropsychologia*, vol. 41, no. 7, pp. 808-817.

Eimer, M. 2000a, "Effects of face inversion on the structural encoding and recognition of faces: Evidence from event-related brain potentials.", *Cognitive Brain Research*, vol. 10, no. 1-2, pp. 145-158.

Eimer, M. 2000b, "The time course of spatial orienting elicited by central and peripheral cues: evidence from event-related brain potentials.", *Biological Psychology*, vol. 53, no. 2-3, pp. 253-258.

Eimer, M. 2000c, "Event-related brain potentials distinguish processing stages involved in face perception and recognition.", *Clinical Neurophysiology*, vol. 111, no. 4, pp. 694-705.

Eimer, M. & McCarthy, R.A. 1999, "Prosopagnosia and structural encoding of faces: evidence from event-related potentials.", *Neuroreport*, vol. 10, no. 2, pp. 255-259

Eimer, M. & Holmes, A. 2002, "An ERP study on the time course of emotional face processing.", *Neuroreport*, vol. 13, no. 4, pp. 427-431.

Eimer, M., Goschke, T., Schlaghecken, F., & Sturmer, B. 1996, "Explicit and implicit learning of event sequences: evidence from event-related brain potentials.", *Journal of Experimental Psychology: Learning, Memory, and Cognition*, vol. 22, no. 4, pp. 970-987.

Eisenberg, N., Fabes, R.A., Miller, P.A., Fultz, J., Shell, R., Mathy, R.M. & Reno, P.R. 1989, "Relation of sympathy and personal distress to pro-social behaviour: a multimethod study.", *Journal of Personality and Social Psychology*, vol. 57, no. 1, pp. 55-66

Ekman, P. 1992, "Facial expressions of emotion: an old controversy and new findings." *Philosophical Transactions of the Royal Society of London. Series B - Biological Sciences*, vol. 335, no. 1273, pp. 63-69

Ekman, P. 1992, "Are there basic emotions?", *Psychological Review*, vol. 99, no. 3, pp. 550-553

Ekman, P. & Friesen, W. V. 1969, "A tool for the analysis of motion picture film or video tape.", *American Psychologist*, vol. 24, no. 3, pp. 240-243.

Ekman, P. & Friesen, W. V. 1969, "Nonverbal leakage and clues to deception.", *Psychiatry*, vol. 32, no. 1, pp. 88-106.

Ekman, P. & Friesen, W. V. 1976, *Pictures of facial affect* Consulting Psychologists Press, Palo Alto, CA.

Ekman, P., Davidson, R. J., & Friesen, W. V. 1990, "The Duchenne smile: emotional expression and brain physiology.", *Journal of Personality and Social Psychology*, vol. 58, no. 2, pp. 342-353.

Elliott, R., Ogilvie, A., Rubinsztein, J. S., Calderon, G., Dolan, R. J., & Sahakian, B. J. 2004, "Abnormal ventral frontal response during performance of an affective go/no go task in patients with mania.", *Biological Psychiatry*, vol. 55, no. 12, pp. 1163-1170.

Ellis, H.D. & Deregowski, J.B. 1981, "Within-race and between-race recognition of transformed and untransformed faces." *American Journal of Psychology,* vol. 94, no. 1, pp. 27-35

Ellis, H. D. & Young, A. W. 1990, "Accounting for delusional misidentification.", *British Journal of Psychiatry*, vol. 157, pp. 239-248.

Ellis, A. W., Young, A. W., & Flude, B. M. 1990, "Repetition priming and face processing - priming occurs within the system that responds to the identity of a face.", *Quarterly Journal of Experimental Psychology Section A-Human Experimental Psychology*, vol. 42, no. 3, pp. 495-512.

Ellis, H. D., Young, A. W., Quayle, A. H., & DePauw, K. W. 1997, "Reduced autonomic responses to faces in Capgras delusion.", *Proceedings of the Royal Society of London Series B-Biological Sciences*, vol. 264, no. 1384, pp. 1085-1092.

Engel, A. K., Koenig, P., Gray, C. M., & Singer, W. 1990, "Stimulus-dependent neuronal oscillations in cat visual cortex: intercolumnar interactions as determined by cross-correlational analysis.", *European Journal of Neuroscience*, vol. 2, pp. 588-606.

Engel, A. K., Roelfsema, P.R., Fries, P., Brecht, M., Singer, W. 1997, "Role of the temporal domain for response selection and perceptual binding." *Cerebral Cortex,* vol. 7 no. 6 pp. 571-82

Engel, A. K., Fries, P., Koenig, P., Brecht, M., & Singer, W. 1999, "Temporal binding, binocular rivalry, and consciousness.", *Consciousness and Cognition*, vol. 8, no. 2, pp. 128-151.

Epstein, R. & Kanwisher, N. 1998, "A cortical representation of the local visual environment.", *Nature*, vol. 392, no. 6676, pp. 598-601.

Epstein, R., Harris, A., Stanley, D., & Kanwisher, N. 1999, "The parahippocampal place area: recognition, navigation, or encoding?", *Neuron*, vol. 23, no. 1, pp. 115-125.

Epstein, R. & Kanwisher, N. 1999, "Repetition blindness for locations: evidence for automatic spatial coding in an RSVP task.", *Journal of Experimental Psychology: Human Perception and Performance*, vol. 25, no. 6, pp. 1855-1866.

Epstein, R. & Kanwisher, N. 2001, "Mnemonic functions of the parahippocampal place area: An event related fMRI study.", *NeuroImage*, vol. 13, no. 6, Supplement 1, p. 663.

Esslen, M., Pascual-Marqui, R. D., Hell, D., Kochi, K., & Lehmann, D. 2004, "Brain areas and time course of emotional processing.", *NeuroImage*, vol. 21, no. 4, pp. 1189-1203.

Etcoff, N. L. 1984, "Selective attention to facial identity and facial emotion.", *Neuropsychologia*, vol. 22, pp. 281-295.

Eugene, F., Levesque, J., Mensour, B., Leroux, J. M., Beaudoin, G., Bourgouin, P., & Beauregard, M. 2003, "The impact of individual differences on the neural circuitry underlying sadness.", *NeuroImage*, vol. 19, no. 2, pp. 354-364.

Farah, M. J. 1996, "Is face recognition 'special'? Evidence from neuropsychology.", *Behavioural Brain Research*, vol. 76, no. 1-2, pp. 181-189.

Farah, M. J. & McClelland, J.L. 1991, "A computational model of semantic memory impairment: modality specificity and emergent category specificity." *Journal of Experimental Psychology – General*, vol. 120, no. 4, pp. 339-357

Farah, M. J. & Aguirre, G. K. 1999, "Imaging visual recognition: PET and fMRI studies of the functional anatomy of human visual recognition.", *Trends in Cognitive Sciences*, vol. 3, no. 5, pp. 179-186.

Farah, M.J., McMullen, P.A. & Meyer, M.W. 1991, "Can recognition of living things be selectively impaired?" *Neuropsychologia*, vol. 29, no. 2, pp. 185-193

Farah, M. J., Levinson, K. L., & Klein, K. L. 1995a, "Face perception and within-category discrimination in prosopagnosia.", *Neuropsychologia*, vol. 33, no. 6, pp. 661-674.

Farah, M. J., Tanaka, J. W., & Drain, H. M. 1995b, "What causes the face inversion effect?", *Journal of Experimental Psychology: Human Perception and Performance*, vol. 21, no. 3, pp. 628-634.

Farah, M. J., Wilson, K. D., Maxwell Drain, H., & Tanaka, J. R. 1995c, "The inverted face inversion effect in prosopagnosia: Evidence for mandatory, face-specific perceptual mechanisms.", *Vision Research*, vol. 35, no. 14, pp. 2089-2093.

Farah, M. J., Wilson, K. D., Drain, M., & Tanaka, J. N. 1998, "What is "special" about face perception?", *Psychological Review*, vol. 105, no. 3, pp. 482-498.

Farah, M. J., Rabinowitz, C., Quinn, G. E., & Liu, G. T. 2003, "Early commitment of neural substrates for face recognition.", *Cognitive Neuropsychology*, vol. 17, no. 1, pp. 117-123.

Fischer, H., Wright, C. I., Whalen, P. J., McInerney, S. C., Shin, L. M., & Rauch, S. L. 2003, "Brain habituation during repeated exposure to fearful and neutral faces: A functional MRI study.", *Brain Research Bulletin*, vol. 59, no. 5, pp. 387-392.

Foucher, J. R., Otzenberger, H., & Gounot, D. 2003, "The BOLD response and the gamma oscillations respond differently than evoked potentials: an interleaved EEG-fMRI study.", *BMC Neurosciences*, vol. 19, no. 4, p. 22.

Foucher, J. R., Otzenberger, H., & Gounot, D. 2004, "Where arousal meets attention: a simultaneous fMRI and EEG recording study.", *NeuroImage*, vol. 22, no. 2, pp. 688-697.

Fries, P., Reynolds, J.H. et al. 2001, "Modulation of oscillatory neuronal synchronisation by selective visual attention.", *Science*, vol. 291, pp. 1560-1563

Friesen, C. K. & Kingstone, A. 1998, "The eyes have it! Reflexive orienting is triggered by nonpredictive gaze.", *Psychonomic Bulletin & Review*, vol. 5, no. 3, pp. 490-495.

Friston, K. J., Ashburner, J., Frith, C. D., Poline, J.-B., Heather, J. D., & Frackowiak, R. S. J. 1995, "Spatial registration and normalisation of images.", *Human Brain Mapping*, vol. 2, pp. 165-189.

Friston, K. J., Price, C. J., Fletcher, P., Moore, C., Frackowiak, R. S. J., & Dolan, R. J. 1996a, "The trouble with cognitive subtraction.", *NeuroImage*, vol. 4, no. 2, pp. 97-104.

Friston, K. J., Stephan, K. M., Heather, J. D., Frith, C. D., Ioannides, A. A., Liu, L. C., Rugg, M. D., Vieth, J., Keber, H., Hunter, K., & Frackowiak, R. S. J. 1996b, "A multivariate analysis of evoked responses in EEG and MEG data.", *NeuroImage*, vol. 3, no. 3, pp. 167-174.

Friston, K. J., Holmes, A. P., & Worsley, K. J. 1999, "How many subjects constitute a study?", *NeuroImage*, vol. 10, pp. 1-5.

Gaetz, W. C. & Cheyne, D. O. 2003, "Localization of human somatosensory cortex using spatially filtered magnetoencephalography.", *Neuroscience Letters*, vol. 340, no. 3, pp. 161-164.

Gainotti, G. 1972, "Emotional behaviour and hemisphere side of lesion.", *Cortex*, vol. 8, pp. 41-55.

Galin, D. & Ornstein, R. 1972, "Lateral specialization of cognitive mode: an EEG study.", *Psychophysiology*, vol. 9, no. 4, pp. 412-418.

Galin, D. & Ornstein, R. 1974, "Individual differences in cognitive style--I. Reflective eye movements.", *Neuropsychologia*, vol. 12, no. 3, pp. 367-376.

Galin, D., Johnstone, J., & Herron, J. 1978, "Effects of task difficulty on EEG measures of cerebral engagement.", *Neuropsychologia*, vol. 16, no. 4, pp. 461-472.

Galin, D., Ornstein, R., Herron, J., & Johnstone, J. 1982, "Sex and handedness differences in EEG measures of hemispheric specialization.", *Brain and Language*, vol. 16, no. 1, pp. 19-55.

Gauthier, I., Williams, P., Tarr, M.J. & Tanaka, J. 1998, Training 'greeble' experts: a framework for studying expert object recognition processes." *Vision Research*, vol. 38, no. 15-16, pp. 2401-2428

Gauthier, I. 2000a, "Visual priming: the ups and downs of familiarity.", *Current Biology*, vol. 10, no. 20, p. R753-R756.

Gauthier, I. 2000b, "What constrains the organization of the ventral temporal cortex?", *Trends in Cognitive Sciences*, vol. 4, no. 1, pp. 1-2.

Gauthier, I. 2000, "Expertise for cars and birds recruits brain areas involved in face recognition.", *Nature Neuroscience*, vol. 3, no. 2, pp. 191-197.

Gauthier, I., 2002, "BOLD activity during mental rotation and viewpoint-dependent object recognition.", *Neuron.*, vol. 34, no. 1, pp. 161-171.

Gauthier, I. & Epstein, R. 2001, "The role of spatial frequencies in face-selective areas: Task-dependent effects.", *NeuroImage*, vol. 13, no. 6, Supplement 1, p. 883.

Gauthier, I. & Nelson, C. A. 2001, "The development of face expertise.", *Current Opinion in Neurobiology*, vol. 11, no. 2, pp. 219-224.

Gauthier, I. & Logothetis, N. L. 2003, "Is face recognition not so unique after all?", *Cognitive Neuropsychology*, vol. 17, no. 1, pp. 125-142.

Gauthier, I., Behnmann, M., & Tarr, M. J. 1999, "Can face recognition really be dissociated from object recognition?", *Journal of Cognitive Neuroscience*, vol. 11, no. 4, pp. 349-370.

Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. 1999, "Activation of the middle fusiform 'face area' increases with expertise in recognizing novel objects.", *Nature Neuroscience*, vol. 2, no. 6, pp. 568-573.

Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C., & Anderson, A. W. 2000, "The fusiform "face area" is part of a network that processes faces at the individual level.", *Journal of Cognitive Neuroscience*, vol. 12, no. 5, p. 912.

Gauthier, I., Tarr, M. J., Moylan, J., Anderson, A. W., Skudlarski, P., & Gore, J. C. 2003, "Does visual subordinate-level categorisation engage the functionally defined fusiform Face Area?", *Cognitive Neuropsychology*, vol. 17, no. 1, pp. 143-163.

George, M. S., Ketter, T. A., Gill, D. S., Haxby, J. V., Ungerleider, L. G., Herscovitch, P., & Post, R. M. 1993, "Brain regions involved in recognizing facial emotion or identity: an oxygen-15 PET study.", *Journal of Neuropsychiatry and Clinical Neurosciences*, vol. 5, no. 4, pp. 384-394.

George, M. S., Ketter, T. A., Parekh, P. I., & Post, R. M. 1994, "Regional blood flow correlates of transient self-induced sadness or happiness.", *Biological Psychiatry*, vol. 35, no. 9, p. 647.

George, M.S., Ketter, T.A., Parekh, P.I., Horwitz, B., Herscovitch, P. & Post, R.M. 1995, "Brain activity during transient sadness and happiness in healthy women.", *American Journal of psychiatry*, vol. 152, no. 3, pp. 341-351

George, M. S., Ketter, T. A., Parekh, P. I., Herscovitch, P., & Post, R. M. 1996, "Gender differences in regional cerebral blood flow during transient self-induced sadness or happiness." *Biological Psychiatry*, vol. 40, no. 9, pp. 859-871.

George, M.S., Ketter, T.A., Parekh, P.I., Rosinsky, N., Ring, H.A., Pazzaglia, P.J., Marangell, L.B., Callahan, A.M. & Post, R.M. 1997 "Blunted left cingulate activation in

mood disorder subjects during a response interference task (the Stroop)." *Neuropsychiatry and Clinical Neuroscience*, vol. 9, no. 1 pp. 55-63

George, P. A. & Hole, G. J. 1995, "Factors influencing the accuracy of age estimates of unfamiliar faces.", *Perception*, vol. 24, no. 9, pp. 1059-1073.

George, J.S., Aine, C.J., Mosher, J.C., Schmidt, D.M., Ranken, D.M., Schlitt, H.A., Wood, C.C., Lewine, J.D., Sanders, J.A. & Belliveau, J.W. 1995, "Mapping function in the human brain with magnetoencephalography, anatomical magnetic resonance imaging and functional magnetic resonance imaging." *Journal of Clinical Neurophysiology*, vol. 12, no. 5, pp. 406-431

Gianotti, L. R. R., Faber, P. L., Pascual-Marqui, R. D., Kochi, K., & Lehmann, D. 2003, "Very early affect-modulated brain electric microstates (f100 msec) during word processing, and their functional tomography". HBM Abstract

Gobbini, M. I., Martin, A., & Haxby, J. V. 2001, "Altered responses to faces due to experimentally-induced familiarity.", *NeuroImage*, vol. 13, no. 6, Supplement 1, p. 408.

Gobbini, M., Leibenluft, E., Santiago, N., & Haxby, J. V. 2004, "Social and emotional attachment in the neural representation of faces.", *NeuroImage*, vol. 22, no. 4, pp. 1628-1635.

Goodale, M. A. & Milner, A. D. 1992, "Separate visual pathways for perception and action.", *Trends in Neurosciences*, vol. 15, no. 1, pp. 20-25.

Goodale, A., Westwood, D. A., & David Milner, A. 2003, "Two distinct modes of control for object-directed action." in *Progress in Brain Research*, Volume 144 edn, Elsevier, pp. 131-144.

Gorodnitsky, I. F., George, J. S., & Rao, B. D. 1995, "Neuromagnetic source imaging with FOCUSS: a recursive weighted minimum norm algorithm.", *Electroencephalography and Clinical Neurophysiology*, vol. 95, no. 4, pp. 231-251.

Gorodnitsky, I. F. & Rao, B. D. 1997, "Sparse signal reconstruction from limited data suing FOCUSS: A re-weighted minimum-norm algorithm.", *IEEE Transactions on Signal Processing*, vol. 45, no. 3, pp. 600-616.

Graham, R. & Cabeza, R. 2001, "Dissociating the neural correlates of item and context memory: an ERP study of face recognition.", *Canadian Journal of Experimental Psychology*, vol. 55, no. 2, pp. 154-161

Graham, R. & Cabeza, R. 2001, "Event-related potentials of recognising happy and neutral faces.", *Neuroreport*, vol. 12, no. 2, pp. 245-248

Gray, C. M., Koenig, P., Engel, A. K., & Singer, W. 1989, "Oscillatory responses in cat visual cortex exhibit intercolumnar synchronisation which reflects global stimulus properties.", *Nature*, vol. 338, pp. 334-337.

Gray, C. M. & Singer, W. 1989, "Stimulus-specific neuronal oscillations in orientation columns of cat visual cortex.", *Proceedings of the National Academy of Sciences of the United States of America*, vol. 86, pp. 1689-1702.

Gray, C. M., Engel, A. K., Koenig, P., & Singer, W. 1990, "Stimulus-dependent neuronal oscillations in cat visual cortex: receptive field properties and feature dependence.", *European Journal of Neuroscience*, vol. 2, pp. 607-619.

Gray, C. M. & McCormick, D. A. 1996, "Chattering cells: Superficial pyramidal neurons contributing to the generation of synchronous oscillations in the visual cortex.", *Science*, vol. 274, pp. 109-113.

Gray, J. M., Young, A. W., Barker, W. A., Curtis, A., & Gibson, D. 1997, "Impaired recognition of disgust in Huntington's disease gene carriers.", *Brain*, vol. 120, pp. 2029-2038.

Gross, C. G., Rocha-Miranda, C. E., & Bender, D. B. 1972, "Visual properties of neurons in inferotemporal cortex of the Macaque.", *Journal Of Neurophysiology*, vol. 35, no. 1, pp. 96-111.

Gross, C. G. & Sergent, J. 1992, "Face recognition", *Current Biology*, vol. 2, no. 5, p. 235.

Gross, J., Kujala, J., Hamalainen, M., Timmermann, L., Schnitzler, A., & Salmelin, R. 2001, "Dynamic imaging of coherent sources: studying neural interactions in the human brain.", *Proceedings of the National Academy of Sciences of the United States of America*, vol. 98, no. 2, pp. 694-699.

Gross, J., Timmermann, L., Kujala, J., Salmelin, R., & Schnitzler, A. 2003, "Properties of MEG tomographic maps obtained with spatial filtering.", *NeuroImage*, vol. 19, no. 4, pp. 1329-1336.

Gur, R. C., Erwin, R. J., Gur, R. E., Zwil, A. S., Heimberg, C., & Kraemer, H. C. 1992, "Facial emotion discrimination: II. Behavioural findings in depression.", *Psychiatry Research*, vol. 42, no. 3, pp. 241-251.

Gur, R. C., Skolnick, B. E., & Gur, R. E. 1994, "Effects of emotional discrimination tasks on cerebral blood flow: regional activation and its relation to performance.", *Brain and Cognition*, vol. 25, no. 2, pp. 271-286.

Gur, R. C., Ragland, J. D., Mozley, L. H., Mozley, P. D., Smith, R., Alavi, A., Bilker, W., & Gur, R. E. 1997, "Lateralised changes in regional cerebral blood flow during performance of verbal and facial recognition tasks: correlations with performance and effort.", *Brain and Cognition*, vol. 33, no. 3, pp. 388-414.

Gur, R. C., Schroeder, L., Turner, T., McGrath, C., Chan, R. M., Turetsky, B. I., Alsop, D., Maldjian, J., & Gur, R. E. 2002a, "Brain activation during facial emotion processing.", *NeuroImage*, vol. 16, no. 3, Part 1, pp. 651-662.

Gur, R. C., Sara, R., Hagendoorn, M., Marom, O., Hughett, P., Macy, L., Turner, T., Bajcsy, R., Posner, A., & Gur, R. E. 2002b, "A method for obtaining 3-dimensional facial expressions and its standardization for use in neurocognitive studies.", *Journal of Neuroscience Methods*, vol. 115, no. 2, pp. 137-143.

Haalman, I. & Vaadia, E. 1998, "Emergence of spatio-temporal patterns on neural activity. *Zeitung für Naturforscher*, vol. 55, no. 7-8, pp. 657-669

Halgren, E., Baudena, P., Heit, G., Clarke, J. M., Marinkovic, K., & Clarke, M. 1994a, "Spatio-temporal stages in face and word processing. I. Depth-recorded potentials in the human occipital, temporal and parietal lobes.", *Journal of Physiology-Paris*, vol. 88, no. 1, pp. 1-50.

Halgren, E., Baudena, P., Heit, G., Clarke, J. M., Marinkovic, K., Chauvel, P., & Clarke, M. 1994b, "Spatio-temporal stages in face and word processing. 2. Depth-recorded potentials in the human frontal and Rolandic cortices.", *Journal of Physiology-Paris*, vol. 88, no. 1, pp. 51-80.

Halgren, E., Baudena, P., Clarke, J. M., Heit, G., Liegeois, C., Chauvel, P., & Musolino, A. 1995a, "Intracerebral potentials to rare target and distracter auditory and visual stimuli. I. Superior temporal plane and parietal lobe.", *Electroencephalography and Clinical Neurophysiology*, vol. 94, no. 3, pp. 191-220.

Halgren, E., Baudena, P., Clarke, J. M., Heit, G., Marinkovic, K., Devaux, B., Vignal, J. P., & Biraben, A. 1995b, "Intracerebral potentials to rare target and distracter auditory and visual stimuli. II. Medial, lateral and posterior temporal lobe.", *Electroencephalography and Clinical Neurophysiology*, vol. 94, no. 4, pp. 229-250.

Halgren, E. 1997, "Psychophysiology of the human hippocampal formation during learning and memory.", *International Journal of Psychophysiology*, vol. 25, no. 1, p. 77.

Halgren, E., Marinkovic, K., & Chauvel, P. 1998, "Generators of the late cognitive potentials in auditory and visual oddball tasks.", *Electroencephalography and Clinical Neurophysiology*, vol. 106, no. 2, pp. 156-164.

Halgren, E., Dale, A. M., Sereno, M. I., Tootell, R. B., Marinkovic, K., & Rosen, B. R. 1999, "Location of human face-selective cortex with respect to retinotopic areas.", *Human Brain Mapping*, vol. 7, no. 1, pp. 29-37.

Halgren, E., Raij, T., Marinkovic, K., Jousmaki, V., & Hari, R. 2000, "Cognitive response profile of the human fusiform face area as determined by MEG.", *Cerebral Cortex*, vol. 10, no. 1, pp. 69-81.

Halgren, E., Dhond, R. P., Christensen, N., Van Petten, C., Marinkovic, K., Lewine, J. D., & Dale, A. M. 2002, "N400-like Magnetoencephalography Responses Modulated by Semantic Context, Word Frequency, and Lexical Class in Sentences.", *NeuroImage*, vol. 17, no. 3, pp. 1101-1116.

Hämäläinen, M. & Ilmoniemi, R. J. 1984, *Interpreting measured magnetic fields of the brain: estimates of current distributions.* , PhD Thesis TKK-F-A559, Helsinki University of Technology, Helsinki, Finland.

Hämäläinen, M. & Sarvas, J. 1989, "Realistic conductivity geometry model of the human head for the interpolation of neuromagnetic data.", *IEEE Transactions on Biomedical Engineering*, vol. 36, no. 2, pp. 165-171.

Hämäläinen, M., Hari, R., Ilmoniemi, R. J., Knuutila, J., & Lounasmaa, O. V. 1993, "Magnetoencephalography - theory, instrumentation and applications to non-invasive studies of the working human brain.", *Review of Modern Physics*, vol. 65, no. 2, pp. 413-497.

Hämäläinen, M. 1995, "Modelling aspects of whole-cortex MEG data.", *Electroencephalography and Clinical Neurophysiology/Electromyography and Motor Control*, vol. 97, no. 4, p. S73-S74.

Hamann, S. & Canli, T. 2004, "Individual differences in emotion processing.", *Current Opinion in Neurobiology*, vol. 14, no. 2, pp. 233-238.

Hamann, S. B. & Adolphs, R. 1999, "Normal recognition of emotional similarity between facial expressions following bilateral amygdala damage.", *Neuropsychologia*, vol. 37, no. 10, pp. 1135-1141.

Hanson, S. J., Matsuka, T., & Haxby, J. V. 2004, "Combinatorial codes in ventral temporal lobe for object recognition: Haxby (2001) revisited: is there a "face" area?", *NeuroImage*, vol. 23, no. 1, pp. 156-166.

Hari, R. 1991, "A neurophysiologist's view on biomagnetic source localisation.," in *Biomagnetic Localisation and 3-D modelling.* , J. Nenonen, H. M. Rajala, & T. Katila, eds., Helsinki University Press, Helsinki.

Hari, R. 1993, "Magnetoencephalography reveals functions of the human brain.", *NIPS*, vol. 8, pp. 213-215.

Hari, R. 1994, "Human cortical functions revealed by magnetoencephalography." In F. Bloom (ed), *Progress in Brain Research 100*, pp.163-168. Elsevier Science B.V.

Hari, R. 1995, "Neuromagnetic studies of human cortical functions.", *Electroencephalography and Clinical Neurophysiology/Electromyography and Motor Control*, vol. 97, no. 4, p. S21.

Hari, R. 1995, "MEG studies of human cortical functions: an introduction.", *Electroencephalography and Clinical Neurophysiology/Electromyography and Motor Control*, vol. 97, no. 4, p. S73.

Hari, R.1999, "Renaissance of human brain rhythms: from description to functional significance.", *Electroencephalography and Clinical Neurophysiology Suppl.* vol. 49 pp. 325-8.

Hari, R. & Forss, N. 1999, "Magnetoencephalography in the study of human somatosensory cortical processing. *Philosophical Transactions of the Royal Society of London. Series B - Biological Sciences*, vol. 354, no. 1387, pp. 1145-54

Hari, R. Levanen, S., Raij, T. 2000, "Timing of human cortical functions during cognition: role of MEG.", *Trends Cognitive Sciences*, vol. 4, no. 12, pp. 455-462.

Hariri, A.R., Bookheimer, S.Y., Mazziotta, J.C. 2000, "Modulating emotional responses: effects of a neocortical network on the limbic system.", *Neuroreport*, vol.17 no. 11(1) pp. 43-8.

Hariri, A. R., Tessitore, A., Mattay, V. S., Fera, F., & Weinberger, D. R. 2002, "The amygdala response to emotional stimuli: A comparison of faces and scenes.", *NeuroImage*, vol. 17, no. 1, pp. 317-323.

Hariri, A. R., Mattay, V. S., Tessitore, A., Kolachana, B., Fera, F., Goldman, D., Egan, M. F., & Weinberger, D. R. 2002, "Serotonin transporter genetic variation and the response of the human amygdala.", *Science*, vol. 297, no. 5580, pp. 400-403.

Hasselmo, M. E., Rolls, E. T., & Baylis, G. C. 1989, "The role of expression and identity in the face-selective responses of neurons in the temporal visual cortex of the monkey.", *Behavioural Brain Research*, vol. 32, no. 3, pp. 203-218.

Hasselmo, M. E., Rolls, E. T., Baylis, G. C., & Nalwa, V. 1989, "Object-centered encoding by face-selective neurons in the cortex in the superior temporal sulcus of the monkey.", *Experimental Brain Research*, vol. 75, no. 2, pp. 417-429.

Hasson, U., Avidan, G., Deouell, L. Y., Bentin, S., & Malach, R. 2003, "Face-selective activation in a congenital prosopagnosic subject.", *Journal of Cognitive Neuroscience*, vol. 15, no. 3, pp. 419-431.

Haxby, J.V., Grady, C.L., Horwitz, B. Ungerleider, L.G., Mishkin, M., Carson, R.E., Herscovitch, P., Schapiro, M.B. & Rapoport, S.I. 1991, Dissociation of object and spatial visual processing pathways in human extrastriate cortex. *Proceedings of the National Academy of Sciences of the United States of America*, vol. 88, no. 5, pp. 162-165

Haxby, J.V., Horwitz, B., Ungerleider, L.G., Maisog, J.M., Pietrini, P., Grady, C.L. 1994, "The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations.", *Journal of Neuroscience.*, vol. 14, no. 11 Pt 1, pp. 6336-53.

Haxby, J. V., Ungerleider, L. G., Clark, V. P., Schouten, J. L., Hoffman, E. A., & Martin, A. 1999, "The effect of face inversion on activity in human neural systems for face and object perception.", *Neuron*, vol. 22, no. 1, pp. 189-199.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. 2000a, "The distributed human neural system for face perception.", *Trends in Cognitive Sciences*, vol. 4, no. 6, pp. 223-233.

Haxby, J. V., Ishai, A., Chao, L. L., Ungerleider, L. G., & Martin, A. 2000b, "Object-form topology in the ventral temporal lobe.", *Trends in Cognitive Sciences*, vol. 4, no. 1, pp. 3-4.

Haxby, J. V., Ida Gobbini, M., Furey, M. L., Ishai, A., & Pietrini, P. 2001, "Distinct, overlapping representations of faces and multiple categories of objects in ventral temporal cortex.", *NeuroImage*, vol. 13, no. 6, Supplement 1, p. 891.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. 2002, "Human neural systems for face recognition and social communication.", *Biological Psychiatry*, vol. 51, no. 1, pp. 59-67.

Heilman, K. M., Scholes, R., & Watson, R. T. 1975, "Auditory Affective Agnosia: Disturbed Comprehension of Affective Speech.", *Journal of Neurology Neurosurgery and Psychiatry*, vol. 38, pp. 69-72.

Heilman, K. M. & Gilmore, R. L. 1998, "Cortical influences in emotion.", *Journal of Clinical Neurophysiology*, vol. 15, no. 5, pp. 409-423.

Heimer, L. 2000 "Basal forebrain in the context of schizophrenia.", *Brain Research and Brain Research Reviews*, vol. 31, no. 2-3, pp. 205-235

Helmholtz, H. v. (1853). "Ueber einige Gesetze der Verteilung elektrischer Stroeme in koerperlichen Leitern, mit Anwendung auf die tierisch-elektrischen Versuche.", *Annals of Physics and Chemistry* vol. 89, pp. 211-23 and 353-377

Henriques, J. B. & Davidson, R. J. 1991, "Left frontal hypoactivation in depression.", *Journal of Abnormal Psychology*, vol. 100, no. 4, pp. 535-545.

Henriques, J. B., Glowacki, J. M., & Davidson, R. J. 1994, "Reward fails to alter response bias in depression.", *Journal of Abnormal Psychology*, vol. 103, no. 3, pp. 460-466.

Hietanen, J. K. & Perrett, D. I. 1996, "Motion sensitive cells in the macaque superior temporal polysensory area: response discrimination between self-generated and externally generated pattern motion.", *Behavioural Brain Research*, vol. 76, no. 1-2, pp. 155-167.

Hillebrand, A. 2000, *The development of constrained source localisation algorithms for human imaging.*, PhD Thesis, The Wellcome Trust Laboratory for MEG Studies, Neuroscience Research Institute, Aston University.

Hillebrand, A. & Barnes, G. R. 2002, "A quantitative assessment of the sensitivity of whole-head MEG to activity in the adult human cortex.", *NeuroImage*, vol. 16, pp. 638-650.

Hillebrand, A. & Barnes, G.R. 2003, "The use of anatomical constraints with MEG beamformers.", *NeuroImage*., vol. 20 no. 4 pp. 2302-13.

Hoffman, E.A, Haxby, J.V. 2000, "Distinct representations of eye gaze and identity in the distributed human neural system for face perception." *Nature Neuroscience*., vol. 3, no.1, pp. 80-4.

Hoffman, E. A., Phillips, M. L., & Haxby, J. V. 2001, "Dynamic changes in facial configuration evoke differential strengths of activity in face-responsive neural regions.", *NeuroImage*, vol. 13, no. 6, Supplement 1, p. 1316.

Holmes, A. P., Blair, R. C., Watson, J. D., & Ford, I. 1996, "Nonparametric analysis of statistic images from functional mapping experiments.", *Journal of Cerebral Blood Flow Metabolism*, vol. 16, no. 1, pp. 7-22.

Holmes, A. P. & Friston, K. J. 1998, "Generalisability, random effects and population interferences.", *NeuroImage*, vol. 7, p. S754.

Holmes, A., Vuilleumier, P., & Eimer, M. 2003, "The processing of emotional facial expression is gated by spatial attention: evidence from event-related brain potentials.", *Cognitive Brain Research*, vol. 16, no. 2, pp. 174-184.

Hornak, J., Rolls, E. T., & Wade, D. 1996, "Face and voice expression identification in patients with emotional and behavioural changes following ventral frontal lobe damage.", *Neuropsychologia*, vol. 34, no. 4, pp. 247-261.

Huiskamp, G. 2001, "General aspects of the electrical activity of the brain." In G. Huiskamp (2001) Physics of medical imaging: EEG and MEG technologies. Available at www.mbfys.kun.nl/~geertjan/mbt2001/chapter2

Huotilainen, M., Winkler, I., Alho, K., Escera, C., Virtanen, J., Ilmoniemi, R. J., Jaaskelainen, I. P., Pekkonen, E., & Naatanen, R. 1998, "Combined mapping of human auditory EEG and MEG responses.", *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, vol. 108, no. 4, pp. 370-379.

Hyman, S. E. 1998, "Brain neurocircuitry of anxiety and fear: implications for clinical research and practice.", *Biological Psychiatry*, vol. 44, no. 12, pp. 1201-1203.

Hyman, S. E. 1998, "A new image for fear and emotion.", *Nature*, vol. 393, no. 6684, pp. 417-418.

Iidaka, T., Omori, M., Murata, T., Kosaka, H., Yonekura, Y., Okada, T., Sadato, N. 2001, "Neural interaction of the amygdala with the prefrontal and temporal cortices in the processing of facial expressions as revealed by fMRI." *Journal of Cognitive Neurosciences.*, vol. 15 no. 13(8), pp. 1035-47.

Ioannides, A. A., Liu, L., Theofilou, D., Dammers, J., Burne, T., Ambler, T., & Rose, S. 2000, "Real time processing of affective and cognitive stimuli in the human brain extracted from MEG signals.", *Brain Topography*, vol. 13, no. 1, pp. 11-19.

Ishai, A., Ungerleider, L. G., Martin, A., & Haxby, J. V. 1997, "FMRI reveals differential activation in the ventral vision pathway during the perception of objects.", *Neuroscience Letters*, vol. 237, no. Supplement 48, p. S25-S26.

Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. 1999, "Distributed representation of objects in the human ventral visual pathway.", *Proceedings of the National Academy of Sciences of the United States of America*, vol. 96, no. 16, pp. 9379-9384.

Ishai, A., Ungerleider, L. G., Martin, A., & Haxby, J. V. 2000, "The representation of objects in the human occipital and temporal cortex.", *Journal of Cognitive Neuroscience*, vol. 12 (Suppl 2), pp. 35-51.

Ishai, A., Ungerleider, L. G., & Haxby, J. V. 2000, "Distributed neural systems for the generation of visual images.", *Neuron*, vol. 28, no. 3, pp. 979-990.

Ishai, A., Haxby, J. V., & Ungerleider, L. G. 2002, "Visual imagery of famous faces: effects of memory and attention revealed by fMRI.", *NeuroImage*, vol. 17, no. 4, pp. 1729-1741.

Itier, R. J. & Taylor, M. J. 2004, "Effects of repetition learning on upright, inverted and contrast-reversed face processing using ERPs.", *NeuroImage*, vol. 21, no. 4, pp. 1518-1532.

Itier, R. J., Lobaugh, N. J., & Taylor, M. J. 2001, "The role of configural changes in face recognition, analysed by PLS.", *NeuroImage*, vol. 13, no. 6, Supplement 1, p. 686.

Jansma, J. M., Ramsey, N. F., Coppola, R., & Kahn, R. S. 2000, "Specific versus non-specific brain activity in a parametric N-back task.", *NeuroImage*, vol. 12, no. 6, pp. 688-697.

Jeffreys, D.A. 1989, "A face responsive potential recorded from the human scalp." *Experimental Brain Research*, vol. 78, no.1, pp. 193-202

Jeffreys, D.A. 1996, "Visual evoked potential evidence for parallel processing of depth– and form– related information in human visual cortex." *Experimental Brain Research*, vol. 111, no. 1, pp. 79-99

Jolicoeur, P., Gluck, M. A., & Kosslyn, S. M. 1984, "Pictures and names: Making the connection.", *Cognitive Psychology*, vol. 16, no. 2, pp. 243-275.

Jones, N. A. & Fox, N. A. 1992, "Electroencephalogram asymmetry during emotionally evocative films and its relation to positive and negative affectivity.", *Brain and Cognition*, vol. 20, no. 2, pp. 280-299.

Jonides, J., Schumacher, E. H., Smith, E. E., Koeppe, R. A., Awh, E., Reuter-Lorenz, P. A., Marschuetz, C., & Willis, C. R. 1998, "The role of parietal cortex in verbal working memory.", *Journal of Neuroscience*, vol. 18, no. 13, pp. 5026-5034.

Joseph, J. E. 2001, "Functional neuroimaging studies of category specificity in object recognition: a critical review and meta-analysis.", *Cognitive and Affective Behavioural Neuroscience*, vol. 1, no. 2, pp. 119-136.

Kanwisher, N. 2001, "Domain-specificity in face perception." *Nature Neuroscience*, vol. 3, no. 8, pp. 759-763

Kanwisher, N. 2001, "Neural events and perceptual awareness", *Cognition*, vol. 79, no. 1-2, pp. 89-113.

Kanwisher, N., Woods, R., Mazziota, J. & Iacoboni, M. 1994, "PET studies of object recognition." *Society for Neurosciences*, Abstracts, vol. 20, p. 184

Kanwisher, N., Chun, M. M., McDermott, J., & Ledden, P. J. 1996, "Functional imaging of human visual recognition", *Cognitive Brain Research*, vol. 5, no. 1-2, pp. 55-67.

Kanwisher, N., McDermott, J., & Chun, M. M. 1997, "The fusiform face area: a module in human extrastriate cortex specialized for face perception.", *Journal of Neuroscience*, vol. 17, no. 11, pp. 4302-4311

Kanwisher, N., Tong, F., & Nakayama, K. 1998, "The effect of face inversion on the human fusiform face area", *Cognition*, vol. 68, no. 1, p. B1-B11.

Kapur, N., Friston, K. J., Young, A. W., Frith, C. D., & Frackowiak, R. S. J. 1995, "Activation of human hippocampal formation during memory for faces: a PET study.", *Cortex*, vol. 31, no. 1, pp. 99-108.

Karnath, H.O., Ferber, S. & Himmelbach, M. 2001, "Spatial awareness is function of the temporal not the posterior parietal lobe." *Nature*, vol. 411, no. 6840, pp. 959-953

Kesler-West, M. L., Andersen, A. H., Smith, C. D., Avison, M. J., Davis, C. E., Kryscio, R. J., & Blonder, L. X. 2001, "Neural substrates of facial emotion processing using fMRI", *Cognitive Brain Research*, vol. 11, no. 2, pp. 213-226.

Kestenbaum, R. & Nelson, C. A. 1992, "Neural and behavioural correlates of emotion recognition in children and adults", *Journal of Experimental Child Psychology*, vol. 54, no. 1, pp. 1-18.

Ketter, T. A., George, M. S., Kimbrell, T. A., Stein, R. M., Willis, M. W., Benson, B. E., Frye, M. A., Cora-Locatelli, G., & Post, R. M. 1996, "Prefrontal and anterior paralimbic dysfunction in primary and secondary mood disorders: evidence of common neural substrates", *European Psychiatry*, vol. 11, no. Supplement 4, pp. 167s-168s.

Kibiuk, L. 2004, http://web.sfn.org/contentPublications/BrainFacts/brainfacts.pdf

Kilgore, W. D. S. & Cupp, D. W. 2002, "Mood and sex of participant in perception of happy faces", *Perceptual and Motor Skills*, vol. 95, no. 1, pp. 279-288.

Kilgore, W.D., Yurgelun-Todd, D.A. 2004a, "Sex-related developmental differences in the lateralised activation of the prefrontal cortex and amygdala during perception of facial affect.", *Perceptual Motor Skills.*, vol. 99 no. 2, pp. 371-91.

Kilgore, W.D., Yurgelun-Todd, D.A. 2004b, "Activation of the amygdala and anterior cingulate during non-conscious processing of sad versus happy faces.", *NeuroImage* vol. 21, no. 4, pp. 1215-23.

Kilts, C., Gideon, D., Egan, G., Gross, R., & Hoffman, J. 1995, "Face emotion processing and pet neuroimaging in schizophrenia", *Schizophrenia Research*, vol. 15, no. 1-2, p. 88.

Kilts, C. D., Egan, G., Gideon, D. A., Ely, T. D., & Hoffman, J. M. 2003, "Dissociable neural pathways are involved in the recognition of emotion in static and dynamic facial expressions", *NeuroImage*, vol. 18, no. 1, pp. 156-168.

Kirita, T. & Endo, M. 1995, "Happy face advantage in recognizing facial expressions", *Acta Psychologica*, vol. 89, no. 2, pp. 149-163.

Kirouac, G. & Dore, F. Y. 1983, "Accuracy and latency of judgment of facial expressions of emotions.", *Perceptual and Motor Skills*, vol. 57, no. 3 (Part1), pp. 683-686.

Kirouac, G. & Dore, F. Y. 1984, "Judgment of facial expressions of emotion as a function of exposure time.", *Perceptual and Motor Skills*, vol. 59, no. 1, pp. 147-150.

Klimesch, W. 1997, "EEG-alpha rhythms and memory processes", *International Journal of Psychophysiology*, vol. 26, no. 1-3, pp. 319-340.

Klimesch, W. 1996a, "Memory processes, brain oscillations and EEG synchronization", *International Journal of Psychophysiology*, vol. 24, no. 1-2, pp. 61-100.

Klimesch, W., Schimke, H., Doppelmayr, M., Ripper, B., Schwaiger, J., & Pfurtscheller, G. 1996b, "Event-related desynchronisation (ERD) and the Dm effect:

Does alpha desynchronisation during encoding predict later recall performance?", *International Journal of Psychophysiology*, vol. 24, no. 1-2, pp. 47-60.

Klimesch, W., Doppelmayr, M., Pachinger, T., & Ripper, B. 1997a, "Brain oscillations and human memory: EEG correlates in the upper alpha and theta band", *Neuroscience Letters*, vol. 238, no. 1-2, pp. 9-12.

Klimesch, W., Doppelmayr, M., Pachinger, T., & Russegger, H. 1997b, "Event-related desynchronisation in the alpha band and the processing of semantic information", *Cognitive Brain Research*, vol. 6, no. 2, pp. 83-94.

Klimesch, W., Doppelmayr, M., Russegger, H., Pachinger, T., & Schwaiger, J. 1998, "Induced alpha band power changes in the human EEG and attention", *Neuroscience Letters*, vol. 244, no. 2, pp. 73-76.

Klimesch, W., Russegger, H., Doppelmayr, M., & Pachinger, T. 1998, "A method for the calculation of induced band power: implications for the significance of brain oscillations", *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, vol. 108, no. 2, pp. 123-130.

Klimesch, W., Vogt, F., & Doppelmayr, M. 1999, "Inter-individual differences in alpha and theta power reflect memory performance", *Intelligence*, vol. 27, no. 4, pp. 347-362.

Klimesch, W., Doppelmayr, M., Schwaiger, J., Auinger, P., & Winkler, T. 1999, "'Paradoxical' alpha synchronization in a memory task", *Cognitive Brain Research*, vol. 7, no. 4, pp. 493-501.

Klimesch, W., Doppelmayr, M., Schwaiger, J., Winkler, T., & Gruber, W. 2000, "Theta oscillations and the ERP old/new effect: independent phenomena?", *Clinical Neurophysiology*, vol. 111, no. 5, pp. 781-793.

Klimesch, W., Doppelmayr, M., Rohm, D., Pollhuber, D., & Stadler, W. 2000, "Simultaneous desynchronisation and synchronization of different alpha responses in the human electroencephalograph: a neglected paradox?", *Neuroscience Letters*, vol. 284, no. 1-2, pp. 97-100.

Klimesch, W., Doppelmayr, M., Yonelinas, A., Kroll, N. E. A., Lazzara, M., Rohm, D., & Gruber, W. 2001, "Theta synchronization during episodic retrieval: neural correlates of conscious awareness", *Cognitive Brain Research*, vol. 12, no. 1, pp. 33-38.

Klimesch, W., Doppelmayr, M., Wimmer, H., Schwaiger, J., Rohm, D., Gruber, W., & Hutzler, F. 2001, "Theta band power changes in normal and dyslexic children", *Clinical Neurophysiology*, vol. 112, no. 7, pp. 1174-1185.

Klimesch, W., Doppelmayr, M., Wimmer, H., Gruber, W., Rohm, D., Schwaiger, J., & Hutzler, F. 2001, "Alpha and beta band power changes in normal and dyslexic children", *Clinical Neurophysiology*, vol. 112, no. 7, pp. 1186-1195.

Klimesch, W., Doppelmayr, M., Stadler, W., Pollhuber, D., Sauseng, P., & Rohm, D. 2001, "Episodic retrieval is reflected by a process specific increase in human electroencephalographic theta activity", *Neuroscience Letters*, vol. 302, no. 1, pp. 49-52.

Klimesch, W. 1999, "Brain Function and Oscillations, Vol. II: Integrative Brain Function. Neurophysiology and Cognitive Processes, edited by Erol Basar", *Trends in Cognitive Sciences*, vol. 3, no. 6, pp. 243-244.

Klimesch, W. 1999, "EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis", *Brain Research Reviews*, vol. 29, no. 2-3, pp. 169-195.

Klimesch, W., Schack, B., Schabus, M., Doppelmayr, M., Gruber, W., & Sauseng, P. 2004, "Phase-locked alpha and theta oscillations generate the P1-N1 complex and are related to memory performance", *Cognitive Brain Research*, vol. 19, no. 3, pp. 302-316.

Klopp, J., Halgren, E., Marinkovic, K., & Nenov, V. 1999, "Face-selective spectral changes in the human fusiform gyrus", *Clinical Neurophysiology*, vol. 110, no. 4, pp. 676-682.

Kohler, C. G., Turner, T., Stolar, N. M., Bilker, W. B., Brensinger, C. M., Gur, R. E., & Gur, R. C. 2004, "Differences in facial expressions of four universal emotions", *Psychiatry Research*, vol. 128, no. 3, pp. 235-244.

Kolb, B. & Taylor, L. 1981, "Affective Behaviour in Patients with Localised Cortical Excisions: Role of Lesion Site and Side", *Science*, vol. 214, pp. 89-91.

Kosaka, H., Omori, M., Murata, T., Iidaka, I., Yamada, H., Okada, T., Takahashi, T., Sadato, N., Itoh, H., Yonekura, Y., & Wada, Y. 2002, "Differential amygdala response during facial recognition in patients with schizophrenia: an fMRI study", *Schizophrenia Research*, vol. 57, no. 1, pp. 87-95.

Kozinska, D., Tretiak, O., Nissanov, J. & Ozturk, C. 1997, "Multidimensional alignment using Euclidean distance transformations. *Graphical Models and Image Processing* vol. 59, no. 6, pp. 373-387

Krause, C. M., Sillanmaki, L., Koivisto, M., Saarela, C., Haggqvist, A., Laine, M., & Hamalainen, H. 2000, "The effects of memory load on event-related EEG desynchronisation and synchronization", *Clinical Neurophysiology*, vol. 111, no. 11, pp. 2071-2078.

Krolak-Salmon, P., Fischer, C., Vighetto, A., & Mauguiere, F. 2001, "Processing of facial emotional expression: spatio-temporal data as assessed by scalp event-related potentials.", *European Journal of Neuroscience*, vol. 13, no. 5, pp. 987-994.

Krolak-Salmon, P., Androdias, G., Honnorat, J., Caudie, C., Bret, P., Hernette, D., & Vighetto, A. 2002, "Beware of optic neuritis!", *The Lancet Neurology*, vol. 1, no. 8, pp. 516-517.

Krolak-Salmon, P., Henaff, M. A., Vighetto, A., Bertrand, O., & Mauguiere, F. 2004, "Early Amygdala Reaction to Fear Spreading in Occipital, Temporal, and Frontal Cortex: A Depth Electrode ERP Study in Human", *Neuron*, vol. 42, no. 4, pp. 665-676.

Krolak-Salmon, P., Henaff, M. A., Vighetto, A., Bertrand, O., & Mauguiere, F. 2004, "Early Amygdala Reaction to Fear Spreading in Occipital, Temporal, and Frontal Cortex: A Depth Electrode ERP Study in Human", *Neuron*, vol. 42, no. 4, pp. 665-676.

Kurucz, J. & Feldmar, G. 1979, "Prosopo-affective agnosia as a symptom of cerebral organic disease.", *Journal of the American Geriatric Society*, vol. 27, no. 5, pp. 225-230.

Kurucz, J., Feldmar, G., & Werner, W. 1979, "Prosopo-affective agnosia associated with chronic organic brain syndrome.", *Journal of the American Geriatric Society*, vol. 27, no. 2, pp. 91-95.

LaBar, K.S., LeDoux, J.E., Spencer, D.D., Phelps, E.A. 1995, "Impaired fear conditioning following unilateral temporal lobectomy in humans.", *Journal of Neurosciences.*, vol. 15 no. 10 pp. 6846-55.

LaBar, K.S., LeDoux, J.E., 1996, "Partial disruption of fear conditioning in rats with unilateral amygdala damage: correspondence with unilateral temporal lobectomy in humans.", *Behavioural Neurosciences.* vol. 110, no. 5, pp. 991-7.

LaBar, K.S., Disterhoft, J.F. 1998, "Conditioning, awareness, and the hippocampus. Hippocampus.", vol. 8, no. 6 pp. 620-6.

LaBar, K. S., Gatenby, J. C., Gore, J. C., LeDoux, J. E., & Phelps, E. A. 1998, "Human amygdala activation during conditioned fear acquisition and extinction: a mixed-trial fMRI study", *Neuron*, vol. 20, no. 5, pp. 937-945.

LaBar, K. S., Gitelman, D. R., Parrish, T. B., & Mesulam, M.-M. 1999, "Neuroanatomic overlap of working memory and spatial attention networks: a functional MRI comparison within subjects", *NeuroImage*, vol. 10, no. 6, pp. 695-704.

LaBar, K. S., Parrish, T. B., Gitelman, D. R., & Mesulam, M.-M. 2000, "Impact of signal-to-noise on functional MRI of the amygdala during emotional picture encoding", *NeuroImage*, vol. 11, no. 5, Supplement 1, p. S231.

LaBar, K. S., Crupain, M. J., Voyvodic, J. T., & McCarthy, G. 2003, "Dynamic perception of facial affect and identity in the human brain", *Cerebral Cortex*, vol. 13, no. 10, pp. 1023-1033.

Lane, R. D., Fink, G. R., Chau, P. M., & Dolan, R. J. 1997, "Neural activation during selective attention to subjective emotional responses.", *Neuroreport*, vol. 8, no. 18, pp. 3969-3872.

Lane, R. D., Reiman, E. M., Ahern, G. L., Schwartz, G. E., & Davidson, R. J. 1997, "Neuroanatomical correlates of happiness, sadness, and disgust.", *American Journal of Psychiatry*, vol. 154, no. 7, pp. 926-933.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. 1990, "Emotion, Attention, and the Startle Reflex", *Psychological Review*, vol. 97, no. 3, pp. 377-395.

Lang, P. J. 1994, "The Varieties of Emotional Experience: A Meditation on James-Lange Theory", *Psychological Review*, vol. 101, no. 2, pp. 211-221.

Lang, P. J. 1995, "The Emotion Probe: Studies of Motivation and Attention", *American Psychologist*, vol. 50, no. 5, pp. 372-385.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. 1998, "Emotion, motivation, and anxiety: brain mechanisms and psychophysiology", *Biological Psychiatry*, vol. 44, no. 12, pp. 1248-1263.

Lang, P. J., Davis, M., & Ohman, A. 2000, "Fear and anxiety: animal models and human cognitive psychophysiology", *Journal of Affective Disorders*, vol. 61, no. 3, pp. 137-159.

Lawrence, N. S., Williams, A. M., Surguladze, S., Giampietro, V., Brammer, M. J., Andrew, C., Frangou, S., Ecker, C., & Phillips, M. L. 2004, "Subcortical and ventral prefrontal cortical neural responses to facial expressions distinguish patients with bipolar disorder and major depression", *Biological Psychiatry*, vol. 55, no. 6, pp. 578-587.

LeDoux, J.E. 1992, "Brain mechanisms of emotion and emotional learning.", Current Opinions in Neurobiology., vol. 2 no. 2, pp. 191-7

LeDoux, J. E. 1993a, "Emotional memory: in search of systems and synapses.", *Annuals of the New York Academy of Sciences.*, vol. 702, pp. 149-157.

LeDoux, J. E. 1993b, "Emotional memory systems in the brain.", *Behavioural Brain Research*, vol. 58, no. 1-2, pp. 69-79.

LeDoux, J. E. 1996, "Emotional networks and motor control: a fearful view.", *Progress in Brain Research*, vol. 107, pp. 437-446.

LeDoux, J. 1998, "Fear and the brain: Where have we been, and where are we going?", *Biological Psychiatry*, vol. 44, no. 12, pp. 1229-1238.

LeDoux, J. E. 2000, "Emotion circuits in the brain.", *Annual Review of Neuroscience*, vol. 23, pp. 155-184.

Leehey, S. Carey, S., Diamond, R. & Cahn, A. 1978, "Upright and inverted faces: the right hemisphere knows the difference. *Cortex*, vol. 14, no. 3, pp. 411-419

Leube, D. T., Erb, M., Grodd, W., Bartels, M., & Kircher, T. T. J. 2001, "Activation of right fronto-temporal cortex characterizes the 'living' category in semantic processing", *Cognitive Brain Research*, vol. 12, no. 3, pp. 425-430.

Leube, D. T., Erb, M., Grodd, W., Bartels, M., & Kircher, T. T. J. 2003, "Successful episodic memory retrieval of newly learned faces activates a left fronto-parietal network", *Cognitive Brain Research*, vol. 18, no. 1, pp. 97-101.

Leube, D. T., Yoon, H. W., Rapp, A., Erb, M., Grodd, W., Bartels, M., & Kircher, T. T. J. 2003, "Brain regions sensitive to the face inversion effect: a functional magnetic resonance imaging study in humans", *Neuroscience Letters*, vol. 342, no. 3, pp. 143-146.

Levy, I., Hasson, U., Avidan, G., Hendler, T., & Malach, R. 2001, "Center-periphery organization of human object areas.", *Nature Neuroscience*, vol. 4, no. 5, pp. 533-539.

Levy, J., Heller, W., Banich, M. T., & Burton, L. A. 1983, "Asymmetry of Perception in Free-Viewing of Chimeric Faces", *Brain and Cognition*, vol. 2, pp. 404-419.

Linkenkaer-Hansen, K., Palva, J. M., Sams, M., Hietanen, J. K., Aronen, H. J., & Ilmoniemi, R. J. 1998, "Face-selective processing in human extrastriate cortex around 120 ms after stimulus onset revealed by magneto- and electroencephalography", *Neuroscience Letters*, vol. 253, no. 3, pp. 147-150.

Linkenkaer-Hansen, K., Nikouline, V. V., & Ilmoniemi, R. J. 2000, "Critical dynamics in the human brain", *NeuroImage*, vol. 11, no. 5, Supplement 1, p. S760.

Lipsey, J. R., Robinson, R. G., Pearlson, G. D., Rao, K., & Price, T. R. 1983, "Mood Change Following Bilateral Hemisphere Brain Injury", *British Journal of Psychiatry*, vol. 143, pp. 266-273.

Liu, J., Harris, A., & Kanwisher, N. 2002, "Stages of processing in face perception: an MEG study.", *Nature Neuroscience*, vol. 5, no. 9, pp. 910-916.

Lopes da Silva, F. H., van Rotterdam, A., Storm van Leeuwen, W., & Tielen, A. M. 1970, "Dynamic characteristics of visual evoked potentials in dog. II. Beta-frequency selectivity in evoked potentials and background activity.", *Electroencephalography and Clinical Neurophysiology*, vol. 29, pp. 260-268.

Lopes da Silva, F. H. 1991, "Neural mechanisms underlying brain waves: from neural membranes to networks.", *Electroencephalography and Clinical Neurophysiology*, vol. 110, pp. 1842-1857.

Lopes da Silva, F. H. 1993, "Computer-assisted EEG diagnosis: Pattern recognition and brain mapping.," in *Electroencephalography: Basic principles, clinical applications and related fields.*, 3rd edn, W. Niedermeyer & F. H. Lopes da Silva, eds., Williams & Wilkins, Baltimore, MD, pp. 1063-1086.

Lu, S. T., Hamalainen, M. S., Hari, R., Ilmoniemi, R. J., Lounasmaa, O. V., Sams, M., & Vilkman, V. 1991, "Seeing faces activates three separate areas outside the occipital visual cortex in man", *Neuroscience*, vol. 43, no. 2-3, pp. 287-290.

Luu, P., Tucker, D. M., & McDougal, L. 1996, "Asymmetric current density as depressives evaluate life events", *Biological Psychiatry*, vol. 39, no. 7, p. 566.

Luu, P., Tucker, D. M., & Makeig, S. 2004, "Frontal midline theta and the error-related negativity: neurophysiological mechanisms of action regulation", *Clinical Neurophysiology*, vol. 115, no. 8, pp. 1821-1835.

Maguire, E.A., Frith, C.D. & Cipolotti, L. 2001, "Distinct neural systems for the encoding and recognition of topography and faces. *NeuroImage*, vol. 13, no. 4, pp. 43-50

Makeig, S. & Jung, T. P. 1996, "Tonic, phasic, and transient EEG correlates of auditory awareness in drowsiness", *Cognitive Brain Research*, vol. 4, no. 1, pp. 15-25.

Makeig, S., Jung, T. P., & Sejnowski, T. J. 2000, "Awareness During Drowsiness: Dynamics and Electrophysiological Correlates", *Canadian Journal of Experimental Psychology*, vol. 54, no. 4, pp. 266-273.

Makeig, S., Jung, T. P., Westerfield, M., & Sejnowski, T. J. 2001, "Imaging event-related brain dynamics", *NeuroImage*, vol. 13, no. 6, Supplement 1, p. 1309.

Makeig, S. 2002, "Response: Event-related brain dynamics - unifying brain electrophysiology", *Trends in Neurosciences*, vol. 25, no. 8, p. 390.

Makeig, S., Westerfield, M., Jung, T. P., Enghoff, S., Townsend, J., Courchesene, T., & Sejnowski, J. 2002, "Dynamic brain sources of visual evoked responses.", *Science*, vol. 295, pp. 690-694.

Makeig, S., Debener, S., Onton, J., & Delorme, A. 2004, "Mining event-related brain dynamics", *Trends in Cognitive Sciences*, vol. 8, no. 5, pp. 204-210.

Marinkovic, K., Dhond, R. P., Halgren, E., & Halgren, E. 2000, "Semantic word processing in auditory modality: Anatomically constrained MEG", *NeuroImage*, vol. 11, no. 5, Supplement 1, p. S366.

Marinkovic, K., Dhond, R. P., Dale, A. M., Glessner, M., Carr, V., & Halgren, E. 2003, "Spatiotemporal Dynamics of Modality-Specific and Supramodal Word Processing.", *Neuron*, vol. 38, no. 3, pp. 487-497.

Maulsby, R.L. 1971, "An illustration of emotionally evoked theta rhythm in infancy: hedonic hypersynchrony.", *Electroencephalography and Clinical Neurophysiology*, vol. 31, no.2, pp. 157-165

Maurer, D. & Barrera, M. E. 1981, "Infants' perception of natural and distorted arrangements of a schematic face.", *Child Development*, vol. 52, no. 1, pp. 196-202.

Mayberg, H. S., Liotti, M., Brannan, S. K., McGinnis, S., Mahurin, R. K., Jerabek, P. A., Silva, J. A., Tekell, J. L., Martin, C. C., Lancaster, J. L., & Fox, P. T. 1999, "Reciprocal limbic-cortical function and negative mood: converging PET findings in depression and normal sadness.", *American Journal of Psychiatry*, vol. 156, no. 5, pp. 675-682.

McCarthy, G. 1995, "Face perception in humans: studies of its neural localization using functional MRI, intracranial ERPs, and magnetoencephalography.", *Electroencephalography and Clinical Neurophysiology/Electromyography and Motor Control*, vol. 97, no. 4, p. S36.

McCarthy, G., Puce, A., Luby, M., Belger, A., & Allison, T. 1996, "Magnetic resonance imaging studies of functional brain activation: analysis and interpretation.", *Electroencephalography and Clinical Neurophysiology*, vol. 47, no. Suppl, pp. 15-31.

McCarthy, G., Luby, M., Gore, J. C., & Goldman-Rakic, P. 1997, "Infrequent events transiently activate human prefrontal and parietal cortex as measured by functional MRI.", *Journal Of Neurophysiology*, vol. 77, no. 3, pp. 1630-1634.

McCarthy, G., Puce, A., Belger, A., & Allison, T. 1999, "Electrophysiological studies of human face perception. II: Response properties of face-specific potentials generated in occipitotemporal cortex.", *Cerebral Cortex*, vol. 9, no. 5, pp. 431-444.

McCarthy, G., Puce, A., Constable, R. T., Krystal, J. H., Gore, J. C., & Goldman-Rakic, P. 2005, "Activation of human prefrontal cortex during spatial and non-spatial working memory tasks measured by functional MRI.", *Cerebral Cortex*, vol. 6, no. 4, pp. 600-611.

McIntosh, A. R., Grady, C. L., Haxby, J. V., Ungerleider, L. G., & Horwitz, B. 1996, "Changes in limbic and prefrontal functional interactions in a working memory task for faces.", *Cerebral Cortex*, vol. 6, no. 4, pp. 571-584.

McKeever, W. F., Van Deventer, A. D., & Suberi, M. 1973, "Avowed, assessed, and familial handedness and differential hemispheric processing of brief sequential and non-sequential visual stimuli", *Neuropsychologia*, vol. 11, no. 2, pp. 235-238.

McKelvie, S.J. 1995, "Emotional expression in upside down faces: evidence for configurational and componential processes", *British Journal of Social Psychology*, vol. 34, no. 3, pp. 325-334

Mechelli, A., Price, C. J., Noppeney, U., & Friston, K. J. 2003, "A dynamic causal modeling study on category effects: bottom-up or top-down mediation?", *Journal of Cognitive Neuroscience*, vol. 15, no. 7, pp. 925-934.

Mechelli, A., Price, C. J., Friston, K. J., & Ishai, A. 2004, "Where bottom-up meets top-down: neuronal interactions during perception and imagery.", *Cerebral Cortex*, vol. 14, no. 11, pp. 1256-1265.

Mechelli, A., Price, C. J., & Friston, K. J. 2001, "Non linear coupling between evoked rCBF and BOLD signals: A simulation study of haemodynamic responses", *NeuroImage*, vol. 13, no. 6, Supplement 1, p. 1310.

Menendez, T., Achenbach, S. Beinder, E., Hofbeck, M., Klingenhammer, L., Singer, H., Moshage, W. & Daniel, W.G. 2001 "Usefulness of magnetocardiography for the investigation of fetal arrhythmias." *American Journal of Cardiology,* vol. 88, no. 3, pp. 334-336

Milner, A. D. & Goodale, M. A. 1993, "Visual pathways to perception and action.", *Progress in Brain Research*, vol. 95, pp. 317-337.

Mineka, S. & Cook, M. 1993, "Mechanisms involved in the observational conditioning of fear.", *Journal of Experimental Psychology - General.* Vol. 122, no. 1 pp. 23-38.

Mishkin, M. & Ungerleider, L. G. 1982, "Contribution of striate inputs to the visuospatial functions of parieto-preoccipital cortex in monkeys", *Behavioural Brain Research*, vol. 6, no. 1, pp. 57-77.

Mishkin, M., Ungerleider, L. G., & Macko, K. A. 1983, "Object vision and spatial vision: two cortical pathways.", *Trends in Neurosciences*, vol. 6, pp. 414-417.

Morita, Y., Morita, K., Yamamoto, M., Waseda, Y., & Maeda, H. 2001, "Effects of facial affect recognition on the auditory P300 in healthy subjects", *Neuroscience Research*, vol. 41, no. 1, pp. 89-95.

Morris, J. S. & Dolan, R. J. 2004, "Dissociable amygdala and orbitofrontal responses during reversal fear conditioning", *NeuroImage*, vol. 22, no. 1, pp. 372-380.

Morris, J. S., Ohman, A., & Dolan, R. J. 1998, "Conscious and unconscious emotional learning in the human amygdala.", *Nature*, vol. 393, no. 6684, pp. 417-418.

Morris, J. S., Scott, S. K., & Dolan, R. J. 1999, "Saying it with feeling: neural responses to emotional vocalizations", *Neuropsychologia*, vol. 37, no. 10, pp. 1155-1163.

Morris, J. S., Buchel, C., & Dolan, R. J. 2001, "Parallel Neural Responses in Amygdala Subregions and Sensory Cortex during Implicit Fear Conditioning", *NeuroImage*, vol. 13, no. 6, pp. 1044-1052.

Morris, J. S., deBonis, M., & Dolan, R. J. 2002, "Human Amygdala Responses to Fearful Eyes", *NeuroImage*, vol. 17, no. 1, pp. 214-222.

Morris, J. S., Frith, C. D., Perrett, D. I., Rowland, D., Young, A. W., Calder, A. J., & Dolan, R. J. 1996, "A differential neural response in the human amygdala to fearful and happy facial expressions.", *Nature*, vol. 383, no. 6603, pp. 812-815.

Morris, J.S., Friston, K.J., Büchel, C., Frith, C.D., Young, A.W., Calder, A.J. & Dolan, R.J. 1998, "A neuromodulatory role for the human amygdala in processing emotional facial expressions." *Brain*, vol. 121, no. 1, pp. 47-57

Moscovitch, M. 1988, "Further analyses of masking functions in laterality studies of face-recognition." *Brain and Cognition,* vol. 7, no. 3, 377-380.

Moscovitch, M. & Radzins, M. 1987 "Backward masking of lateralised faces by noise, patterns and spatial frequency." *Brain and Cognition*, vol. 6, no. 1, pp. 72-90

Moscovitch, M. & Melo, B. 1997, "Strategic retrieval and the frontal lobes: evidence from confabulation and amnesia." *Neuropsychologia*, vol. 35, no. 7, pp. 1017-1034

Moses, Y., Ullman, S., & Edelman, S. 1996, "Generalization to novel images in upright and inverted faces.", *Perception*, vol. 25, no. 4, pp. 443-461.

Mosher, J. C., Lewis, P., & Leahy, R. M. 1992, "Multiple dipole modelling and localisation from spatio-temporal MEG data.", *IEEE Transactions on Biomedical Engineering*, vol. 39, pp. 541-557.

Mosher, J. C. & Leahy, R. M. 1998, "Recursive MUSIC: A framework for EEG and MEG source localisation.", *IEEE Transactions on Biomedical Engineering*, vol. 45, no. 11, pp. 1342-1354.

Mukamel, R., Harel, M., Hendler, T., & Malach, R. 2004, "Enhanced temporal non-linearities in human object-related occipito-temporal cortex.", *Cerebral Cortex*, vol. 14, no. 5, pp. 574-585.

Murray, J. E., Yong, E., & Rhodes, G. 2000, "Revisiting the perception of upside-down faces.", *Psychological Science*, vol. 11, no. 6, pp. 492-496.

Nakamura, A., Yamada, T., Abe, Y., Nakamura, K., Sato, N., Horibe, K., Kato, T., Kachi, T., & Ito, K. 2001, "Age-related changes in brain neuromagnetic responses to face perception in humans", *Neuroscience Letters*, vol. 312, no. 1, pp. 13-16.

Nakamura, K., Mikami, A., & Kubota, K. 1992, "Activity of single neurons in the monkey amygdala during performance of a visual discrimination task", *Journal Of Neurophysiology*, vol. 67, no. 6, pp. 1447-1463.

Nakamura, K., Sugiura, M., Kato, T., Nakamura, A., Hatano, K., Nagumo, S., Kubota, K., Fukuda, H., Kojima, S., Kawashima, R., & Ito, K. 1999, "Activation of the right inferior frontal cortex during assessment of facial emotion.", *Journal Of Neurophysiology*, vol. 82, no. 3, pp. 1610-1614.

Nakamura, K., Kawashima, R., Sato, N., Nakamura, A., Sugiura, M., Kato, T., Hatano, K., Ito, K., Fukuda, H., Schormann, T., & Zilles, K. 2000, "Functional delineation of the human occipito-temporal areas related to face and scene processing - A PET study", *Brain*, vol. 123, pp. 1903-1912.

Narumoto, J., Yamada, H., Iidaka, T., Sadato, N., Fukui, K., Itoh, H., Yonekura, Y. 2000, "Brain regions involved in verbal or non-verbal aspects of facial emotion recognition." *Neuroreport.*, vol. 3 no. 11(11) pp. 2571-6.

Nelson, C. A. & Kestenbaum, R. 1991, "Neural and behavioural correlates of emotion recognition in children", *International Journal of Psychophysiology*, vol. 11, no. 1, p. 59.

Neuper, C. & Pfurtscheller, G. 2001, "Event-related dynamics of cortical rhythms: frequency-specific features and functional correlates", *International Journal of Psychophysiology*, vol. 43, no. 1, pp. 41-58.

Nichols, T. E. & Holmes, A. P. 2002, "Nonparametric permutation tests for functional neuroimaging: a primer with examples.", *Human Brain Mapping*, vol. 15, no. 1, pp. 1-25.

Nishijo, H., Ono, T., & Nishino, H. 1988, "Single neuron responses in amygdala of alert monkey during complex sensory stimulation with affective significance.", *Journal of Neuroscience*, vol. 8, no. 10, pp. 3570-3583.

Nishijo, H., Ono, T., & Nishino, H. 1988, "Topographic distribution of modality-specific amygdalar neurons in alert monkey.", *Journal of Neuroscience*, vol. 8, no. 10, pp. 3556-3569.

Nishitani, N. 2003, "Dynamics of cognitive processing in the human hippocampus by neuromagnetic and neurochemical assessments", *NeuroImage*, vol. 20, no. 1, pp. 561-571.

Nishitani, N., Nagamine, T., Ikeda, A., & Shibasaki, H. 1995, "Late auditory event-related magnetic fields studied with whole head magnetoencephalography", *Electroencephalography and Clinical Neurophysiology/Electromyography and Motor Control*, vol. 97, no. 4, p. S123-S124.

Nishitani, N., Nagamine, T., & Shibasaki, H. 1997, "Auditory and visual novel magnetic fields studied with magnetoencephalography", *Electroencephalography and Clinical Neurophysiology*, vol. 103, no. 1, p. 201.

Nunez, P. L. 1981, *Electric fields of the brain.* Oxford University Press, Oxford / New York.

Nunez, P. L. 1986, "The brain's magnetic field: some effects of multiple sources on localisation methods.", *Electroencephalography and Clinical Neurophysiology*, vol. 63, pp. 75-82.

Nunez, P. L. 1995, *Neocortical dynamics of human EEG rhythms.* Oxford University Press, Oxford / New York.

Nyberg, L., Persson, J., & Nilsson, L. G. 2002, "Individual differences in memory enhancement by encoding enactment: relationships to adult age and biological factors", *Neuroscience & Biobehavioral Reviews*, vol. 26, no. 7, pp. 835-839.

Ojemann, J. G., Ojemann, G. A., & Lettich, E. 1992, "Neuronal activity related to faces and matching in human right non-dominant temporal cortex.", *Brain*, vol. 115, no. 1, pp. 1-13.

Orozco, S. & Ehlers, C. L. 1998, "Gender differences in electrophysiological responses to facial stimuli", *Biological Psychiatry*, vol. 44, no. 4, pp. 281-289.

Orozco, S., Wall, T. L., & Ehlers, C. L. 1999, "Influence of Alcohol on Electrophysiological Responses to Facial Stimuli", *Alcohol*, vol. 18, no. 1, pp. 11-16.

Pare, D. & Gaudreau, H 1996 "Projection cells and interneurons of the lateral and basolateral amygdala: distinct firing patterns and differential relation to theta and delta rhythms in conscious cats." *Journal of Neuroscience*, vol. 16, no. 10, pp. 3334-3350

Pare, D., Collins, D. R., & Pelletier, J. G. 2002, "Amygdala oscillations and the consolidation of emotional memories", *Trends in Cognitive Sciences*, vol. 6, no. 7, pp. 306-314.

Pascual-Marqui, R. D. 1997, "Low resolution brain electromagnetic tomography (LORETA)", *Electroencephalography and Clinical Neurophysiology*, vol. 103, no. 1, pp. 25-26.

Pascual-Marqui, R. D., Michel, C. M., & Lehmann, D. 1994, "Low resolution electromagnetic tomography: a new method for localizing electrical activity in the brain", *International Journal of Psychophysiology*, vol. 18, no. 1, pp. 49-65.

Pascual-Marqui, R.D., Esslen, M. Koch, K. & Lehmann, D. 2002, "Functional imaging with low-resolution brain electromagnetic tomography (LORETA): a review." *Methods Find Experimental Clinical Pharmacology*, vol. 24 Suppl. C, pp. 91-95

Pelletier, J. G. & Pare, D. "Role of amygdala oscillations in the consolidation of emotional memories", *Biological Psychiatry*, vol. In Press, Corrected Proof.

Penny, W. D., Kiebel, S. J., Kilner, J. M., & Rugg, M. D. 2002, "Event-related brain dynamics", *Trends in Neurosciences*, vol. 25, no. 8, pp. 387-389.

Perrett, D.I., Rolls, E.T. & Caan, W. 1982, "Visual neurons responsive to faces in monkey temporal cortex." *Experimental Brain Research*, vol. 47, no. 3, pp. 329-342

Perrett, D. I., Smith, P. A., Potter, D. D., Mistlin, A. J., Head, A. S., Milner, A. D., & Jeeves, M. A. 1984, "Neurones responsive to faces in the temporal cortex: studies of functional organization, sensitivity to identity and relation to perception.", *Human Neurobiology*, vol. 3, no. 4, pp. 197-208.

Perrett, D. I., Smith, P. A., Mistlin, A. J., Milner, A. D., & Jeeves, M. A. 1985, "Visual cells in the temporal cortex sensitive to face view and gaze direction.", *Proceedings of the Royal Society of London Series B-Biological Sciences*, vol. 223, no. 1232, pp. 293-317.

Perrett, D.I., Mistlin, A.J., Chitty, A.J., Smith, P.A., Potter, D.D., Broennimann, R. & Harries, M. 1988, "Specialised face processing and hemispheric asymmetry in man and monkey: evidence from single unit and reaction time studies." *Behavioural Brain Research*, vol. 29, no. 3, pp. 245-258

Perrett, D. I., Hietanen, J. K., Oram, M. W., & Benson, P. J. 1992, "Organization and functions of cells responsive to faces in the temporal cortex.", *Philosophical Transactions of the Royal Society of London. Series B - Biological Sciences*, vol. 335, no. 1273, pp. 23-30.

Perrett, D. I., Oram, M. W., & Ashbridge, E. 1998, "Evidence accumulation in cell populations responsive to faces: an account of generalisation of recognition without mental transformations", *Cognition*, vol. 67, no. 1-2, pp. 111-145.

Pfurtscheller, G. 1992, "Event-related synchronisation (ERS): an electrical correlate of cortical areas at rest.", *Electroencephalography and Clinical Neurophysiology*, vol. 83, pp. 62-69.

Pfurtscheller, G., Neuper, C., & Mohl, W. 1994, "Event-related desynchronisation (ERD) during visual processing", *International Journal of Psychophysiology*, vol. 16, no. 2-3, pp. 147-153.

Pfurtscheller, G., Stancak, J., & Neuper, C. 1996a, "Event-related synchronization (ERS) in the alpha band -- an electrophysiological correlate of cortical idling: A review", *International Journal of Psychophysiology*, vol. 24, no. 1-2, pp. 39-46.

Pfurtscheller, G., Stancak, J., & Neuper, C. 1996b, "Post-movement beta synchronization. A correlate of an idling motor area?", *Electroencephalography and Clinical Neurophysiology*, vol. 98, no. 4, pp. 281-293.

Pfurtscheller, G. & Lopes da Silva, F. H. 1999a, "Event-related EEG/MEG synchronisation: basic principles.", *Clinical Neurophysiology*, vol. 110, pp. 1842-1847.

Pfurtscheller, G. & Lopes da Silva, F. H. 1999b, "Functional meaning of event-related desynchronisation (ERD) and synchronisation (ERS)" in G. Pfurtscheller & F. H. Lopes da Silva, (Eds) *Handbook of electroencephalography and clinical neurophysiology.*, Elsevier

Pfurtscheller, G. 2001, "Functional brain imaging based on ERD/ERS", *Vision Research*, vol. 41, no. 10-11, pp. 1257-1260.

Phillips, C., Rugg, M.D. & Friston, K.J. 2002, "Anatomically informed basis functions for EEG source localisation: combining functional and anatomical constraints." *NeuroImage*, vol. 16, no. 3(1), pp. 678-685

Phillips, M. L., Young, A. W., Senior, C., Brammer, M., Andrew, C., Calder, A. J., Bullmore, E. T., Perrett, D. I., Rowland, D., Williams, S. C. R., Gray, J. A., & David, A. S. 1997, "A specific neural substrate for perceiving facial expressions of disgust", *Nature*, vol. 389, no. 6650, pp. 495-498.

Phillips, M. L., Bullmore, E. T., Howard, R., Woodruff, P. W. R., Wright, I. C., Williams, S. C. R., Simmons, A., Andrew, C., Brammer, M., & David, A. S. 1998a, "Investigation of facial recognition memory and happy and sad facial expression perception: an fMRI study", *Psychiatry Research-Neuroimaging*, vol. 83, no. 3, pp. 127-138.

Phillips, M. L., Young, A. W., Scott, S. K., Calder, A. J., Andrew, C., Giampietro, V., Williams, S. C. R., Bullmore, E. T., Brammer, M., & Gray, J. A. 1998b, "Neural responses to facial and vocal expressions of fear and disgust", *Proceedings of the Royal Society of London Series B-Biological Sciences*, vol. 265, no. 1408, pp. 1809-1817.

Phillips, M. L., Young, A. W., Senior, C., Brammer, M., Andrew, C., Calder, A. J., Bullmore, E. T., Williams, S. C. R., Gray, J. A., & David, A. S. 1998c, "Specific neural substrates for disgust and fear in normal and clinical groups", *Biological Psychiatry*, vol. 43, p. 247.

Phillips, M.L., Williams, L., Senior, C. Bullmore, E.T., Brammer, M.J., Andrew, C., Williams, S.C. & David, A.S. 1999, "A differential neural response to threatening and non-threatening negative facial expressions in paranoid and non-paranoid schizophrenics.", *Psychiatry Research*, vol. 92, no. 1, pp. 11-31

Phillips, M.L. Medford, N. Young, A.W., Williams, L. William, S.C.R., Bullmore, E.T, Gray, J., Brammer, M. 2001, "Time courses of left and right amygdalar responses to fearful facial expressions", *NeuroImage*, vol. 13, no. 6

Phillips, M. L. 2003, "Understanding the neurobiology of emotion perception: implications for psychiatry", *British Journal of Psychiatry*, vol. 182, pp. 190-192.

Phillips, M. L., Drevets, W. C., Rauch, S. L., & Lane, R. 2003a, "Neurobiology of emotion perception I: the neural basis of normal emotion perception", *Biological Psychiatry*, vol. 54, no. 5, pp. 504-514.

Phillips, M. L., Drevets, W. C., Rauch, S. L., & Lane, R. 2003b, "Neurobiology of emotion perception II: implications for major psychiatric disorders", *Biological Psychiatry*, vol. 54, no. 5, pp. 515-528.

Pierret, A., Peronnet, F. Echallier, J.F. 1994, "A behavioural and electrophysiological study of the comparison of size discrepant shapes. *Journal of Physiology* – Paris, vol. 88, no. 5, pp. 279-290

Pinel, J. 1997, *Biopsychology* (2nd Ed) Boston: Allyn & Bacon

Pizzagalli, D., Koenig, T., Regard, M., & Lehmann, D. 1998, "Faces and emotions: brain electric field sources during covert emotional processing", *Neuropsychologia*, vol. 36, no. 4, pp. 323-332.

Pizzagalli, D., Koenig, T., Regard, M., & Lehmann, D. 1999, "Affective attitudes to face images associated with intra-cerebral EEG source location before face viewing", *Cognitive Brain Research*, vol. 7, no. 3, pp. 371-377.

Pizzagalli, D., Lehmann, D., Koenig, T., Regard, M., & Pascual-Marqui, R. D. 2000, "Face-elicited ERPs and affective attitude: brain electric microstate and tomography analyses", *Clinical Neurophysiology*, vol. 111, no. 3, pp. 521-531.

Pizzagalli, D. A., Lehmann, D., Hendrick, A. M., Regard, M., Pascual-Marqui, R. D., & Davidson, R. J. 2002, "Affective Judgments of Faces Modulate Early Activity (~160 ms) within the Fusiform Gyri", *NeuroImage*, vol. 16, no. 3, Part 1, pp. 663-677.

Polikar, R. 1995 http://users.rowan.edu/~polikar/WAVELETS/WTpart1.html

Ponomarenko, A. A., Korotkova, T. M., & Haas, H. L. 2003, "High frequency (200 Hz) oscillations and firing patterns in the basolateral amygdala and dorsal endopiriform nucleus of the behaving rat", *Behavioural Brain Research*, vol. 141, no. 2, pp. 123-129.

Power, M.J. & Dalgleish, T. 1997, *"Cognition and emotion: from order to disorder."* Hove, England: Psychology Press

Puce, A., Allison, T., Gore, J. C., & McCarthy, G. 1995, "Face-sensitive regions in human extrastriate cortex studied by functional MRI.", *Journal Of Neurophysiology*, vol. 74, no. 3, pp. 1192-1199.

Puce, A., Allison, T., Asgari, M., Gore, J. C., & McCarthy, G. 1996, "Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study.", *Journal of Neuroscience*, vol. 16, no. 16, pp. 5205-5215.

Puce, A., Allison, T., Benton, S., Gore, J. C., & McCarthy, G. 1998, "Temporal cortex activation in humans viewing eye and mouth movements.", *Journal of Neuroscience*, vol. 18, no. 6, pp. 2188-2199.

Puce, A., Allison, T., & McCarthy, G. 1999, "Electrophysiological studies of human face perception. III: Effects of top-down processing on face-specific potentials.", *Cerebral Cortex*, vol. 9, no. 5, pp. 445-458.

Puce, A., Castiello, U., Syngeniotis, A., & Abbott, D. 2001, "The human STS integrates form and motion", *NeuroImage*, vol. 13, no. 6, Supplement 1, p. 931.

Rämä, P., Martinkauppi, S., Linnankoski, I., Koivisto, J., Aronen, H. J., & Carlson, S. 2001, "Working Memory of Identification of Emotional Vocal Expressions: An fMRI Study", *NeuroImage*, vol. 13, no. 6, pp. 1090-1101.

Rapcsak, S. Z., Comer, J. F., & Rubens, A. B. 1993, "Anomia for Facial Expressions: Neuropsychological Mechanisms and Anatomical Correlates", *Brain and Language*, vol. 45, no. 2, pp. 233-252.

Rauch, S. L., Whalen, P. J., Shin, L. M., McInerney, S. C., Macklin, M. L., Lasko, N. B., Orr, S. P., & Pitman, R. K. 2000, "Exaggerated amygdala response to masked facial stimuli in posttraumatic stress disorder: a functional MRI study", *Biological Psychiatry*, vol. 47, no. 9, pp. 769-776.

Ray, W. J. & Cole, H. W. 1985a, "EEG activity during cognitive processing: influence of attentional factors.", *International Journal of Psychophysiology*, vol. 3, no. 1, pp. 43-48.

Ray, W. J. & Cole, H. W. 1985b, "EEG alpha activity reflects attentional demands, and beta activity reflects emotional and cognitive processes.", *Science*, vol. 228, no. 4700, pp. 750-752.

Reiman, E. M., Lane, R. D., Ahern, G. L., Schwartz, G. E., Davidson, R. J., Friston, K. J., Yun, S. L., & Chen, K. 1997, "Neuroanatomical correlates of externally and internally generated human emotion.", *American Journal of Psychiatry*, vol. 154, no. 7, pp. 918-925.

Rhodes, G., Jefferey, L., Watson, T.L., Jaquet, E., Winkler, L. & Clifford, C.W.H. 1995, "Orientation-contingent face aftereffects and implications for face coding mechanisms.", *Current Biology*, vol. 14, no. 23, pp. 2119-2123

Rippon, G. (in press) Electroencephalography. In C. Senior, T. Russell & Gazzaniga (Eds) Methods of the mind: The study of human cognition. Publishers

Robinson, S. E. & Vrba, J.(1999?) "Functional Neuroimaging by Synthetic Aperture Magnetometry (SAM)." *Conference Proceedings Biomagnetism*. 11th International Conference on Biomagnetism.

Rodriguez, E., George, N., Lachaux, J. P., Renault, B., & Varela, F. J. 1999, "Perception's shadow: long-distance synchronization of human brain activity.", *Nature*, vol. 397, no. 6718, pp. 430-433.

Rolls, E. T. 1984, "Neurons in the cortex of the temporal lobe and in the amygdala of the monkey with responses selective for faces.", *Human Neurobiology*, vol. 3, no. 4, pp. 209-222.

Rolls, E. T. 1990, "A theory of emotion and its application to understanding the neural basis of emotion.", *Cognition & Emotion*, vol. 4, pp. 161-190.

Rolls, E. T. 1994, "Brain mechanisms for invariant visual recognition and learning", *Behavioural Processes*, vol. 33, no. 1-2, pp. 113-138.

Rolls, E. T. 2000, "Précis of the brain and emotion", *Behavioural and Brain Sciences*, vol. 23, no. 2, p. 177-+.

Rolls, E. T. 2000, "Memory systems in the brain", *Annual Review of Psychology*, vol. 51, pp. 599-630.

Rolls, E. T. 2003, "Vision, emotion and memory: from neurophysiology to computation", *International Congress Series*, vol. 1250, pp. 547-573.

Rolls, E. T., Baylis, G. C., & Hasselmo, M. E. 1987, "The responses of neurons in the cortex in the superior temporal sulcus of the monkey to band-pass spatial frequency filtered faces", *Vision Research*, vol. 27, no. 3, pp. 311-326.

Rolls, E. T., Critchley, H. D., Wakeman, E. A., & Mason, R. 1996, "Responses of neurons in the primate taste cortex to the glutamate ion and to inosine 5'-monophosphate", *Physiology & Behaviour*, vol. 59, no. 4-5, pp. 991-1000.

Romani, G. L. 1987, "The inverse problem in MEG studies: an instrumental and analytical perspective." *Phys Med Biol.*, 32(1) pp. 23-31.

Romani, G. L. 1989, "Fundamentals of neuromagnetism.," in *Advances in biomagnetism.*, S. J. Williamson et al., eds., Plenum Press, New York.

Rosch, E., Mervis, C. B., Gray, W. D., Johnson, D. M., & Boyes-Braem, P. 1976, "Basic objects in natural categories", *Cognitive Psychology*, vol. 8, no. 3, pp. 382-439.

Rossion, B., Delvenne, J.-F., Debatisse, D., Goffaux, V., Bruyer, R., Crommelinck, M., & Guerit, J.-M. 1999, "Spatio-temporal localization of the face inversion effect: an event-related potentials study", *Biological Psychology*, vol. 50, no. 3, pp. 173-189.

Rossion B, Gauthier I, Tarr MJ, Despland P, Bruyer R, Linotte S, & Crommelinck M 2000, "The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain.", *Neuroreport*, vol. 11, no. 1, pp. 69-74.

Rossion, B., Curran, T., & Gauthier, I. 2002, "A defence of the subordinate-level expertise account for the N170 component", *Cognition*, vol. 85, no. 2, pp. 189-196.

Rossion, B., Joyce, C. A., Cottrell, G. W., & Tarr, M. J. 2003, "Early lateralisation and orientation tuning for face, word, and object processing in the visual cortex", *NeuroImage*, vol. 20, no. 3, pp. 1609-1624.

Rusalova, M. N. & Kostiunina, M. B. 2003, "Psychophysiological study of the information theory of emotions using the model of positive emotion", *Abstract only.*

Sachs, G., Steger-Wuchse, D., Kryspin-Exner, I., Gur, R. C., & Katschnig, H. 2004, "Facial recognition deficits and cognition in schizophrenia", *Schizophrenia Research*, vol. 68, no. 1, pp. 27-35.

Sackeim, H. A. & Gur, R. C. 1978, "Lateral asymmetry in intensity of emotional expression", *Neuropsychologia*, vol. 16, no. 4, pp. 473-481.

Sala, J. B., Rama, P., & Courtney, S. M. 2003, "Functional topography of a distributed neural system for spatial and nonspatial information maintenance in working memory", *Neuropsychologia*, vol. 41, no. 3, pp. 341-356.

Salmelin R, Hari R. 1994, "Characterization of spontaneous MEG rhythms in healthy adults." *Electroencephalography and Clinical Neurophysiology*, 91(4) pp. 237-48.

Sams, M., Hietanen, J. K., Hari, R., Ilmoniemi, R. J., & Lounasmaa, O. V. 1997, "Face-specific responses from the human inferior occipito-temporal cortex", *Neuroscience*, vol. 77, no. 1, pp. 49-55.

Sarter, M. & Bruno, J.P. 2000, "Cortical cholinergic inputs mediation arousal, attentional processing and dreaming: differential afferent regulation of the basal forebrain by telencephalic and brain stem afferents.", *Neuroscience*, vol. 95, no. 4, pp. 933-952

Schendan, H. E. & Kutas, M. 2002, "Neurophysiological evidence for two processing times for visual object identification", *Neuropsychologia*, vol. 40, no. 7, pp. 931-945.

Schendan, H.E., Ganis, G. & Kutas, M. 1998, "Neurophysiological evidence for visual perceptual categorisation of words and faces within 150ms. *Psychophysiology*, vol. 35, no. 3, pp. 240-251

Scherg, M. & Berg, P. 1991, "Use of prior knowledge in brain electromagnetic source analysis.", *Brain Topography*, vol. 4, no. 2, pp. 143-150.

Schmolck, H. & Squire, L. R. 2001, "Impaired perception of facial emotions following bilateral damage to the anterior temporal lobe", *Neuropsychology*, vol. 15, no. 1, pp. 30-38.

Schneider, F., Gur, R. C., Gur, R. E., & Muenz, L. R. 1994, "Standardized mood induction with happy and sad facial expressions", *Psychiatry Research*, vol. 51, no. 1, pp. 19-31.

Schupp, H. T., Junghofer, M., Weike, A. I., & Hamm, A. O. 2003, "Attention and emotion: an ERP analysis of facilitated emotional stimulus processing", *Neuroreport*, vol. 14, no. 8, pp. 1107-1110.

Schupp, H. T., Ohman, A., Junghofer, M., Weike, A. I., Stockburger, J., & Hamm, A. O. 2004, "The Facilitated Processing of Threatening Faces: An ERP Analysis", *Emotion*, vol. 4, no. 2, pp. 189-200.

Schutter, D. J. L. G., Putman, P., Hermans, E., & van Honk, J. 2001, "Parietal electroencephalogram beta asymmetry and selective attention to angry facial expressions in healthy human subjects", *Neuroscience Letters*, vol. 314, no. 1-2, pp. 13-16.

Schutter, D. J. L. G., de Haan, E. H. F., & van Honk, J. 2004, "Functionally dissociated aspects in anterior and posterior electrocortical processing of facial threat", *International Journal of Psychophysiology*, vol. 53, no. 1, pp. 29-36.

Schweinberger, S. R., Sommer, W., & Stiller, R. M. 1994, "Event-related potentials and models of performance asymmetries in face and word recognition", *Neuropsychologia*, vol. 32, no. 2, pp. 175-191.

Schweinberger, S. R., Pfutze, E. M., & Sommer, W. 1995, "Repetition Priming and Associative Priming of Face Recognition: Evidence From Event-Related Potentials", *Journal of Experimental Psychology: Learning, Memory, and Cognition*, vol. 21, no. 3, pp. 722-736.

Schweinberger, S.R., Herholz, A. & Sommer, W. 1997, "Recognising famous voices: influence of stimulus duration and different types of retrieval cues." *Journal of Speech, Language and Hearing Research*, vol. 40, no. 2, pp. 453-563

Schweinberger, S. R. & Soukup, G. R. 1998, "Asymmetric Relationships Among Perceptions of Facial Identity, Emotion, and Facial Speech", *Journal of Experimental Psychology: Human Perception and Performance*, vol. 24, no. 6, pp. 1748-1765.

Schweinberger, S.R., Burton, A.M. & Kelly, S.W. 1999, "Asymmetric dependencies in perceiving identity and emotion: experiments with morphed faces." *Perception and Psychophysiology*, vol. 61, no. 6, pp. 1102-1115

Schweinberger, S. R., Pickering, E. C., Jentzsch, I., Burton, A. M., & Kaufmann, J. M. 2002, "Event-related brain potential evidence for a response of inferior temporal cortex to familiar face repetitions", *Cognitive Brain Research*, vol. 14, no. 3, pp. 398-409.

Schweinberger, S.R., Baird, L.M., Blumler, M., Kaufmann, J.M., Mohr, B. 2003, "Interhemispheric cooperation for face recognition but not for affective facial expressions." *Neuropsychology*, vol. 41, no. 4, pp. 407-414

Scott, S. K., Young, A. W., Calder, A. J., Hellawell, D. J., Aggleton, J. P., & Johnson, M. 1997, "Impaired auditory recognition of fear and anger following bilateral amygdala lesions", *Nature*, vol. 385, no. 6613, pp. 254-257.

Seeck, M. & Grusser, O.J. 1992, "Category-related components in visual evoked potentials: photographs of faces, persons, flowers and tools as stimuli." *Experimental Brain Research*, vol. 92, no. 2, pp. 338-49.

Sekihara, K., Takeuchi, F., Kuriki, S., Koizumi, H. 1994, "Reduction of brain noise influence in evoked neuromagnetic source localization using noise spatial correlation." *Physics and Medical Biology*, vol. 39, no.6, pp. 937-46.

Sekuler, A.B., Gaspar, C.M., Gold, J.M. & Bennett, P.J. 2004, "Inversion leads to quantitative, not qualitative, changes in face processing.", *Current Biology*, vol. 14, pp. 391-396

Senior, C. 2003, "Beauty in the brain of the beholder", *Neuron*, vol. 38, no. 4, pp. 525-528.

Serences, J. T. 2004, "A comparison of methods for characterizing the event-related BOLD timeseries in rapid fMRI.", *NeuroImage*, vol. 21, no. 4, pp. 1690-1700.

Serences, J. T., Yantis, S., Culberson, A., & Awh, E. 2004, "Preparatory activity in visual cortex indexes distractor suppression during covert spatial orienting.", *Journal of Clinical Neurophysiology*, vol. 92, no. 6, pp. 3538-3545.

Serences, J.T., Schwarzbach, J., Courtney, S.M. Golay, X. & Yantis, S. 2004, "Control of object-based attention in human cortex." *Cerebral Cortex*, vol. 14, no. 12, pp. 1346-1357

Sergent, J. 1994, "Brain-imaging studies of cognitive function. *Trends in Neuroscience*, vol. 17, no. 6, pp. 221-117

Sergent, J. & Signoret, J. L. 1992a, "Functional and anatomical decomposition of face processing: evidence from prosopagnosia and PET study of normal subjects.", *Philosophical Transactions of the Royal Society of London. Series B - Biological Sciences*, vol. 335, no. 1273, pp. 55-61.

Sergent, J. & Signoret, J. L. 1992b, "Varieties of functional deficits in prosopagnosia.", *Cerebral Cortex*, vol. 2, no. 5, pp. 375-388.

Sergent, J. & Signoret, J. L. 1994, "Implicit access to knowledge derived from unrecognised faces in prosopagnosia.", *Cerebral Cortex*, vol. 2, no. 5, pp. 389-400.

Sergent, J., Ohta, S., & MacDonald, B. 1992, "Functional neuroanatomy of face and object processing. A positron emission tomography study.", *Brain*, vol. 115, no. 1, pp. 15-36.

Sergent, J., MacDonald, B. & Zuck, E. 1994, "Structural and functional organization of knowledge about faces and proper names – a positron emission tomography study. *Attention & Performance*, vol. 15, pp. 203-228

Shuttleworth, E. C. J., Syring, V., & Allen, N. 1982, "Further observation on the nature of prosopagnosia.", *Brain and Cognition*, vol. 1, pp. 307-322.

Silberman, E. K. & Weingartner, H. 1986, "Hemispheric lateralisation of functions related to emotion", *Brain and Cognition*, vol. 5, no. 3, pp. 322-353.

Singer, W. 1990, "The formation of cooperative cell assemblies in the visual cortex.", *Journal of Experimental Biology*, vol. 153, pp. 177-197.

Singer, W., Gray, C. M., Engel, A. K., Koenig, P., Artola, A., & Brocher, S. 1990, "Formation of cortical cell assemblies.", *Cold Spring Harb Symposium Quantum Biology*, vol. 55, pp. 939-952.

Singer, W. 1993, "Synchronisation of cortical activity and its putative role in information processing and learning.", *Annual Review of Physiology*, vol. 55, pp. 349-374.

Singer, W. & Gray, C. M. 1995, "Visual feature integration and the temporal correlation hypothesis.", *Annual Review of Neuroscience*, vol. 18, pp. 555-586.

Singer, W., Engel, A. K., Kreiter, A. K., Munk, M. H. J., Neuenschwander, S., & Roelfsema, P. R. 1997, "Neuronal assemblies: necessity, signature and detectability", *Trends in Cognitive Sciences*, vol. 1, no. 7, pp. 252-260.

Singh, K. D., Holliday, I. E., Furlong, P. L., & Harding, G. F. A. 1997, "Evaluation of MEG/EEG co-registration strategies using Monte Carlo simulation.", *Electroencephalography and Clinical Neurophysiology*, vol. 102, pp. 81-85.

Singh, K. D., Barnes, G. R., Hillebrand, A., Forde, E. M. E., & Williams, A. L. 2002, "Task-Related Changes in Cortical Synchronization Are Spatially Coincident with the Haemodynamic Response", *NeuroImage*, vol. 16, no. 1, pp. 103-114.

Singh, K. D., Barnes, G. R., & Hillebrand, A. 2003, "Group imaging of task-related changes of cortical synchronisation using non-parametric permutation testing.", *NeuroImage*, vol. 19, pp. 1589-1601.

Sobotka, S.S., Davidson, R.J. & Senulis, J.A. 1992, "Anterior brain electrical asymmetries in response to reward and punishment.", *Electroencephalography and Clinical Neurophysiology*, vol. 83, no. 4, pp. 236-247

Sprengelmeyer, R., Young, A. W., Calder, A. J., Karnat, A., Lange, H., Homberg, V., Perrett, D. I., & Rowland, D. 1996, "Loss of disgust - Perception of faces and emotions in Huntington's disease", *Brain*, vol. 119, pp. 1647-1665.

Sprengelmeyer, R., Young, A. W., Sprengelmeyer, A., Calder, A. J., Rowland, D., Perrett, D., Homberg, V., & Lange, H. 1997, "Recognition of facial expressions: Selective impairment of specific emotions in Huntington's disease", *Cognitive Neuropsychology*, vol. 14, no. 6, pp. 839-879.

Sprengelmeyer, R., Rausch, M., Eysel, U. T., & Przuntek, H. 1998, "Neural structures associated with recognition of facial expressions of basic emotions.", *Proceedings of the Royal Society of London Series B-Biological Sciences*, vol. 265, no. 1409, pp. 1927-1931.

Streit, M., Wolwer, W., Ihl, R., Brinkmeyer, J., & Gaebel, W. 1997, "EEG correlates of facial affect recognition and visual object recognition in schizophrenia", *Biological Psychiatry*, vol. 42, no. 1, Supplement 1, p. 141S.

Streit, M., Ioannides, A. A., Liu, L., Wolwer, W., Dammers, J., Gross, J., Gaebel, W., & Mueller-Gartner, H. W. 1999, "Neurophysiological correlates of the recognition of facial expressions of emotion as revealed by magnetoencephalography.", *Brain Research: Cognitive Brain Research*, vol. 7, no. 4, pp. 481-491.

Streit, M., Wolwer, W., Brinkmeyer, J., Ihl, R., & Gaebel, W. 2000, "Electrophysiological correlates of emotional and structural face processing in humans", *Neuroscience Letters*, vol. 278, no. 1-2, pp. 13-16.

Streit, M., Dammers, J., Simsek-Kraues, S., Brinkmeyer, J., Wolwer, W., & Ioannides, A. 2003, "Time course of regional brain activations during facial emotion recognition in humans", *Neuroscience Letters*, vol. 342, no. 1-2, pp. 101-104.

Suberi, M. & McKeever, W. F. 1977, "Differential right hemispheric memory storage of emotional and non-emotional faces", *Neuropsychologia*, vol. 15, no. 6, pp. 757-768.

Sugase, Y., Yamane, S., Ueno, S., & Kawano, K. 1999, "Global and fine information coded by single neurons in the temporal visual cortex.", *Nature*, vol. 400, no. 6747, pp. 869-873.

Sukov, W. & Barth, D.S. 1998, "Three-dimensional analysis of spontaneous and thalamically evoked gamma oscillations in auditory cortex. *Journal of Neurophysiology*, vol. 79, no. 6, pp. 2875-2884

Surguladze, S., Brammer, M. J., Senior, C., & Phillips, M. 2001, "Differential responses to negative vs. positive facial expressions in depressive patients", *Biological Psychiatry*, vol. 49, no. 8, p. 135.

Surguladze, S., Brammer, M., & Phillips, M. 2002, "Trends in BOLD response during processing emotional cues in depression", *European Psychiatry*, vol. 17, no. Supplement 1, p. 113.

Surguladze, S. A., Brammer, M. J., Young, A. W., Andrew, C., Travis, M. J., Williams, S. C. R., & Phillips, M. L. 2003, "A preferential increase in the extrastriate response to signals of danger", *NeuroImage* , vol. 19, no. 4, pp. 1317-1328.

Surguladze, S. A., Young, A. W., Senior, C., Brebion, G., Travis, M. J., & Phillips, M. L. 2004, "Recognition Accuracy and Response Bias to Happy and Sad Facial Expressions in Patients With Major Depression", *Neuropsychology*, vol. 18, no. 2, pp. 212-218.

Suslow, T., Dannlowski, U., Lalee-Mentzel, J., Donges, U. S., Arolt, V., & Kersting, A. 2004, "Spatial processing of facial emotion in patients with unipolar depression: a longitudinal study", *Journal of Affective Disorders*, vol. 83, no. 1, pp. 59-63.

Swithenby, S. J., Bailey, A. J., Braeutigam, S., Josephs, O. E., Jousmaki, V., & Tesche, C. 1998, "Neural processing of human faces: a magnetoencephalographic study.", *Experimental Brain Research*, vol. 118, no. 4, pp. 501-510.

Talairach, J. & Tournoux, P. 1988, *Co-Planar Stereotaxic Atlas of the Human Brain.* Thieme, New York.

Tallon-Baudry, C., Bertrand, O., Bouchet, P., & Pernier, J. 1995, "Gamma-range activity evoked by coherent visual stimuli in humans.", *European Journal of Neuroscience*, vol. 7, pp. 1285-1291.

Tallon-Baudry, C., Bertrand, O., Delpeuch, C., & Pernier, J. 1996, "Stimulus specificity of phase-locked and non-phase-locked 40Hz visual responses in humans.", *Journal of Neuroscience*, vol. 16, pp. 4240-4249.

Tallon-Baudry, C., Bertrand, O., Delpeuch, C., & Pernier, J. 1997, "Oscillatory gamma-band (30-70Hz) activity induced by a visual search task in humans.", *Journal of Neuroscience*, vol. 17, no. 2, pp. 722-734.

Tallon-Baudry, C., Bertrand, O., Peronnet, F., & Pernier, J. 1998, "Induced gamma-band activity during the delay of a visual short-term memory task in humans.", *Journal of Neuroscience*, vol. 18, no. 11, pp. 4244-4256.

Tallon-Baudry, C. & Bertrand, O. 1999, "Oscillatory gamma activity in humans and its role in object representation.", *Trends in Cognitive Sciences*, vol. 3, pp. 151-162.

Tanaka, J. W. & Farah, M. J. 1993, "Parts and wholes in face recognition.", *Quarterly Journal of Experimental Psychology Section A-Human Experimental Psychology*, vol. 46, no. 2, pp. 225-245.

Tanaka, K., Saito, H., Fukada, Y., & Moriya, M. 1991, "Coding visual images of objects in the inferotemporal cortex of the macaque monkey.", *Journal Of Neurophysiology*, vol. 66, no. 1, pp. 170-189.

Taniguchi, M., Kato, A., Fujita, N., Hirata, M., Tanaka, H., Kihara, T., Ninomiya, H., Hirabuki, N., Nakamura, H., & Robinson, S. E. 2000, "Movement-Related

Desynchronisation of the Cerebral Cortex Studied with Spatially Filtered Magnetoencephalography", *NeuroImage*, vol. 12, no. 3, pp. 298-306.

Tarr, M. J. & Gauthier, I. 2000, "FFA: a flexible fusiform area for subordinate-level visual processing automat zed by expertise.", *Nature Neuroscience*, vol. 3, no. 8, pp. 764-769.

Tarr, M. J. & Gauthier, I. 1998, "Do viewpoint-dependent mechanisms generalize across members of a class?", *Cognition*, vol. 67, no. 1-2, pp. 73-110.

Taylor, M. J., McCarthy, G., Saliba, E., & Degiovanni, E. 1999, "ERP evidence of developmental changes in processing of faces", *Clinical Neurophysiology*, vol. 110, no. 5, pp. 910-915.

Taylor, M. J., Itier, R. J., Allison, T., & Edmonds, G. E. 2001a, "Direction of gaze effects on early face processing: eyes-only versus full faces", *Cognitive Brain Research*, vol. 10, no. 3, pp. 333-340.

Taylor, M. J., Edmonds, G. E., McCarthy, G., & Allison, T. 2001b, "Eyes first! Eyes-processing develops before face processing in children.", *Neuroreport*, vol. 12, pp. 1671-1676.

Tesche, C. D. 1996, "MEG imaging of neuronal population dynamics in the human thalamus." *Electroencephalography and Clinical Neurophysiology Suppl.*, vol. 47, pp.81-90.

Thompson, P. 1980, "Margaret Thatcher: a new illusion.", *Perception*, vol. 9, pp. 483-484

Tomarken, A. J., Davidson, R. J., & Henriques, J. B. 1990, "Resting frontal brain asymmetry predicts affective responses to films.", *Journal of Personality and Social Psychology*, vol. 59, no. 4, pp. 791-801.

Tomarken, A. J. & Davidson, R. J. 1994, "Frontal brain activation in repressors and nonrepressors.", *Journal of Abnormal Psychology*, vol. 103, no. 2, pp. 339-349.

Tong, F., Nakayama, K., Moscovitch, M., Weinrib, O., & Kanwisher, N. 2003, "Response Properties of the Human Fusiform Face Area", *Cognitive Neuropsychology*, vol. 17, no. 1, pp. 257-279.

Tovee, M. J. 1998a, "Face processing: Getting by with a little help from its friends", *Current Biology*, vol. 8, no. 9, p. R317-R320.

Tovee, M. J. 1998b, "Is Face Processing Special?", *Neuron*, vol. 21, no. 6, pp. 1239-1242.

Tow, P.M. & Whitty C.W. 1953, "Personality changes after operations on the cingulate gyrus in man". *Journal of Neurochemistry*, vol. 16, no. 3, pp.186-93

Tranel, D., Bechara, A., Damasio, H., & Damasio, A. R. 1998, "272 Neural correlates of emotional imagery", *International Journal of Psychophysiology*, vol. 30, no. 1-2, p. 107.

Treisman, A. M. & Kanwisher, N. G. 1998, "Perceiving visually presented objects: recognition, awareness, and modularity", *Current Opinion in Neurobiology*, vol. 8, no. 2, pp. 218-226.

Tsao, D. Y., Vanduffel, W., Sasaki, Y., Fize, D., Knutsen, T. A., Mandeville, J. B., Wald, L. L., Dale, A. M., Rosen, B. R., & Van Essen, D. C. 2003, "Stereopsis Activates V3A and Caudal Intraparietal Areas in Macaques and Humans", *Neuron*, vol. 39, no. 3, pp. 555-568.

Tucker, D. M., Watson, R. T., & Heilman, K. M. 1977, "Discrimination and Evocation of Affectively Intoned Speech in Patients with Right Parietal Disease", *Neurology*, vol. 27, pp. 947-958.

Tucker, D.M. 1981, "Lateral brain function, emotion, and conceptualisation." *Psychological Bulletin*, vol. 89, no 1, pp. 19-46.

Ukai, S., Shinosaki, K., Ishii, R., Ogawa, A., Mizuno-Matsumoto, Y., Inouye, T., Hirabuki, N., Yoshimine, T., Robinson, S. E., & Takeda, M. 2002, "Parallel distributed processing neuroimaging in the Stroop task using spatially filtered magnetoencephalography analysis", *Neuroscience Letters*, vol. 334, no. 1, pp. 9-12.

Ukai, S., Shinosaki, K., Ishii, R., Ogawa, A., Mizuno-Matsumoto, Y., Inouye, T., Hirabuki, N., Yoshimine, T., Robinson, S. E., & Takeda, M. 2002, "Spatially filtering MEG analysis estimates propagation of cortical activities during the Stroop task", *International Congress Series*, vol. 1232, pp. 409-413.

Valentine, T. 1988, "Upside down faces: A review of the effect of inversion on recognition", *British Journal of Psychology*, vol. 79, pp. 471-491.

van Honk J, Schutter DJ, d'Alfonso A, Kessels RP, Postma A, de Haan EH. 2001, Repetitive transcranial magnetic stimulation at the frontopolar cortex reduces skin conductance but not heart rate: reduced gray matter excitability in orbitofrontal regions. *Archives General Psychiatry*, vol. 58, no.10, pp. 973-4.

van Honk, J., Hermans, E. J., d'Alfonso, A. A. L., Schutter, D. J. L. G., van Doornen, L., & de Haan, E. H. F. 2002, "A left-prefrontal lateralised, sympathetic mechanism directs attention towards social threat in humans: evidence from repetitive transcranial magnetic stimulation", *Neuroscience Letters*, vol. 319, no. 2, pp. 99-102.

van Honk, J., Tuiten, A., van den Hout, M., Koppeschaar, H., Thijssen, J., de Haan, E., Verbaten, R. 1998, "Baseline salivary cortisol levels and preconscious selective attention to threat. A pilot study. *Psychoneuroendocrinology*, vol. 23, no. 7, pp. 741-747

van Honk, J., Kessels, R. P. C., Putman, P., Jaeger, G., Koppeschaar, H. P. F., & Postma, A. 2003, "Attentionally modulated effects of cortisol and mood on memory for emotional faces in healthy young males", *Psychoneuroendocrinology*, vol. 28, no. 7, pp. 941-948.

van Veen, B. D., van Drongelen, W., Yuchtman, M., & Suzuki, A. 1997, "Localisation of brain electrical activity via linearly constrained minimum variance spatial filtering.", *IEEE Transactions on Biomedical Engineering*, vol. 44, no. 9, pp. 867-880.

Vermeire, B.A. & Hamilton, C.R. 1998, "Inversion effect for faces in split-brain monkeys. *Neuropsychologia*, vol. 36, no. 10, pp. 1003-1014

Vogt, B. A., Crino, P. B., & Vogt, L. J. 1992a, "Reorganization of cingulate cortex in Alzheimer's disease: neuron loss, neuritic plaques, and muscarinic receptor binding.", *Cerebral Cortex*, vol. 2, no. 6, pp. 526-535.

Vogt, B. A., Finch, D. M., & Olson, C. R. 1992b, "Functional heterogeneity in cingulate cortex: the anterior executive and posterior evaluative regions.", *Cerebral Cortex*, vol. 2, no. 6, pp. 435-443.

von Stein, A. & Sarnthein, J. 2000, "Different frequencies for different scales of cortical integration: from local gamma to long range alpha/theta synchronization. *International Journal of Psychophysiology*, vol. 38, no. 3, pp. 301-313

Vrba, J. 1997, "Baseline optimisation for noise cancellation systems.", Proceedings – 19th International Conference, IEEE/EMBS, Chicago, Illinois

Vrba, J. 2002, "Magnetoencephalography: the art of finding a needle in a haystack", *Physica C: Superconductivity*, vol. 368, no. 1-4, pp. 1-9.

Vrba, J. & Robinson, S. E. 2001, "Signal Processing in Magnetoencephalography", *Methods*, vol. 25, no. 2, pp. 249-271.

Vuilleumier, P. 2002, "Facial expression and selective attention", *Current Opinion in Psychiatry*, vol. 15, no. 3, pp. 291-300.

Vuilleumier, P. 2002, "Perceived gaze direction in faces and spatial attention: a study in patients with parietal damage and unilateral neglect", *Neuropsychologia*, vol. 40, no. 7, pp. 1013-1026.

Vuilleumier, P. & Schwartz, S. 2000, "Modulation of visual perception by eye gaze direction in patients with spatial neglect and extinction.", *Neuroreport*, vol. 12, no. 10, pp. 2101-2104

Vuilleumier, P., Armony, J. L., Clarke, K., Husain, M., Driver, J., & Dolan, R. J. 2002, "Neural response to emotional faces with and without awareness: event-related fMRI in a parietal patient with visual extinction and spatial neglect", *Neuropsychologia*, vol. 40, no. 12, pp. 2156-2166.

Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. 2001, "Effects of Attention and Emotion on Face Processing in the Human Brain: An Event-Related fMRI Study", *Neuron*, vol. 30, no. 3, pp. 829-841.

Wang, J. Z. 1993, "Minimum-norm least-squares estimation: magnetic source images for a spherical model head." *IEEE Transactions on Biomedical Engineering*, 40(4): 387-96.

Watanabe, S., Kakigi, R., & Puce, A. 2003, "The spatiotemporal dynamics of the face inversion effect: A magneto- and electro-encephalographic study", *Neuroscience*, vol. 116, no. 3, pp. 879-895.

Werheid, K., Alpay, G., Jentzsch, I., & Sommer, W. 2005, "Priming emotional facial expressions as evidenced by event-related brain potentials", *International Journal of Psychophysiology*, vol. 55, no. 2, pp. 209-219

Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. 1998, "Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge.", *Journal of Neuroscience*, vol. 18, no. 1, pp. 411-418.

Whalen, P.J., Bush, G., McNally, R.J., Wilhelm, S., McInerney, S.C., Jenike, M.A. & Rauch, S.L. 1998, "The emotional counting Stroop paradigm: a functional magnetic resonance imaging probe of the anterior cingulate affective division.", *Biological Psychiatry*, vol. 44, pp. 1219-1228

Whalen, P. J., Shin, L. M., McInerney, S. C., Fischer, H., Wright, C. I., & Rauch, S. L. 2001, "A functional MRI study of human amygdala responses to facial expressions of fear versus anger.", *Emotion*, vol. 1, no. 1, pp. 70-83.

Wikswo Jr, J. P. 1989, "Biomagentic source and their models.," in *Advances in Biomagnetism*, S. J. Williamson et al., eds., Plenum Press, New York.

Wild, B., Erb, M., Bartels, M., & Grodd, W. 2000, "fMRI of perception of emotionally expressive faces and its interaction with facial movements.", *NeuroImage*, vol. 11, no. 5, Supplement 1, p. S829.

Wild, B., Erb, M., & Bartels, M. 2001, "Are emotions contagious? Evoked emotions while viewing emotionally expressive faces: quality, quantity, time course and gender differences.", *Psychiatry Research*, vol. 102, no. 2, pp. 109-124.

Wild, B., Erb, M., Eyb, M., Bartels, M., & Grodd, W. 2003, "Why are smiles contagious? An fMRI study of the interaction between perception of facial affect and facial movements.", *Psychiatry Research: Neuroimaging*, vol. 123, no. 1, pp. 17-36.

Williams, L. M., Senior, C., David, A. S., Loughland, C. M., & Gordon, E. 2001a, "In search of the "Duchenne smile": Evidence from eye movements.", *Journal of Psychophysiology*, vol. 15, no. 2, pp. 122-127.

Williams, L. M., Phillips, M. L., Brammer, M. J., Skerrett, D., Lagopoulos, J., Rennie, C., Bahramali, H., Olivieri, G., David, A. S., Peduto, A., & Gordon, E. 2001b, "Arousal dissociates amygdala and hippocampal fear responses: evidence from simultaneous fMRI and skin conductance recording.", *NeuroImage*, vol. 14, no. 5, pp. 1070-1079.

Williamson SJ, Kaufman L. 1990, "Evolution of neuromagnetic topographic mapping.", *Brain Topography*, vol. 3, no. 1, pp113-27.

Wilson, F.A. & Goldman-Rakic, P.S. 1994, "Viewing preferences of rhesus monkeys related to memory for complex pictures, colours and faces.", *Behavioural Brain Research*, vol. 60, no. 1, pp. 79-89

Wojciulik, E. & Kanwisher, N. 1999, "The generality of parietal involvement in visual attention.", *Neuron*, vol. 23, no. 4, pp. 747-764.

Young, A. W. 1998, *Face and mind.* Oxford University Press, Oxford.

Young, A. W., Flude, B. M., Hay, D. C., & Ellis, A. W. 1993a, "Impaired discrimination of familiar from unfamiliar faces.", *Cortex*, vol. 29, no. 1, pp. 65-75.

Young, A. W., Newcombe, F., deHaan, E. H., Small, M., & Hay, D. C. 1993b, "Face perception after brain injury. Selective impairments affecting identity and expression.", *Brain*, vol. 116, no. 4, pp. 941-959.

Young, A. W., Hellawell, D. J., VanDeWal, C., & Johnson, M. 1996, "Facial expression processing after amygdalotomy.", *Neuropsychologia*, vol. 34, no. 1, pp. 31-39.

Young, A. W., Rowland, D., Calder, A. J., Etcoff, N. L., Seth, A., & Perrett, D. I. 1997, "Facial expression megamix: Tests of dimensional and category accounts of emotion recognition.", *Cognition*, vol. 63, no. 3, pp. 271-313.

Yovel, G. & Kanwisher, N. 2004, "Face perception: domain specific, not process specific.", *Neuron*, vol. 44, no. 5, pp. 889-898.

Zarahn, E., Aguirre, G. K., & D'Esposito, M. 1997, "Empirical analyses of BOLD fMRI statistics.", *NeuroImage*, vol. 5, no. 3, pp. 179-197.

Zarahn, E., Aguirre, G. K., & D'Esposito, M. 1999, "Temporal isolation of the neural correlates of spatial mnemonic processing with fMRI.", *Cognitive Brain Research*, vol. 7, no. 3, pp. 255-268.

Zarahn, E. 2000, "Testing for neural responses during temporal components of trials with BOLD fMRI.", *NeuroImage*, vol. 11, no. 6, pp. 783-796.

Zigmond, A.S. & Snaith, R.P. 1983, "The hospital anxiety and depression scale.", *Acta Scandinavia*, vol. 67 pp. 361-370.

Zurowski, B., Gostomzyk, J., Gron, G., Weller, R., Schirrmeister, H., Neumeier, B., Spitzer, M., Reske, S. N., & Walter, H. 2002, "Dissociating a common working memory network from different neural substrates of phonological and spatial stimulus processing.", *NeuroImage*, vol. 15, no. 1, pp. 45-57.

http://www.4dneuroimaging.com/About4D/Experience.html

http://www.tristantech.com/prod_biomagnet.html

http://www.ctf.com/products/meg/ctf/overview.html

http://www.aston.ac.u.uk/lhs/research/nri/meg/intro/forward.shtml#volumeconductor

http://users.rowan.edu/~polikar/WAVELETS/WTpart1.html

http://nbs.neuro-bs.com/presentation/download

www.ece.drexel.edu/ICVC/Align/align11.html

http://www/aston.ac.uk/lhs/staff/singhkd/mri3dX/

http://cvc.edu/projects/yalefaces/yalefaces.html.

Appendix A1

TableA1: summary of the spatial correlates of face processing and facial emotional processing

Authors	Method & Experimental Design	Contrast	Findings	
Blair, Morris, Frith, Perrett & Dolan (1999)	PET; passive viewing of facial expressions	Emotional (anger) vs. neutral expressions		
Breiter et al. (1996)	**FMRI; passive viewing of facial expressions**	**Emotional (fear / happy) vs. neutral expression**	**Amygdala, fusiform gyrus**	
Critchely et al. (2000)	FMRI; passive viewing of emotional expressions (happy, angry and neutral) (Ekman & Friesen Series); task: either emotion (explicit) or gender discrimination (implicit)	Emotional (anger / happy) vs. neutral expressions	High valence facial expressions: Increases in BOLD in left inferior and lateral temporal lobe visual cortices i.e. fusiform and middle temporal gyri); left hippocampus; amygdala-hippocampal junction; pulvinar nucleus of the thalamus; bilateral cerebellum; left retro-splenium Deactivation (i.e. increases BOLD in control condition) in left insula and cerebellum; right superior temporal gyrus Explicit processing of facial expressions: Right posterior hippocampus; bilateral fusiform gyrus; left putamen; middle temporal gyrus; deactivation of right cerebellum Implicit processing of facial expressions: Left insula; inferior prefrontal lobe; bilateral amygdala-hippocampal junction; putamen; Deactivation in left inferior frontal gyrus (Broca's area); retro-splenium; cerebellum; bilateral posterior cingulate; middle temporal gyri	

			Processing mixed vs. neutral expressions: Left fusiform gyrus (BA37); right cerebellum; left peristriate (BA18); left retro-splenium (BA30); left amygdala-hippocampal junction; left posterior hippocampus; left pulvinar (thalamus) (BA27); left middle temporal gyrus (BA21);	
George et al. (1997)	**PET; Recognition of emotional expressions**	**Emotion vs. identity**		
Hariri, Bookheimer & Mazziotta (2000)	FMRI; matching and labelling of emotional expressions	Emotion (fear / anger) vs. control	Match vs. control: bilateral amygdala; right thalamus; right fusiform gyrus; Label vs. control: right PFC; right fusiform gyrus; Match vs. label: bilateral amygdala; right thalamus; Label vs. Match: right PFC; right fusiform gyrus;	
Iidaka et al. (2001)	FMRI; viewing of emotional expressions; label emotion as positive or negative, rate intensity on 5-point scale (= explicit task)	Emotional (positive / negative) vs. neutral expressions	Averaging face condition: Bilateral prefrontal cortices (BA44, BA46, BA9); fusiform gyrus (BA37); medial temporal pole; right parieto-occipital lobe; Negative minus neutral: Left amygdala; right orbito-frontal cortex (BA11); bilateral superior temporal gyrus (BA38); right middle temporal gyrus (BA21) Positive minus neutral: No significant voxels Positive minus negative expressions: Right angular gyrus (BA39) Negative minus positive expressions: Left middle temporal gyrus (BA21); left inferior frontal gyrus (BA44); left precentral gyrus (BA4)	

			Signal change in the left amygdala showed positive correlation with signal change in the left inferior frontal gyrus (BA45).	
Kesler-West et al. (2001)	FMRI; processing facial emotions (taken from Ekman & Friesen; Bowers et al.; Izard & Büchler and photographs taken in own laboratory; Upon face presentation, concentration on facial expression	Emotional (anger / fear / happy / sad) vs. neutral expressions	Anger: right fusiform gyrus (BA19, BA37, BA39); right lateral occipital gyrus (BA18); left inferior frontal gyrus (BA45, BA47); left fusiform gyrus (BA37, BA19); left precentral sulcus (BA44, BA6); superior frontal gyrus (BA9) Fear: left inferior frontal gyrus (BA47); Happy: medial frontal gyrus; cingulate sulcus (BA32, BA10) Sad: left fusiform gyrus (BA19) Neutral vs. scrambled: bilateral fusiform gyri; bilateral amygdalae / entorhinal cortices; right superior temporal sulcus; right inferior occipital gyrus; bilateral inferior frontal gyri; right angular gyrus; bilateral lingual gyri (face processing regions rather than emotional expression regions?)	
Morris, Friston, Büchel et al. (1998)	PET; viewing of facial expressions of fear or happiness (Ekman Series); gender discrimination task (implicit emotion processing)	Emotional (fear) vs. neutral expression; correlation with increasing fear and happiness intensities	Fear vs. happy: Left amygdala; left cerebellum; right superior frontal gyrus (BA6); left cingulate gyrus Happy vs. fear Right middle temporal gyrus (BA21); right putamen; left superior parietal lobule (BA5, BA7); left calcarine sulcus; Emotional vs. neutral contrast: Left occipito-temporal sulcus; right orbito-frontal cortex; left pulvinar	
Nakamura et al.	PET; passive viewing of emotional	Emotional (anger /	Right inferior frontal cortex (46 32 -4)(46 32	

(1999)	expressions coloured photographs, categorised into calm, happy, sad, angry, surprised, disgusted or others task = facial emotion discrimination (positive, i.e. happy) vs. neutral, i.e. calm vs. negative, i.e. sad or angry control task: colour discrimination; facial attractiveness	happy / sad) vs. neutral expressions	0); lateral occipital cortices (right: 34 -88 -6); left orbitofrontal cortex Left inferior frontal cortex did not exhibit any significant activation during the assessment of facial emotion Right hemisphere more active than left; no specific increases in rCBF on amygdala	
Narumoto et al. (2000)	FMRI; recognition of facial and verbal / vocal emotional expressions vs. gender discrimination (visual and vocal) thus = 4 delayed-matching tasks	Matching of emotional expressions (anger / fear / happy / surprise / sad / disgust) vs. gender matching	<u>Emotion vs. rest:</u> bilateral middle frontal gyrus (BA9); right inferior frontal gyrus (BA47); supplementary motor area (SMA) (BA6); left premotor cortex (PMC) (BA6); left sensorimotor cortex (SMC) (BA4); thalamus; midbrain; bilateral superior parietal lobe (BA7); right inferior parietal lobe (BA39); left precuneus (BA7); right inferior temporal gyrus (BA37); left fusiform gyrus (BA19); right lingual gyrus (BA18); bilateral cuneus (BA19); bilateral cerebellum <u>Emotion vs. Gender Task:</u> right inferior frontal gyrus (BA47); left fusiform gyrus (BA19, BA37); right lingual gyrus (BA18) <u>Non-verbal facial emotion matching vs. verbal facial emotion task:</u> left inferior frontal gyrus (BA10); right middle frontal gyrus (BA46); right cerebellum <u>Verbal facial emotion task vs. non-verbal facial emotion matching:</u> right lingual gyrus (BA18); left fusiform gyrus (BA19)	

Phillips, Bullmore et al. (1998)	FMRI; perception of sad and happy facial expressions (from Recognition Memory Test RMT; Warrington 1984 and Ekman & Friesen 1976). Facial expression perception task using block design; task = identification of emotional expressions	Emotional (sad / happy) vs. neutral expressions	Happy vs. Neutral: left anterior cingulate gyrus (BA24); bilateral medial frontal cortex; bilateral posterior cingulate gyri (BA23, BA30, BA31); left supramarginal gyrus (BA40); right putamen; right dorsolateral prefrontal cortex Phase analysis activation due to presentation of happy faces Sad vs. Neutral: left supramarginal gyrus (BA40); right dorsolateral prefrontal cortex (BA45); left middle occipital gyrus (BA18) Phase analysis signal increase due to presentation of neutral faces	
Phillips et al. (1999)	FMRI: passive viewing of facial expressions	Emotion (anger / fear / disgust) vs. neutral expressions		
Phillips, Young et al. (1998)	FMRI; facial expressions of fear and disgust	Emotion (fear / disgust) vs. neutral expressions		
Phillips et al. (1997)	FMRI; perception of facial expressions	Emotion (fear / disgust) vs. neutral		
Sergent, Ohta, MacDonald & Zuck (1994)	**PET; passive viewing of emotional expressions**	**Emotion vs. neutral expressions**		
Sprengelmeyer, Rausch, Eysel & Przuntek (1998)	FMRI; recognition of facial expression	Emotion (disgust / fear / anger) vs. neutral expressions		
Vuilleumier & Schwartz (2001)	FMRI; effects of attention and emotion on face processing	Emotion (fear) vs. neutral expressions		
Whalen et al. (2001)	FMRI; passive viewing of emotional expressions	Emotion (fear / anger) vs. neutral		

		expressions		
Williams et al. (2001)	FMRI; passive viewing of facial expressions	Emotion (fear) vs. neutral expressions		
Dolan et al. (1996)			Medial frontal and cingulate gyri	
Gur e al. (2002)	FMRI; Colour photographs of actors and actresses posing 5 different emotional expressions at 3 different intensities; task = emotion discrimination i.e. positive or negative (= explicit task) or age discrimination (= implicit task)	Emotion (happiness, sadness, anger, fear & disgust)	Emotion minus Age: Bilateral amygdala; left hippocampus; left parahippocampal gyrus; bilateral cingulate; bilateral fusiform gyri; left thalamus; bilateral inferior frontal gyri; Age minus Emotion: Bilateral cingulate; bilateral fusiform gyri; left thalamus; bilateral inferior frontal gyri; left occipital lobe;	
Killgore & Yurgelun-Todd (2004)	FMRI; B&W photographs of facial expressions of happiness, sadness and neutral; from Erwin et al. (1992); masked facial affect task, i.e. brief presentation of faces; task = gender discirmination	Emotional (masked) (happy, sad) vs. neutral expressions	Hypothesised activation: Masked happiness (masked by neutral expression): Left amygdala (BA28); right amygdala (BA34); left anterior cingulate (BA32, BA24); right anterior cingulate (BA32); Masked sadness (masked by neutral expressions): Left anterior cingulate (BA32) Conjunction (masked happiness plus masked sadness): Left amygdala (BA34); left anterior cingulate (BA32) Masked happiness minus masked sadness: Right amygdala (BA28); left anterior cingulate (BA23, BA24, BA10, BA24); right anterior cingulate (BA24) Masked sadness minus masked happiness:	

			Nothing significant Non-hypothesised activation: Masked happiness: Right inferior temporal gyrus (BA37); left inferior occipital gyrus (BA19) Masked sadness: Right lingual gyrus (BA18) Conjunction (masked happiness plus masked sadness): Bilateral cerebellum; right inferior temporal gyrus; right superior occipital gyrus	
Esslen et al. 2004			Happiness: left frontal, left & right temporal activation; bilateral anterior and posterior cingulate gyri; upper medial frontal regions Sadness: left and right prefrontal cortices; (trend towards significance in anterior cingulate gyrus) Disgust: anterior cingulate gyrus, left frontal cortex (trend towards significance in right frontal cortex) Anger: right frontal lobe & medial frontal gyrus; (trend towards significance in left frontal lobe) Fear: bilateral frontal lobes; right temporal lobe	
Kosaka et al. (2002)	FMRI; positive or negative facial expression discrimination task (i.e. judge which face = more emotional)	Emotional (happy / angry / disgusted / sad) vs. neutral expressions;	Positive face discrimination: bilateral amygdala	
Author	**Method & Experimental Design**	**Contrast**	**Findings**	
Pizzagalli et al. 1999	EEG; FFT dipolar approximation; Face stimuli from Szondi – test; rating of how much a face was liked			

	or disliked			
Pizzagalli et al. 2002	EEG; LORETA; Face stimuli from Szondi test; assessment of affective content / appeal (i.e. liked face / disliked face) post 'scan' NB: Szondi portraits do not display marked emotional expressions, thus according to the authors are well suited for the investigation of individual differences in affective judgement	Comparison of liked to disliked faces; of faces to control stimuli	GFP latency pf N170 = identical for liked and disliked faces (158ms); liked faces elicited a stronger N170 than disliked faces (4.47μV to 4.3μV) over bilateral occipito-parietal areas RoI – FFG: liked faces elicited stronger activity than disliked faces, overall activity significantly stronger at right compared to left sides Whole brain LORETA – liked faces evoked stronger activity than disliked faces in right parietal lobe, supramarginal gyrus (BA40) Liked faces vs. neutral faces: higher GFP for liked compared to neutral faces (as well as disliked faces)	
Eimer & Holmes (2002)	EEG; comparisons of ERPs to emotional compared to neutral stimuli; upright fearful & neutral faces, control = houses and inverted faces; task = indicate by button press immediate stimulus representations, refrain from answering all other trials	Emotional (fear) to neutral expressions	ERPs to fearful faces more positive than ERPs elicited by neutral faces ERP latency differences between fearful & neutral faces at 115ms; significant emotional expression effect in 110-150ms latency interval at fronto-central electrodes; at 155-200ms enhanced positivities for fearful faces at fronto-central electrodes; Emotional expression effects reliably fronto-central, between 250 and 1000ms; at posterior sites between 455 and 1000ms	
Esslen et al. 2004	EEG; LORETA; photographs from Ekman & Friesen series; task = place self into mood expressed by faces	Emotional (happy / sad / angry / fearful / disgusted) vs. neutral expressions	At 70ms: sad & disgust expressions At 100ms: happy, sad, disgust & fear expressions At 138 ms – 200ms: all five emotion expressions Happiness: at 138-205ms – bilateral frontal areas (trend); at 244-290ms – bilateral ventromedial frontal and temporal areas & parietal areas; at	

			361-467ms – ACC (trend) Sadness: at 103-123ms – left postcentral areas (secondary somatosensory cortex, SII; at 138-197ms – right PFC; at 220-260ms: bilateral ventromedial & orbitofrontal areas; right PFC; left and extended right temporal areas; right occipital cortex; left superior frontal cortex; 279-346ms – right frontal cortex; bilateral PCC and occipital lobe (trend); 447-474ms – right frontal, temporal and parieto-occipital areas Disgust: 138-189ms – right frontal cortex; 205-252ms – right frontal cortex; 443-478ms – bilateral frontal areas; ACC extended to premotor areas Anger: 349-431ms – right frontal lobe; superior frontal gyrus (trend); 452-467ms – right PFC Fear: 256-306ms –left temporal areas; right frontal pole (trend); 322-342ms – right temporal cortex	
Esslen et al. 2004			Strong activation in right fusiform gyrus, BA37; primary and secondary visual cortices (BA17, BA18)	
Eimer & Holmes (2002)		Upright faces vs. inverted faces; faces vs. houses	Late positivity attenuated and shorter-lived for inverted faces; ERP correlates of face recognition at 200ms; Upright vs. Inverted Faces: latency delay for inverted faces (183ms) compared to upright faces (178ms) Face vs. House: faces showed enhanced N170	
Eimer 2000			ERP correlates of face recognition at 200ms	
Bentin & Deouell			ERP correlates of face recognition at 200ms	

(2000)				
Sams et al. (1997)	MEG; ECDs; concentrate on image, no specific task	Faces vs. control stimuli (pointillised faces; everyday objects; white square on grey background)	Faces vs. pointillised faces: right occipital cortex from 120ms; differences largest at 160ms; field patterns stronger for faces compares to pointillised faces (v weak activity over occipital cortex) Faces compared to other control stimuli: non-systematic; different for each control category In all RPs, ECDs point towards the centro-parietal and occipito-parietal regions, yet outside primary projection areas MEG deflections at 80-400ms at occipital regions Inferior occipito-temporal cortex; peaking at about 150-170ms; fisrt MEG responses appear to peak at about 80-100ms, from striate and extrastriate areas	

Appendix 2

Table A2– Summary of results

200 ms	Face versus House	Face versus Scrambled	Face versus Baseline
2-8Hz			
8-13Hz			
13-25Hz	Right parietal lobe; postcentral gyrus; BA3* 33 –33 60 t = +5.54; p < 0.01 Right parietal lobe; angular gyrus* 42 -66 30 t = +4.97; p < 0.05	Right inferior parietal lobule; BA40* 39 -57 48 t =+6.27; p < 0.01 Right parietal lobe; postcentral gyrus * 36 -36 54 t =+5.35; p < 0.05 Right parietal lobe; angular gyrus* 45 –66 33 t =+5.03; p < 0.05 Right occipital lobe; subgyral regions 24 -72 -6 t =+5.83; p < 0.01 Right occipital lobe; cuneus* 18 -90 3 t =+4.99; p < 0.05	Cluster size = 1371, p < 0.01 (threshold = 2) Cluster size = 82, p < 0.05 (threshold = 4) Left temporal lobe, limbic regions -21 –9 -42 t = +4.6; p = 0.068 Left posterior lobe -21 –57 -45 t = +4.56, p = 0.076 left inferior temporal gyrus -33 –9 -45 t = +4.17, p > 0.05
25-40Hz	Cluster size = 951; p < 0.05 Right parietal lobe; precuneus*	Cluster size = 330; p < 0.05 Right parietal lobe; postcentral gyrus*	Right occipital lobe; cuneus; BA18*

	6 -69 36 vx: t =+3.77 ; p > 0.05 Right occipital lobe; cuneus; BA19* 21 -90 36 vx: t =+3.75 ; p > 0.05 Right occipital lobe; precuneus* 24 -78 24 vx: t =+3.54; p > 0.05	21 -45 66 T =+4.65; p = 0.08 Right parietal lobe; sub-gyral regions 24 -39 48 T =+4.47; p > 0.05 Cluster size = 5238; p < 0.01 In addition to above Left temporal lobe; sub-gyral regions* -27 -51 15 T =+4.39; p > 0.05	15 –84 15 t = +7.72; p < 0.005 left occipital lobe; cuneus* -3 –87 9 t = +6.73, p < 0.05 left lingual gyrus* -6 –87 0 t = +6.36, p < 0.005
5-40Hz	Right temporal lobe; superior temporal gyrus* 51 -48 18 T =+5.54; p < 0.01 Right inferior frontal gyrus; BA44* 60 9 18 T =+4.72; p < 0.05	Right temporal lobe; sub-gyral regions* 42 -66 -3 T =+6.7; p < 0.01 Right superior parietal lobule; BA7* 39 -60 51 T =+6.68; p < 0.01 Right parietal lobe; postcentral gyrus; BA3* 39 -30 36 T =+6.06; p < 0.01 Left temporal lobe; middle temporal gyrus* -54 -51 0 T =+4.88; p < 0.05 Right occipital lobe; cuneus; BA7* 18 -78 27 T =+5.03; p < 0.05 Right limbic lobe* 36 -6 -36 T =+5.88; p < 0.01	

500ms	Face versus House	Face versus Scrambled	
2-8Hz			
8-13Hz	Right cerebellum; posterior lobe* 45 -84 -33 T = +5.44; p < 0.05 Right inferior occipital gyrus* 30 -99 -15 T = +4.19; p = 0.184	Right middle occipital gyrus* 33 -87 15 T = +6.09; p < 0.01	
13-25Hz	Right temporal lobe; sub-gyral regions* 33 -66 6 **T = +5.61 ; p < 0.005** Right parietal lobe; sub-gyral regions* 27 -54 30 T = +5.56 ; p < 0.01 Right parietal lobe; angular gyrus* 42 -69 30 T = +5.49 ; p < 0.01 **Left parietal lobe; sub-gyral regions*** -21 -45 48 T = +4.99 ; p < 0.05	Right temporal lobe; superior temporal gyrus* 45 -57 15 T = +6.51; p < 0.005 Right cerebellum; sub-lobar regions* 27 -42 24 T = +6.23 ; p < 0.005 Right inferior parietal lobule* 36 -54 39 T = +5.21; p < 0.05 Left inferior parietal lobule* -30 -51 45 t = +4.33; p < 0.05	
25-40Hz	Right occipital lobe; sub-gyral regions* 24 -72 27 T = +5.33 ; p < 0.01 Right parietal lobe; precuneus* 15 -66 33	Right parietal lobe; postcentral gyrus* 33 -36 54 T = +6.52 ; p < 0.005 Right parietal lobe; sub-gyral* 33 -54 39	

	T = +5.21; p < 0.01 Right limbic lobe; cingulate gyrus; BA31* 12 -45 36 T = +4.83 ; p < 0.05 Right parietal lobe; precuneus; BA7* 12 -42 51 T = +4.77 ; p < 0.05 Left parietal lobe; postcentral gyrus* 51 -27 57 T = +4.6; p < 0.05 Left inferior frontal gyrus^ -36 21 -6 T = -5.14; p < 0.05	T = +5.72 ; p < 0.01 Right temporal lobe; superior temporal gyrus* 45 -45 15 T = +4.93 ; p < 0.05 Left frontal lobe; sub-gyral regions* -18 21 27 T = +4.8 ; p < 0.05	
5-40Hz			

TableA2:Significant results as revealed in SnPM for the two time-windows. Results significant at cluster level are underlined, the size and significance level of the cluster are given. All other results reached significance at voxel level.
^ denotes decreases in event-related spectral power; * denotes increases in event-related spectral power.

Appendix A3

Table A3– Summary of results

400 ms	Upright face versus Baseline	Inverted face versus baseline	Upright face versus inverted face
2-8Hz			
8-13Hz			
13-25Hz	Right parietal lobe, precuneus, BA7^ 6 -60 51 t = -5.44, p < 0.05 Left parietal lobe, precuneus^ -9 -75 45 t = -5.3, p < 0.05	Left occipital lobe cuneus, BA19^ -15 -84 30 t = -7.16, p < 0.01 Right superior parietal lobule^ 27 -72 48 t = -6.95, p < 0.01 Right parietal lobe; precuneus area^ 12 -69 48 t = -6.64, p < 0.05 Right middle occipital gyrus^ 27 -84 0 t = -5.34, p < 0.05	
25-40Hz	Right middle occipital gyrus^ 30 -84 12 t = -5.75, p < 0.05 Right parietal lobe; postcentral gyrus: BA2^ 24 -42 69 t = -5.41, p < 0.05	Cluster size = 1611, p < 0.05 Right temporal lobe^ 51 -54 -9 t = -4.59 Cluster size = 216, p < 0.05 Left inferior temporal gyrus, BA20^	

		-33 -9 -45 t = -4.98	
5-40Hz			
200 ms	**Upright face versus Baseline**	**Inverted face versus baseline**	**Upright face versus inverted face**
2-8Hz			
8-13Hz	Left posterior lobe* -45 –69 -48 t = +5.17, p < 0.05	Right middle temporal gyrus* 36 –78 21 t = +5.26, p < 0.05 Right middle temporal gyrus, BA39* 51 –75 24 t = +5.41, p < 0.05	
13-25Hz			
25-40Hz			
5-40Hz	Cluster size = 515, p < 0.05 Right occipital lobe, lingual gyrus, BA18 3 –90 –9 t = 4.83 Right occipital lobe, BA18 6 –87 6 t = 4.23	Right middle temporal gyrus 42 –66 21 t = +6.77, p < 0.01 Right occipital lobe, sub-gyral regions 27 –72 24 t = +6.3; p < 0.01 Right occipital lobe, cuneus	

		-15 –90 15 t = + 6.2, P < 0.01 Right occipital lobe, lingual gyrus 9 –87 -15 t = +5.42, p < 0.05 Left superior frontal gyrus^ -30 54 -9 t = - 5.38, p < 0.05	

TableA3:Significant results as revealed in SnPM for the two time-windows. Results significant at cluster level are underlined, the size and significance level of the cluster are given.All other results reached significance at voxel level.
^ denotes decreases in event-related spectral power; * denotes increases in event-related spectral power.

Appendix 4

Table A4– Summary of results

	Happy versus Sad Faces	**Happy versus Scrambled**	**Sad versus Scrambled**	**All faces versus Scrambled Images**
2-8Hz				
8-13Hz		**400ms** cluster size = 619, $p < 0.05$ Left middle frontal gyrus* -27 42 57 T = +5.39, $p < 0.05$		
13-25Hz		**400ms** **cluster size = 4** **Left superior frontal gyrus*** -12 51 24 T = +4.94, $p < 0.05$		**200ms** cluster size = 1823, $p < 0.05$ **Left middle frontal gyrus^** -36 45 30 T = -5.74; **400ms** cluster size = 6770, $p < 0.05$ Left superior frontal gyrus* 48 39 -27 T = + 5.43
25-				**200ms** cluster size = 5619, $p < 0.05$

40Hz		**400ms** cluster size = 1394, $p < 0.05$ Right limbic lobe; parahippocampal gyrus, amygdala* -27 42 57 T = +4.54,		Left temporal lobe; fusiform gyrus; BA37 ^ -51 -45 -24 T = -4.17; Left cerebellum, culmen^ -3 -57 -24 T = -3.85; Left middle temporal gyrus^ T = -3.78; -60 -45 -6
5-40Hz				

Table A4: Significant results as revealed in SnPM. Significance is reached at cluster level, the size and significance levels of the cluster are given. ^ denotes decreases of event-related spectral power; * denotes increases in event-related spectral

Appendix 5

400 ms	Happy versus Sad	Happy versus Neutral	Sad versus Neutral
2-8Hz			
8-13Hz	Cluster size = 17, $p < 0.05$ right middle frontal gyrus, BA9 15 63 21 t = -5.6 right superior frontal gyrus 57 18 36 t = -5.6		
13-25Hz			
25-40Hz			
5-40Hz			
400 ms	**Happy versus Sad**	**Happy versus Neutral**	**Sad versus Neutral**
2-8Hz			
8-13Hz			

13-25Hz			
25-40Hz		Cluster size = 1126, P < 0.05 Right frontal lobe, sub-gyral regions* 24 24 –3 t = + 4.97, p < 0.05 vx: p = 0.065	
5-40Hz			
200 ms	**Happy versus baseline**	**Sad versus baseline**	**Neutral versus baseline**
2-8Hz			
8-13Hz			
13-25Hz	Cluster size = 7242m P < 0.05 Left frontal lobe, precentral gyrus^ -48 –3 39 t = -4.66 Left medial frontal gyrus, BA6 -57 3 48 t = -4.59		
5-40Hz	Cluster size = 5713, p < 0.05		Right superior parietal

	Right middle frontal gyrus^ 36 0 60 t = -4.81 Left superior frontal gyrus^ -18 54 27 t = -3.9		lobule 30 -57 40 t = +6.37, p < 0.05
All faces versus baseline	**200 ms**	**400**	
2-8Hz			
8-13Hz	Left occipital lobe, cuneus, BA19* -3 96 25 t= +4.2, p > 0.05		
13-25Hz			
25-40Hz			
5-40Hz	Left occipital lobe, lingual gyrus BA18* -18 -81-3 t = +4.8, P < 0.05		

TableA5:Significant results as revealed in SnPM for both time-windows. Results significant at cluster level are underlined, the size and significance level of the cluster are given. All other results reached significance at voxel level.
^ denotes decreases in event-related spectral power; * denotes increases in event-related spectral power.