

**EFFECTS OF SPATIAL FREQUENCY ON THE M170
NEUROMAGNETIC RESPONSE TO FACES AND
OBJECTS: A DEVELOPMENTAL MEG STUDY**

by

Jennifer Barrie
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APPROVAL

Name: Jennifer Barrie

Degree: Master of Arts (Psychology)

Title of Thesis: Effects of Spatial Frequency on the M170
Neuromagnetic Response to Faces and Objects:
A Developmental MEG Study

Chair: Dr. John McDonald
Assistant Professor

Dr. Mario Liotti
Senior Supervisor
Associate Professor

Dr. Anthony Herdman
Supervisor
Assistant Professor

External Examiner: Dr. Jason Barton
Professor
Division of Neurology
Department of Medicine
University of British Columbia

Date Defended : July 24, 2007



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ABSTRACT

Previous research suggests that adults more accurately identify faces in Low Spatial Frequency (LSF), which is supported by holistic processing, compared to High SF, supported by localized processing. The current study used magnetoencephalography to record the face-specific neuromagnetic M170 response to faces and butterflies presented in LSF, Broad SF and HSF. Child, adolescent and adult participants made face/object discriminations. Sensors of interest over left and right occipito-temporal scalp regions were grand-averaged over the 6 conditions. Results indicated that the peak M170 neuromagnetic response was greater and occurred earlier with increasing age. In adults, LSF faces elicited an earlier peak response compared to HSF faces. Similarly, in adolescents LSF faces elicited an earlier peak M170 response than HSF faces; however, in children there was no effect of SF on the latency of the peak M170 response. Results suggest an advantage of holistic face processing in adolescents and adults, but not children.

Keywords: Face processing, M170, Development, Magnetoencephalography

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1: GENERAL INTRODUCTION

Faces are an integral part of our everyday social interactions and are an essential component of interpersonal relationships and socio-emotional functioning (Adolphs, Sears, & Piven, 2001). From a very young age, children orient preferentially to faces, looking longer at human faces and tracking a face-like object with more interest and for a greater extent of time compared to any other object (Henderson, McCulloch, & Herbert, 2003; Morton & Johnson, 1991). This preference ensures that infants receive a wealth of exposure to faces early in life, as they are more likely to notice faces than other objects. Perhaps as a result of this vast amount of exposure to faces, humans develop expertise in face processing and face recognition (Tanaka, 2001; for an alternative explanation see, Kanwisher, 2000).

It is still not clear what the underlying properties of human faces are that allow them to be processed so efficiently and at such a young age, but one possible candidate is spatial frequency content. Infants show a low spatial frequency advantage for individual face recognition at birth (de Heering, Turati, Rossion, Bulf, Goffaux, & Simion, in press). Other authors have suggested that it is the first- and second-order configuration of a face that facilitates face processing (Hayden, Ramesh, Corbly, & Joseph, 2007; Johnson, 2005). First-order configuration refers to the fact that two eyes are above a nose, above a mouth; whereas second-order relational information refers to the distance

between eyes or the distance between the nose and the mouth. Studies have shown that by five months of age, infants are sensitive to disruption of first- and second-order configuration, evidenced by inverting faces or changing the distance between the eyes (Hayden et al., 2007). Similarly, some authors have proposed that it is the structural characteristics of a face that attract an infant's attention. These characteristics include that faces are top-heavy (i.e. more stimulus content in the upper half of a face), a characteristic for which infants show a visual preference as demonstrated by studies showing that infants look preferentially at stimuli with dark elements in the upper half of a ovular shape (Johnson, 2005; Macchi Cassia, Valenza, Pividori & Simion, 2002), and that there are congruent spatial relations between the inner features and the outer contour of a face (Macchi Cassia et al., 2002; Turati, Valenza, Leo, & Simion, 2005).

Despite this early preference for faces, children are consistently poorer at identifying and recognizing faces than adults. One possible explanation for this observation is that children rely primarily on the featural information to identify, recognize and derive information from faces whereas adults seem to rely on the general gestalt of the face (Carey & Diamond, 1977; Schwarzer, 2000; Turati et al., 2005). The goal of the current study was to examine the effect of spatial frequency modulations on face and object processing and track the developmental course of its effect.

Holistic Face Processing in Adults

In 1969, Yin identified that humans were disproportionately impaired at recognizing inverted faces compared to any other inverted object. In this paper, Yin tentatively proposed that the reason for this disproportionate impairment was that humans rely on the general configuration of the whole face to identify it (1969). Since then, much research has been conducted, replicating the face inversion effect and supporting the hypothesis that faces are processed holistically (e.g. Farah, Tanaka, & Drain, 1995; Tanaka & Farah, 1993).

Holistic processing refers to perceiving a face as a single whole, a gestalt (Taylor, Batty, & Itier, 2004), and the holistic processing hypothesis states that a face is encoded as a whole, and is not broken down into its individual features (Itier & Taylor, 2004b). This is advantageous for rapidly deriving information from faces. However, it results in disproportionately impaired processing when the face can no longer be processed as a whole. When faces are inverted, for example, the first-order configuration and the overall gestalt of the face are disrupted. As such, the face can no longer be perceived as a single gestalt, and must be processed featurally, relying on individual facial features to identify it as a face (Rossion, Gauthier, Goffaux, Tarr, & Crommelink, 2002). The consequence of such featural processing is the disproportionately delayed response time and decreased accuracy at identifying an inverted face compared to an upright faces (Rossion et al., 2002; Yin, 1969).

Since Yin's paper (1969), numerous tasks have been designed to examine holistic face processing (Maurer, Le Grand, & Mondloch, 2002 for a

review). Two very commonly used behavioural paradigms include the part-whole paradigm and the composite face paradigm (Goffaux & Rossion, 2006). In their seminal study using the part-whole paradigm, Tanaka and Farah (1993) demonstrated that participants who were trained to name a series of faces were better at identifying facial features embedded in the whole face than when the features were presented in isolation. This part-whole effect has since been replicated using unfamiliar stimuli, with participants consistently identifying features of a face better when presented within the whole face than when presented separately (Farah, Wilson, Drain, & Tanaka, 1998; Goffaux & Rossion, 2006). This paradigm demonstrates that face parts are processed in reference to other parts of the face as the recognition of features is facilitated when presented within the whole face.

Correspondingly, Young, Hellawell and Hay (1987) found that participants were significantly slower to name the top half of a familiar face when it was combined with a bottom half of a different familiar face, compared to when the top and bottom parts of a same face were misaligned. This finding has since been replicated in multiple studies with unfamiliar faces (e.g. Le Grand, Mondloch, Maurer, & Brent, 2004; Goffaux & Rossion, 2006) and suggests that healthy adults look at the whole face, even when attempting to recognize only half. This further supports that faces are processed holistically.

Spatial Frequency and Face Processing

More recently, studies presenting faces in different spatial frequencies have been used to determine how faces are processed. The visual system

receives input from the outside world in complex luminance arrays that are broken down into distinct neural signals, representing luminance across various spatial regions. Spatial frequencies refer to luminance variations at different scales, and different spatial frequencies convey different types of information for visual processing (Goffaux & Rossion, 2006). Low spatial frequencies (LSF) represent coarse visual information, whereas high spatial frequencies (HSF) represent fine visual information, as demonstrated in Figure 1-1. Studies have further reported a linear relationship between spatial frequency and reaction time, with reaction times increasing with spatial frequency (Greenlee & Breitmeyer, 1989) whereas others have identified an overall advantage for holistic processing, labelled the global advantage (Amirkhiabani & Lovegrove, 1999). This was especially relevant to face processing whereby, LSF relays coarser information, such as shading cues or pigmentation, more conducive to holistic processing, and HSF conveys information pertinent to analyzing the featural cues of the face, supported by localized processing (Goffaux & Rossion, 2006). It is thought that there is an adaptive, evolutionary advantage in being able to quickly recognize a familiar face and recognize information about sex, age and mood in faces at an early age (e.g. Kanwisher & Yovel, 2006; Turati et al., 2005), and the ability to process faces based on the coarse information provided by LSF may provide this underlying mechanism.

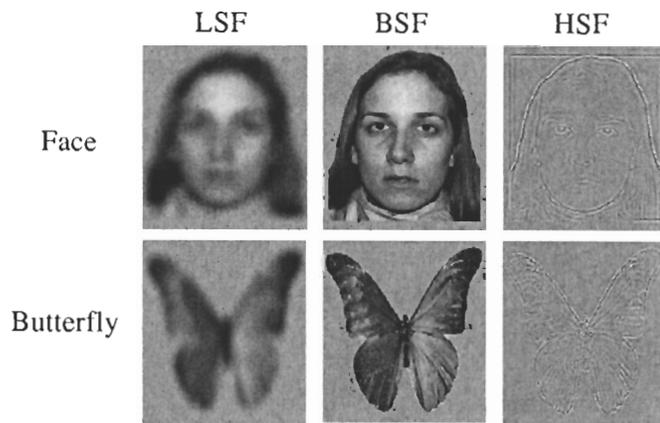


Figure 1-1 Example of faces and butterflies presented in LSF, broad-band spatial frequency and HSF.

In a series of behavioural studies, Goffaux and Rossion (2006) demonstrated that holistic face processing was supported by LSF. This study employed the traditional part-whole and composite face paradigms and presented faces in LSF, HSF and medium range spatial frequency. Goffaux and Rossion demonstrated greater impairment at identifying facial features presented in isolation and greater difficulty identifying the top half of a face when it was combined with a different bottom, when the face was presented in LSF than when presented in HSF. They interpreted these findings as indicating that LSF supports holistic processing, as participants showed greater impairment on tasks designed to assess holistic processing when faces were presented in LSF (2006).

Given the vast amount of research suggesting that faces are processed holistically, as demonstrated in various studies using the face inversion effect, the whole-part paradigm, and the composite face effect (e.g. Farah et al., 1995;

Goffaux, Gauthier, & Rossion, 2003; Maurer et al., 2002; Savig & Bentin, 2001; Tanaka & Farah, 1993; Young et al., 1987; Yin, 1969), it can be presumed that faces are better processed in LSF. However, this has not yet been conclusively determined. Whereas some studies suggest a LSF advantage for face processing (e.g. Goffaux & Rossion, 2006; Halit, de Haan, Schyns, & Johnson, 2006), other studies have found that medium-range spatial frequencies are critical for face recognition (e.g. Costen, Parker, & Craw, 1996). In light of such inconsistencies in the literature, it has been proposed that the spatial frequency bands required for face processing depend on the task at hand (e.g. Schyns, 1998; Schyns & Oliva, 1999). In their review, Ruiz-Soler and Beltran proposed that more demanding tasks, such as an identification task, benefits from processing the higher spatial frequencies (2006); leading one to conclude that for a simpler task, such as the face-object discrimination task that was employed in my studies, participants would benefit from relying primarily on lower spatial frequencies. Goffaux and colleagues came to a similar conclusion in a study where participants were asked to identify differences between a distracter face and a target face (Goffaux, Hault, Michel, Vuong, & Rossion, 2005). When the difference between faces was at the configural level (e.g. metric distance between the eyes), participants were better at detecting the difference when faces were presented in LSF. Conversely, when the difference was featural (e.g. eyes, nose or mouth), there was a performance advantage when faces were presented in HSF (Goffaux et al., 2005).

The Neural Mechanisms of Face Processing in Adults

Early neural markers of Face Processing: M/N170 and M/P100

In recent years, electroencephalography (EEG) and magnetoencephalography (MEG) have proven to be powerful tools at understanding the neural mechanisms of face processing. Studies using EEG and MEG have revealed selective responses to faces compared to nonface objects elicited within 200 ms from face onset. One of the most reliable findings from studies using EEG is a component of the event-related potential (ERP) showing preferential response to faces compared to nonface objects. Identified by Bentin and colleagues in 1996, many studies have since replicated this finding and examined the properties of this so called face-specific N170 component (e.g. Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000; Itier & Taylor, 2004a; Itier & Taylor, 2004b; Savig & Bentin, 2001). The N170 is a negative deflection occurring approximately 170 ms after stimulus onset that shows an earlier and greater peak response to faces, and parts of faces (specifically the eyes) (Eimer, 1998) compared to nonface objects (Bentin et al., 1996; Eimer, 2000; Itier & Taylor, 2004a; Itier & Taylor, 2004b; Savig & Bentin, 2001). This negative polarity is largest over the posterior-inferior scalp areas above the temporal-occipital lobes, with a more robust modulation over the right hemisphere than the left (Bentin et al., 1996; Bentin & Deouell, 2000; Itier & Taylor, 2004a; Savig & Bentin, 2001). The N170 is thought to be associated with an early visual mechanism involved with the analysis of features and early recognition of the face (Liu, Harris & Kanwisher, 2002).

A component occurring within the first 140 ms to 200 ms after stimulus onset has also been identified using MEG. Recorded maximally on posterior-lateral sensors, this component, the M170, often shows similar sensitivity to faces compared to other objects as the N170 (e.g. Itier, Herdman, George, Cheyne, & Taylor, 2006; Liu, et al., 2002; Xu, Liu, & Kanwisher, 2005), although it does not always behave like the N170 and whether or not this is the magnetic equivalent of the N170 remains debated (Itier et al., 2006).

Modulation of an earlier ERP component, the P1, (occurring approximately 100ms after stimulus onset), has also been reported in the face ERP literature. The P1 has been reliably found for visual stimuli and is sensitive to contrast; however, whether or not it reflects an early face processing mechanism remains unclear. Some studies have reported that, from a young age, the latency of the P1 is shorter for faces compared to other objects (e.g. Itier & Taylor, 2002b). Similarly, the M100, has also been identified in recent MEG studies as showing greater peak amplitude in response to faces compared to other objects over occipital sites (Liu et al., 2002; Xu et al., 2005).

The N170 and the Face Inversion Effect

Research using EEG has also shown that the N170 is modulated by the inversion of a face. Inverted faces elicit enhanced N170 amplitudes and delayed latencies compared to the presentation of an upright face. This effect is not observed in case of inverted versus upright objects (Eimer, 2000; Goffaux et al., 2003; Rossion et al., 1999; Rossion et al., 2000; Rossion, Gauthier, Goffaux, Tarr, & Crommelink, 2002; Savig & Bentin, 2001). The face inversion ERP effects

have been explained by a disruption of global processing, and the consequent need to rely on local features. These results complement behavioural findings and suggest that this loss of configural face information may increase the difficulty and slow face processing (e.g. Rossion et al., 1999). Similarly, the M170 has also shown delayed latency in response to inverted compared to upright faces, although some studies have failed to find an effect of amplitude (e.g. Itier et al., 2006).

Some research has also reported an effect of inversion on the P1/M100 component. Studies using ERPs have reported that, from a young age the latency of the P1 is shorter in children, and the amplitude smaller in adults, in response to inverted versus upright faces (Itier & Taylor, 2002b). Likewise, Itier and colleagues (2006) found a slight but consistent delay in response to inverted compared to upright faces on the peak latency of the M170 component. Nevertheless, an effect of inversion on the P1 has not been reported in all studies (e.g. Rossion et al, 1999).

The N170 and Spatial Frequency

As with evidence from behavioural studies, electrophysiological results for the effect of spatial frequency modulations on the N170 response are thus far inconclusive. A study employing upright and inverted faces and cars as stimuli demonstrated that the N170 amplitude was selectively modulated by spatial frequency content (Goffaux, Gauthier, & Rossion, 2003). Faces and cars in broad-pass and LSF elicited the typical face-specific N170 effect, being that faces elicited earlier peak responses than objects and inverted faces elicited a

delayed and enhanced peak response compared to upright faces. However, the face inversion effect and the face-specific effect were absent in the HSF condition (Goffaux et al., 2003). The authors concluded that the source of early processing differences between faces and objects was due to the more efficient and quicker extraction of coarse, holistic information, available in LSF, crucial for perceiving a face. This study also reported that for faces, the N170 amplitude significantly decreased from BSF to LSF to HSF. Similarly, Hsiao and colleagues recorded MEG responses to upright and inverted human faces presented in BSF, LSF, middle spatial frequencies (MSF) and HSF, and reported longer latencies to inverted compared to upright faces in BSF and LSF. This groups also found that M170 responses to LSF faces showed longer latencies and smaller amplitudes compared to BSF faces, whereas there were no latency or amplitude differences between BSF, MSF and HSF faces (Hsiao, Hsieh, Lin, & Chang, 2005).

However, a second ERP study failed to find an effect of spatial frequency on the neural response to faces and objects. Holmes, Winston and Eimer (2005) found enhanced N170 amplitudes for faces compared to nonfaces across LSF, BSF and HSF. They concluded that the structural encoding of faces operates in a uniform manner across spatial frequencies (Holmes et al., 2005). No effects of amplitude or latency were reported. My study attempted to address the lack of clarity in the literature thus far and further clarify the effect of spatial frequency on the M170 neuromagnetic response.

The Development of Face Processing

Behavioural Findings

Despite the plethora of research on face processing in adults, our knowledge of the developmental trajectory of human's ability to readily process and recognize faces is limited. It is well documented that, in contrast to adults' expert ability, children are much poorer at recognizing faces (Taylor et al., 2004). However, why this is and how the adult level of expertise for face processing develops remains unclear.

Carey and Diamond (1977) argued for a qualitative change in face processing that occurs around 10 years of age as they failed to find the face inversion effect in children younger than 10 years but identified in children older than 10 years. These authors concluded that younger children were relying on a featural strategy to process faces and that holistic face processing developed around age 10, a hypothesis that was further supported by a face categorization study that identified the face inversion effect in 10 year olds, but failed to find it in seven year olds (Schwarzer, 2000). This finding would seem a straight forward explanation for children's relative weakness at processing faces. However, many studies have since failed to find support for this hypothesis.

In contrast to the hypothesis of a qualitative switch in processing mode, the face inversion effect has been identified in children as young as 5 and 6 years of age (Brace et al., 2001; Mondloch, Le Grand, & Maurer, 2002; Tanaka, Kay, Grinnell, Stansfield, & Szechter, 1998), suggesting that from a young age, children process faces holistically. Interestingly, Brace and colleagues (2001)

found that children between the ages of 2 and 4 responded faster to inverted faces compared to upright faces, indicating that a qualitative switch in processing mode may occur at some point during childhood. Further, adding to the inconsistency in the literature, some studies have reported increasing inversion effects with age, arguing for a gradual quantitative change over childhood (e.g. Mondloch et al., 2002), whereas other have not (e.g. Tanaka et al., 1998). In general, the N170 shows a gradually decreasing latency over time, again supporting gradual, quantitative change (Taylor et al., 2004). Thus, the development of face processing remains unclear.

Early Neural Markers of Face Processing in Children

Compared to the adult literature, only a few studies have examined the neural mechanisms of face processing in children although there is a growing body of research using EEG and MEG to examine the neural mechanisms of face processing. In infants, research has identified two components, which are believed to be the equivalent of the adult N170, namely, an N290 and a P400. These are hypothesized to merge into the single N170 seen in older individuals (deHaan, Johnson, & Halit, 2003). The infant N290 is a negative deflection occurring over the posterior midline and paramidline electrodes that reflects an effect of inversion. The infant P400 has also been proposed as a precursor to the adult N170. Although it has a different polarity than the N170, the P400 is more prominent in lateral posterior electrodes and has shorter peak latencies in response to faces compared to objects (deHaan et al., 2003).

In 4 year olds, the N170 has been identified at approximately 270ms after stimulus onset. This wave is largest at parieto-temporal electrode sites, as in adults, and shows decreasing latency throughout childhood, reaching adult levels during adolescence (Taylor et al., 2004; Taylor, McCarthy, Saliba, & Degiovanni, 1999). Studies have also generally demonstrated increased N170 amplitude across development, with faces in 10-11 and 12-13 year olds eliciting a relatively small peak N170 that increased throughout adolescence, reaching adult levels by roughly 15 years of age for explicit face processing tasks (e.g. Taylor et al., 2004).

Moreover, Taylor and colleagues identified the commonly reported longer latency and increased negativity to inverted than upright faces in children aged 12 years and older (2004). However, in contrast to the adult literature, in children aged 4 to 9 years, the N170 latency was longer for upright compared to inverted faces. Likewise, in children aged 4 to 11 years of age, the N170 amplitude was greater for upright faces than inverted faces (Taylor et al., 2004). In opposition, Itier and Taylor (2004d) found the typical face inversion effect in children as young as 8 years, with inverted faces eliciting a later and greater peak response than upright faces.

In a series of four studies examining implicit and explicit face processing with upright, inverted and emotional faces to examine the development of the N170 component, Taylor and colleagues reported two negative peaks, an earlier less reliable peak that was absent in older children but present in 65% of children younger than 12 years, and a later more dominant peak (2004). However, this

bifid peak has not been reported in all studies. For example, in children aged 4 to 14 years, Taylor and colleagues (1999) did not detect an N170 with a double negative peak in a study using faces and cars among other distracter stimuli, and butterflies as targets. Similarly, using an implicit processing task with emotional faces Batty and Taylor (2006) did not report a bifid N170 in children aged 4 to 15. Finally, a study examining the effect of face inversion and contrast-reversal on the development of the N170 also failed to report a double negative peak (Itier & Taylor, 2004d).

As is evident, the literature remains inconclusive about the developmental trajectory of the N170 ERP component. Nonetheless, the data seem to converge on the fact that, in children, faces elicit an N170 that is later and has a less negative peak amplitude than adults. Across development, faces elicit an earlier and greater amplitude N170 component that seems approaches the typical, adult N170 at some point during mid-adolescence. Although an explanation for the delayed N170 in children remains inconclusive, there are several hypotheses about the development of social functioning (face processing included) and the maturation of the brain in general that may be applicable.

One common developmental explanation for slower face processing in children than in adults includes the “brain maturational” view. This view states that the maturation of a specific brain region is related to newly emerging sensory, motor and cognitive functioning. This model suggests that the basic mechanism for face processing is in place from birth but that different, more complex brain regions develop over time (Johnson, 2006) resulting in improved

face processing. A second view is the “interactive specialization” model, which is based on evidence suggesting that some cortical regions begin with poorly defined functions, such that they are partially activated in a wide range of different contexts and by different tasks, that later become fine tuned to specific tasks during development. This model predicts that increasing specialization and more focal localization of cortical processes to faces would occur during development (Johnson, 2006), resulting in faster, more accurate processing of faces.

Research on anatomical brain development may also provide insight into the development of face processing and the M/N170 component. Studies employing fMRI suggest that there is a continuous increase in the volume of white matter, arguably due to intra-cortical myelination, throughout adolescence and a concurrent decrease in grey matter volume in certain cortical regions, as a result of synaptic pruning (Luna & Sweeney, 2004; Paus, 2005; Sowell, Thompson, Tessner, & Toga, 2001). These processes allow for increased specialization of brain functioning. Synaptic pruning permits more efficient localization of brain function, enhancing the ability of discrete brain areas to engage in higher-order cognitive processing, such as working memory and planning; whereas, myelination increases the speed of neural transmission, allowing the integration of different brain regions that support such higher-order cognitive functions (Luna & Sweeney, 2004). Although such studies have primarily been conducted on frontal lobe processes, such as working memory and executive functions, they may be applicable to social cognition functions,

such as face processing, suggesting increased specialization of brain areas for face processing and enhanced speed of neural transmission in response to faces with development.

Magnetoencephalography

My study employed MEG to determine the effect of spatial frequency on the M170 neuromagnetic response in children, adolescents and adults. MEG is a noninvasive, online technique for investigating neuronal activity in the human brain (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993) and provides millisecond information about the time course of neural activity. As MEG is not distorted by irregularities and variation in the skull bone, MEG can also provide good spatial resolution of approximately 1-2 cm (Hämäläinen et al., 1993). However, MEG is less sensitive to completely radial sources than EEG.

MEG data, like EEG data, can be time- and phase-locked to a specific event, such as the presentation of a face, to create an event-related field (ERF). ERFs reflect neuronal activity that is associated with stimulus processing and is phase-locked to that stimulus (e.g. Puce, Allison, Spencer, Spence & McCarthy, 1997). Averaging over a large number of trials of the specific event facilitates detecting the magnetic flux associated with that event and creating a waveform representative of the event of interest.

As mentioned above, MEG has been used to detect and study the properties of the M170 neuromagnetic response (e.g. Harris & Nakayama, 2007a; Harris & Nakayama, in press; Hsaio et al., 2005; Itier et al., 2006; Liu et al., 2002; Xu et al., 2005). The advantage of using MEG for the current study was

that MEG, beyond possessing excellent temporal resolution as is afforded by EEG, additionally allows for better spatial resolution than EEG (Hämäläinen et al., 1993). As a large body of research exists regarding the location of face generators in the brain, being able to project the source of the M170 into brain space may provide important convergent information about neural generators of the M170. In adults, it is well documented that faces are processed in a region in the ventral occipital cortex called fusiform gyrus (e.g. Deffke et al., 2007; Hsaio et al., 2005; Itier et al., 2006; Kanwisher & Yovel, 2006; Liu et al., 2002; Xu et al., 2005), commonly referred to as the fusiform face area (FFA). EEG/MEG studies have demonstrated that the N/M170 is primarily generated in the region of FFA, with right hemispheric dominance (Deffke et al., 2007; Hsaio et al., 2005; Itier, et al, 2006; Itier & Taylor, 2004c). Research using functional Magnetic Resonance Imaging (fMRI) has also found that this brain region, particularly in the right hemisphere, shows greater hemodynamic response to faces compared to nonface objects (e.g Kanwisher & Yovel, 2006; Liu et al., 2002; Xu et al., 2005; Vuilleumier, Armony, Driver & Dolan, 2003).

Current Study

My studies investigated the effect of spatial frequency on the M170 neuromagnetic response to faces and objects. The first study was conducted with a group of adults, aged 19 years and older, whereas the second was conducted with a group of children between the ages of 9 and 12 years, and a group of adolescents, aged 15 to 17 years. In both studies, faces and butterflies were presented in LSF, BSF (broad-band spatial frequencies) and HSF (see

Figure 1-1 for example of stimuli) while participants were sitting under an array of SQUID magnetometers.

Study 1

Study 1 had three primary goals. The first goal was to compare the reaction times in response to faces and butterflies presented in LSF, BSF and HSF in a normative group of adult participants. Based on previous research that has indicated that faces are primarily supported by holistic processing, that holistic processing is supported by LSF (Goffaux & Rossion, 2003) and that the task in my studies was a simple face-nonface discrimination task, I predicted that participants would respond faster to faces presented in LSF than BSF or HSF. This would further support an advantage of holistic processing for faces. The second goal was to characterize the influence of various spatial frequencies on the M170 response to faces and objects in a normative adult sample. The final goal was to estimate the brain source generators of the M170 response.

Study 2

Study 2 had the main goal of clarifying the developmental trajectory of the behavioural responses and the M170 electromagnetic response elicited by faces and butterflies in LSF, BSF and HSF by comparing the pattern of response, time course and neuromagnetic flux of the M170 in adults, adolescents and children. Understanding the typical developmental course is an essential step before attempting to study development in populations known to have face processing deficits, such as Autism Spectrum Disorder (ASD). This study hoped to provide

insight into the developmental course of the early neural mechanisms of face processing, documenting differences in terms of peak M170 latency and amplitude differences, as well as elucidating the effect of spatial frequency on the M170 across development. This, to my knowledge, has not previously been examined.

2: STUDY 1

The purpose of this study was to examine how varying the spatial frequency of face and nonface stimuli affected face processing as reflected by modulations of the M170 component in adults. The nonface stimuli employed for this study were butterflies, which were chosen due to their intuitive similarity to faces: both are biological; both are symmetrical, and they have a similar shape.

Given the body of research suggesting that faces are processed holistically in adults, I predicted that faces would be processed differently in LSF than in HSF. More specifically, as a simple face-nonface discrimination task was employed, I hypothesized that LSF cues would be available more rapidly than HSF cues, resulting in faster reaction times to LSF faces compared to HSF faces, and an earlier and greater peak M170 amplitude for LSF compared to HSF faces. I predicted that BSF faces would be processed faster than HSF faces and slower than LSF faces. I also hypothesized that these effects would be specific to faces.

Finding the hypothesized effect of spatial frequency in faces would suggest a LSF advantage for simple tasks. This would support previous research using the face inversion task (Yin, 1969), the part-whole paradigm (Tanaka & Farah, 1993), and composite faces (Young et al., 1987) demonstrating that faces are processed holistically in healthy adults. However, if an overall effect of spatial frequency is identified, this would support previous hypotheses that LSF

information is available earlier than HSF information (Greenlee & Breitmeyer, 1989), and would indicate an overall advantage of holistic processing (e.g. Amirkhiabani & Lovegrove, 1999). This would also further indicate strict processing of LSF information within magnocellular pathways and HSF information within parvocellular pathways (e.g. Vuilleumier et al., 2004).

A second goal of this project was to conduct source analysis on the data, using Brain Electrical Source Analysis (BESA) software to estimate the brain source generators of the M170 response. An extensive body of literature exists indicating that there is an area in the brain along the fusiform gyrus that responds specifically to faces. Known as the fusiform face area (FFA), research using functional Magnetic Resonance Imaging (fMRI) has shown that this brain region in the occipito-temporal cortex shows preferential hemodynamic response to faces compared to nonface objects (e.g. Kanwisher & Yovel, 2006; Xu et al., 2002; Vuilleumier et al., 2004). Additionally, the source of the M170 has been projected to this region in the brain using MEG (e.g. Hsaio et al., 2005; Itier et al., 2006). Therefore, it was predicted that the source of the M170 would project to the region of the fusiform gyrus, within the occipito-temporal cortex.

Methods

Participants

A total of 13 healthy adults (aged 19 and older) with normal or corrected-to-normal vision participated in this experiment. One male participant was excluded due to a past history of epileptic seizures. The 12 remaining participants ($M_{age} = 26.2$ years, 5 women) self-reported right-handedness and had

no history of neurological or psychiatric disorder. Adult participants were graduate or undergraduate students in the Department of Psychology at Simon Fraser University, Burnaby, British Columbia and either volunteered or participated for course credit.

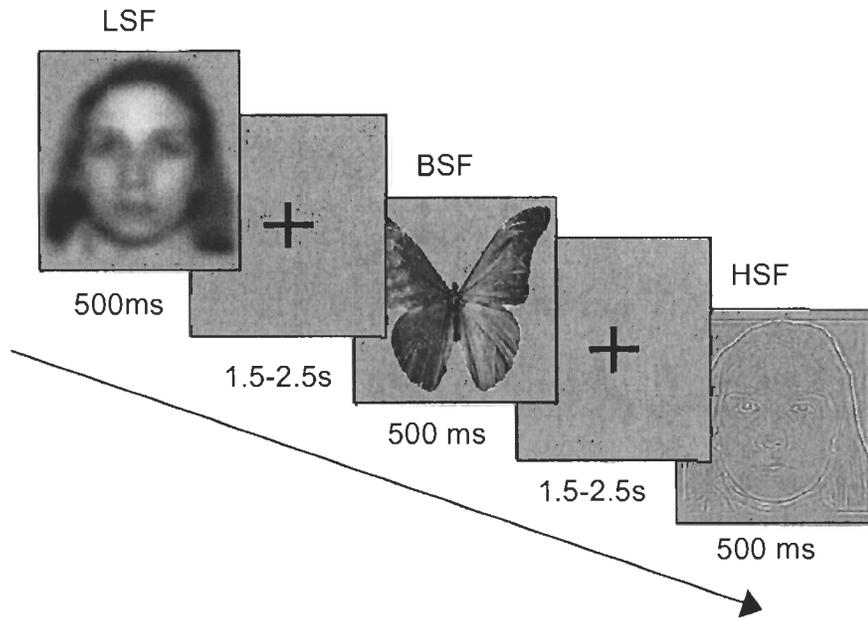


Figure 2-1 Illustration of faces and butterflies as presented in Study 1 and 2.

Stimuli

Stimuli consisted of 150 grey-scale photographs of front-view human faces and 150 grey-scale photographs of front-view butterflies. Faces and butterflies were presented in LSF, BSF and HSF, forming a total of six conditions. Figure 1-1 shows examples of stimuli used in this experiment. Fifty stimuli per condition were presented, for a total of 300 stimuli. Each stimulus set was filtered, preserving either the full-range of spatial frequencies (broad-band spatial frequency, BSF), the HSF ranges or the LSF ranges. The spatial frequency

content in the original stimuli (BSF) was filtered using a high-pass cut-off that was >23 cycle/degree for the HSF stimuli, and a low-pass cut-off that was <8 cycles/degree was for the LSF stimuli. Average luminance did not differ according to image type (mean luminance across stimuli for LSF, BSF and HSF: 115, 112, 118 on a 256 grey-level scale). All stimuli were viewed at a distance of 30 cm on a 42 cm x 32 cm screen.

Procedure

Participants sat in a dimly lit and magnetically shielded room at the Down Syndrome Research Foundation in Burnaby, British Columbia, and were instructed not to move their heads. Participants practiced the task until they were comfortable with the button box before starting the experiment. Participants were instructed to make face-nonface discriminations, regardless of spatial frequency, while viewing the stimuli. The stimuli appeared one by one, in a randomized order, at the centre of the screen on a grey background for 500 ms, followed by a randomized jittered inter-stimulus interval, averaging 2000 ms (range: 1500 ms-2500 ms), as demonstrated in Figure 2-1. Participants reported as quickly and as accurately as possible the type of stimulus presented by pressing a button for face or a button for nonface with their thumbs. The experiment was divided into three roughly 5-minute blocks, with intervening short breaks of approximately 45 to 60 seconds. After a short break, the experimenter resumed the experiment. Accuracy and response time were calculated from participants' button presses.

Magnetoencephalography (MEG) recording

Whole-head MEG was measured in a magnetically shielded room while the participant sat with his or her head surrounded by the helmet shaped OMEGA 151-channel MEG system (VSM MedTech Inc., CTF Systems Inc, Coquitlam, B.C). Each MEG sensor consisted of an axial first-order gradiometer, which were approximately 4.2 cm apart, with a 5 cm baseline and a 2 cm diameter. This system included a reference array that allowed third-order spatial gradient environmental noise cancellation (Xiang, Wilson, Otsubo, Ishii, & Chuang, 2001). Synthetic third-order gradient noise cancellation minimizes environmental noise and maximizes measurement of low frequency ranges (Fife et al., 1999). Data were recorded with the third-order gradients noise cancellation. To facilitate registration of the MEG sensors with the subject's head shape, coils were placed at the location of three fiducial points, e.g., the nasion, and the two pre-auricular points. The 3-D locations of such fiducial points, along with an average of about 150 points on the head surface, were recorded for each subject at the end of the session using a 3-D digitizer (Polhemus Inc., Vermont, USA).

Data analyses

Sensor space

MEG signals were bandpass filtered at .5-40 Hz and signals were baseline corrected using a 100 ms time interval (-100ms to 0ms). Trials contaminated with ocular movements and other artefacts (fields greater than 2 picoTesla) within the 0-500ms post-stimulus interval were removed from further analyses.

After the data were pre-processed, artefact-free trials were averaged for each condition and participant. Grand-averages were then computed across participants for each of the six conditions. These grand-averages were used in combination with an examination of the grand-averaged topographical map to determine a group of four sensors in the left and right hemisphere for which the M170 neuromagnetic response was greatest. Figure 2-2 shows that these sensors were selected over the occipito-temporal cortex and consisted of sensors MRT 24, 33, 34, 43 in the right, and MLT 24, 33, 34, 43 in the left. These sensors of interest (SOI) were subsequently collapsed to create a left and right clustered channel, used in subsequent analyses. The reason for choosing multiple channels for analyses was to compensate for slightly different positioning of each participant's head in the MEG helmet.

Next, grand-averages were computed from the left and right SOIs for each condition. These grand-averages were then used to determine the mean peak amplitude for each condition. The peak M170 response was searched for in the 140 ms to 200 ms post-stimulus interval. A grand-averaged peak latency was identified for each condition and each participant's peak M170 response was subsequently selected within a +/- 30 ms window of that peak latency.

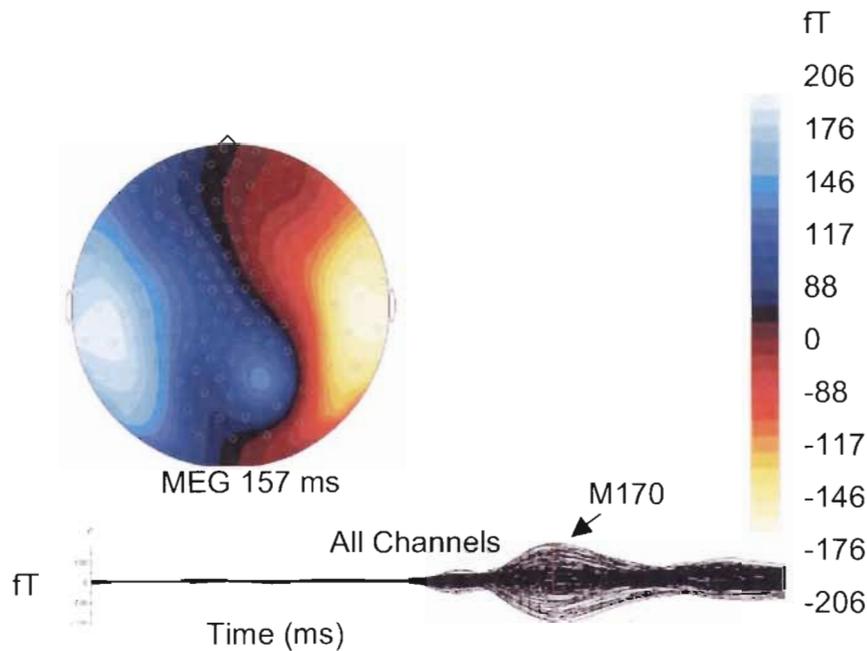


Figure 2-2 Topographical head map of faces averaged across LSF, BSF and HSF at mean latency of peak M170 ERF, used to select left and right SOIs.

Source space

Source analysis was conducted using Brain Electrical Source Analysis (BESA) software. A 100 ms pre-stimulus baseline correction was performed and a 30 Hz lowpass filter was applied. For each participant, averaged LSF, BSF, HSF face and butterfly event-related fields (ERFs) were used to create that participant's source model. Initially, separate models were created for each condition, for each participant (for a total of 72 models). This was performed in order to determine if the location and orientation of the dipoles were significantly different across conditions. Repeated-measures ANOVAs revealed no differences in location or orientation for any of conditions; therefore, I averaged ERFs from the six conditions to increase the signal-to-noise ratio, and to create a

single model for each participant. An M170 peak was detected by visual inspection within 140-200ms post-stimulus and dipoles were fit based on a 20 ms window around this peak. Each participant's model was created by fitting the M170 with a single pair of symmetric dipoles, with no other constraints (location and orientation left to vary). Participant's own source models were then applied to BSF, HSF and LSF face and butterfly conditions. Source waveforms were extracted and grand-averaged peak amplitudes and latencies of the M170 across the six conditions were statistically analyzed.

Statistical Analyses

In both the sensor and source domain, an effect of stimulus type refers to a difference between faces and butterflies whereas an effect of spatial frequency refers to a difference between HSF, LSF and BSF. Analyses were conducted using 2 x 3 repeated-measures Analysis of Variance (ANOVA), within-subject factors being stimulus type (face and butterfly) and spatial frequency (LSF, BSF, HSF). The alpha level was set to .05 and degrees of freedom were corrected using the Greenhouse-Geisser epsilon method, to correct for violations of sphericity in the data. In case of significant interactions, post-hoc comparisons were carried out to identify significant contrasts which were found on an exploratory basis. Paired-samples *t*-tests, with Bonferroni correction to control for familywise error were employed.

A-priori defined paired-samples *t*-tests were employed in case of effects that were predicted by our hypotheses, regardless of the significance of the ANOVA's interaction.

For the MEG analysis in sensor space, I focused on the right SOI based on past research indicating the right hemisphere's preferential role in face processing (e.g. Bentin et al.,1996; Hsaio et al., 2005; Itier et al., 2006). Similarly, analyses were conducted on the source waveforms from the right dipole only.

Results

Behavioural Performance

Participants were fast and accurate at discriminating between faces and butterflies in LSF, BSF and HSF. Table 2-1 reports mean accuracy and standard deviation for each condition. Mean reaction times (RT) and standard deviations for faces and butterflies in HSF, LSF and BSF are presented in Table 2-2. RTs were analyzed using a repeated-measures ANOVA. Results revealed a main effect of spatial frequency ($F(2,10)=5.25, p=.01$). No main effect of stimulus type ($F(1,11)=.23, p=.64$), and a marginally significant stimulus by spatial frequency interaction ($F(2,10)=3.22, p=.06$) were found.

Table 2-1 Mean accuracy (percent hits) and standard deviation in parentheses for faces and butterflies presented in LSF, BSF and HSF.

	LSF	BSF	HSF
Face	94 (2)	94 (3)	96 (2)
Butterfly	96 (1)	98 (1)	97 (2)

Given the a priori prediction of differential RT effects for faces as a function of spatial frequency, planned paired-samples *t*-tests were carried out.

Participants were significantly slower to respond to HSF faces compared to LSF faces ($t_{11}=-5.01, p<.001$), whereas RT to LSF and BSF faces were not significantly different ($t_{11}=-1.30, p=.22$). In contrast, effects of spatial frequency in the butterfly condition were not significant (HSF vs. LSF butterflies, $t_{11}=-1.18, p=.26$; LSF vs. BSF butterflies, $t_{11}=1.91, p=.08$).

Table 2-2 Mean reaction times (ms) and standard deviation in parentheses for faces and butterflies presented in HSF, LSF and BSF.

	LSF	BSF	HSF
Face	469 (63)	468 (70)	479 (68)
Butterfly	476 (59)	473 (54)	483 (55)

MEG Sensor Analysis

M170 Latency

Repeated-measures ANOVA results revealed a significant main effect of spatial frequency ($F_{2,10}=22.44, p<.001$), with earlier latency for LSF than HSF, and a marginally significant main effect of stimulus type, with faces occurring earlier than butterflies ($F(1,11)=4.05, p=.07$). Importantly, however, the interaction of stimulus type by spatial frequency was significant ($F_{2,22}=12.17, p=.001$). Grand-average mean latencies and standard error of the means (SEM) are illustrated in Figure 2-3.

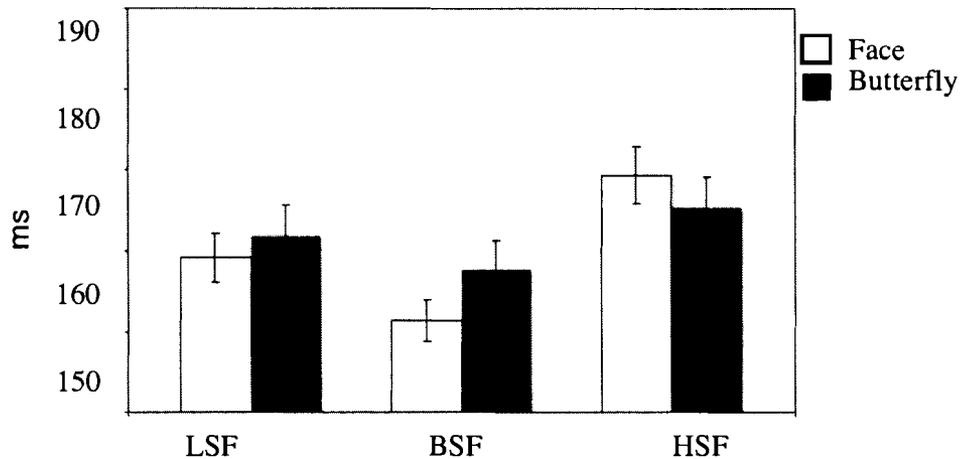


Figure 2-3 Grand-average mean M170 peak latency (ms) elicited by faces and butterflies presented in LSF, BSF and HSF. Error bars are standard errors of the mean (SEMs).

A priori pairwise comparisons of faces across the three spatial frequencies revealed that HSF faces elicited a peak neuromagnetic response that was significantly later than that elicited by LSF faces ($t_{11}=6.74$, $p<.001$) and that LSF faces peaked significantly later than BSF faces ($t_{11}=4.32$, $p=.001$). Pairwise comparisons of butterflies across the three spatial frequencies revealed that there was no difference between HSF and LSF butterflies ($t_{11}=.17$, $p=.87$), but that BSF butterflies elicited an M170 that peaked significantly earlier ($t_{11}=2.66$, $p=.02$). Figure 2-4 illustrates grand-averaged ERF waveforms.

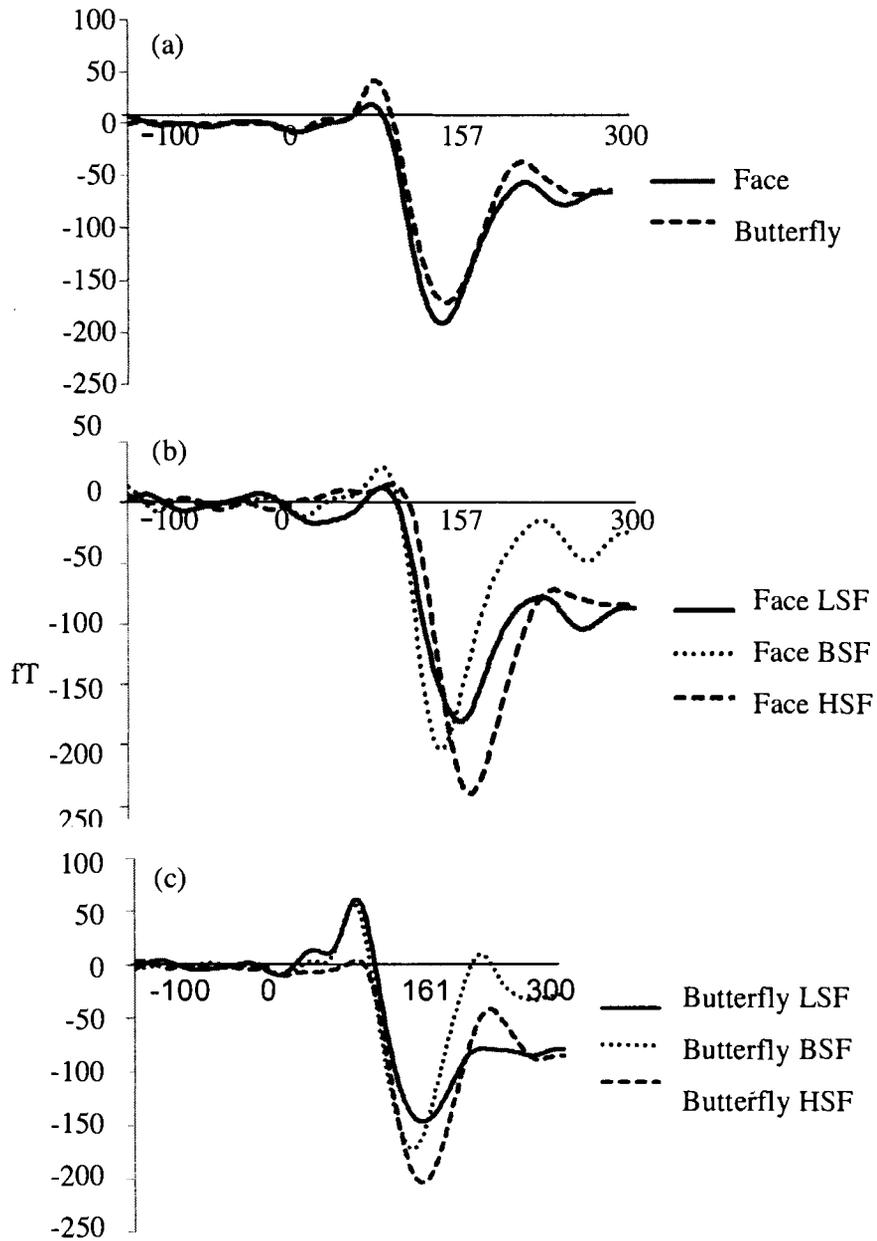


Figure 2-4 Grand-averaged M170 waveforms elicited by (a) faces and butterflies averaged across SF, (b) faces and (c) butterflies presented in LSF, BSF and HSF, recorded from right SOI.

Given the significant stimulus type by spatial frequency interaction, Bonferroni-corrected post-hoc comparisons were carried out to identify other significant yet unpredicted contrasts (alpha value= .02). In LSF and BSF, faces occurred earlier than butterflies ($t_{11}=-2.66$, $p=.02$ and $t_{11}=-3.36$, $p=.01$, respectively). Please note that while Figure 2-3 suggests a possible reverted effect for the HSF, the contrast did not approach significance ($t_{11}=1.32$, $p=.21$).

M170 Amplitude

ANOVA results revealed a main effect of stimulus type, ($F(1,11)=8.15$, $p=.02$), with faces eliciting greater M170 amplitude than butterflies (across spatial frequency), as well as a main effect of spatial frequency ($F(2,10)=25.26$, $p<.001$). However, no interaction between stimulus type and spatial frequency was found ($F(2,22)=.43$, $p=.65$).

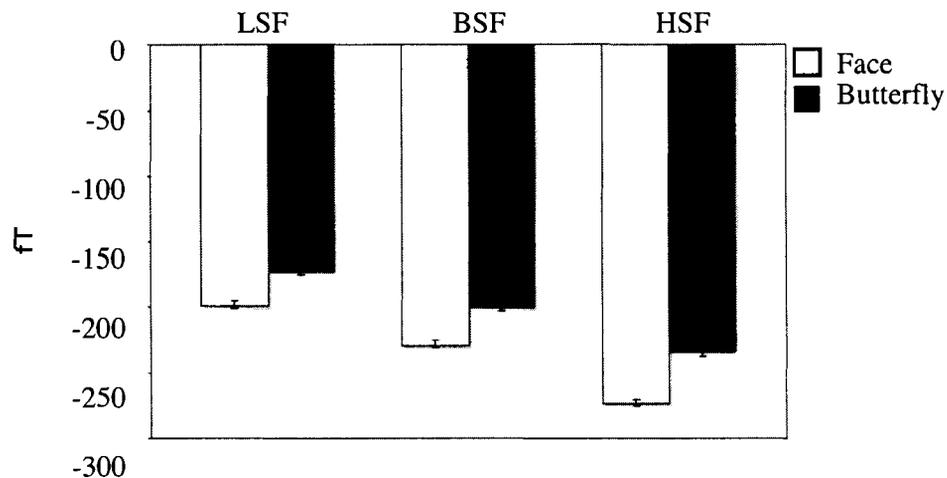


Figure 2-5 Grand-averaged mean amplitude (fT) elicited by faces and butterflies presented in LSF, BSF and HSF, recorded from right SOI. Error bars are SEMs.

To test the a priori predictions regarding the M170 amplitude, comparisons of faces across the three spatial frequencies revealed that HSF faces elicited a significantly greater M170 amplitude than LSF faces ($t_{11}=6.71$, $p<.001$), and that BSF faces elicited a greater M170 amplitude than LSF faces ($t_{11}=2.48$, $p=.03$). Similar results were observed for the butterfly condition, with HSF butterflies eliciting greater M170 amplitude than LSF butterflies ($t_{11}=3.91$, $p=.002$), and BSF butterflies also eliciting a greater peak neuromagnetic flux than LSF butterfly ($t_{11}=3.51$, $p=.01$). Figure 2-5 illustrates mean M170 amplitudes and Figure 2-4 demonstrates M170 waveforms. Note the overall greater M170 amplitude for faces than butterflies and for HSF than LSF stimuli.

Brain Electrical Source Analysis (BESA)

M170 source dipole modelling was conducted successfully on 11 of 12 participants. The bilateral dipoles generally went to the region of the occipito-temporal cortex as located on BESA's template brain (see Table 2-3 for Talarach coordinates and Figure 2-6 for a BESA template brain with 11 dipoles, demonstrating location of solutions). Source models fit well and had an average residual variance of 28% (see Table 2-4 for residual variances for each model) and were considered good models to conduct further statistical analyses.

Table 2-3 Dipole locations (in Talarach coordinates) for right hemisphere of 11 generated dipole solutions and mean dipole location.

Participant	X	Y	Z
1	25.76	-48.02	11.29
2	32.06	-42.26	8.62
3	22.21	-27.27	-8.42
4	30.11	-67.12	-9.22
5	29.51	-65.78	-12.53
6	26.65	-54.24	6.18
7	33.89	-52.52	3.42
8	29.7	-46.74	-7.86
9	31.19	-63.37	-1.00
10	41.46	-54.16	3.94
11	39.54	-57.43	-3.98
Mean	31.10	-52.63	-0.86

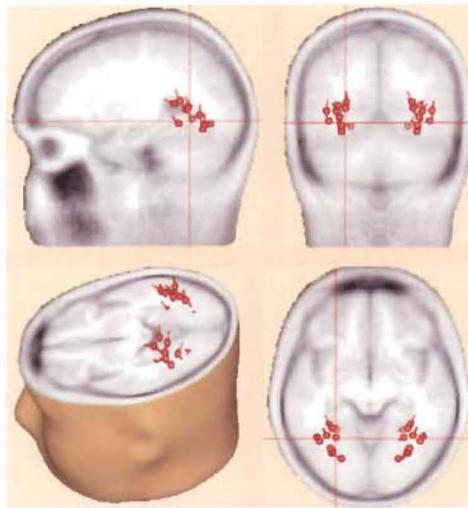


Figure 2-6 Location of dipoles, placed in BESA template brain to demonstrate distribution of 11 bilateral dipoles fit to M170 ERF.

Table 2-4 Residual variance (percent) of model after fitting bilateral dipole around peak M170 ERF.

Participant	LSF face	BSF face	HSF face	LSF butterfly	BSF butterfly	HSF butterfly
1	17.94	36.19	22.41	15.67	18.13	12.03
2	32.83	37.74	38.04	33.65	32.83	39.17
3	22.82	19.38	17.15	45.24	67.02	46.22
4	24.89	17.67	17.36	20.25	20.08	21.74
5	40.91	30.96	14.16	42.96	68.79	45.59
6	8.12	3.85	3.87	12.85	8.75	3.87
7	15.01	9.822	8.32	14.15	11.17	11.87
8	61.36	43.68	37.99	30.35	29.53	22.45
9	24.63	42.85	30.03	63.30	30.94	17.66
10	37.77	28.04	34.76	49.38	54.53	40.54
11	19.42	23.54	15.45	34.21	32.02	33.80
Mean	27.79	26.70	21.78	32.91	33.98	26.81
SD	14.78	13.16	11.85	16.34	20.88	14.89

M170 Latency

ANOVA results of the source waveforms revealed a main effect of spatial frequency ($F(2,10)=40.28, p<.001$), but no effect of stimulus type, ($F(1,11)=.73, p=.41$). As for the sensors data, there was a significant stimulus by spatial frequency interaction ($F(2,22)=13.37, p=.001$). Figure 2-7 graphs means and SEMs for each condition. A priori paired samples t -tests on LSF, BSF and HSF faces revealed that the M170 peak latency was later for HSF faces than for LSF faces ($t_{11}=6.96, p<.001$), and that LSF faces peaked significantly later than BSF faces ($t_{11}=5.01, p<.001$). For butterflies, it was found that the M170 elicited by HSF butterflies occurred later than that elicited by LSF butterflies ($t_{11}=2.36, p=.04$), and that the M170 for LSF and BSF butterflies was not significantly

different ($t_{11}=1.65, p=.13$). Figure 2-9 illustrates grand-average M170 waveforms elicited by faces and butterflies averaged across SF, as well faces and butterflies in LSF, BSF and HSF.

Post-hoc paired samples t -tests ($\alpha = .02$) revealed that BSF faces were occurring significantly earlier than BSF butterflies ($t_{11}=4.39, p<.001$). No significant differences between faces and butterflies in LSF ($t_{11}=-.97, p=.35$) and HSF ($t_{11}=1.72, p=.11$) were identified.

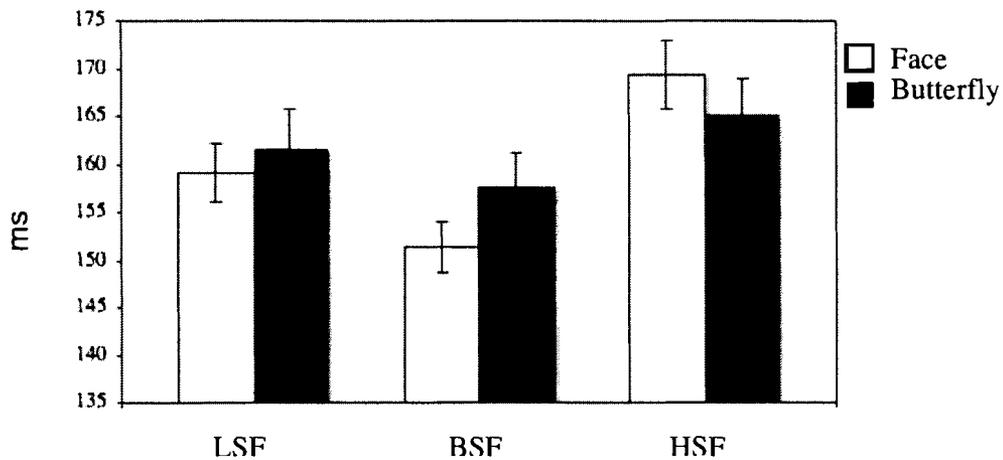


Figure 2-7 Grand-averaged mean latency (ms) of the M170 peak dipole. Error bars are SEMs.

M170 Amplitude

ANOVA results of the M170 amplitudes from the source waveforms showed a main effect of stimulus type, with faces eliciting a greater M170 electromagnetic response than butterflies ($F(1,11)=17.15, p=.002$), as well as a main effect of spatial frequency ($F(2,10)=8.24, p=.004$), with HSF eliciting a greater M170 amplitude than BSF and LSF. As for the sensors space data, the

interaction between stimulus type and spatial frequency was far from significance ($F(2,10)=.61, p=.55$). See Figure 2-8 for a graph of condition means and SEMs. A priori paired sampled t-tests revealed that BSF faces and LSF faces elicited similar M170 amplitudes ($t_{11}=-.56, p=.59$). However, HSF faces had a greater neuromagnetic peak flux than LSF faces ($t_{11}=2.89, p=.02$). Results for butterflies demonstrated the same pattern across spatial frequencies as faces. BSF and LSF butterflies did not have significantly different peak amplitudes ($t_{11}= -1.37, p=.20$), but HSF butterflies had a greater peak amplitude than LSF butterflies ($t_{11}=2.89, p=.01$).

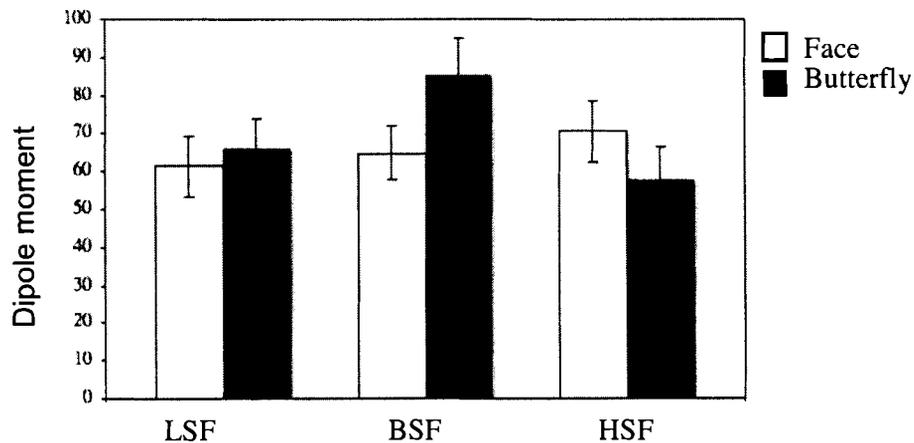


Figure 2-8 Grand-average mean amplitude elicited by faces and butterflies presented in LSF, BSF and HSF, obtained from M170 source waveforms. Error bars are SEMs.

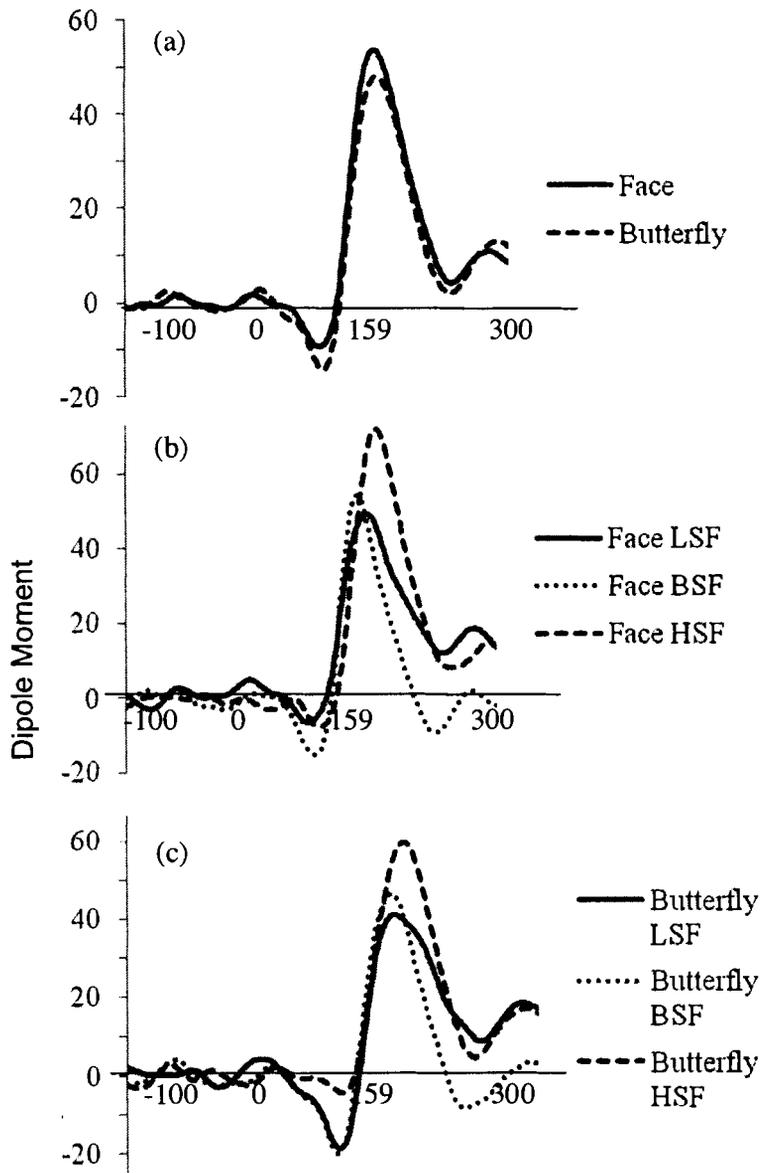


Figure 2-9 Grand-average M170 right source waveforms elicited by (a) faces and butterflies, averaged across SF, (b) faces and (c) butterflies presented in LSF, BSF, and HSF.

Discussion

Results from the current experiment indicated that, as hypothesized, adult participants responded faster to BSF and LSF faces than to HSF faces, indicating a behavioural advantage for discriminating faces when LSF information is available, as has been previously reported in the literature (e.g. Goffaux & Rossion, 2006). This experiment further indicated that this advantage for holistic information was specific to faces as participants were equally fast to respond to butterflies in LSF, BSF and HSF.

Because an effect of spatial frequency was found in the face condition but not in the butterfly condition, the behavioural results from this study fail to support the previous suggestions that spatial frequencies are processed on a gradient with lower spatial frequencies being available earlier than higher spatial frequencies or an overall advantage to holistic information, as has been reported elsewhere (Amirkhiabani & Lovegrove, 1999; Greenlee & Breitmeyer, 1989).

This study also found that the M170 neuromagnetic response was modulated by changes in spatial frequency. As hypothesized, LSF faces elicited an earlier peak electromagnetic flux than HSF faces, supporting the notion that holistic processing is important in face recognition.

In opposition to what was reported by Goffaux and colleagues (2003), the data from my study also indicated that LSF faces elicited a smaller peak neuromagnetic response than HSF faces. In contrast as well to Hsiao and colleagues (2005), my study found the BSF faces also elicited a smaller peak M170 amplitude than HSF faces. Although this effect was not hypothesized, and

at first glance may appear counterintuitive, an fMRI study using a similar manipulation of spatial frequency with neutral and emotional faces found greater activations in the FFA and other extrastriate areas to HSF than LSF faces (Vuilleumier et al., 2004). This is consistent with my data. However, Vuilleumier and colleagues (2004) interpreted this finding as indicating that visual recognition systems in ventral extrastriate cortex encode predominantly HSF information, and are relatively insensitive to LSF information. They invoked the parvocellular-magnocellular dual pathway model to explain that HSF information in faces travels via the ventral cortical pathway to the fusiform, whereas as LSF information travels via the magnocellular pathway to subcortical structures, such as the amygdala, ultimately minimizing the role of LSF in face processing.

In contrast to this interpretation, my study suggested that LSF plays an important role in face processing. As previously mentioned, M170 peak latencies were faster for LSF than HSF faces, and this effect was specific for faces. In addition, RT findings indicated faster categorization of LSF than HSF faces, but not butterflies, also arguing for the selective precedence of holistic face processing. Together these findings indicate the role of LSF information in face processing and suggest that the distinction between parvocellular and magnocellular pathways for HSF and LSF faces may be less distinct than suggested by Vuilleumier and colleagues (2004).

The result of later peak latencies and increased neuromagnetic flux in response to HSF compared to LSF (and BSF) faces may be explicable by considering the well-documented effect that inverted faces have on the N170

ERP component. More specifically, the results from this study indicate that HSF faces elicited a peak neuromagnetic response that was delayed and greater than the response elicited by LSF (and BSF) faces. This, to my knowledge, has not previously been reported. Several studies have consistently reported that inverted faces elicit a peak N170 amplitude that is later and greater than the peak amplitude elicited by upright faces (e.g. Eimer, 2000; Goffaux et al., 2003; Rossion et al., 1999; Rossion et al., 2000; Rossion, et al., 2002). Although this finding has been difficult to interpret, it has been suggested that inverted faces may require additional processing due to the disruption of configural and holistic information (e.g. Rossion et al., 1999; Rossion et al., 2002). The current results seem to mimic the face inversion effect on the N170/M170 component and, in conjunction with present behavioural data, suggests that, in the absence of holistic information (i.e., HSF faces) faces require increased processing to be perceived. These results corroborate the essential role that holistic information plays in face perception (e.g. Farah et al., 1995; Goffaux, Gauthier, & Rossion, 2003; Maurer et al., 2002; Savig & Bentin, 2001; Tanaka & Farah, 1993; Young et al., 1987; Yin, 1969).

A secondary finding of my study was the result that LSF faces elicited a delayed peak response compared to BSF faces in adults. Similar to behavioural studies that found an overall advantage in terms of accuracy and response time to BSF and medium-range spatial frequencies (Ruiz-Soler & Beltran, 2006), this suggests an overall advantage to faces presented with the full range of spatial frequencies available. The delayed latency of the peak response for LSF faces

may reflect an effect of masking. The expertise hypothesis of face perception states that faces are not “special” (as would be argued by some authors, e.g. Kanwisher, 2000), but are objects of expertise due to increased exposure to faces relative to other objects from a young age (e.g. Tanaka, 2001). Humans are exposed to faces on a daily basis; however, faces presented in LSF are not seen everyday. Although it is beneficial to be able to rapidly decipher socio-emotional information from faces with limited information (as would be provided by lower spatial frequencies) (e.g. Kanwisher & Yovel, 2006; Turati et al., 2005), humans are not accustomed to seeing faces presented with blurred featural information. The faces to which humans have developed expertise are intact faces with the full range of spatial frequencies available to the observer. Such logic may also explain, in part, the delayed processing of HSF faces compared to BSF faces, as humans are not accustomed to identifying faces with solely featural information intact.

In terms of the M170 latency, as with faces, BSF butterflies occurred earlier than HSF and LSF butterflies. This suggests that, as with faces, there is an advantage to viewing objects with the full spatial frequency spectrum available. However, in contrast to what was noted with faces, the peak amplitudes elicited by LSF did not occur earlier than those elicited by HSF butterflies. The peak latencies to LSF and HSF butterflies were not significantly different. Unlike with faces, and in conjunction with reaction time findings, there does not appear to be an advantage of holistic processing for objects.

As for M170 peak amplitudes, similar to what was identified in faces, LSF butterflies elicited smaller peak neuromagnetic responses compared to BSF butterflies, which in turn elicited a smaller peak response than did HSF butterflies. This finding may indicate that, regardless of stimulus type, more processing is required for stimuli presented in HSF. Nevertheless, the current study failed to show that there is an overall advantage for holistic information, because response time to HSF, BSF and LSF butterflies were not significantly different and M170 latencies to LSF butterflies were not elicited significantly shorter than to HSF butterflies.

Additionally, as has been well documented in the literature, this study found that faces elicited greater peak amplitudes than butterflies. Similar to what was reported by Goffaux and colleagues (2003), the present investigation failed to detect this face typical effect in the HSF condition, but did detect it in the BSF and LSF conditions. This further supports an overall advantage of holistic face processing.

As predicted, source analysis of the M170 ERF identified a bilateral source in the visual extrastriate cortex, in the region of the fusiform gyrus as has previously been identified using EEG/MEG (e.g. Deffke et al., 2007; Itier et al., 2006; Itier & Taylor, 2004c; Liu et al., 1999). Although the average Talaraich coordinates of the dipoles were slightly more dorsal than the fusiform gyrus (by about 5-10 mm), this may reflect the absence of individual structural MRIs to more accurately localize the source of the M170. Alternatively, it may indicate a source in the Superior Temporal Sulcus, which has previously been identified as

showing enhanced activation to faces and is dorsal to the fusiform gyrus (e.g. Itier et al., 2006). Additionally, although upon visual inspection there were clear M100 effects (especially in the butterfly condition), I did not model this source. Doing so may have improved the fit of the model, and this may also explain why sources are slightly more dorsal than anticipated. Nonetheless, although the Talarach coordinates must be interpreted with caution, because of the aforementioned absence of individual structural MRIs and source modelling error, results appear to confirm that the fusiform gyrus is a likely generator of the M170, among other possible generators in the extrastriate cortex.

Finally, statistical analyses of peak latency and amplitude for the right M170 source waveforms closely replicated the scalp results, strengthening results from the current study and further suggesting that the source of the M170 (and its modulation by stimulus type and spatial frequency) is likely originating in the vicinity of the fusiform gyrus.

3: STUDY 2

The purpose of the present study was to (1) investigate the role of spatial frequency in face processing in children (9-12 years) and adolescents (15-17 years), and (2) examine the developmental trajectory of face processing from pre-adolescence to adulthood. In adults, it is well documented that faces are supported by holistic processing; however, in children this advantage for holistic processing has not always been identified (Diamond & Carey, 1977; Schwarzer, 2000; Taylor et al., 2004). This study employed a simple face-nonface discrimination task that successfully demonstrated a recognition (response time for identification) advantage for low spatial frequency (LSF) faces compared to high spatial frequency (HSF) faces in adults (see Study 1), to examine holistic versus featural processing in children and adolescents.

In terms of reaction time, I hypothesized that adolescents would respond more rapidly to LSF faces than to HSF faces. Likewise, I predicted that LSF faces would elicit a shorter and greater M170 latency than HSF faces. Finally, no effect of spatial frequency was expected in the nonface condition. These findings would replicate adult results, and indicate that holistic face processing has developed by mid-adolescence. However, if this same effect of spatial frequency is identified in the nonface condition, this would suggest that an overall advantage for holistic information exists in adolescents (e.g. Greenlee & Breitmeyer, 1989; Boeschoten et al., 2005), as discussed in Study 1.

In children, I hypothesized that a similar pattern of results would emerge as was predicted with adolescents. Thus, I hypothesized that children would respond more rapidly to LSF faces compared to HSF faces and that this effect would be specific to faces. Also, I predicted that LSF faces would elicit a shorter M170 latency than would HSF faces and, again, this effect would be specific to faces. These findings would indicate that, for simple face-nonface discrimination tasks, children primarily rely on holistic information, available in LSF.

However, given current inconsistencies reported in the literature, with some studies failing to find support for holistic face processing in children, it was also possible that children would not demonstrate an advantage to LSF faces. This would manifest in HSF faces being responded to as quickly as LSF faces, and these both being slower than or equal to BSF faces. Further, in terms of M170 latency, there would be no overall effect of spatial frequency for faces, with LSF and HSF faces not eliciting significantly different peak M170 latencies. Finally, if children respond faster to HSF faces and show a shorter M170 latency to HSF faces compared to LSF and BSF faces, this would suggest an advantage of featural processing in children, ultimately supporting Diamond and Carey's (1977) initial suggestion that there is a qualitative switch in face processing mode across development, with younger children processing faces featurally.

Finally, in terms of developmental trajectory, I predicted that children would have the slowest reaction times to faces and butterflies and that there would be no difference between adolescents and adults given past findings of adult-like N170 in 15 year old (e.g. Taylor et al., 2004). I hypothesized the M170

in adults would have the shortest latencies and greatest neuromagnetic flux whereas the child M170 would have the longest peak latencies and smallest neuromagnetic flux in response to faces and butterflies. As the adolescents in this experiment were older (i.e. 15-17 years), I hypothesized that the M170 in adolescents would not be significantly different from the M170 in adults. This would suggest that adult levels of face expertise have been attained by mid- to late-adolescence, as has previously been documented (Taylor et al., 2003).

Methods

Participants

A total of 12 typically developing adolescents and 13 typically developing children (aged: 15-17 and 9-12, respectively) with normal or corrected-to-normal vision participated in this experiment. One female adolescent and one female child were excluded due to an error with data collection. The 11 remaining adolescents ($M_{age} = 15.5$; 5 female; 10 right-handed) and 12 remaining children ($M_{age} = 10.5$; 8 female; 12 right-handed) had no history of neurological or psychiatric disorder. Participants were paid \$20.00 to participate in the study and were recruited through newspaper advertisements, poster advertisements and personal contacts.

Stimuli

The stimuli were identical to those used in Study 1.

Procedure

The experimental procedures were identical to those used in Study 1, with the exception that a parent or researcher sat in the MEG suite with the participant during the experiment.

Magnetoencephalography (MEG) recording

All MEG recording procedures were identical to those used in Study 1.

Data analyses

Sensor space

All data analyses procedures were performed in an identical manner to those in Study 1, with the exception that trials contaminated with ocular movements and other artefacts within 0-300ms post-stimulus were rejected and excluded from all analyses. In adolescents, the SOIs were MRT 24, 33, 34, 43, in the right, and sensors MLT 14, 24, 25, 34, in the left. For children, the SOIs were MRT 34,35,43,44, in the right, and MLT 34,35,43,44 in the left (see Figure 3-1 for topographical maps used to pick SOIs).

M170 peaks for each participant were picked following the procedure employed in Study 1. Also, 50% of the child participants in this study had a double negative M170 peak. I relied on the scalp topography to determine the appropriate peak. In all participants, the earlier peak showed similar scalp activity as was observed in adolescents and adults (as demonstrated in Figure 3-1) whereas the second peak showed a more anterior scalp distribution. Additionally,

the first peak was more reliably recorded, was observed in all participants, and had a great peak neuromagnetic response than the second peak.

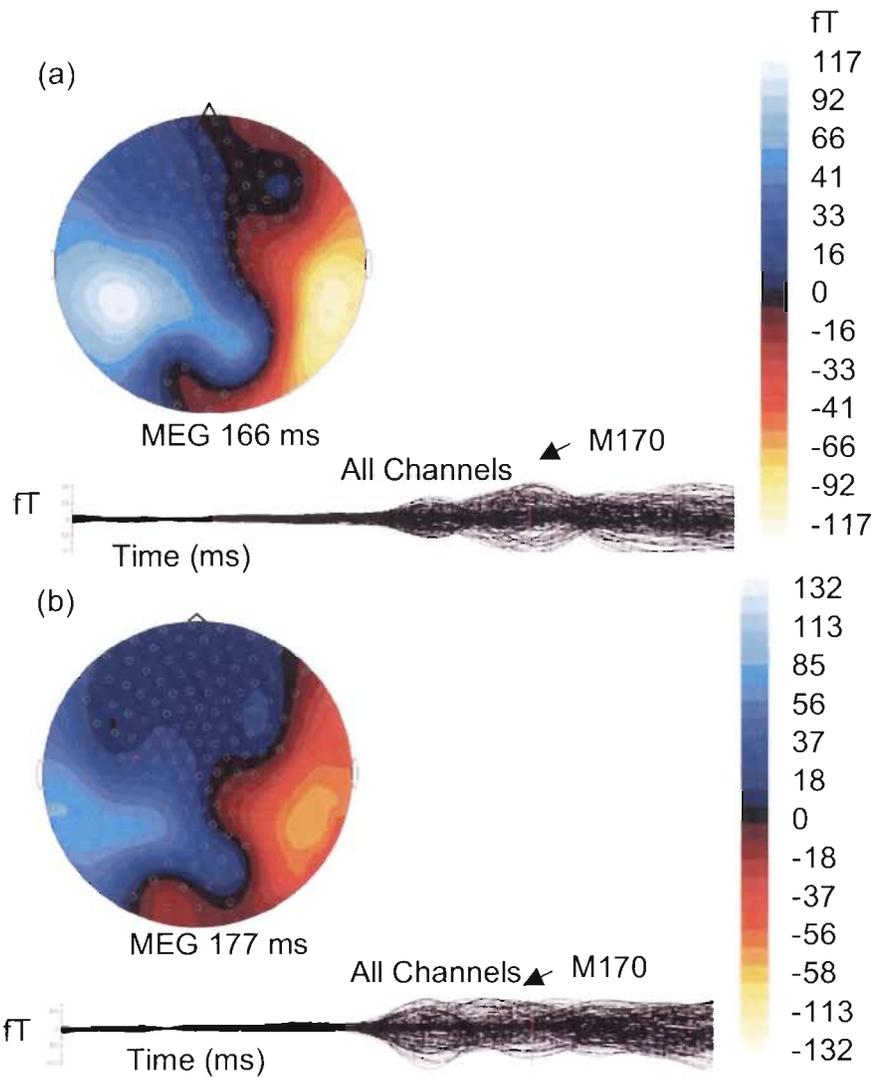


Figure 3-1 Grand-averaged topographical head maps of the M170 elicited by faces, averaged across LSF, BSF and HSF, at peak neuromagnetic flux in (a) adolescents and (b) children, demonstrating where sensors of interests were chosen over the left and right hemispheres.

Statistical Analyses

Within-group statistical analyses were conducted using the same procedures as in Study 1. Across group analyses were conducted using 2 x 3 repeated-measures ANOVAs, with stimulus type and spatial frequency serving as the within-subject variables and age group membership serving as the between-subjects variable. Whenever there was an interaction with age group (spatial frequency by age group or stimulus type by age group interaction), post hoc comparisons were conducted using Bonferroni corrected independent samples *t*-tests to further examine differences between the three age groups.

Results

Behavioural Performance

Adolescent Group

Participants were fast and accurate at discriminating between faces and butterflies in LSF, BSF and HSF (accuracy was above 90% for all conditions, except HSF faces). Means and standard deviations of response accuracy are shown in Table 3-1. The mean reaction times (RT) for faces and butterflies in HSF, LSF and BSF (see Table 3-2), were analyzed using a repeated-measures ANOVA, which revealed a main effect of spatial frequency ($F(2,9)=9.283$, $p=.004$). No main effect of stimulus type ($F(1,10)=.735$, $p=.41$) and no stimulus by spatial frequency interaction ($F(2,22)=2.212$, $p=.16$) were found.

Table 3-1 Adolescent group's mean accuracy (percent) and standard deviation in parenthesis for faces and butterflies presented in LSF, BSF and HSF.

	LSF	BSF	HSF
Face	93 (6)	94 (6)	74 (10)
Butterfly	91 (7)	93 (7)	93 (6)

When the a priori predictions were run on the face condition across spatial frequencies, paired-samples *t*-tests revealed that participant's reaction times to LSF faces were on average faster than they were to HSF faces ($t_{11}=2.945$, $p=.02$). Further, participants responded faster to LSF faces compared to BSF faces ($t_{11}=2.218$, $p=.05$). Finally comparisons run on the effect of spatial frequency in the butterfly condition revealed no differences in RT between HSF, LSF and BSF, $p>.05$.

Table 3-2 Adolescent group's mean reaction times (ms) and standard deviation in parentheses for faces and butterflies presented in HSF, LSF and BSF.

	LSF	BSF	HSF
Face	479 (74)	470 (80)	493 (68)
Butterfly	469 (89)	476 (85)	484 (78)

Child Group

Participants were fast and accurate at discriminating between faces and butterflies in LSF, BSF and HSF. Accuracy was above 80% for all conditions, as shown in Table 3-3. The mean reaction times (RT) for faces and butterflies in HSF, LSF and BSF, presented in Table 3-4, were analyzed using a repeated-

measures ANOVA. ANOVA results found a main effect of spatial frequency ($F(2,10)=4.347, p=.043$). However, no main effect of stimulus type ($F(1,11)=2.143, p=.17$) and no stimulus by spatial frequency interaction ($F(2,10)=.881, p=.40$) were found.

Table 3-3 Child group's mean accuracy (percent) and standard deviation in parenthesis for faces and butterflies presented in LSF, BSF and HSF.

	LSF	BSF	HSF
Face	87 (10)	85 (11)	86 (12)
Butterfly	82 (13)	85 (15)	83 (15)

When the a priori predictions were run on the face condition across spatial frequencies, paired-samples *t*-tests failed to reveal significant differences in RT to LSF faces compared to HSF faces ($t_{11}=1.57, p=.14$) and between LSF and BSF faces ($t_{11}=.75, p=.47$). Comparison of the effect of spatial frequency in the butterfly condition revealed no differences in RT between HSF, LSF and BSF.

Table 3-4 Child group's mean reaction times (ms) and standard deviation in parentheses for faces and butterflies presented in HSF, LSF and BSF.

	LSF	BSF	HSF
Face	555 (101)	550 (99)	587 (115)
Butterfly	540 (83)	545 (104)	556 (86)

MEG Sensor Analysis

M170 Latency: Adolescent Group

ANOVA results revealed that there was no main effect of stimulus type, $F(1,10)=.20, p=.67$. A main effect of spatial frequency ($F(2,10)=22.02, p<.001$) was found but no stimulus type by spatial frequency interaction was identified ($F(2,10)=1.24, p=.31$).

A priori pairwise comparisons of faces across the three spatial frequencies revealed that HSF faces elicited a peak neuromagnetic response that was significantly later than that elicited by LSF faces ($t_{10}=4.79, p=.001$) and that the M170 elicited by LSF faces peaked significantly later than the M170 elicited by BSF faces ($t_{10}=3.72, p=.004$). Pairwise comparisons of butterflies across the three spatial frequencies revealed that there was no difference between HSF and LSF butterflies ($t_{10}=1.92, p=.09$), and no difference between LSF and BSF butterflies ($t_{10}=1.22, p=.25$). Figure 3-2 is a graph of means and SEMs of M170 latencies.

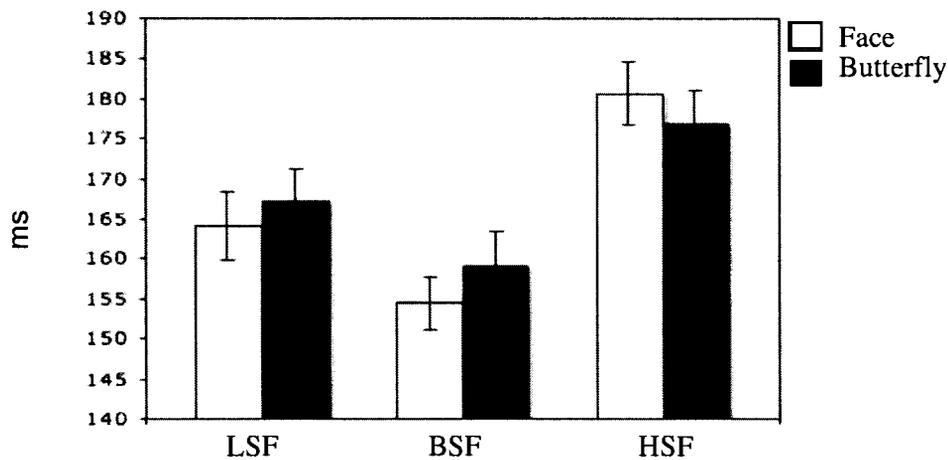


Figure 3-2 Adolescent grand-averaged mean latency (ms) elicited by faces and butterflies presented in LSF, BSF and HSF, recorded from right SOI. Error bars are standard errors of the means (SEMs).

M170 Amplitude: Adolescent Group

ANOVA results revealed a main effect of stimulus type ($F(1,10)=8.61$, $p=.02$), with faces eliciting greater neuromagnetic response than butterflies. No effect of spatial frequency ($F(2,9)=.28$, $p=.71$) and no interaction between stimulus type and spatial frequency ($F(2,20)=.06$, $p=.87$) were identified. Figure 3-3 graphs means and SEMs of amplitudes across the six conditions.

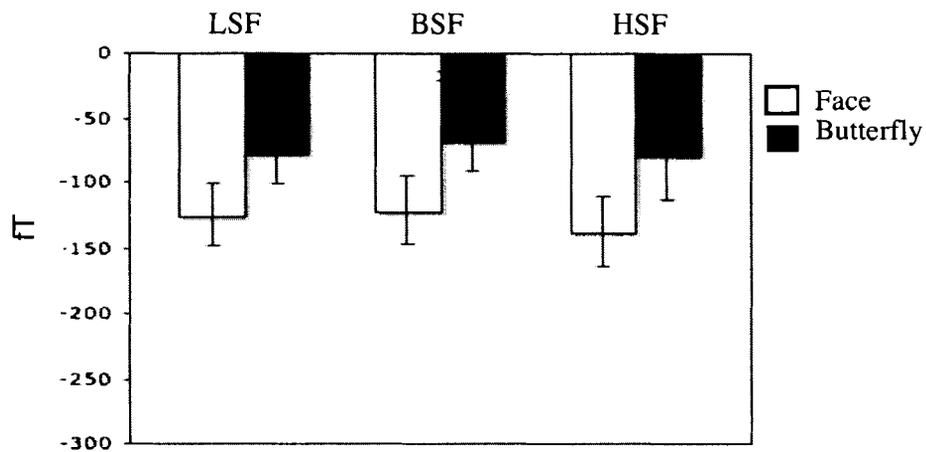


Figure 3-3 Adolescent grand-averaged mean amplitudes (fT) elicited by faces and butterflies presented in LSF, BSF and HSF and recorded from right SOI. Error bars are SEMs.

M170 Latency: Child Group

ANOVA results revealed no main effect of stimulus type, ($F(1,11)=.47$, $p=.51$), no main effect of spatial frequency, ($F(2,10)=2.89$, $p=.08$) and no stimulus by spatial frequency interaction, ($F(2,10)=.67$, $p=.51$). Mean latencies and SEMs for faces and butterflies across SF are shown in Figure 3-6, and appear to show a similar pattern as was observed in the adolescent group of $BSF < LSF < HSF$.

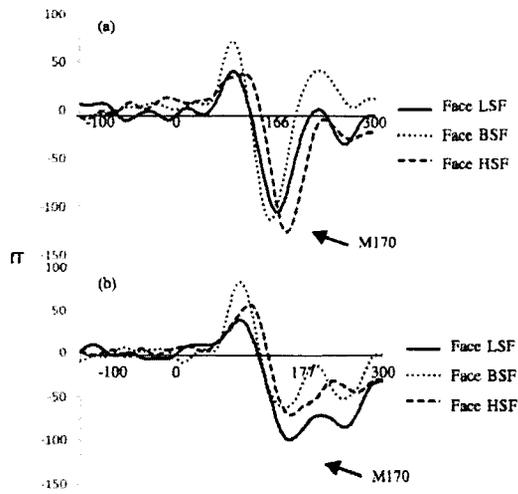


Figure 3-4 Grand-average M170 ERF in (a) adolescents and (b) children elicited by faces in LSF, BSF, and HSF. Recorded from right SOI.

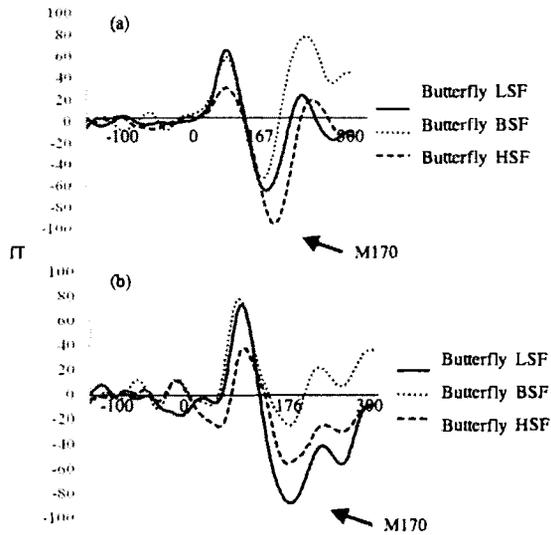


Figure 3-5 Grand-average M170 ERF in (a) adolescents and (b) children elicited by butterflies in LSF, BSF, and HSF. Recorded from right SOI.

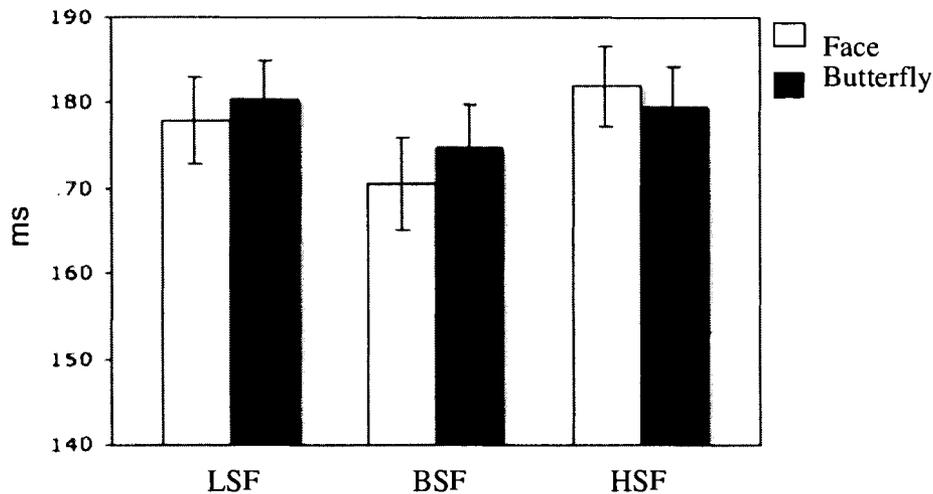


Figure 3-6 Grand-average mean M170 peak latency (ms) in the child group elicited by faces and butterflies presented in LSF, BSF and HSF, recorded from right ROI. Error bars are SEMs.

M170 Amplitude: Child Group

ANOVA results showed that there was a marginally significant effect of stimulus, ($F(1,10)=4.17, p=.07$), with a trend for faces to elicit larger peak amplitudes than butterflies. A main effect of spatial frequency was found ($F(2,10)=10.16, p=.001$), but no stimulus type by spatial frequency interaction was identified ($F(2,22)=1.79, p=.19$). See Figure 3-7 for a graph of mean amplitudes across the six conditions in the child group.

A priori comparisons revealed no difference between HSF and LSF faces ($t_{11}=1.64, p=.13$), but LSF faces elicited a larger peak response than BSF faces ($t_{11}=-2.17, p=.05$). Similarly, results for butterfly indicated no significant difference between HSF and LSF butterflies ($t_{11}=1.74, p=.11$); although, there was a significant difference between LSF and BSF butterflies ($t_{11}=-4.18, p=.002$).

Figures 3-4(b) and 3-5(b) show grand-averaged ERF waveforms elicited by faces and butterflies presented in LSF, BSF and HSF.

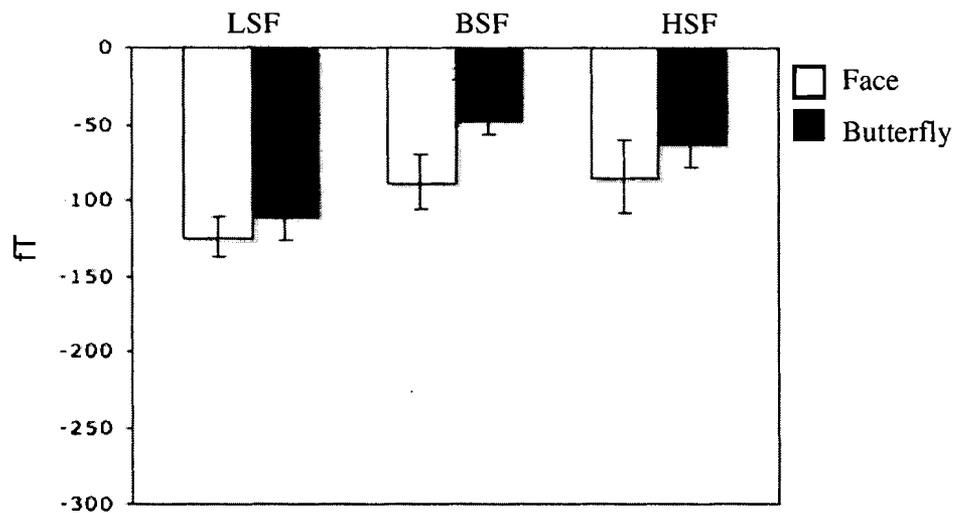


Figure 3-7 Grand-average mean amplitude (fT) in child group, elicited by faces and butterflies presented in LSF, BSF and HSF, recorded from right SOIs. Error bars are SEMs.

Developmental Trajectory of Face Processing

Behavioural Results: Reaction Time

ANOVA results revealed that there was an overall effect of spatial frequency ($F(2,30)=7.94, p=.002$) and a significant spatial frequency by stimulus type interaction ($F(2,62)=3.70, p=.04$). No overall effect of stimulus type ($F(1,31)=2.53, p=.12$), no stimulus type by age group interaction ($F(2,31)=.65, p=.53$) and no spatial frequency by age group interaction ($F(2,62)=1.61, p=.19$)

were found. The three way interaction between age group, spatial frequency and stimulus type was not significant.

M170 Latency

ANOVA results of the M170 latency revealed a significant effect of spatial frequency ($F(2,30)=42.96, p<.001$), a significant spatial frequency by age group type interaction ($F(4,62)=2.79, p=.04$), and a significant spatial frequency by stimulus type interaction ($F(2,30)=7.04, p=.003$). No effect of stimulus type ($F(1,31)=.96, p=.33$), no interaction between stimulus type and age group ($F(4,62)=1.22, p=.31$) and no age group by spatial frequency by stimulus type interaction ($F(4,62)=.23, p=.92$) were found.

Bonferroni corrected independent samples *t*-tests ($\alpha=.004$) were conducted to examine the interaction between age group and spatial frequency. Results revealed no significant differences between the adult and adolescent groups for any of the six conditions. The M170 in children peaked significantly later in children compared to adults for LSF faces ($t_{22}=3.22, p=.004$) and BSF faces ($t_{22}=4.04, p=.001$). There was no difference in M170 peak latency between children and adults for any of the other conditions. Figure 3-8 shows grand-averaged M170 ERFs elicited by faces and butterflies, averaged across SF, in adults, adolescents and children.

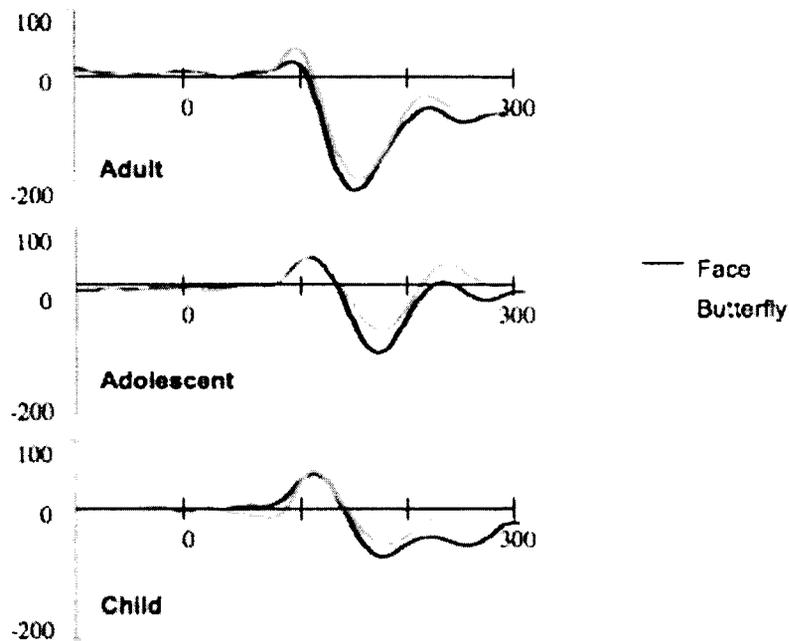


Figure 3-8 Grand-averaged M170 ERF of face and butterflies averaged across spatial frequency in (a) adult, (b) adolescent and (c) child groups, recorded from right SOI.

M170 Amplitude

ANOVA results revealed a significant effect of stimulus type ($F(1,31)=21.03, p<.001$), a significant effect of spatial frequency ($F(2,32)=6.29, p=.009$) and a significant spatial frequency by age group interaction ($F(4,62)=5.68, p<.001$). A stimulus type by age group interaction ($F(2,32)=1.71, p=.19$), a stimulus type by spatial frequency ($F(2,31)=.75, p=.56$) and a age group by spatial frequency by stimulus type interaction ($F(4,64)=.69, p=.43$) were not found.

Bonferroni corrected independent samples *t*-tests ($\alpha = .004$) were conducted to further examine the interaction between spatial frequency and age group and revealed that adolescents had significantly smaller peak M170

amplitudes than adults in response to HSF faces ($t_{21}=3.66$, $p=.001$), HSF butterflies ($t_{21}=3.81$, $p=.001$), LSF butterflies ($t_{21}=3.29$, $p=.003$) and BSF butterflies ($t_{21}=4.56$, $p<.001$). Children had smaller peak M170 amplitudes than adults in response to HSF faces ($t_{22}=5.32$, $p<.001$), BSF faces ($t_{22}=4.29$, $p<.001$), HSF butterflies ($t_{22}=5.03$, $p<.001$) and BSF butterflies ($t_{22}=7.59$, $p<.001$).

Discussion

The current experiment demonstrated that adolescents, like adults in Study 1, were faster to respond to LSF faces compared to HSF faces, indicating faster discrimination of faces when they are presented holistically. In contrast, children did not demonstrate such an advantage, showing a lack of significant RT differences in response to faces and butterflies presented in LSF, BSF and HSF. Although this was a null result making it difficult to interpret, this finding may suggest, as some previous authors have reported (e.g. Carey & Diamond, 1977; Schwarzer, 2000), that children do not demonstrate a behavioural advantage to faces presented holistically, whereas adolescents do. Alternatively, it may be that a larger sample size is required to elicit such an effect due to increased variability in the child group.

Further, as has previously been reported (Taylor et al., 2004) this study found that the child group was generally less accurate at discriminating between faces and butterflies than the adolescent and adult groups, although this group was nonetheless able to accurately discriminate between faces and butterflies with roughly 84% accuracy. Of note, the adolescent group was the least accurate at identifying HSF faces, less accurate than any condition in the child condition

and roughly 19% less accurate than they were at discriminating any of the other conditions, at 74% accuracy. Although this may suggest that on average the adolescent group was attending less to HSF faces, it more likely indicates a particular difficulty at identifying faces presented featurally, in the absence of holistic information, in this sample.

The present study also found that there was an effect of spatial frequency on the latency of the M170 peak response in adolescents, but not for children. In adolescents, faces presented in LSF elicited an earlier peak M170 compared to HSF faces, an effect that was specific to faces. This pattern was the same as was noted in the adult group, in Study 1. Furthermore, in the adolescent age group, the latency of the M170 elicited by LSF faces was slower than that elicited by BSF faces, as was also observed in the adult group and previously discussed in Study 1.

In children, however, no significant M170 latency differences were found between faces or butterflies presented in LSF, HSF, and BSF. Again, although null results are difficult to interpret, this finding may suggest that children do not process faces holistically, processing them similarly to objects, whereas the adolescents show a faster processing of faces presented holistically. This finding is similar to the one reported by Taylor and colleagues (2004) in a study with upright and inverted faces. This study reported the typical N170 face inversion effect in children older than 11-12 years of age; however in younger children, they found that upright faces elicited an N170 with a longer latency and greater negativity than inverted faces. These findings suggest the development of holistic

face processing during adolescents. Alternatively, as previously discussed, effects in my study may have been minimized in the child group due to increased variability in the data.

In terms of peak M170 amplitude, adolescents and children demonstrated the typical trend of faces eliciting a larger electromagnetic response than nonface objects. The amplitude of the M170 was not modulated by spatial frequency in the adolescent group. However, in the child group it was. Interestingly, in opposition to what was reported in adults in Study 1, children showed a greater neuromagnetic flux to faces presented in LSF compared to BSF faces. In the adult literature, such increased negativity has been interpreted as indicating the recruitment of more processing to perceive a face, usually the result of having to rely on a suboptimal processing strategy (e.g. Rossion et al., 1999). Thus, this finding may indicate that more processing is involved in recognizing a face presented holistically for children, even on a very simple discrimination task. Considered in combination with the behavioural literature indicating that children do not show a disadvantage for inverted compared to upright faces, as is observed in adults (e.g. Carey & Diamond, 1977; Schwarzer, 2000), past electrophysiology research on the N170 ERP component (e.g. Taylor et al., 2004), and behavioural and M170 latency data from my study, this suggests that children do not show a LSF advantage to face processing as adolescents and adults do. This is in contrast to several studies which have reported a typical face inversion effect in children, both behaviourally (e.g. Brace et al., 2001; Mondloch et al., 2002; Tanaka et al., 1998) and at the neural level (Itier & Taylor, 2004d)

and is at odds with my initial hypotheses that, because this was a simple face-object discrimination task, children would show a LSF face advantage.

Analysis of the developmental trajectory of face processing in this study suggested that by mid-adolescence, adolescents are processing faces in a qualitatively similar manner to adults, meaning that a similar pattern of results was observed in the adult and adolescent group in response to LSF and HSF faces. Unexpectedly, however, the overall M170 peak amplitude in the adolescent group were more similar to the child M170 than to the adult M170 values. This contradicts some previous research (e.g. Taylor et al., 2004) that has reported adult-level N170s in adolescence by 15 years of age, and rather indicates that the M170 continues to develop throughout adolescence until adulthood.

In comparison to adolescent and adult groups, the M170 in the child group was smaller in amplitude, more variable in latency and failed to show face typical M170 effects. Interestingly, this finding is similar to a recent fMRI study that found that children failed to show consistent face-selective activation in typical face regions of the brain (Scherf, Behrmann, Humphreys, & Luna, 2007) which was attributed to reduced face-selectivity and extent of activation in regions typically associated with face processing, less overall volume and more variability in localization. Such findings likely explain the current MEG findings, which also suggest that there is a lack of face-selectivity to faces in children. Possible reasons for this lack of specificity include previously discussed mechanisms of brain development, such as increased myelination and synaptic pruning which

help to specialize certain brain regions for certain tasks (e.g. Luna & Sweeney, 2004; Paus, 2005; Sowell et al., 2001). In addition to neuronal specialization, with increased exposure to faces across development and an increasing need to recognize more faces, humans need to refine their ability to identify and recognize faces.

In combination with past ERP and fMRI studies, the current experiment suggests that a possible reason for less accurate and less efficient face recognition in childhood reflects a combination of a less specific, less localized brain region for faces and a lack of LSF advantage.

Conclusion

The current study has several limitations. Notably, sample size for the adolescent and, particularly, the child group was small, especially in light of more variable performance and greater susceptibility to artefacts in young people. Additionally, the age ranges chosen for the adolescent and child groups may have been too broad, ultimately diluting within-group effects. There may have also been hormonal changes and other such differences between participants, especially between males and females, arising from puberty in the child group. Given the small sample size, I could not examine such within-group variability that may be confounding the effect of SF on face processing.

Nonetheless, the current study replicated previous findings that the early mechanisms of face processing change across development; however, this study suggested that these early mechanisms continue to develop until early adulthood rather than reaching adult levels by mid-adolescence. Thus, the current findings

suggest that the benefit for holistic face processing, which appears to be absent in children in this study, develops by mid-adolescence but that adult levels of expertise continue to develop until adulthood, at least at the neural level.

4: GENERAL CONCLUSION

The current experiments provide a framework for future research examining the effect of spatial frequency in populations with deficits in face processing, such as Autism Spectrum Disorder (ASD). Understanding the behavioural and neural mechanisms of face processing in typically developing children and healthy adults is an important first step in attempting to understand the development of face processing in patient populations. The study of spatial frequency modulations on face and nonface processing is particularly relevant to the study of populations with ASD, in light of research suggesting that individuals with ASD generally attend to local aspects of a stimulus (e.g. Rondan & Deruelle, 2006) and, more specifically, that individuals with ASD rely more on HSF information than LSF information to process face information (Deruelle, Rondan, Gepner, & Tardif, 2004). Future studies can examine the effect of spatial frequency on the M170 in participants with ASD and compare this with typical development. This may elucidate the neural mechanisms of face processing in ASD, which remain poorly understood.

REFERENCE LIST

- Adolphs, R., Sears, L., & Piven, J. (2001). Abnormal processing of social information from faces in autism. *Journal of Cognitive Neuroscience*, 13, 232-240.
- Amirkhiani, G. & Lovegrove, W. J. (1999). Do the global advantage and interference effects covary? *Perception & Psychophysics*, 61, 1308-1319.
- Batty, M. & Taylor, M. J. (2006) The development of emotional face processing during childhood. *Developmental Science*, 9, 207-220.
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8, 551-565.
- Bentin, S. & Deouell, L. Y. (2000). Structural encoding and identification in face processing: ERP evidence for separate mechanisms. *Cognitive Neuropsychology*, 17, 35-55.
- Brace, N. A., Hole, G. J., Kemp, R. I, Pike, G. E., Van Duuren, M., & Norgate, L. (2001). Developmental changes in the effect of inversion: Using a picture book to investigate face recognition. *Perception*, 30, 85-94.
- Carey, S. & Diamond, R. (1977). From piecemeal to configurational representation of faces. *Science*, 195, 312-314.
- Costen, N. P., Parker, D. M., & Craw, I. (1996). Effects of high-pass and low-pass spatial filtering on face identification. *Perception & Psychophysics*, 58, 602-612.
- de Haan, H., Johnson, M. J., & Halit, H (2003). Development of face-sensitive event-related potentials during infancy: A review. *International Journal of Psychophysiology*, 51, 45-58.
- de Heering, A., Turati, C., Rossion, B., Bulf, H., Goffaux, V., & Simion, F. (in press). Newborns' face recognition is based on spatial frequencies below 0.5 cycles per degree. *Cognition*.
- Deruelle, C. Rondan, C., Gepner, B., & Tardif, C., (2004). Spatial frequency and face processing in children with autism and Asperger syndrome. *Journal of Autism and Developmental Disorder*, 34, 199-210.
- Eimer, M. (1998). Does the face-specific N170 component reflect the activity of a specialized eye processor? *Neuroreport*, 14, 1737-1747.

- Eimer, M. (2000). Effects of face inversion on the structural encoding and recognition of faces: Evidence from event-related brain potentials. *Cognitive Brain Research*, 10, 145-158.
- Farah, M. J., Tanaka, J. W., & Drain, H. M. (1995). What causes the face inversion effect? *Journal of Experimental Psychology: Human Perception and Performance*, 21, 628-634.
- Farah, M. J., Wilson, K. D., Drain, M., & Tanaka, J. M. (1998). What is "special" about face perception? *Psychological Review*, 105, 482-498.
- Fife, A. A., Vrba, J., Robinson, S. E., Anderson, G., Betts, K., Burbank, M. B., Cheyne, D., Cheung, T., Govorkov, S., Haid, G., Haid, V., Hunter, C., Kubik, P. R., Lee, S., McKay, J., Reichl, E., Schroyen, C., Sekachev, I., Speak, P., Taylor, B., Tillotson, & M., Sutherling, W. (1999). Synthetic gradiometer systems for MEG. *IEEE Transactions on Applied Superconductivity*, 9, 4063-4068.
- 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 process faces at the individual level. *Journal of Cognitive Neuroscience*, 12, 495-504.
- Goffaux, V., Gauthier, I., & Rossion, B. (2003). Spatial scale contribution to early visual differences between face and object processing. *Cognitive Brain Research*, 16, 416-424.
- Goffaux, V., Hault, V., Michel, C., Vuong, Q. C., & Rossion, B. (2005). The respective role of low and high spatial frequencies in supporting configural and featural processing of faces. *Perception*, 34, 77-76.
- Goffaux, V. & Rossion, B. (2006). Faces are "spatial"--holistic face perception is supported by low spatial frequencies. *Journal of Experimental Psychology*, 32, 1023-1039.
- Greenlee, M. W. & Breitmeyer, B. G. A choice reaction time analysis of spatial frequency discrimination. *Vision Research*, 29, 1575-1586.
- Halit, H., de Haan, M., Schyns, P. G., & Johnson, M. H. (2006). Is high-spatial frequency information used in the early stages of face detection? *Brain Research*, 1117, 154-161.
- Hämäläinen, M., Hari, R., Ilmoniemi, R. J., Knuutila, J., & Lounasmaa, O. V. (1993). Magnetoencephalography: Theory, instrumentation, and application to noninvasive studies of the working human brain. *Review of Modern Physics*, 65, 413-397.
- Harris, A. & Nakayama, K. (2007a). Rapid face-selective adaptation of an early extrastriate component in MEG. *Cerebral Cortex*, 17, 63-70.
- Harris, A. & Nakayama, K. (in press). Rapid adaptation of the M170 response: Importance of face parts. *Cerebral Cortex*.

- Hayden, A., Bhatt, R. S., Reed, A., Corbly, C. R., & Joseph, J. E. (2007). The development of expert face processing: Are infants sensitive to normal differences in second-order relational information. *Journal of Experimental Child Psychology*, 97, 85-98.
- Henderson, R.M., McCulloch, D. L., & Herbert, A. M. (2003). Event-related potentials (ERPs) to schematic faces in adults and children. *International Journal of Psychophysiology*, 51, 59-67.
- Holmes, A., Winston, J. S., & Eimer, M. (2005). The role of spatial frequency information for ERP components sensitive to face and emotional facial expression. *Cognitive Brain Research*, 25, 508-520.
- Hsiao, F. J., Hsieh, J. C., Lin, Y. Y., & Chang, Y. (2005). The effects of face spatial frequencies on cortical processing revealed by magnetoencephalography. *Neuroscience Letter*, 380, 54-59.
- Itier, R. J., Herdman, A. T., George, N., Cheyne, D., & Taylor, M. J. (2006). Inversion and contrast-reversal effects on face processing assessed by MEG. *Brain Research*, 1115, 108-120.
- Itier, R. J. & Taylor, M. J. (2002a). Inversion and contrast polarity reversal effect both encoding and recognition processes of unfamiliar faces: A repetition study using ERPs. *Neuroimage*, 15, 353-372.
- Itier, R. J. & Taylor, M. J. (2002b). Effects of repetition and configural changes on the development of face recognition processes. *Developmental Science*, 7, 469-487.
- Itier, R. J., & Taylor, M. J. (2004a). Effects of repetition learning on upright, inverted and contrast-reversed face processing using ERPs. *NeuroImage*, 21, 1518-1532.
- Itier, R. J. & Taylor, M. J. (2004b). N170 or N1? Spatiotemporal differences between object and face processing using ERPs. *Cerebral Cortex*, 14, 132-142.
- Itier, R. J. & Taylor, M. J. (2004c). Source analysis of the N170 to faces and objects. *NeuroReport*, 15, 1261-1265.
- Itier, R. J. & Taylor, M. J. (2004d). Face inversion and contrast-reversal effects across development: In contrast to the expertise theory. *Developmental Science*, 7, 246-260.
- Johnson, M. H. (2006). Developing a social brain. *Acta Paediatrica*, 96, 3-5.
- Johnson, M. H. (2005). Subcortical face processing. *Nature Review Neuroscience*, 6, 766-774.
- Kanwisher, N. (2000). Domain specificity in face perception. *Nature Neuroscience*, 3, 759-763.

- Kanwisher, N. & Yovel, G. (2006). The fusiform face area: a cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 361, 2109-2128.
- Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2004). Impairment in holistic face processing following early visual deprivation. *Psychological Science*, 32, 762-768.
- Liu, J., Harris, A., & Kanwisher, N. (2002). Stages of processing in face perception: An MEG study. *Nature Neuroscience*, 5, 910-916.
- Luna, B. & Sweeney, J. A. (2004). The emergence of collaborative brain function: FMRI studies of the development of response inhibition. *Annual New York Academia of Sciences*, 1021, 296-309.
- Macchi Cassia, V., Valenza, E., Pividori, D., & Simion, F. (2002). Can a nonspecific bias toward top-heavy patterns explain newborns' face preference? *Psychological Science*, 15, 379-383.
- Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Sciences*, 80, 347-371.
- Mondloch, C. J., Le Grand, R., & Maurer, D. (2002). Configural face processing develops more slowly than featural face processing. *Perception*, 31, 553-566.
- Morton, J. & Johnson, M. H. (1991). CONSPEC and CONLERN: A two-process theory of infant face recognition. *Psychological Review*, 98, 164-181.
- Paus, T. (2005). Mapping brain maturation and cognitive development during adolescent. *Trends in Cognitive Science*, 9, 60-68.
- Puce, A., Allison, T., Spencer, S. S., Spencer, D. D., & McCarthy, G. (1997). Comparison of cortical activation evoked by faces measured by intracranial field potentials and functional MRI Two case studies. *Human Brain Mapping*, 5, 298-305.
- Rondan, C. & Deruelle, C. (2007). Global and configural visual processing in adults with autism and Asperger syndrome.
- Rossion, B., Delvenne, J., Debatisse, D., Goffaux, V., Bruyer, R., Crommelink, M., & Guérit, J. (1999). Spatio-temporal localizations of the face inversion effect: An event-related potentials study. *Biological Psychology*, 50, 173-189.
- Rossion, B., Gauthier, V., Goffaux, M. J., Tarr, M., & Crommelinck, M. (2002). Expertise training with novel objects leads to left-lateralized facelike electrophysiological responses. *Psychological Science*, 13, 250-257.

- Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., & Crommelinck, M. (2000). Effects of face inversion on the structural encoding and recognition of faces: Evidence from event-related brain potentials. *Neuroreport*, *10*, 145-158.
- Ruiz-Soler, M. & Beltran, F. S. (2006). Face perception: An integrative review of the role of spatial frequencies. *Psychological Research*, *70*, 273-292.
- Savig, N. & Bentin, S. (2001). Structural encoding of human and schematic faces: Holistic and part-based processes. *Journal of Cognitive Neuroscience*, *13*, 937-951.
- Scherf, K. S., Behrmann, M., Humphreys, K., & Luna, B. (2007). Visual category-selectivity for faces, places and objects emerges along the different developmental trajectories. *Developmental Science*, *10*, F15-F30.
- Schyns, P. G. (1998). Diagnostic recognition: Task constraints, object information and their interactions. *Cognition*, *67*, 147-179.
- Schyns, P. G. & Oliva, A. (1999). Dr. Angry and Mr. Smile: When categorization flexibility modifies the perception of faces in rapid visual presentations. *Cognition*, *69*, 243-265.
- Schwarzer, R. (2000). Development of face processing: The effect of face inversion. *Child Development*, *71*, 391-401.
- Sowell, E. R., Thompson, P. M., Tessner, K. D., & Toga, A. W. (2001). Mapping continued brain growth and gray matter density reduction in dorsal frontal cortex: Inverse relationships during postadolescent brain maturation. *Journal of Neuroscience*, *15*, 8819-8829.
- Tanaka, J. (2001). The entry point of face recognition: Evidence for face expertise. *Journal of Experimental Psychology: General*, *130*, 534-543.
- Tanaka, J. W. & Farah, M. J. (1993). Parts and whole in face recognition. *Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology*, *46*, 225-245.
- Tanaka, J. W., Kay, J. B., Grinnell, E., Stansfield, B., & Szetcher, L. (1998). Face recognition in young children: When the whole is greater than the sum of its parts. *Visual Cognition*, *5*, 479-496.
- Taylor, M. J., Batty, M., & Itier, R. J. (2004). The faces of development: A review of early face processing over childhood. *Journal of Cognitive Neuroscience*, *15*, 1426-1442.
- Taylor, M. J. McCarthy, G., Saliba, E., & Degiovanni, E. (1999). ERP evidence of developmental changes in processing of faces. *Clinical Neurophysiology*, *110*, 910-915.

- Turati, C., Valenza, E., Leo, I., & Simion, F. (2005). Three-month-olds' visual preference for faces and its underlying visual processing mechanism. *Journal of Experimental Child Psychology, 90*, 255-273.
- Vuilleumier, P., Aromony, J. L., Drive, J., & Dolan, R. J. (2004). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nature Neuroscience, 6*, 624-631.
- Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology, 81*, 141-145.
- Young, A. W., Hellowell, D., & Hay, D. C. (1987). Configurational information in face perception. *Perception, 16*, 747-759.
- Xiang, J., Wilson, D., Otsubo, H., Ishii, R., & Chuang, S. (2001). Neuromagnetic spectral distribution of implicit processing of words. *Cognitive Neuroscience and Neuropsychology, 12*, 3923-3927.
- Xu, Y., Liu, J., & Kanwisher, N. (2005). The M170 is selective for faces, not for expertise. *Neuropsychologia, 43*, 588-597.