FAMILIARITY MODIFIES EARLY PERCEPTUAL FACE PROCESSING AS REVEALED BY EVENT-RELATED POTENTIALS

FAMILIARITY MODIFIES EARLY PERCEPTUAL FACE PROCESSING AS REVEALED BY EVENT-RELATED POTENTIALS

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Abstract

Accurate face recognition plays a critical role in developing and maintaining social relationships. Typically developing adults show expertise when processing faces, demonstrated by their ability to recognize new faces even after a single exposure. Furthermore, face recognition is superior for highly familiar faces associated with rich semantic information. Although semantic processes mediate familiar face recognition, it is unclear what processes mediate unfamiliar face recognition. The main objective of my thesis was to identify unique neural mechanisms underlying familiar versus unfamiliar face recognition and to detail how these mechanisms change as a result of learning. I used event-related potentials (ERPs) to assess the stages of face processing affected by familiarity.

In Chapter 1, I reviewed the literature contrasting familiar and unfamiliar face recognition processes from cognitive and neural perspectives.

In Chapter 2, I identified processes involved in unfamiliar face recognition by recording ERPs to repeated presentations of unfamiliar faces in upright and inverted orientations. Inverted faces portray the same structural information as upright faces but with novel orientation that disrupts identity processing. Repeated exposure to an upright face (and not an inverted face) produced repetition priming at an early perceptual stage reflected by the N170 component, suggesting that unfamiliar face recognition is mediated by early perceptual representation.

In Chapter 3, I directly tested whether semantic information modifies early perceptual face processing. I recorded ERPs to new faces that were learned over a five-day session with either person-specific or irrelevant information. N170 repetition priming was observed for all faces except those learned with person-specific information, suggesting that relevant semantic information, and not merely perceptual experience, changes early perceptual face processing.

In Chapter 4, I assessed the relationship between N170 and N400 recognition processes. Specifically, I examined whether top-down semantic processes reflected by the N400 modulate early identity processes reflected by the N170. I constructed composite faces by combining facial features from different famous individuals; the facial features conveyed incongruous identity information so that when the face was processed as a whole it was perceived to be novel. Both familiar faces and composite faces failed to elicit N170 repetition priming but did elicit a similar N400 response, suggesting that familiar face recognition can be achieved with very little facial information. Moreover, these results suggest that the retrieval of semantically relevant information during familiar face recognition occurs even in the presence of incongruous perceptual information and that such processing modulates early perceptual processes.

Together, these results demonstrate the interplay between memory and perception (which I summarize and discuss in Chapter 5), revealing different mechanisms of face recognition as a function of person-specific information. Unfamiliar face recognition takes place at the perceptual stage reflected by the N170 and is revealed through repetition priming. As an unfamiliar face becomes well known, its recognition processes shift to a later semantic stage reflected by the N400 and such semantic processes seem to modulate early perceptual processes. This knowledge has advanced our understanding of face processing at cognitive and neural levels.

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Preface

This thesis includes two published manuscripts (Heisz, Watter, & Shedden, 2006. Automatic face identity encoding at the N170. Vision Research, 46, 4604-4614; Heisz & Shedden, 2009. Semantic learning modifies perceptual face processing. Journal of Cognitive Neuroscience, 21, 1127-1134) and one submitted manuscript (Heisz & Shedden. ERP evidence for semantic retrieval associated with familiar faces and incongruent parts). I was the lead researcher for all projects, assisted by my PhD supervisor Judith M. Shedden in aspects of experimental design and manuscript editing. For one of the projects (Heisz, Watter & Shedden, 2006) Scott Watter also assisted in aspects of experimental design and manuscript editing.

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Chapter 1

Introduction

Appropriate human social interactions rely on accurate face recognition as well as immediate access to associated person-specific information. The general major contribution of my thesis was to demonstrate that person-specific information feeds back to modify early perceptual face processing. I demonstrated this by using event-related potentials (ERPs) neuroimaging technique, identifying unique neural mechanisms that underlie familiar versus unfamiliar face recognition and detailing how these mechanisms change during person learning.

Throughout this dissertation I use the term familiarity, colloquially defined as the quality of being well known. More formally, *visual familiarity* refers to perceptual experience processing the structural face image, and *familiar/familiarity* refers to visual familiarity plus associated person-specific information or semantics. I use the terms *person-specific information* and *semantics* (interchangeably) to mean general information about the person, including personal traits, intentions, and transient mental states, biographical facts and episodic memories (c.f., Gobbini & Haxby, 2007). Although not the focus of this dissertation, there seems to be additional distinction among familiar faces including own-face and personally familiar faces (Taylor et al., 2009).

The distinction of visual familiarity versus visual-plus-semantic familiarity fits well with Bruce and Young's (1986) functional model of face recognition. The model has three main processing modules that are central to face recognition. The first stage is called "Structural Encoding", and produces a physical extraction of the face image (i.e., pictorial code). Structural encoding also produces more abstract representations of the facial features and their configuration. This structural face information feeds into the second stage called "Face Recognition Unit (FRU)", which is thought to reflect a structural identity code, capturing aspects of the individual face that make it unique. Note that a structural identity code differs from a pictorial code in that a structural identity code is a more abstract representation of a particular face image, sensitive to the invariant aspects of the face. There is one FRU for each previously viewed individual face. As a result of visual familiarity, familiar faces are thought to have a more elaborate FRU than unfamiliar faces. Thus, a sense of familiarity can be established by structural identity code alone.

However, a sense of familiarity is generally not sufficient for appropriate social interaction. The structural identity code (along with the individual's voice, name) can act to retrieve the associated identity-specific semantic code. This type of information is represented by the third stage called "Person Identity Node (PIN)", which is thought to represent broad details about the person, such as biographical facts and episodic memories. There is one PIN for each known individual. Accessing the PIN provides a feeling of knowing (or person recognition), which is important for guiding appropriate social behaviour. PINs are thought to be part of the general cognitive system of semantic memory. Importantly, PINs are thought to feedback to modulate processing at the earlier stage of FRUs; this was originally supported by associated (related) face priming (Bill Clinton's face primes Hillary Clinton's face; Bruce & Valentine, 1986) and is further corroborated by the general findings of my thesis.

To further place my thesis within the context of the current literature, I discuss three topics central to face recognition: 1) the physical attributes needed for accurate face recognition, 2) the neural regions that subtend face processing, and 3) the timing of face-related processes. Throughout these topics I emphasize the similarities and differences between familiar and unfamiliar face recognition processes.

1.1 The physical attributes needed for accurate face recognition

Faces are a highly homogenous stimulus class, with the same parts in the same arrangement, and individuating faces by physical appearance is not as easy as it may seem. Fortunately, faces have many different cues to identity. Individual variation in facial features (e.g., size, shape, colour, texture), the spacing between features, and the contour of the face could be used to identification. However, in most cases, recognition seems to rely on integrating face parts into a coherent unit or holistic representation (Farah, Wilson, Drain & Tanaka, 1998; Sergent, 1984).

There is a complex nomenclature used to describe the different ways in which features combine into a whole (for review, see Maurer, Le Grand & Mondloch, 2002). Although these distinctions are not central to my thesis, it is important to define the three main conceptualizations of whole face information: first-order relational information, second-order relational information, and holistic processing. First-order relational information refers to the homogenous arrangement of facial features, with two eyes above a nose above a mouth, which is true of all face images. This representation is very robust such that any image arranged according to first-order relations tends to be perceived as a face. For example, Archimbaldo's paintings portray fruits and vegetables arranged in typical facial configuration, and although the collection is not actually a face, it is perceived as one (Hulten, 1987). Second-order relational information refers to the spatial distance between features, which is somewhat confounded with the size and shape of features. Unlike first-order relations, second-order relational information differs across individual faces and therefore, is thought to play an important role in facial identity. Holistic processing means to consider the face as a whole unit or gestalt, and seems to be dependent on the detection of first-order relations. A hallmark of holistic processing is that individual features are not represented in isolation when presented in the context of a whole face.

The main purpose for discussing part versus whole face information is to show that the contribution of part information for identification depends on face familiarity. We know that familiar faces are recognized faster and more accurately than unfamiliar faces (Burton, Wilson, Cowen, & Bruce, 1999; Bruce, 1982; Ellis, Shepherd, & Davies, 1979; Klatzky & Forrest, 1984; Young, Hay, McWeeny, Flude & Ellis, 1985) even when image quality is poor (Burton et al., 1999) and image context is variable (i.e., changes in viewpoint; Bruce, 1982). Interestingly, this superior recognition for familiar faces seems to be accompanied by improved ability to use part-based facial identity cues for recognition (O'Donnell & Bruce, 2001).

In the following section, I describe two classic whole face manipulations: face inversion effect and composite face effect, which do not distinguish between familiar and unfamiliar face recognition. I also present evidence for enhanced part-based processing in familiar facial recognition.

Whole face manipulations

Inversion effect. To invert a stimulus is to rotate it 180° in the picture plane. Yin (1969) measured the effect of stimulus inversion on the recognition of faces and other mono-oriented objects (e.g., house, airplanes). Although inversion disrupted recognition of all the objects, it disproportionally disrupted face recognition. Based on verbal reports made at the end of the experiment, Yin speculated that participants were using different strategies to remember objects versus faces; objects seemed to be encoded using a more analytical or detailed strategy, whereas upright faces seemed to be encoded using a more relational or holistic strategy.

Indeed, relational or holistic information seems to be most disrupted by face inversion. For example, Rhodes and colleagues (1993) manipulated faces by adding paraphernalia (e.g., adding glasses) or changing relational information (e.g., spacing between eyes). Each face was presented in original and modified versions, and participants determined which version of the face they had seen in the study phase. Participants easily recognized upright study faces but had difficulty recognizing inverted study faces especially when discriminating between original versus relationally manipulated versions. These results demonstrate that inversion disrupts second-order relational processing and this directly affects face recognition.

Familiar faces are not immune to the inversion effect. Compared to familiar object recognition, inversion disproportionally disrupts familiar face recognition

(Scapinello & Yarmey, 1970; Yarmey, 1971). In fact, one of the most striking displays of the inversion effect was first demonstrated using Margaret Thatcher's face (Thompson, 1980). Thatcherizing a face involves inverting the eyes and mouth while keeping the rest of the face in usual upright orientation. Upright Thatcherized faces are grotesque and look very different from the original face image, whereas inverted Thatcherized faces appear normal and are difficult to distinguish from the original face image (Bartlett & Searcy, 1993). This illusion reveals how little relational (first-order and second-order) information we are able to extract from the whole face when it is inverted, even when the face is familiar.

It is also difficult to learn a relational processing strategy for inverted faces. Robbins & McKone (2003) tested this by training participants to discriminate between inverted facial images of identical twins. Although identical twins were used to minimize the distinctiveness of features, participants were still able to find small featural differences between faces (i.e., eyebrow shape) and this featural information was sufficient for identification. Importantly, when the distinguishing feature was not available (i.e., by occluding the eyebrows), participants were unable to identify the inverted faces and were unable to recognize the individual across different (untrained) inverted facial images. Similar pattern-based learning was observed when participants were trained to discriminate between 10 inverted facial images; although participants learned to identify individual inverted faces, the learning did not transfer to new inverted images (Hussain, Sekuler, & Bennett, 2009). In contrast, similar recognition deficits are not observed for upright faces (Robbins & McKone, 2003).

It is important to note that non-face stimuli can show inversion effects. Like faces, a stimulus of expertise (e.g., Dog show judges viewing inverted dog bodies) can be disproportionally disrupted by inversion (Diamond & Carey, 1986). Furthermore, non-expertise objects and faces can show equal disruption by inversion when performance is assessed by perceptual sensitivity rather than recognition accuracy (Matheson & McMullen, 2009). These suggest that relational processing may not be face-specific but rather a processing strategy that can be used to recognize all visual stimuli.

In summary, inversion disrupts our ability to processes relational information, and such information seems to play an important role in both familiar and unfamiliar face recognition.

Composite face effect. Composite faces are created by combining the top half of one person's face with the bottom half of a different person's face (Hole, 1994; Young, Hellawell & Hay, 1987). When the two halves are aligned, the juxtaposition of different individuals represented by the top and bottom halves produces the strong perception of a completely novel face. In contrast, when the two halves are misaligned via slight horizontal displacement, the composite face illusion disappears and the two halves can be recognized separately.

Young and colleagues (1987) were the first to demonstrate the composite face effect. They combined the top and bottom halves of different famous faces and had participants name the famous individual represented by the top half (or bottom half). Participants were slower to name the famous individual represented by the top half (or bottom half) when the two halves were aligned than when they were misaligned. This demonstrates holistic processing in that the incongruent information from the composite face interferes with part-based recognition when the composite halves are arranged in typical face configuration.

The original paradigm was modified to test composites of unfamiliar faces (Hole, 1994; Hole, George & Dunsmore, 1999). Instead of naming, participants determined whether two composites had the same top-halves or not. Importantly, it was difficult for participants to correctly perceive two top halves as the same when they were aligned with different bottom halves. Thus, even for a composite made of unfamiliar halves, the incongruent information from the irrelevant half interferes with the correct perception of the relevant half. This suggests that holistic processing is engaged when face parts (familiar or unfamiliar) are aligned in a typical face configuration.

Recent work has examined the limits of holistic processing by manipulating the extent of misalignment between composite face halves (Taubert & Alais, 2009). In particular, composite face halves were misaligned either horizontally (as in the original studies) or vertically. Although holistic processing was disrupted by the slightest (i.e., a quarter-width of the face) horizontal misalignment, holistic processing was not disrupted by the same amount of vertical misalignment. Vertical misalignment may be less disruptive to holistic processing than horizontal misalignment because vertical variation among feature distance is more naturalistic. Moreover, with vertical misalignment (and not with horizontal misalignment), features remain in proper first-order configuration.

In summary, the composite face illusion demonstrates our propensity for holistic processing when typical face parts are arranged in proper facial configuration, and this is true regardless of face familiarity.

Part-based face manipulations

Individual variation of the size and shape of features (e.g., eyes, nose, mouth) are also important for face recognition. Tanaka and Farah (1993) tested this by examining participants' ability to identify the features of a newly familiarized face in isolation and in the context of the whole face. Overall participants were about 10% better at identifying facial features in the context of the whole face than in isolation. Control stimuli (i.e., scrambled faces, inverted faces and houses) failed to show a similar whole-over-part advantage, suggesting that information provided by the whole is especially important for face recognition. However, participants were still quite good at recognizing features in isolation and identification by eyes alone was about 80% correct.

This makes sense given that the eyes seem to contain the most diagnostic information for facial identification. Evidence for this comes from various psychophysical techniques (Gosselin & Schyns, 2001; Sekuler, Gaspar, Gold & Bennett, 2004). For example, in the response classification technique external noise is added to a face image; the distribution of noise across the image is randomly varied from trial-to-trial to determine regions in which noise consistently affects performance. In a recognition task, noise masking the eyes and eye region consistently impairs performance (Sekuler et al., 2004). Although unfamiliar faces are often used in these techniques, each face is presented up to a thousand times and therefore, may become visually familiar at some point during the experiment.

Indeed, the eyes seem to be particularly important for familiar face recognition. O'Donnell and Bruce (2001) demonstrated this by making specific featural manipulations to familiar and unfamiliar faces, including changes to the eyes, hair, mouth, or chin. Original and manipulated versions of the same face were presented side-by-side and participants were asked to determine if the two faces were physically identical or not. Overall, participants were good at detecting hairstyle change but poor at detecting chin or mouth changes. Importantly, participants were better at detecting changes to the eyes of familiar faces than unfamiliar faces, suggesting a greater sensitivity to identity information conveyed by the eyes of familiar faces. This fits with data from eye-tracking studies whereby participants spend more time looking at the eyes of familiar than unfamiliar faces (Althoff & Cohen, 1999) and show increased sampling of the eyes as new faces become familiar (Heisz & Shore, 2008). The eyes may act as important cues, encouraging the retrieving stored facial representations of familiar individuals. These stored representations may help to fill in the missing structural detail, creating a somewhat complete representation of the whole face and allowing for more accurate recognition of highly familiar faces with very little perceptual input.

In summary, the whole face plays an important role in recognition as evinced by the inversion and the composite face effects. The eyes also contain important identity information and we are most sensitive to this information when a face is (at least) visually familiar.

1.2 The neural regions that subtend face processing

Despite the structural complexity of faces, the brain seems to effortlessly create high fidelity percepts. Not surprisingly, there has been much interest in understanding exactly how this works, and over the last two decades we have made good progress. In the following section, I first describe the basic functional organization of the visual system and then get into more detail about the main structures that subtend face-related processes.

Functional organization of the visual system

The retina (at the back of the eyes) is the first structure to process any visual stimuli, encoding the brightness and frequency of reflected light in a topographic fashion. Retinal ganglion cells from each eye project into separate layers of the lateral geniculate nucleus (LGN) of the thalamus, which is an important gateway to primary or striate visual cortex (V1) of the occipital lobe. V1 receives information from both eyes and processes rudimentary properties of the stimulus, such as the orientation of edges and lines, luminance, and contrast. V1 projects into extrastriate visual cortex (V2, V3), which is the initial stage for colour, form and motion processing. Two functionally separate pathways project from V2: the *dorsal pathway* to posterior parietal cortex, which is primarily involved in motion perception or vision-for-action, and the *ventral pathway* to inferior temporal cortex, which is primarily involved in form and colour perception or vision-for-perception (Goodale & Milner, 1992). Areas within each stream are organized in hierarchical fashion, such that higher visual areas process more complex visual information.

Face-sensitive neural areas

An important question for face researchers concerns the specificity of brain processes for face stimuli. Although the brain seems to respond differently to faces compared to other objects, it is unclear whether this reflects the workings of face-specific or all-purpose visual processes. Given their crucial social function, special mechanisms may have evolved for processing faces (see McKone, Kanwisher, & Duchaine, 2007 for recent review). However, faces may show special processing because they are the only stimulus class with which most typically developing humans have expertise—we are highly practiced at individuating faces (e.g., Bob) whereas we tend to process most objects at the basic level (e.g., as a table or car; Anaki & Bentin, 2009; Tanaka, 2001). Individual level processing may place higher demands on the visual system than basic level processing (Tarr & Cheng, 2003). Indeed, highly familiar objects (e.g., the Eiffel tower; Anaki & Bentin, 2009) and objects-of-expertise (e.g., a dog to a dog expert; Gauthier, Tarr, Anderson, Skurdlarski, & Gore, 1999) can elicit individual level processing and seem to be processed in a face-like manner.

Although the specificity of face processing is still under debate, there has been a tremendous amount of work investigating the brain's response to face stimuli. In the following section, I will be describing face-sensitive brain areas but it is important to keep in mind that these areas may or may not be face-specific.

Neuropsychological case studies

Our initial understanding of neural face processing came from a rare form of brain damage called prosopagnosia, which renders patients unable to recognize individual faces (see Barton, 2008; Behrmann & Avidan, 2005; Rossion, 2008a, for recent reviews). The acquired form of prosopagnosia tends to result from bilateral or right hemisphere lesions in occipital temporal cortex, selectively disrupting face processes while leaving other cognitive and visual processes intact. Although there have been some cases in which prosopagnosia affects familiar but not unfamiliar face recognition, and vice versa (Malone, Morris, Kay & Levin, 1982), the precise brain regions responsible for these familiarity-specific impairments are difficult to localize by lesion alone.

Face cells in monkeys

Further insight into human face processing came from single-cell recordings of awake, anesthetized monkeys (although note that monkey brains are not exactly equivalent to human brains). This technique involves inserting a microelectrode into the brain to measure action potentials of single neurons. Some cells within monkey temporal cortex are sensitive to faces, facial features and direction of eye gaze (see Desimone, 1991; Gross, 2008; Perrett, Misdin & Chitty, 1987; for reviews). These face cells seem to cluster within the inferior temporal gyrus and the superior temporal sulcus. Importantly, no single cell responds to a particular individual face. Instead, each cell seems to have a graded response to many faces; the magnitude of each cell's response depends on the physical characteristics of the face image, suggesting a distributed network of multiple cells may respond to an individual face (see Quiroga & Panzeri, 2009 for a discussion of sparse coding).

Functional magnetic resonance imaging (fMRI)

Our understanding of face processing burgeoned with the development of functional brain imaging, providing a non-invasive way to measure human brain function. Functional magnetic resonance imaging (fMRI) measures blood-oxygen-level dependency. Although fMRI is an indirect measure of brain activity, its high spatial resolution can identify brain regions that are recruited for face processing. Results of fMRI experiments indicate face-sensitive generators within at least three distinct areas of the visual pathway: the superior temporal sulcus region (STS), the inferior occipital gyrus (IOG), and the middle fusiform gyrus (MFG). The STS is most sensitive to the changeable aspects of a face, including expression, eye gaze, and head orientation, whereas the IOG and MFG are most sensitive to the invariant individuating aspects of a face (Haxby, Hoffman, & Gobbini, 2000).

Both the occipital (Gauthier et al., 2000) and fusiform (Kanwisher, McDermott, & Chun, 1997) face areas (localized to the IOG and MFG, respectively) are sensitive to faces, showing greater activation to faces than non-face objects especially in the right hemisphere. Although both face areas are sensitive to whole face manipulation, the occipital face area seems less sensitive, suggesting that it may be able to represent features more independently (Schiltz & Rossion, 2006). Critically, right occipital and fusiform face areas show greater activity in response to unfamiliar faces than familiar faces (Rossion, Schiltz, & Crommelinck, 2003), suggesting that the recruitment of these face areas may be affected by prior processing of a particular face.

1.3 The timing of face-related processes

The timing of neural face processing reveals important information about the different stages involved in face recognition. Event-related potential (ERP) neuroimaging technique can capture the precise time course of neural processes with millisecond resolution. ERP acquisition usually involves placing electrodes on the scalp; the electrodes record the electroencephalogram (EEG) signal, time locked to the onset of a particular event. The EEG signal is subjected to signal processing which includes filtering and rejection of artifacts. The voltage activity of like events is averaged, and the resulting ERP waveform depicts changes in brain voltage (amplitude) over time. ERP waveforms consist of a series of peaks or components, identified by their time and sign of deflection, which are thought to be indicative of specific psychological (e.g., sensory, cognitive, motor) stages.

There has been much work using ERPs to investigate the neurocognitive processes of face recognition. However, to fully appreciate these findings, it is important to have a basic understanding of how the ERP signal is generated by the brain. In the following section, I first describe ERP neural-level activity and then discuss three ERP components implicated in face processing: N170, N250 and N400.

Event-related potentials (ERPs)

ERPs reflect postsynaptic potentials, initiated by the binding of neurotransmitters to the apical dendrites of the postsynaptic cell membrane. This causes ion channels to open or close, allowing ions to move across the membrane, creating a gradient change at the apical dendrite part of the neuron. To equilibrate this gradient change, ions either move in or out of the cell body and basal dendrites parts of the same neuron. This creates a tiny dipole across the neuron, with net positivity at one end and a net negativity at the other end. Importantly, the dipole generates an open field meaning that its current spreads through the brain (conductor) and can be measured at distal locations (e.g., the scalp). Since electrical activity has nearly the same velocity as light, voltage changes recorded at the scalp reflect the precise timing of neural activity.

Although the dipole of a single neuron is too small to measure at the scalp, simultaneous dipoles of a population of spatially aligned neurons can sum to create an equivalent current dipole that is large enough to be measured at the scalp. Cortical pyramidal cells are well suited for ERP, with long apical dendrites aligned in parallel, and perpendicular to the cortical surface. Moreover, populations of pyramidal cells are densely interconnected. If a population of pyramidal cells receives the same input (from cortical or subcortical sources), the ensuing activity would likely generate a sizable dipole, measurable by scalp electrodes.

The particular voltage response measured at the scalp depends on the position and orientation of the dipole. Dipole current diffuses through the brain following a path of least resistance. When the current reaches the skull (resistor) it tends to spread laterally. This causes the spatial smearing of the voltage signal, and explains why neighboring scalp electrodes tend to have a similar amplitude response. The smeared voltage signal also makes it extremely difficult to localize dipole-generating neural populations, and thus, ERP is characterized as having low spatial resolution. Although there are mathematical techniques for solving the inverse problem of inferring dipole source(s) from voltage patterns, any given voltage pattern may have resulted from an infinite number of dipole configurations. Even when the solution is spatially constrained (e.g., by using spatial information from structural MRI), dipole source modeling can still be highly erroneous.

Early perceptual face processing

N170

All visual stimuli produce P1-N1 morphology, with a positive peak at approximately 100 ms (P1) immediately followed by at negative peak at approximately 150 ms (N1). Both components are maximally recorded over lateral occipital cortex and are implicated in early visual structural processing. In addition, faces elicit an N170 response. The N170 is a negative going ERP component that peaks between 140 ms and 190 ms post-stimulus onset and is maximally recorded over occipiotemporal cortex. As with most evoked potentials, the cortical source underlying the N170 has been difficult to localize. This is partly because the ERP signal provides poor spatial resolution, and partly because the N170 seems to reflect the activation of multiple generators at various brain regions, including bilateral fusiform gyri, (superior, middle and inferior) temporal gyri, and bilateral precuneus (e.g., Corrigan et al., 2009). Consistent with the right hemisphere bias reported in some prosopagnosia cases and fMRI studies, N170 face-related effects tend to be larger over the right hemisphere than the left hemisphere (Rossion, Joyce, Cottrell, & Tarr, 2003).

As an index of early perceptual face processing, the N170 amplitude is larger for faces than non-face stimuli (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Carmel & Bentin, 2002; Eimer, 2000b; George, Evans, Fiori, Davidoff, & Renault, 1996; Sagiv &

Bentin, 2001). Although sensitive to human faces, the N170 can show larger amplitude for animal faces (Rousselet, Mace, Fabre-Thorpe, 2004) and face-like objects (Churches, Baron-Cohen, & Ring, 2009) compared to other non-face objects, suggesting sensitivity to general processes of face detection. Since all faces have the same parts arranged in the same configuration, part and/or whole information could be used for face detection. In turn, much research has examined the N170 response to various part and whole face manipulations.

In general, whole face manipulations tend to enhance and delay the typical face-related N170 response. This is true for inverted faces (Bentin et al., 1996; Eimer, 2000b; Heisz, Watter, & Shedden, 2006a, 2006b; Itier, Alain, Sedore, & McIntosh, 2007; Itier & Taylor, 2002, 2004; Rossion et al., 2000), upright Thatcherized faces (Carbon, Schweinberger, Kaufmann, & Leder, 2005; Milivojevic, Clapp, Johnson & Corballis, 2003), and misaligned composite faces (Letourneau & Mitchell, 2008; Jacques & Rossion, 2009). The delay is thought to reflect slower, less automatic processing of these unusual stimuli. The amplitude enhancement is thought to reflect the recruitment of additional neural generators, and this is supported by different scalp voltage distributions for manipulated versus typical faces (Carbon et al., 2005; Itier et al., 2007; Jacques & Rossion, 2009).

Part-based manipulations also affect the N170 but in a much less systematic way. N170 amplitude is larger for whole facial images than for facial images lacking internal features (e.g., eyes, nose, mouth) or external features (e.g., head contour, hair; Eimer, 2000b). Compared to whole faces, isolating the nose or lips reduces and delays the N170 response (Bentin et al., 1996), whereas isolating the eyes enhances the N170 response (Bentin et al., 1996; Itier, Alain, Sedore, & McIntosh, 2007). The enhanced eye response is accompanied by a shift in scalp voltage distribution, and together these results have been interpreted as reflecting the additional recruitment of eye-selective neural generators of the superior temporal sulcus and fusiform gyrus (Bentin et al., 1996; Itier et al., 2007; Itier & Batty, 2009).

So, it seems as though the N170 is sensitive to both whole face information as well as information conveyed by the eyes. Interestingly, this maps to the type of information needed for accurate face recognition, suggesting that N170 may reflect early identity processes. However, initial tests failed to find any difference in the N170 response to familiar versus unfamiliar faces (Eimer, 2000a; Bentin & Deouell, 2000), and thus, it was presumed that N170 processes reflected face detection and not identity processing. This prompted researchers to look at later time components (like the N250 and the N400) for familiarity effects.

Before I discuss the later stages of face processing reflected by the N250 and N400 ERP components, I will review two different but converging literatures that report similar N170-like early face processing effects: intracranial N200 and M170 component.

N200

The N200 reflects an ERP component recorded from strips of electrodes placed on the surface of the ventral occipitotemporal cortex. These electrodes are implanted in patients with intractable epilepsy to help localize focal seizures. Compared to scalp recorded

ERP, the location of neural activity recorded by an intracranial electrode strip can be better established.

The N200 is a negative going component that peaks approximately 200 ms post-stimulus onset and shows similar response properties to the scalp-recorded N170 described above. In particular, the N200 is evoked for faces and not for non-face stimuli (e.g., cars, nouns, butterflies; Allison, Puce, Spencer, & McCarthy, 1999). Its amplitude response is sensitive to external (face contour) and internal (especially the eyes but also the nose and mouth) faces parts (McCarthy, Puce, Belger, & Allison, 1999), and shows equally large amplitude for upright and inverted faces (McCarthy et al., 1999).

Like the N170, the N200 amplitude does not differ for familiar and unfamiliar faces (Barbeau et al., 2008; Puce, Allison, & McCarthy, 1999). However, it is sensitive to face repetition, with decreased amplitude for single (but not habitual) repetition of the same unfamiliar face (Puce et al., 1999). Moreover, electrical stimulation of sites at which the N200 is maximally recorded can disrupt the inability to name famous faces (Allison et al., 1994; Puce et al., 1999), suggesting there may an important connection between early face representation and later semantics that is mediated by processed reflected by the N200.

M170

Magnoencephalography (MEG) captures the magnetic field produced by neuronal electrical potentials. Recall that EEG reflects neuronal electrical potentials and thus, these two neuroimaging techniques are closely related. Notably, the MEG M170 component—occurring around 170 ms and localized to the fusiform gyrus (Deffke et al., 2007)—displays similar response properties to the ERP N170 component.

The M170 is sensitive to facial images. Its amplitude is larger for faces than non-face stimuli (e.g., houses, animals, hands, and other common objects; Lui, Higuchi, Marantz, & Kanwisher, 2000; Xu, Liu, & Kanwisher, 2005) but also shows sensitivity to face-like stimuli, such as primate faces and car fronts (Hadjikhani, Kveraga, Naik, & Ahifors, 2009; Schweinberger, Kaufmann, Moratti, Keil, & Burton, 2007). The M170 amplitude is larger for frontal face images compared to profile face images (Lui et al., 2000) and is delayed when a face is presented upside-down than when presented upright (Itier, Herdman, George, Cheyne, & Taylor, 2006; Lui et al., 2000; Schweinberger et al., 2007).

The M170 response seems to reflect processes underlying face categorization. Most work supporting this idea has used the double-pulse adaptation paradigm (Jefferys, 1996), whereby two stimuli (S1, S2) are presented with a short interstimulus interval, and the ratio of S2 M170 amplitude to S1 M170 amplitude is calculated. Repetition suppression refers to a reduction in the M170 amplitude to S2 relative to S1. A whole face image immediately preceded by a different whole face image (in photographic, two-tone or line-drawn forms) elicits greater repetition suppression than a whole face image immediately preceded by a house image (Harris & Nakayama, 2007). Greater repetition suppression is also seen when a whole face is preceded face parts in isolation (e.g., eyes, nose, mouth) than by a house image, suggesting that features alone may cue face categorization (Harris & Nakayama, 2008).

Importantly, repetition suppression is greatest when a whole face is immediate preceded by a different whole image of the same face, suggesting that the M170 is also sensitivity to facial identity (Harris & Nakayama, 2008). Likewise, the M170 amplitude is larger for personally familiar than unfamiliar faces (Kloth et al., 2006), suggesting that early identity processing at the M170 may be modulated by later semantic processes.

Given the similarities in response properties, N170, N200 and M170 components are thought to reflect similar (if not the same) neural processes.

Later stages of face processing

N250

The N250 is a negative going component that peaks approximately 250 ms post-stimulus onset. It is maximally recorded over inferiotemporal cortex and localized to generators of the fusiform gyrus (e.g., Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002). The N250 seems to reflect processes involved in individual (subordinate) level categorization. Its amplitude is larger for one's own face than unfamiliar faces (Tanaka, Curran, Porterfield, & Collins, 2006). However, unfamiliar task relevant (target) faces can show an increase in N250 amplitude with repeated exposure (Tanaka et al., 2006). Furthermore, non-face objects (i.e., cars, blobs) produce an enhanced N250 amplitude response following individual (subordinate) level training but not basic level training (Krigolson, Pierce, Holroyd, & Tanaka, 2009; Scott, Tanaka, Sheinberg, & Curran, 2008).

The N250 also shows a repetition effect, whereby repeating the same face elicits an increase in the N250 amplitude, often referred to as N250r (note: this is not repetition suppression as seen at the N170 and N400, see discussion below). The N250r is larger for immediate repetition than for delayed repetitions (Schweinberger, Pickering, Burton, & Kaufmann, 2002) and larger when the exact same image is repeated rather than subsequent presentations of different images of the same person (Schweinberger, Pickering, Jentzsch, Burton et al., 2002), suggesting sensitivity to perceptual face repetition. The N250r is also larger for familiar than unfamiliar faces (Engst, Martin-Loeches, & Sommer, 2006; Schweinberger, Pickering, Burton et al., 2002) and for familiar than unfamiliar buildings (Engst et al., 2006). Furthermore, the N250r increases after repeatedly viewing a previously unfamiliar face (Herzmann & Sommer, 2007). Taken together, N250 processes seem to perceptual matching, which seems to be more fluent for perceptually experienced (visually familiar) visual stimuli.

Critically, the N250r is task dependent, with a larger response for direct (i.e., identity matching) tasks than indirect (i.e., non matching) tasks. This is particularly important as it suggests N250 processes are not necessarily automatic process. Furthermore, this may be why I failed to observe N250r effects in my experiments discussed in Chapters 2 and 3; in both of these experiments, face identity was not task relevant. The focus of the thesis is on the N170 effects and future work will explore the N250 details.

N400

The N400 is a negative going ERP component that peaks approximately 400 ms post-stimulus onset and is maximally recorded over centroparietal cortex. The N400 seems to reflect the activity of generators in the anterior medial temporal lobe (McCarthy, Nobre, Bentin, & Spencer, 1995). The N400 was first described in response to semantically anomalous sentence endings, such as "The pizza was too hot to cry" (Kutas & Hillyard, 1980). Time-locking ERPs to the onset of the semantically anomalous word "cry" elicited large N400 response; replacing the word "cry" with a less semantically anomalous word (e.g., "drink") elicited a moderate N400 response, whereas replacing the word "cry" with a semantically congruent word (e.g., "eat") elicited no N400 response. Thus, the N400 was established as an index of the degree of semantic mismatch between the preceding words and the sentence ending, whereby the preceding words set up the context in which certain sentence endings were more or less expected.

Since this initial study, N400 semantic processing effects have been observed with other stimuli, including faces. Face-related N400 effects are observed using a repetition-priming paradigm in which the first face sets up the context and second subsequently presented face either matches or not. Participants typically perform a 1-back identity-matching task to encourage matching between the first and second faces. If the first face is familiar, it will elicit a N400 response, which is thought to reflect activation of semantic information associated with the face image (Bentin & Deouell, 2000; Eimer, 2000a; Heisz & Shedden, submitted). If the second face is the same familiar face, it will not elicit an N400 response because it matches perfectly with the preceding face. The difference between the N400 amplitude response to first and second face images is referred to as a repetition effect. A larger repetition effect (i.e., repetition priming) is indicative of a better match between the faces as seen when the same familiar face is immediately repeated; whereas no N400 repetition is indicative of no match between the faces as seen when two semantically unrelated familiar faces are sequentially presented

(Barrett, Rugg, & Perrett, 1988; Eimer, 2000a;Engst et al., 2006; Herzmann, Schweinberger, Sommer & Jentzsch, 2004; Schweinberger, Pfütze & Sommer, 1995; Schweinberger, Pickering, Burton, et al., 2002). Importantly, N400 priming occurs when a familiar face follows its name (Pickering & Schweinberger, 2003) or a familiar face follows the face of a related individual (Schweinberger et al., 1995), suggesting that N400-based matching reflects abstract or conceptual processes.

Importantly, familiar faces tend to elicit N400 effects while unfamiliar faces do not. This is not too surprising as familiar faces are associated with semantic person-specific information. In contrast, unfamiliar faces are associated with little or no semantic information and therefore rely less on N400 semantic processes.

Face-related components (N170, N250, N400) have been mapped onto the function face model proposed by Bruce and Young's (1986). N170 processes are thought to reflect the first stage of structural encoding, extracting the perceptual details of the facial image. N250 processes are thought to reflect the second stage: Face Recognition Unit (FRU), involved in processing of a structural identity code. Finally, N400 processes are thought to reflect Person Identity Node (PIN) processing or accessing person-specific semantic information.

1.4 The scope of my thesis

In the current studies, I sought to identify the unique neural mechanisms that underlie familiar versus unfamiliar face recognition, with particular interest in how these mechanisms change during learning. I used ERPs to assess the stages of face processing that may be affected by familiarity.

At the time I began my thesis, we knew that face recognition differs according to familiarity and that N400 processes play an important role in familiar face recognition but we did not know how individual unfamiliar faces are recognized and how these recognition processes change as new faces become familiar. A critical difference between familiar and unfamiliar faces is that familiar faces are associated with a rich network of person-specific information. According to the current face recognition model, different aspects of a person act as effective retrieval cues resulting in superior recognition of highly familiar individuals (for relevant models, see Bruce & Young, 1986; Burton, Bruce & Johnston, 1990; Burton, Bruce & Handcock, 1999). In contrast, unfamiliar faces are associated with little or no person-specific information and therefore recognition may be based primarily on perceptual matching.

With this in mind, I reexamined the N170 literature and found a collection of studies that involved perceptual matching. These studies used a repetition-priming paradigm similar to that used to investigate the N400 effects, whereby the first face is presented followed by the second face, and participants determine if the two faces represent the same individual. Although some studies reported N170 effects for repeated faces, other did not, and many researchers remained skeptical of the N170 as an index of early identity processing. However, I realized there was a simple reason for this lack of consistency: N170 repetition effects were being reported for unfamiliar faces (Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009; Campanella et al., 2000; George, Jemel, Fiori, & Renault, 1997; Guillaume & Tiberghien, 2001; Heisz & Shedden, 2009; Heisz, Watter, & Shedden, 2006a, 2006b; Jaques, d'Arripe, & Rossion, 2007; Itier & Taylor, 2002, 2004) but not for familiar faces (Schweinberger, Pickering, Burton & Kaufmann, 2002; Schweinberger, Pickering, Jentzsch, Burton & Kaufmann, 2002) and from this I built my thesis.

In my first experiment (Chapter 2), I examined whether the N170 repetition effect was sensitive to face identity. I recorded ERPs to repeated unfamiliar faces presented in upright and inverted orientation (Heisz, Watter, & Shedden, 2006b). Although upright and inverted faces are of equal perceptual complexity, inversion disrupts typical identity processing (e.g., Yin, 1969). I assessed the automaticity (i.e., processing that is done spontaneously or without intention) of unfamiliar face recognition at the N170 by having participants perform a 1-back location-matching task in which face identity is task irrelevant. N170 repetition priming was observed for upright faces but not inverted faces, suggesting that the N170 is sensitive to automatic identity processes of upright faces.

In my second set of experiments (Chapter 3), I directly tested whether semantic information modifies early perceptual face processing. I recorded ERPs to new faces that were learned over a five-day session with either person-specific or irrelevant information (Heisz & Shedden, 2009). N170 repetition priming was observed for all faces expect those learned with person-specific information, suggesting that relevant semantic information, and not merely perceptual experience, changes early perceptual face processing as reflected by the N170.

In my third set of experiments (Chapter 4), I assessed the relationship between N170 and N400 recognition processes. Specifically, I examined whether top-down semantic processes (reflected by the N400) modulate early identity processes (reflected by the N170). I constructed composite faces by combining facial features from different famous individuals; the facial features conveyed incongruous identity information so that when the face was processed as a whole it was perceived to be novel. Critically, the N170 repetition effect is thought to reflect whole-face matching (Jacques & Rossion, 2009). Although our composite faces were being processed holistically, both familiar faces and composite faces failed to elicit N170 repetition priming. In contrast, both familiar faces and composite faces did elicit a similar N400 response, suggesting that familiar face recognition can be achieved with very little facial information. These results demonstrate the retrieval of semantically relevant information during familiar face recognition even in the presence of unfamiliar perceptual information and that such associated semantic processing modulates early perceptual processes.

In summary, I have demonstrated the interplay between memory and perception, revealing different mechanisms of face recognition as a function of person-specific information. Unfamiliar face recognition takes place at the perceptual stage reflected by the N170 and is revealed through repetition priming. As an unfamiliar face becomes well known, its recognition processes shift to a later semantic stage reflected by the N400. This knowledge has advanced our understanding of face processing at cognitive and neural levels.

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Chapter 2

Automatic face identity encoding at the N170

Jennifer J. Heisz, Scott Watter & Judith M. Shedden

2.1 Preamble

Unfamiliar faces are associated with little or no semantic information and thus, recognition processes are based primarily on perceptual matching. Given that the N170 component is thought to reflect an early perceptual face processing stage, I hypothesized that N170 repetition effect may be a potential mechanism for unfamiliar face recognition processes.

In this chapter, I describe an experiment in which I assessed the automaticity of unfamiliar face recognition at the N170. I define automaticity as processing that is spontaneously or without intention. To test automaticity, I had participants perform a 1-back location-matching task in which face identity is task irrelevant. To test specificity of face processing, I contrasted the repetition of upright versus inverted face processing. Inverted faces are good control stimuli because they portray the same low-level information as upright faces but with novel orientation that disrupts identity processing. Repeated exposure to an upright face (and not an inverted face) produced repetition priming at an early perceptual stage reflected by the N170 component. This suggests that N170 processes mediate automatic identity processing of unfamiliar faces.

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Automatic face identity encoding at the N170

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Abstract

The N170 event-related potential component is currently under investigation for its role in face identity processing. Using a location-matching paradigm, in which face identity is task irrelevant, we observed a progressive decrease in N170 amplitude to multiple repetitions of upright faces presented at unattended locations. In contrast, we did not observe N170 habituation for repeat presentations of inverted faces. The findings suggest that the N170 repetition effects reflect early face identity processes that are part of familiarity acquisition of new faces.

Keywords: Face perception; Event-related potentials; Attention; Inversion effect

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1. Introduction

A considerable amount of research has been devoted to contrasting familiar and unfamiliar face processing, yet little research has investigated the mechanisms by which novel faces become familiar. Currently, the event-related potential (ERP) component N170 is under investigation for its role in the acquisition of face familiarity.

The N170 is thought to reflect the detection and global processing of facial images. Larger N170 responses are evoked in response to facial stimuli than non-face objects and scrambled faces (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Carmel & Bentin, 2002; Eimer, 2000b; George, Evans, Fiori, Davidoff, & Renault, 1996; Rossion et al., 2000; Sagiv & Bentin, 2001). The N170 component is attenuated and delayed in response to facial images lacking internal (e.g. eyes, nose, mouth) or external features (e.g. head contour, hair) (Eimer, 2000b). Inverting a face image impairs normal face recognition abilities via the disruption of configural information (e.g. Yin, 1969; for a review see Maurer, LeGrand, & Mondloch, 2002). Consequently, N170 responses evoked by inverted faces are delayed and enhanced (Eimer, 2000a, 2000b, 2000c; Itier & Taylor, 2002; Rossion et al., 1999; Rossion et al., 2000), possibly revealing the greater effort required to recognize inverted faces or recruitment of additional neurons that respond to non-face objects.

Initial reports suggested face recognition processes were captured by later ERP components only. Differences between novel and famous faces were observed at N400 and P600, such that the responses were enhanced for famous versus unfamiliar faces (Bentin & Deouell, 2000; Eimer, 2000a). Famous face repetition effects were also observed at these later ERP components (Eimer, 2000c; Pfutze, Sommer, & Schweinberger, 2002; Schweinberger, Pickering, Burton, & Kaufmann, 2002a; Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002b; Schweinberger, Huddy, & Burton, 2004). These studies did not show repetition effects for unfamiliar face repetition at these late components (Eimer, 2000c; Schweinberger et al., 2002a).

A comparison of repeated presentations of unfamiliar and famous faces revealed earlier N170 repetition effects for unfamiliar faces. Caharel, Poiroux, and Bernard (2002) measured ERP modulation during passive viewing of one's own face, a famous face and an unfamiliar face, with each image repeated 100 times in random order. Familiarity effects were observed at the N170 such that the N170 amplitude was significantly attenuated in response to repetitions

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of an unfamiliar face but not for repetitions of one's own face or a famous face. Similar results were found by Henson et al. (2003) who showed repetition effects at the N170 for unfamiliar faces, and not for famous faces. Note the contrast with later components in which repetition effects were observed at later ERP components for famous faces, and not for unfamiliar faces as described above. These early versus late ERP effects demonstrate processing differences between highly familiar faces and newly learned faces.

A general finding is that the amplitude of the N170 decreases in response to repeat versus solitary presentations of unfamiliar faces (Campanella et al., 2000; George, Jemel, Fiori, & Renault, 1997; Guillaume & Tiberghien, 2001; Heisz, Watter, & Shedden, 2006; Itier & Taylor, 2002; Itier & Taylor, 2004). The N170 repetition effects are observed across short (e.g. Itier & Taylor, 2002) and long (George et al., 1997) repetition lags. Repetition effects at the N170 are observed for repeat presentation of photos portraying the same individual even when the same face is presented with different facial expressions (Guillaume & Tiberghien, 2001), different image backgrounds (Guillaume & Tiberghien, 2001), or different physical images (Campanella et al., 2000). N170 repetition effects are typically observed when the experimental task requires explicit evaluation of face identity (Campanella et al., 2000; George et al., 1997; Guillaume & Tiberghien, 2001; Itier & Taylor, 2002; Itier & Taylor, 2004) but are also observed when face identity is task irrelevant (Heisz et al., 2006). Taken together these findings suggest that N170 amplitude modulation for unfamiliar face repetitions is part of early identity processes and may reflect mechanisms that underlie familiarity acquisition for new faces.

Using an identity-matching task, Itier and Taylor (2002) reported N170 amplitude attenuation to repeated face images compared to new images regardless of whether the images were upright, inverted or contrast-reversed. This effect was reproduced in a follow-up study (Itier & Taylor, 2004) which used upright, inverted and contrast-reversed facial images in a target identification task. Their task consisted of a learning phase in which a target face was presented 10 times. The learning phase was immediately followed by a test phase in which the target was repeated 12 times amongst 20 new facial images of the same type and participants' task was to identify the targets. For upright, inverted and contrast-reversed images, there was a decrease in N170 amplitude in response to the last half of target face repetitions relative to non-target faces, and a decrease in N170 latency in response to all target face repetitions relative to non-target faces.

The observation of N170 habituation to repeated inverted and contrast-reversed images may seem counter to the hypothesis that the N170 repetition effects reflect early identity processing. Both inversion (Yin, 1969) and contrast-reversal (Galper, 1970) of facial images disrupt normal face recognition processes. Specifically, these image manipulations disrupt perception of configural relationships among features (Lewis & Johnston, 1997; Rhodes, Brake, & Atkinson, 1993). In addition, evidence suggests that inverted faces are recognized via featural processing rather than via holistic face recognition processes (Rhodes, 1988; Rhodes et al., 1993; Searcy & Bartlett, 1996; Tanaka & Sengco, 1997).

However, it is possible that the N170 repetition effects for inverted and contrast-reversed faces are a consequence of the task demands. Specifically, when identity is part of the task, effort is made to extract identity from the image. Thus, a task which requires identity matching may show repetition effects for faces even when they are inverted or contrast-reversed. Previous experiments have demonstrated that attending to the identity of the face does modify processing at the N170. One study compared tasks involving face recognition versus digit detection (with digits superimposed on the face image) (Eimer, 2000a, 2000c). N170 peak latency was delayed for both upright and inverted faces in the digit detection task compared to the face recognition task. Moreover, when spatial attention was directed toward the face the N170 amplitude response was enhanced relative to when attention was directed away from the face toward the digit (Holmes, Vuilleumier, & Eimer, 2003).

If the repetition effect for inverted faces is due to identity processing that is imposed by task demands that direct attention to face identity, then it might be possible to reduce the repetition effect by drawing attention away from face identity. We know that identity of upright faces is processed automatically (Tanaka, 2001) and that inverted faces do not show the same advantage (Maurer et al., 2002). Therefore, a task in which face identity is not relevant might reveal repetition effects for upright faces that do not occur for inverted faces which are more difficult to identify. This would lend support to the hypothesis that the N170 repetition effects are related to face identity processing.

Heisz et al. (2006) used a location-matching task in which face identity was not relevant. A face was presented on each trial in one of four possible spatial locations and the task was to indicate whether the current face occurred in the same or different visuospatial location as the face on the previous trial. Behavioural responses and P3 amplitudes showed sensitivity to face identity when faces were presented at attended visuospatial locations but not when faces were presented at unattended visuospatial locations. The N170 repetition effect was also sensitive to visuospatial attention, showing a more progressive habituation when faces were presented in unattended locations (amplitude decreased for each repeated face up to four sequential repeats) versus attended locations (amplitude decreased for the first repeated face only). The claim was made that the N170 reflected automatic face identity processing and that amplitude reductions reflected increased ease of processing when faces were repeated. Heisz et al. (2006) suggested that in attended visuospatial locations, the identity process reflected by the N170 reengaged after the initial repeated face because attention to the spatial location of the face resulted in attention to the identity of the face even though identity was not task relevant. However, in unattended visuospatial locations this reengagement of identity processing did not occur, revealing the progressive habituation of the N170.

We used the same location-matching task as Heisz et al. (2006) with an additional set of inverted face stimuli. Alternating runs of novel and repeat faces in upright and inverted form were presented. On each trial, a face was presented in one of four possible locations, and the task was to indicate whether the face appeared in the same or different visuospatial location as the previous face. We found a progressive habituation of the amplitude of the N170 to repeated upright faces in unattended locations, consistent with Heisz et al. (2006). An amplitude decrease for the first repeated upright face only was observed in attended locations, similar to other work (Campanella et al., 2000; George et al., 1997; Guillaume & Tiberghien, 2001; Heisz et al., 2006; Itier & Taylor, 2002, 2004). Finally, no N170 amplitude habituation occurred when repeated faces were inverted regardless of whether they were presented in attended or unattended visuospatial locations.

2. Methods

2.1. Participants

Thirty-four volunteers (31 female, mean age 19 years) from the McMaster University community participated in the study. Five subjects were eliminated due to excessively noisy EEG. All but two subjects were right handed and all subjects reported normal or corrected-to-normal vision. Informed consent was obtained from each participant. Eligible participants received course credit for their participation, and the remainder volunteered without compensation.

2.2. Apparatus and stimuli

Stimulus presentation and manual response measurement were controlled with Presentation® experimental software (Version 0.80, www.neurobs.com), running on a Pentium 4 computer under the Windows 2000 operating system with a 17-in. color CRT display at a resolution of 1024 x 768 pixels and a frame rate of 75 Hz. The experiment was run in a dimly lit room, with a fixed chin rest to maintain a constant viewing distance of 80 cm. Stimuli were 177 black-and-white pictures of Caucasian male (85) and female (92) faces with neutral expressions. These stimuli were adapted from a larger set of stimulus photographs courtesy of Dr. Daphne Maurer's Visual Development Laboratory, Department of Psychology, Neuroscience and Behaviour, McMaster University, originally acquired and processed as described in Mondloch, Geldart, LeGrand, and Maurer (2003). All the faces were unknown to the subjects and the faces were without glasses, jewelry, or other extraneous items. An elliptical image mask was used to isolate each face from mid forehead to lower chin (including eyebrows and outer margins of the eyes, as shown in Fig. 1). The 8-bit (256-level) grey scale images had a mean pixel luminance value of 166.0, with a standard deviation (contrast equivalent) of 12.3. Faces were presented within an ever-present placeholder box, with width of 85 mm and, height of 104 mm centered on the display. Within the center of the box was a 1 mm square fixation point, which was occluded by the face stimuli when they were presented. Elliptical face stimuli with a width of 60 mm and height of 90 mm were presented on a white background, in one of the four corners of the constant box, with 2 mm vertical and horizontal separation from the nearest sides of the box. The spatial extent of the faces within the placeholder box was large enough that they overlapped adjacent locations by 19.5 mm in width and 40 mm in height. With the constant viewing distance of 80 cm, face stimuli were ≈6.4 degrees of visual angle high and 4.3 degrees of visual angle wide.

2.3. Procedure

The experimental procedure is depicted in Fig. 1. The experiment consisted of four experimental sessions each lasting ≈10 min. Each session contained all 177 face stimuli divided into two subsets: upright and inverted; all faces maintained the same orientation for the entire experiment. Blocks of upright and inverted face trials were alternated throughout each session. Within each block, runs of repeat faces (e.g., four or five presentations of the same face) were alternated with runs of novel faces (e.g., three or four presentations of different faces). Stimulus order was randomized for each session so that a repeated face in one session might be presented only once as a novel face in the following session (and vice versa). Because the same 177 faces were used in all three sessions, familiarity with the set increased accordingly. Each session contained ≈300 trials, with self-paced breaks provided every 80 trials, dividing each session into four approximately equal blocks.

Prior to each session, participants received a brief training block in which the same upright face was presented for 16 trials. Participants were instructed to keep their eyes fixated on the central fixation point. Faces were presented in one of the four corners of the placeholder box for 200 ms, with an interstimulus interval that was randomly jittered from 1000 to 1300 ms. Participants performed a continuous, running 1-back location-matching task, determining whether the current face stimulus was in the same visuospatial location or a different visuospatial location as the immediately preceding face. Visuospatial location of each face stimulus was determined randomly with equal probability of occurrence in each of the four possible visuospatial locations, giving expected probabilities of same-location and different-location trials of 25% and 75%, respectively. Subjects responded with their right index and middle fingers on the "1" and "2" keys of the keypad on a standard computer keyboard to denote same-location and different-location responses, with response key mapping counterbalanced across subjects. Participants were required to respond to every face stimulus except the first one of a continuous-performance block. Subjects were instructed to ignore face identity, and both speed and accuracy were emphasized.

2.4. Electrophysiology

The continuous EEG (132 channels, BioSemi ActiveTwo, www.biosemi.com) was sampled at 512 Hz, using a left hemisphere parietal electrode (CMS) as reference. ERP averaging and analyses were performed using EEProbe software (ANT, www.ant-software.nl). The continuous EEG file for each subject was digitally filtered from 0.03 to 30 Hz. The EEG file was re-referenced to a common average reference for the N170 component and re-referenced to linked mastoids for analysis of the P3 component. Eye-blinks were identified and corrected using both automated and manual detection procedures via EEProbe software. Epochs contaminated with other eye movements and large artifacts were rejected. A 1000 ms recorded EEG epoch, including a 100 ms pre-stimulus baseline and a 900 ms interval following stimulus onset, was chosen for ERP averaging. ERP waveforms were then averaged separately for each condition. Only trials with correct responses were included.

2.5. Data analysis

Repeated measures analyses of variance (ANOVA) were conducted for both mean reaction time for correct responses and mean error rate in a 3-way design with the following conditions: stimulus orientation (upright, inverted), visuospatial location (different, same), and face identity (novel, repeat). Behavioural data were collapsed over experimental sessions and serial position.

The P1 component was isolated using a time window ranging from 50 to 150 ms, obtained via inspection of the grand average waveforms. Analysis of the P1 component was conducted on the same electrode set as in

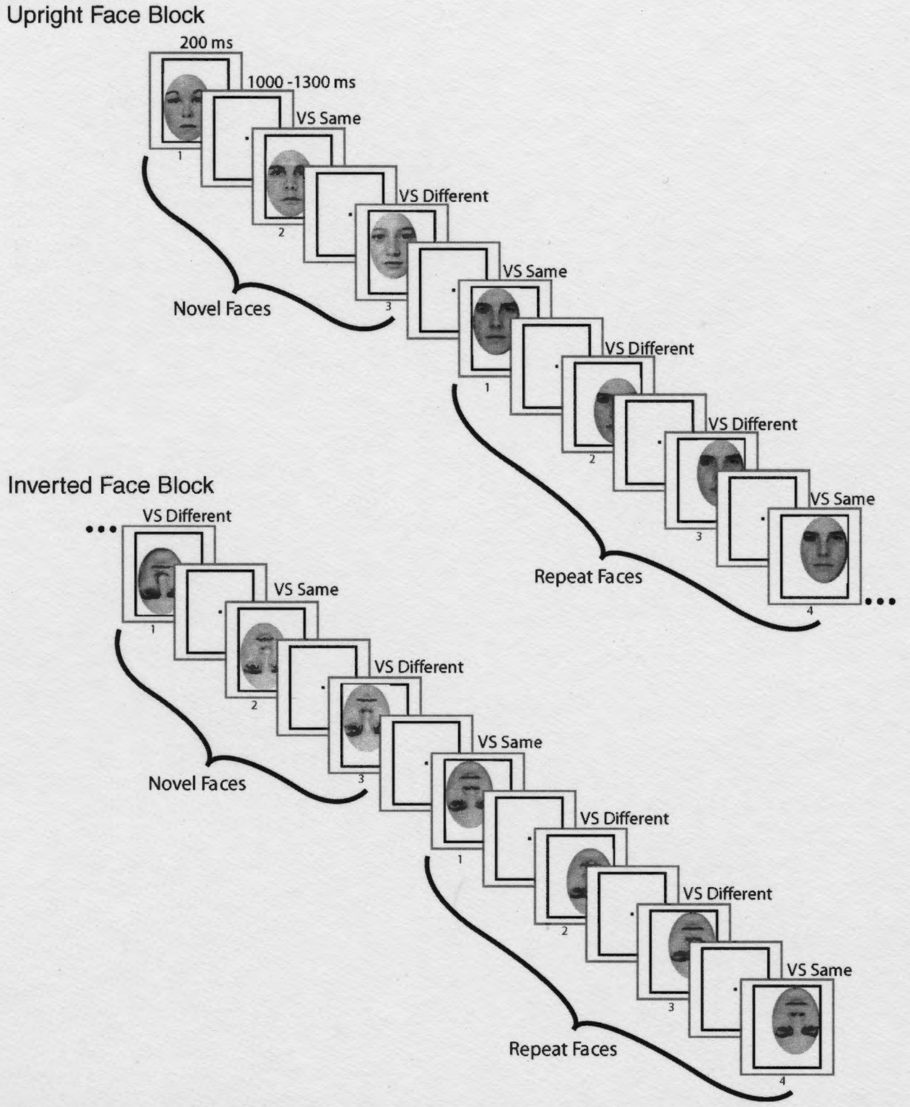

Fig. 1. The figure depicts some of the possible combinations of face orientation (upright vs. inverted), face identity (novel vs. repeat), visuospatial (VS) location (same vs. different) and serial position that participants experienced throughout the experiment. Faces were presented randomly at one of the four corners of an ever-present box on the computer screen, with subjects judging whether the current face stimulus was in the same or a different visuospatial location compared with the location of the previous face. Faces were presented for 200 ms in blocks of upright and inverted faces alternating runs of three or four novel faces and four or five repeated presentations of the same face, with 1000–1300 ms between stimuli.

N170 analysis. Repeated measures ANOVA with Greenhouse-Geisser correction applied when necessary was conducted for P1 peak amplitude in a 5-way design with the following conditions: hemisphere (left, right), stimulus orientation (upright, inverted), visuospatial location (different, same), face identity (novel, repeat), serial position (1, 2, 3, 4).

ERP analysis of the N170 components focussed on an occipital-parietal region of interest which exhibited maximal N170 amplitude. A set of eight electrodes were assessed, four electrodes from each of left and right hemispheres. For each subject individual waveforms were inspected to determine the optimal location at which to capture maximal N170 amplitude effects and the analysis of all N170 conditions was conducted for that electrode pair. Electrode locations corresponding to locations defined by the 10–20 system: P03/P04, P05/P06, an electrode pair slightly lateral in location to P03/P04, and an electrode pair slightly medial in location to P05/P06. The N170 component was isolated using a time window ranging from 120 to 200 ms, obtained via inspection of the grand average waveforms. Repeated measures ANOVAs with Greenhouse-Geisser correction when needed were conducted on N170 amplitudes and latencies to examine differences across serial positions for runs of novel and repeated upright faces as well as runs of novel and repeated inverted faces. Initially, a five factor $2 \times 2 \times 2 \times 2 \times 4$ ANOVA with factors of hemisphere (left, right), stimulus orientation (upright, inverted), visuospatial location (different, same), face identity (novel, repeat), and serial position (1, 2, 3, 4) was run, and based on a significant 5-way interaction, ANOVA analyses were done on the following effects. Two factor 2×4 ANOVAs with factors of hemisphere (left, right) and serial position (1, 2, 3, 4) were done separately for upright novel and repeat faces, and inverted novel and repeat faces, at same and different locations.

Effects of face identity and visuospatial location on P3 component amplitudes were assessed over a parietal region of interest, comprised of electrodes Pz (corresponding to the 10–20 system coordinates) and two neighbouring electrodes on either side of the midline. P3 mean amplitude effects (average amplitudes across a 450–580 ms window, obtained via inspection of the grand average waveforms) were assessed with a 3-way repeated measures ANOVA with factors of stimulus orientation (upright, inverted), visuospatial location (different, same), and face identity (novel, repeat). ERP data were collapsed over experimental sessions and serial position.

FCz amplitudes were assessed over a frontal region of interest, comprised of electrodes FCz (corresponding to the 10–20 system coordinates) and two neighbouring electrodes on either side of the midline. FCz (average amplitudes across a 450–580 ms window, obtained via inspection of the grand average waveforms) were assessed with a 3-way repeated measures ANOVA with factors of stimulus orientation (upright, inverted), visuospatial location (different, same), and face identity (novel, repeat). ERP data were collapsed over experimental sessions and serial position.

3. Results

3.1. Behavioral results

Fig. 2 illustrates mean error rate and reaction time performance for upright and inverted face stimuli, presented as repeat and novel face stimuli at different and same visuospatial locations. Behavioral performance was impaired for novel faces presented at the same visuospatial location: there were increases in both error rate and response time for novel faces at same location relative to repeat faces at same location, and novel and repeat faces at different locations. These observations were supported by a 2-way interaction of location and face identity for errors: $F(1,28) = 14.319$, $p < 0.01$; and reaction time: ($F(1,28) = 6.345$, $p < 0.05$). The 3-way interaction between face orientation, location, and face identity was not significant for either error rate ($F < 1$) or reaction time performance ($F(1,28) = 2.159$, $p =$ n.s.).

3.2. P1 results

Fig. 3 illustrates mean P1 responses. Mean P1 amplitudes were larger for inverted relative to upright face stimuli, $F(1,28) = 21.134$, $p < 0.05$. Larger P1 amplitudes were observed for face stimuli presented at same relative to different visuospatial locations, $F(1,28) = 18.526$, $p < 0.05$. This observation is consistent with greater allocation of attention to "same" locations compared to "different" locations. There was also a significant 3-way interaction between hemisphere, orientation and face identity, $F(1,28) = 5.515$, $p < 0.05$. This effect was due to larger P1 amplitudes for novel than repeat upright faces detected at the right hemisphere electrode sites, suggesting an early sensitivity to novel upright (but not novel inverted) faces (Bonferroni $t(28) = 2.625$, $p < 0.01$ and $t(28) = 0.299$, $p =$ n.s., for upright and inverted, respectively). There were no significant interactions involving serial position.

3.3. N170 results

Fig. 3 (waveforms) and Fig. 4 (line graphs) illustrate mean N170 responses. Based on a significant 5-way interaction, $F(3,84) = 3.615$, $p < 0.05$, analyses were conducted to examine hemisphere by serial position for each of upright novel and repeat faces, and inverted novel and repeat faces, at same and different visuospatial locations. A progressive decrease in N170 amplitudes occurred for upright repeated faces at different (unattended) visuospatial locations, main effect of serial position: $F(3,84) = 3.135$, $p < 0.05$. The progressive decrease in N170 amplitude was most predominant in the right hemisphere compared to the left hemisphere, 2-way interaction between serial position and hemisphere: $F(3,84) = 8.020$, $p < 0.001$. This observation was supported by a significant linear trend of serial position, $F(1,28) = 6.739$, $p < 0.05$, and a significant linear trend of serial position by hemisphere, $F(1,28) = 22.414$, $p < 0.001$. In contrast, we did not observe a progressive habituation of the N170 amplitude for inverted repeated faces at different visuospatial locations, $F(3,84) = 0.723$, $p =$ n.s. N170

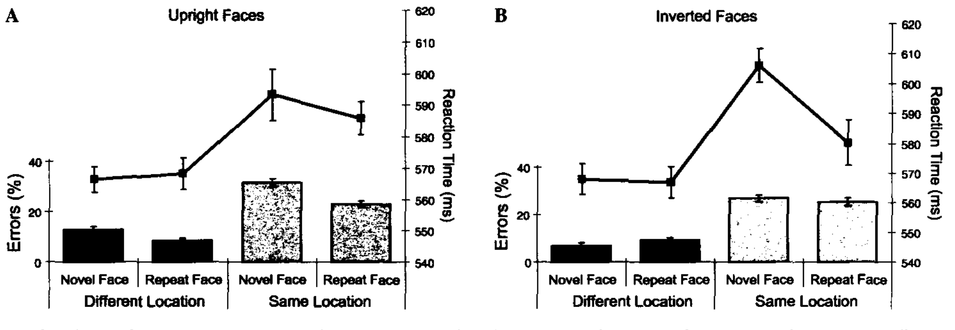

Fig. 2. Mean reaction time and mean percentage errors for (A) upright and (B) inverted, novel vs. repeat faces presented at same vs. different visuospatial locations. Mean reaction time is represented by the line graph, left axis and mean percentage errors is represented by the bar graph, right axis. Error bars indicate standard errors. Overall, performance was impaired for novel faces presented in the same visuospatial location.

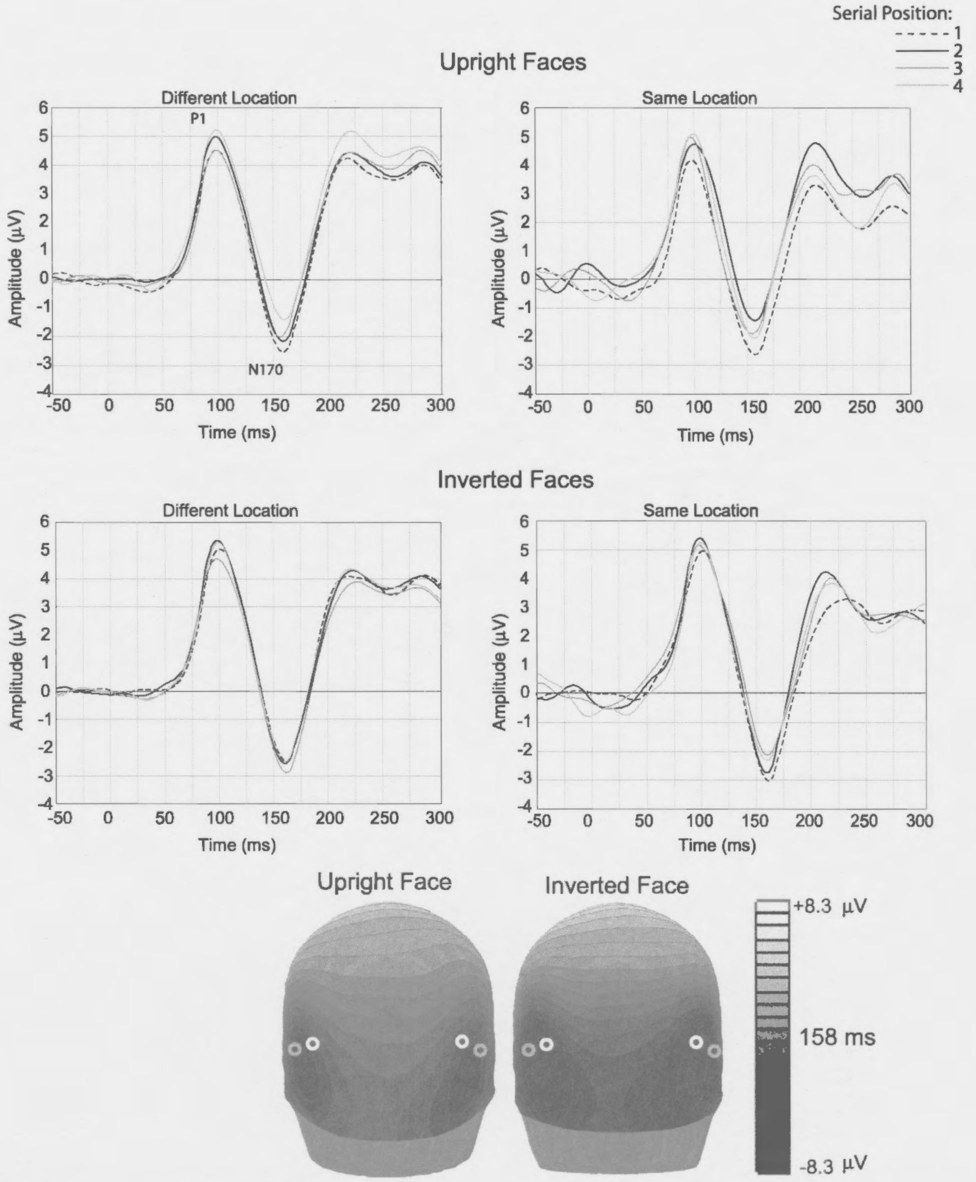

Fig. 3. Grand mean N170 component morphology for upright and inverted repeated face stimuli at different vs. same visuospatial locations. Grand mean scalp topographies illustrating N170 amplitude effects at 158 ms. Scalp voltage distributions are displayed for upright and inverted repeat faces presented at same locations. The white dots denote the location of electrodes used in N170 analysis, which are slightly medial and superior to P6/P7. The grey dots denote the electrode locations P6/P7 for reference.

habituation was not observed for novel upright faces presented at different locations, $F(3,84) = 0.099$, $p = \text{n.s.}$, or for novel inverted faces presented at different locations, $F(3,84) = 2.228$, $p = \text{n.s.}$

There was also a decrease in N170 amplitude for the initial (but not subsequent) upright face repetition at same visuospatial locations in both hemispheres; the effect was significant in the right hemisphere and supported by a significant 2-way interaction between serial position and hemisphere: $F(3,84) = 3.640$, $p < 0.05$. N170 habituation was not observed for repeat upright face presented at same locations, this observation supported by a null result of linear trend for serial position, $F(1,28) = 0.696$, $p = \text{n.s.}$ We did not observe a decrease in N170 amplitude for the initial inverted face repetition at same visuospatial locations, $F(3,84) = 0.639$, $p = \text{n.s.}$ N170 habituation was not observed

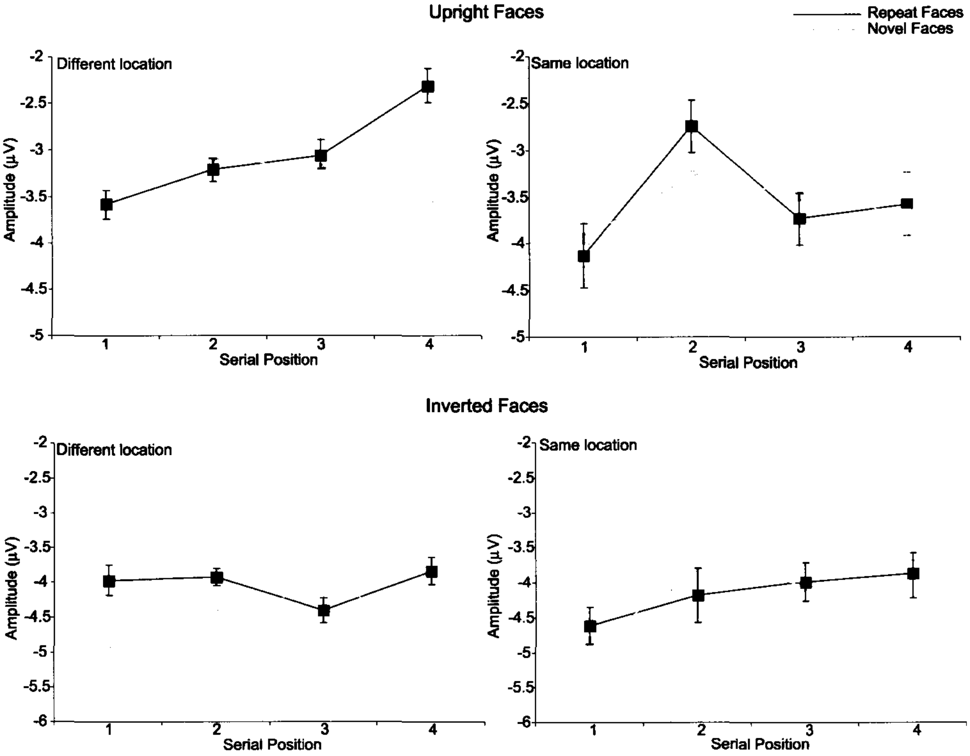

Fig. 4. Grand means of N170 amplitudes illustrating upright and inverted, novel vs. repeat face stimuli at different vs. same visuospatial locations. Repetition effects occurred for upright faces but not for inverted faces. Error bars indicate standard errors.

for novel upright faces presented at same locations, $F(3,84) = 0.188$, $p = \text{n.s}$, or for novel inverted faces presented at same locations, $F(3,84) = 1.918$, $p = \text{n.s.}$

No significant N170 latency effects were observed.

3.4. P3 results

Fig. 5A illustrates mean P3 amplitude responses for upright and inverted face stimuli, presented as repeat and novel face stimuli at different and same visuospatial locations. Overall, greater P3 mean amplitude responses were elicited for upright relative to inverted faces, $F(1,28) = 6.876$, $p < 0.05$. P3 mean amplitude was larger for faces presented at same versus different locations, $F(1,28) = 64.257$, $p < 0.05$. Amplitudes were larger for novel compared to repeated faces, $F(1,28) = 6.425$, $p < 0.05$, and this interacted with location and orientation $F(1,28) = 5.244$, $p < 0.05$. This 3-way interaction can be explained as follows. P3 amplitudes were larger for upright novel faces (10.8 µV) relative to repeat faces (9.0 µV) presented at same (attended) visuospatial locations (Bonferroni $t(28) = 3.600$, $p < 0.01$), whereas no differences were observed between novel (6.3 µV) and repeat (6.2 µV) faces presented at different locations (Bonferroni $t(28) = 0.576$, $p = \text{n.s.}$). P3 amplitudes were equivalent for inverted novel versus repeat faces presented at same visuospatial locations (9.3 µV vs. 9.2 µV, respectively; Bonferroni $t(28) = 0.256$, $p = \text{n.s.}$) and for inverted novel versus repeat faces presented at different locations (5.9 µV vs. 5.7 µV, respectively; Bonferroni $t(28) = 0.875$, $p = \text{n.s.}$). These observations suggest that upright and inverted faces are treated differently at this stage of processing. In particular, P3 amplitude at Pz is sensitive to the difference between repeat and novel faces when the faces are upright and in the attended visuospatial location, but not when they are inverted or in the unattended visuospatial location.

3.5. FCz results

At FCz there was an identity effect observed that was in the same time window as the identity effect at Pz. The pattern was the same as that observed at Pz in that the identity effect occurred at same but not different locations. The pattern was different than that observed at Pz in that at same locations, novel faces produced larger amplitudes than repeat faces for both upright and inverted faces, whereas at Pz this occurred for upright faces only. Fig. 5B shows the waveforms at FCz and Fig. 6 shows the topographies of the

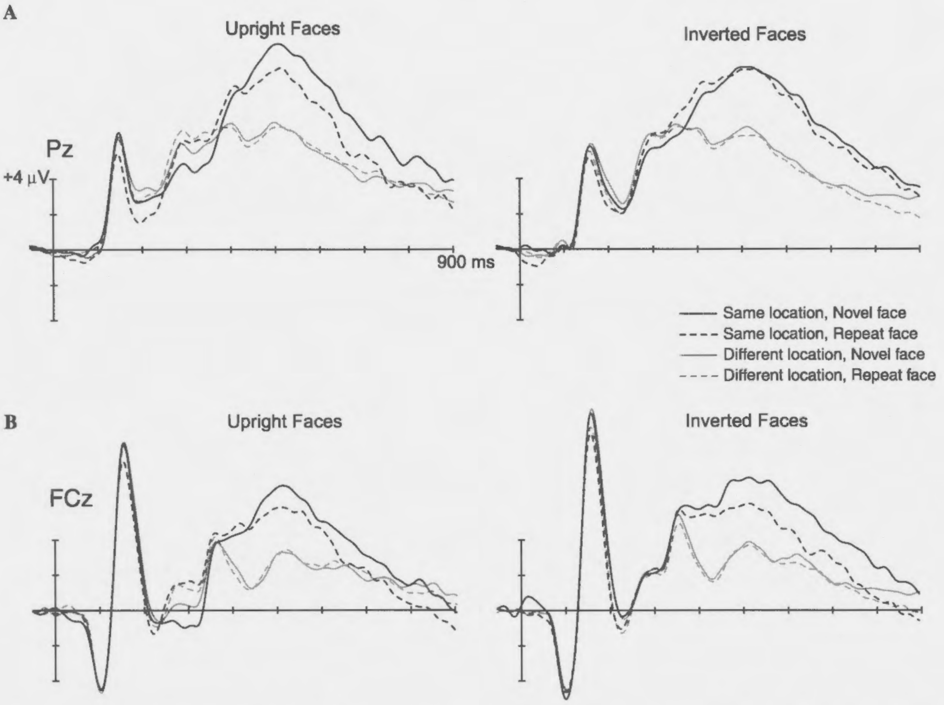

Fig. 5. (A) Grand mean waveforms observed at electrode Pz illustrating P3 morphology for upright and inverted face stimuli presented as novel vs. repeat faces at same vs. different visuospatial locations. Overall, faces presented at same visuospatial locations elicited larger P3 mean amplitudes than faces presented at different visuospatial locations. At same visuospatial locations, novel faces elicit larger P3 responses than repeat faces for upright faces only, and not for inverted faces. (B) Grand mean waveforms at electrode FCz showing positivity in same time window as P3. At same visuospatial locations only, upright and inverted faces produced a more positive component for novel compared to repeated faces.

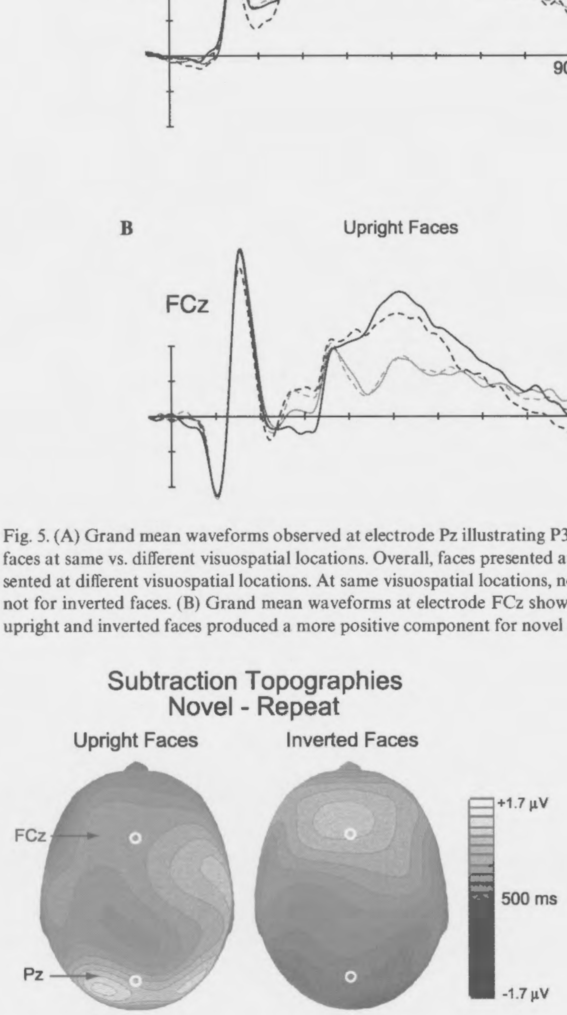

Fig. 6. Grand mean subtraction topographies illustrating novel—repeat difference at parietal and frontal sites at 500 ms (see Fig. 5 for the associated waveforms).

novel minus repeated faces difference for upright and inverted orientations at 500 ms. Mean FCz amplitude was larger for faces presented at different relative to same locations, $F(1,28) = 58.591$, $p < 0.05$. Amplitudes were larger for novel compared to repeated faces, $F(1,28) = 6.088$, $p < 0.05$, and this interacted with location, $F(1,28) = 11.809$, $p < 0.05$. This 2-way interaction can be explained as follows. Larger FCz amplitudes were observed for novel faces relative to repeat faces presented at same (attended) visuospatial locations (Bonferroni $t(28) = 3.165$, $p < 0.01$), whereas no differences were observed between novel and repeat faces presented at different locations (Bonferroni $t(28) = -1.062$, $p =$ n.s.). Importantly, a 3-way interaction between face orientation, location and face identity was not significant, $F(1,28) = 0.526$, $p =$ n.s. The topographies illustrate the contrast between the P3 results at Pz (for which the novel versus repeat difference occurs only for upright faces) and the FCz results (for which both upright and inverted faces show a novel versus repeat difference).

4. Discussion

The N170 ERP component is currently under investigation for its sensitivity to novel face repetitions and the acquisition of familiarity with particular faces. Recent studies have reported a decrease in the amplitude of the N170 in response to face repetitions (Campanella et al., 2000; George et al., 1997; Guillaume & Tiberghien, 2001; Heisz et al., 2006; Itier & Taylor, 2002, 2004). A particularly sensitive measure of the N170 habituation effect is observed when attention is directed away from face identity. For example, using a visuospatial location matching task in which face identity was not relevant, Heisz et al. (2006) reported a progressive decrease in the N170 amplitude for up to three repetitions of the same face presented in unattended locations. These findings were interpreted as support for a hypothesis that the N170 activity represents relatively early and automatic face identity processing. Indeed, it has been suggested that tasks that do not require explicit evaluation of the face identity, provide a more pure measure of the automaticity of face processing (Gauthier et al., 2000). However, it was not clear from the Heisz et al. (2006) study whether the N170 habituation was due primarily to face identity priming or had a large component of perceptual priming, because the repeated faces were also perceptually identical. In the present study, we used inverted faces to test the hypothesis that the N170 habituation reflects a change in face identity processing mechanisms. If the N170 habituation was due to identity processing, then in the current experiment inverted faces would not produce the same progressive habituation as upright faces because extracting identity from inverted faces is relatively difficult (Eimer, 2000a, 2000b, 2000c; Rossion et al., 1999).

Using the same 1-back visuospatial location matching paradigm we replicated the Heisz et al. (2006) results showing a progressive decrease in N170 amplitude for each repetition of the same face when the repetitions occurred in unattended visuospatial locations. To demonstrate that face identity was not being explicitly evaluated at different locations, Heisz et al. (2006) analyzed the P3 ERP component. The amplitude of the P3 has been reported to effectively index allocation of cognitive resources (Kramer & Strayer, 1988; Kramer, Strayer, & Buckley, 1991; Watter, Geffen, & Geffen, 2001; Wickens, Kramer, Vanasse, & Donchin, 1983). The present P3 findings for upright faces replicated those of Heisz et al. (2006) by revealing a larger P3 for novel versus repeat faces when they appeared in the same location as the previous trial, but the P3 amplitude was not sensitive to face repetition when the faces appeared in different visuospatial locations. Some studies report larger P3 amplitudes for repeated versus novel faces (Itier & Taylor, 2002, 2004; Paller, Bozic, Ranganath, Grabowecky, & Yamada, 1999; Paller, Gonslaves, Grabowecky, Bozic, & Yamada, 2000), however in those studies the tasks required responses to repeated face identity, and in our study the faces were not relevant to the response, so this difference in response processing may have contributed to the different pattern we observed. We posit that the larger P3 for novel versus repeat faces indicates that attention was captured by the identity properties of the novel face stimulus and that this greater attention to identity did not occur when the face was presented in a different visuospatial location.

Inverted face stimuli produced similar P3 amplitude differences such that P3 amplitude for same visuospatial locations was much larger than different visuospatial locations. However, the novel versus repeat difference at same visuospatial locations did not occur for inverted faces at the parietal P3,[1] suggesting that even at attended locations, attention was not captured by identity of the inverted faces to the same extent that this occurred for upright faces.

The behavioural responses were consistent with the P3 results. Both upright and inverted faces produced more errors and longer reaction times when faces were presented in the same visuospatial location as the stimulus on the previous trial, supporting the idea that the perceptual properties of same-location stimuli interfered with behavioural performance despite being irrelevant to the task. Similar to the behavioural results of Heisz et al. (2006), this effect was larger for novel faces. It is possible that attention was captured by the novel stimulus which interfered more with response processing than the repeated stimulus. In general, the effects of stimulus properties on response time, accuracy, and the P3 were much larger when stimuli were presented to the same (attended) visuospatial location.

The establishment of unattended face processing at different locations via P3 and behavioral data, and replication of the N170 habituation to upright face repetition, allowed us to test the N170 habituation effect in response to face inversion. Our claim is that when face identity is not relevant to the task, face processing at unattended locations reflects a relatively purer representation of habituation of automatic face processing, consistent with the conclusion made by Heisz et al. (2006). Attention to a face stimulus, whether it is due to task relevance or focus of spatial attention, results in substantial optimal engagement of face identity processes, and these processes reengage with each repetition of the face. In this situation, a decrease in N170 amplitude is observed only for the first repetition (that is, the second presentation) of a previously novel face. When attention is directed away, as it was in our study by making face identity task irrelevant and by presenting faces outside the locus of spatial attention, face identity processes do not reengage with each face and habituation of the N170 occurs, with N170 amplitude observed to decrease progressively over several repetitions of the same face.

In contrast to the progressive decrease in the N170 amplitude for upright faces presented at unattended locations, we did not observe N170 habituation for inverted faces. Inverted faces do not share some of the processing advantages afforded to upright faces (Rossion et al., 1999; Yin, 1969). The processing difference of upright versus inverted faces likely reflects greater expertise for upright faces, including the relative ease with which upright faces are perceived and processed at an individual level (Tanaka, 2001). The identity processing impairment for inverted faces is thought to result from the disruption of second-order relations—the spatial relationships among the features of the face (Leder & Bruce, 2000; Yin, 1969; for reviews see: Maurer et al., 2002; Valentine, 1988). Extraction of second-order relational information from a face is thought to occur early in face processing (Freire, Lee, & Symons, 2000) and may possibly be reflected in the N170. The N170 response to inverted faces is characteristically later and larger compared with upright faces, suggesting

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[1] There was a novel—repeat difference at frontal sites, which may suggest an additional generator sensitive to stimulus repetition.

greater N170-related processing is required when information is more difficult to extract (Eimer, 2000a, 2000b, 2000c; Itier & Taylor, 2002; Rossion et al., 1999).

Our observed lack of N170 habituation for repeated inverted face stimuli fits well with these prior findings. Compared to upright faces, poorer extraction of physical second-order relations would lead to impaired processing of identity properties of inverted faces. We suggest that identity representations for upright faces are established relatively efficiently, requiring less N170-related processing on subsequent viewings of the same stimulus. In contrast, identity representations of inverted faces are established relatively inefficiently. Without a strong identity representation of a face stimulus, the N170 response to the repetition of an inverted face would not habituate until a sufficient identity representation had been established.

This study was designed to address the question of whether identity processing underlies the N170 habituation effect. The critical point for this paper is that N170 habituation at unattended locations was observed for repeated upright faces, but did not occur for repeated inverted faces, supporting the idea that N170 habituation is related to face identity. Campanella et al. (2000) found that contiguous presentations of photographs that preserved face identity but not the physical properties of the face stimulus caused a decrease in the N170 amplitude, inferring that the N170 repetition effect reflects identity processing rather than perceptual priming.[2] However, Itier and Taylor (2002) reported a decrease in N170 amplitude in response to single repetitions of both upright, inverted, and contrast reversed faces. This suggests that the N170 repetition effect may reflect perceptual priming because inversion and contrast reversal impairs identity processing. Inverted faces are processed differently from upright faces in part because processing face identity is less fluent for inverted faces than upright faces. However, the automatic face identity process still operates when an inverted face is presented, and habituation of the N170 may be observed if this process is allowed to complete. For example, other studies have observed N170 habituation for repeated inverted faces (Itier & Taylor, 2002, 2004). The difference between those studies and the current study is the nature of the task. When face identity is task relevant, N170 habituation to repeated inverted faces is observed. When face identity is not task relevant, we do not observe N170 habituation to repeated inverted faces. The present study extends these findings and explains the conflict in the published results by showing that the N170 repetition effect does not occur for inverted faces when identity of the face stimulus is not task relevant, lending support to the hypothesis that the N170 repetition effect reflects habituation of face identity processing.

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[2] It would be interesting to test whether the results from our study would replicate with different photographs of the same individual.

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Chapter 3

Semantic learning modifies perceptual face processing

Jennifer J. Heisz & Judith M. Shedden

2.1 Preamble

N170 repetition priming is a potential mechanism for unfamiliar face recognition. Interestingly, repetition priming is not seen for highly familiar faces. A critical difference between familiar and unfamiliar faces is that familiar faces are associated with a rich network of person-specific information. Such semantic information is thought to allow for a more conceptual representation of the individual. In turn, the recognition of familiar faces associated with rich semantic information may be less dependent on perceptual processes reflected by the N170.

In this chapter, I directly test whether semantic learning modifies the N170 response. I used a five-day learning paradigm, in which one group of participants learned faces with person-specific semantic information and another group of participants learned faces with irrelevant information. ERPs were recorded on Day 1 (when all faces were unfamiliar) and Day 5 (after learning). Only faces learned with person-specific information showed a reduction in the N170 repetition effect, suggesting that relevant semantic information, and not merely perceptual experience, changes early perceptual face processing.

Semantic Learning Modifies Perceptual Face Processing

Jennifer J. Heisz and Judith M. Shedden

Abstract

■ Face processing changes when a face is learned with personally relevant information. In a five-day learning paradigm, faces were presented with rich semantic stories that conveyed personal information about the faces. Event-related potentials were recorded before and after learning during a passive viewing task. When faces were novel, we observed the expected N170 repetition effect—a reduction in amplitude following face repetition. However, when faces were learned with personal information, the N170 repetition effect was eliminated, suggesting that semantic information modulates the N170 repetition effect. To control for the possibility that a simple perceptual effect contributed to the change in the N170 repetition effect, another experiment was conducted using stories that were not related to the person (i.e., stories about rocks and volcanoes). Although viewers were exposed to the faces an equal amount of time, the typical N170 repetition effect was observed, indicating that personal semantic information associated with a face, and not simply perceptual exposure, produced the observed reduction in the N170 repetition effect. These results are the first to reveal a critical perceptual change in face processing as a result of learning person-related information. The results have important implications for researchers studying face processing, as well as learning and memory in general, as they demonstrate that perceptual information alone is not enough to establish familiarity akin to real-world person learning. ■

INTRODUCTION

Many differences exist in our recognition of familiar and unfamiliar faces. Familiar faces are recognized faster and more accurately than unfamiliar faces (Burton, Wilson, Cowen, & Bruce, 1999; Klatzky & Forrest, 1984; Bruce, 1982; Ellis, Shepherd, & Davies, 1979). We rely on different facial information to identify familiar and unfamiliar faces; when identifying familiar faces, we tend to focus on the eye and eye region, whereas when identifying unfamiliar faces, we tend to scan the entire face image (Heisz & Shore, 2008; Althoff & Cohen, 1999). These differences have led many to theorize that different neurological processes subserve familiar and unfamiliar face recognition. In the following experiments, we investigate differences in familiar and unfamiliar face recognition processing as reflected in the repetition effect of the event-related potential (ERP) N170 component.

The N170 is a negative-going component that peaks approximately 170 msec poststimulus onset. It is maximally recorded over the occipito-temporal cortex and is typically larger over the right hemisphere than the left hemisphere. Mainly implicated in perceptual (physical; bottom–up) face processing, the amplitude of the N170 is larger for faces than nonface objects (Carmel & Bentin, 2002; Sagiv & Bentin, 2001; Eimer, 2000a; George, Evans, Fiori, Davidoff, & Renault, 1997; Bentin, Allison, Puce, Perez, & McCarthy, 1996) and is larger for whole facial images compared to facial images lacking internal features (e.g., eyes, nose, mouth) or external features (e.g., head contour, hair) (Eimer, 2000a). Although the N170 is sensitive to both facial features and facial configuration (i.e., the spatial relations among the features of a face) (Bentin, Golland, Flevaris, Robertson, & Moscovitch, 2006; Boutsen, Humphreys, Praamstra, & Warbrick, 2006; Caharel, Fiori, Bernard, Lalonde, & Rebai, 2006; Itier, Latinus, & Taylor, 2006; Latinus & Taylor, 2005, 2006; Carbon, Schweinberger, Kaufmann, & Leder, 2005; Schyns, Jentzsch, Johnson, Schweinberger, & Gosselin, 2003), the right hemisphere is particularly sensitive to changes in facial configuration, whereas the left hemisphere is particularly sensitive to changes in facial features (Scott & Nelson, 2006).

Facial identity processing is revealed through the N170 repetition effect. Characterized by a reduction in the N170 amplitude following immediate face presentations (Heisz, Watter, & Shedden, 2006a, 2006b; Itier & Taylor, 2002, 2004; Guillaume & Tiberghien, 2001; Campanella et al., 2000; George, Jemel, Fiori, & Renault, 1997), the N170 repetition effect is observed for repeated presentation of the same image (Heisz et al., 2006a, 2006b; Itier & Taylor, 2002, 2004; George, Jemel, et al., 1997), as well as successive presentation of two images portraying the same individual with different

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facial expressions (Guillaume & Tiberghien, 2001), different background images (Guillaume & Tiberghien, 2001), or completely different physical images (Campanella et al., 2000), suggesting that the effect cannot be explained as perceptual habituation. Importantly, N170 repetition effects are only observed for unfamiliar faces. The N170 repetition effect is not observed for highly familiar or famous faces (Schweinberger, Pickering, Burton, & Kaufmann, 2002; Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002). Caharel, Poiroux, and Bernard (2002) demonstrated this dissociation in a passive viewing task in which observers viewed 100 repetitions of one's own face, a famous face, and an unfamiliar face. The N170 amplitude response in the right hemisphere was attenuated for repetitions of an unfamiliar face only; the attenuation did not occur for repetitions of one's own face and repetitions of a famous face. Similarly, another study reported repetition effects for unfamiliar, and not for famous faces (Henson et al., 2003).

A critical difference between familiar and unfamiliar faces is the amount of person-specific information associated with the face. Highly familiar faces are associated with a rich network of person-specific information, whereas unfamiliar faces are associated with little or no information. According to the current face recognition model, person-specific information aids in our identification of a particular individual (Burton, Bruce, & Hancock, 1999; Burton, Bruce, & Johnston, 1990; Bruce & Young, 1986). Different aspects of a person can be used to retrieve relevant information, resulting in superior memory for highly familiar individuals. Unfamiliar faces do not afford such recognition benefits because they lack associated information, resulting in recognition based primarily on perceptual processing. We hypothesize that perceptual identity processing is reflected in the N170 repetition effect, which is observed for unfamiliar faces because perceptual processing is the primary mode of recognition. In contrast, the N170 repetition effect is not observed for familiar faces because both perceptual processing and semantic processing support recognition. Indeed, other top-down processes (e.g., expectations, attention) modify processing at the N170 by activating facial representations (Jemel, Pisani, Calabria, Crommelinck, & Bruyer, 2003; Bentin, Sagiv, Mecklinger, Friederici, & von Crammon, 2002; Eimer, 2000b). Accordingly, the N170 repetition effect elicited by an unfamiliar face should be reduced or eliminated after acquiring person-specific information.

In the present experiments, we used a 5-day learning paradigm to examine the influence of face learning on the N170 repetition effect. In a between-subjects design, one group of subjects learned faces with related stories (i.e., stories that conveyed person-specific information) and another group of subjects learned faces with unrelated stories (i.e., stories about rocks and other inanimate objects). ERPs were recorded before and after learning. Prior to learning when all faces were unfamiliar, we expected all faces to elicit the N170 repetition effect because perceptual processing alone would support recognition. After learning faces with related stories, we expected a reduction of the N170 repetition effect because both perceptual and semantic processing would support recognition. In contrast, after learning faces with unrelated stories, we expected to observe the N170 repetition effect because recognition would remain supported by perceptual processing.

METHODS

Subjects

Twenty volunteers from the McMaster University community participated in the experiment, 10 volunteers were randomly assigned to learn faces with related stories (5 men, mean age = 20.6 years, 2 left-handed) and 10 volunteers were randomly assigned to learn faces with unrelated stories (3 men, mean age = 20.1 years, 2 left-handed). All subjects reported normal or corrected-to-normal vision. Informed consent was obtained from each observer. Eligible observers received course credit plus $15.00 for their participation, and the remainder received $40.00 compensation. All procedures complied with the tricouncil policy on ethics (Canada) and were approved by the McMaster Ethics Research Board.

Stimuli

Stimulus presentation and manual response measurement were controlled by Presentation experimental software (Version 9.9, www.neuro-bs.com), running on a Pentium 4 Computer under Windows XP operating system. The stimuli were displayed on a 17-in. color CRT display at a resolution of 1280 × 1024 and a frame refresh rate of 85 Hz. Participants were seated 80 cm from the display and the experiment was run in a dimly lit room.

The face stimuli consisted of 10 colored images of Caucasian individuals (5 men) with neutral expressions. Faces were without glasses and a black wrap concealed clothing. Faces were adopted from a larger set provided by Dr. Daphne Maurer's Visual Developmental Lab, Department of Psychology, Neuroscience and Behaviour, McMaster University (Geldart, Maurer, & Henderson, 1999). Facial images were presented at the center of the display on a gray background, approximately 4.8° of visual angle wide and 6.0° of visual angle high. The average luminance value for each face image was approximately 19.7 cd/m^2. Eight images (4 males, 4 females) were selected per subject and assigned to a particular condition; the assignment of face stimuli to particular conditions was counterbalanced across subjects.

The story stimuli consisted of related stories and unrelated stories. P. Darren Parker, a graduate of Television

Production and Writing, Humber College, composed the related stories. The related stories captured "A-week-in-the-life-of" four unique and interconnected characters. The stories were divided into five sections of approximately equivalent length (~4.5 min) and narrated to subjects in chronological order over five consecutive days. Each section represented "A-day-in-the-life-of" the four characters, conveying new information about them while building on information from previous sections. Whenever a specific character appeared in the narrated story, that character's face was presented visually. In total, two characters appeared in the story approximately 21 min each (main characters), and two characters appeared in the story approximately 3 min each (sub characters). The unrelated stories were created from compilation of geographical articles about various inanimate objects, such as rocks and volcanoes. The articles were randomly assigned to one of five sections with approximately equivalent length (~4.5 min) and narrated to subjects over five consecutive days. Each section presented new information that was completely unrelated to the information from previous sections. As in the related story condition, two faces were presented for approximately 21 min each and two faces were presented for approximately 3 min each, so that both groups were exposed to the faces at the same time and for the same duration; the content of the stories was the only difference between the two groups.

The story stimuli were recorded in a sound attenuated room, with Shure Professional head-worn Dynamic Microphone and Marantz Professional CD Recorder. Audacity editing suite was used to segment the audiofiles, minimize noise, and equate loudness across each separate wavefile. The same female voice was used to create all auditory stimuli. Auditory stimuli were presented using Labtec remote computer speakers mounted in front of the participant, presented at approximately 60 dB or the level of a normal conversation.

Procedure

The experiment was conducted over five consecutive days. In a between-subjects design, one group of subjects learned faces with related stories (i.e., stories that conveyed person-specific information) and the other group of subjects learned faces with unrelated stories (i.e., stories about rocks and other inanimate objects). During the learning sessions, a face was presented at the center of the display and subjects were instructed to keep their eyes on the face image; eye movements were recorded to ensure this. While viewing the face image, subjects in the related story condition listened to related stories about the individual and subjects in the unrelated story condition listened to stories about rocks and other inanimate objects. For the group that learned faces with related stories, the face image presented on the display always corresponded with the character being described in the story. When the story shifted to another character, the new character's face replaced the previous character's face, allowing the visual face image and auditory character-related story to be associated for each character. The group that learned faces with unrelated stories saw the same sequence of faces (with the same stimulus onset times and durations for each face), but in this condition, the faces did not relate to the content of the story. In other words, we presented both groups with identical visual stimuli and varied the auditory stimuli, such that one group heard person-related stories characterizing the faces and the other group heard unrelated stories about rocks and other inanimate objects. Following each learning session, subjects answered questions about the story content to encourage them to pay attention to the stories. Approximately 2 months after the learning session, we tested 8 of the 10 subjects from the related story condition for their memory of the faces; each subject was 100% correct at naming the characters' faces.

ERPs were recorded before and after learning. Each ERP session lasted approximately 1 hr. The prelearning ERP session consisted of six face stimuli: four learned faces (i.e., faces presented during the learning session) and two control faces (i.e., faces presented in ERP sessions only). The postlearning ERP session consisted of eight stimuli, four learned faces, and four control faces (i.e., the 2 control faces from the prelearning ERP session plus 2 new control faces). Faces were presented for 750 msec followed by an interstimulus interval of 750 msec, during which a fixation point was presented. Faces were presented in pseudorandomized order; each face was presented approximately 200 times, half of which were immediate repetitions. Subjects performed a passive viewing task in which they were instructed to consider each face's identity. This passive viewing paradigm was adopted from Caharel et al. (2002).

Electrophysiology

The ActiveTwo BioSemi electrode system was used to record continuous electroencephalographic (EEG) activity from 128 Ag/AgCl scalp electrodes plus 4 addition electrodes placed at the outer canthi and just below each eye for recording horizontal and vertical eye movements. Two additional electrodes, common mode sense (CMS) active electrode and driven right leg (DRL) passive electrode, were also used. These electrodes replace the "ground" electrodes used in conventional systems (www.biosemi.com/faq/cms&drl.htm). Because the BioSemi system is an active electrode system, there is no conventional reference electrode; a monopolar signal is stored for each active electrode and all re-referencing is done in software after acquisition. The continuous signal was acquired with an open band pass from DC to 150 Hz and digitized at 512 Hz. The signal was band-pass filtered off-line at 0.1 to 30 Hz and re-referenced to a common average reference.

ERP averaging and analysis were performed using EEProbe software (ANT; www.antsoftware.nl). EEG and EOG artifacts were removed using a ±35-μV deviation over 200-msec intervals on all electrodes. Blink artifacts were selected manually and corrected by a subtraction of VEOG propagation factors via a regression algorithm on EOG components (using EEProbe signal processing software). A 1000-msec recorded EEG epoch, including 100 msec prestimulus baseline and 900 msec interval following stimulus onset, was chosen for ERP averaging. ERP waveforms were then averaged separately for each electrode for each experimental condition.

Data Analysis

ERP analysis of the N170 component focused on an occipito-temporal region of interest, which exhibited maximal N170 amplitude. Over left and right hemispheres, a set of four adjacent electrode pairs was examined, forming a cluster around P7/P8 (also called T5/T6 in the 10–20 system), such that the distance between the adjacent electrodes was 2 cm (center to center) posterior and inferior to P7/P8. This is the electrode location most commonly associated with N170 effects in the literature (e.g., Rossion & Jacques, 2008; Itier et al., 2006) and displayed the largest peak-to-peak amplitude between P1 and N170 (~6 μV). For each subject, the pair from this cluster that showed maximal N170 effects was selected for analysis. The amplitude of the N170 component was isolated using a time window ranging from 120 to 200 msec, obtained via inspection of the grand-average waveforms. Repeated measures analysis of variance (ANOVA) was conducted for N170 peak amplitude in a five-way design with one between-subject factor of group (faces learned with related stories, faces learned with unrelated stories) and four within-subject factors of session (prelearning, postlearning), hemisphere (right, left), face type (learned, control), and repetition (preceeded by the same face, preceded by a different face).

RESULTS

Initial statistical analyses were conducted to determine whether there were any differences between responses to main and sub character faces, and between responses to the different control faces. Repeated measures ANOVA tests revealed no main effects or interactions of main versus sub character faces with factors of session and repetition (all *F*s < 0.7). Separate repeated measures ANOVA showed no main effects or interactions between the different control faces with factors of session and repetition (all *F*s < 0.8). Therefore, all subsequent analyses collapsed over individual faces and focused on two categories of faces: learned faces (presented during the ERP sessions and during the 5 days of stories) and control faces (presented only during the ERP sessions).

Two figures illustrate the results. Figure 1 depicts grand-average waveforms for the N170 ERP component elicited in the right versus left hemispheres during prelearning versus postlearning sessions. Learned faces and control faces are compared between subjects in the related versus unrelated story conditions, and the N170 repetition effect is reflected in the amplitude differences for faces preceded by the same face image versus faces preceded by a different face image. Figure 2 depicts the difference in left and right hemisphere N170 repetition effect between pre- and postlearning sessions for learned and control faces in the related and unrelated story conditions (e.g., subtract the postlearning repetition effect from the prelearning repetition effect for each condition). A positive value indicates a reduction in the N170 repetition effect following learning, whereas a negative value indicates an enhancement in the N170 repetition effect following learning.

Based on a significant five-way interaction [$F(1, 18) = 5.271$, $p < .05$], separate analyses were conducted to focus on key issues. The first set of analyses involved two repeated measures ANOVA tests carried out separately for the related and unrelated stories groups.

Faces learned with ***unrelated*** stories revealed a simple main effect of repetition [$F(1, 9) = 22.327$, $p < .01$], such that N170 amplitudes were reduced for faces preceded by the same face compared to faces preceded by a different face. Importantly, this repetition effect did not interact with session. No other main effects or interactions were observed in the unrelated stories condition, and the remaining analyses focus on the related stories group.

Faces learned with ***related*** stories revealed a significant four-way interaction of session, hemisphere, face type, and repetition [$F(1, 9) = 6.621$, $p < .05$]. We further examined the repetition effect by collapsing the data in two different sets of analyses. First, we analyzed the prelearning and postlearning sessions separately using a three-factor (Hemisphere × Face type × Repetition) repeated measures ANOVA. This allowed us to ask directly whether the repetition effect differed between learned and control faces within each of the two ERP sessions. The prelearning session revealed a simple main effect of repetition [$F(1, 9) = 10.177$, $p < .05$], such that N170 amplitudes were reduced for faces preceded by the same face compared to faces preceded by a different face. Importantly, this effect did not interact with face type, showing that both learned and control faces produced the same repetition effects in the prelearning session. No other main effects or interactions were observed in the prelearning session. The postlearning session revealed a simple main effect of repetition [$F(1, 9) = 76.976$, $p < .001$], and a significant two-way interaction between face type and repetition [$F(1, 9) = 5.635$, $p < .05$], such that N170 repetition effects were smaller for learned faces compared to control faces [$t(9) = -2.374$, $p < .05$]. This result supports the hypothesis that

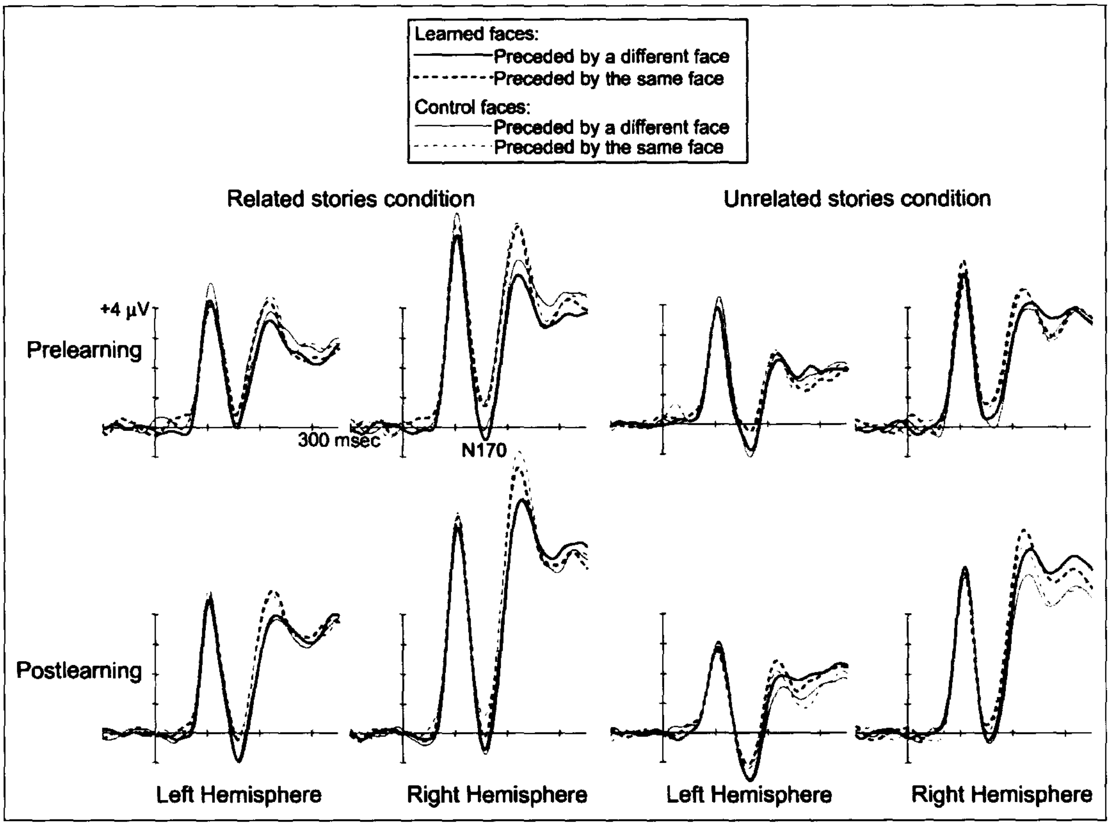

Figure 1. Grand-average waveforms for the N170 ERP component measured at P7/P8 (also called T5/T6) during prelearning versus postlearning sessions. Learned faces and control faces are compared between subjects in the related versus unrelated story conditions, and the N170 repetition effect is reflected in the amplitude differences for faces preceded by the same face image versus faces preceded by a different face image.

the repetition effect for learned and control faces differs following the 5 days of related stories about the learned faces.

Second, we analyzed the learned and control faces separately using a three-factor (Hemisphere × Session × Repetition) repeated measures ANOVA to directly compare the shift in the N170 repetition effect across the pre- and postlearning sessions. There was a main effect of session for both analyses due to larger amplitudes overall in the postlearning session compared to the prelearning session [learned faces: $F(1, 9) = 11.341, p < .01$; control faces: $F(1, 9) = 6.414, p < .05$]. The control faces revealed a simple main effect of repetition [$F(1, 9) = 50.033$, $p < .001$], such that N170 amplitudes were reduced for faces preceded by the same face compared to faces preceded by a different face. Importantly, the repetition effect for the control faces did not interact with session. No other main effects or interactions were observed for the control faces.

Learned faces revealed a simple main effect of repetition [$F(1, 9) = 19.003$, $p < .01$], and a three-way interaction between session, hemisphere, and repetition [$F(1, 9) = 5.094, p = .05$]. For the prelearning session, repetition effects were observed in both right [$t(9) = -3.640$, $p = .005$] and left [$t(9) = -2.414$, $p = .039$] hemispheres. However, during the postlearning session, repetition effects were only observed in the left hemisphere [$t(9) = -3.629, p = .005$]. The N170 repetition effect was not observed for learned faces in the right hemisphere [$t(9) = -1.458, p = ns$]. In other words, the N170 repetition effect, which was largest over the right hemisphere in the prelearning session, was eliminated over the right hemisphere after learning faces with related stories.

DISCUSSION

We examined the influence of face learning on perceptual face processing. Across five consecutive days, subjects viewed previously novel faces while either listening to stories about the individuals or listening to unrelated stories (i.e., stories about rocks and other inanimate

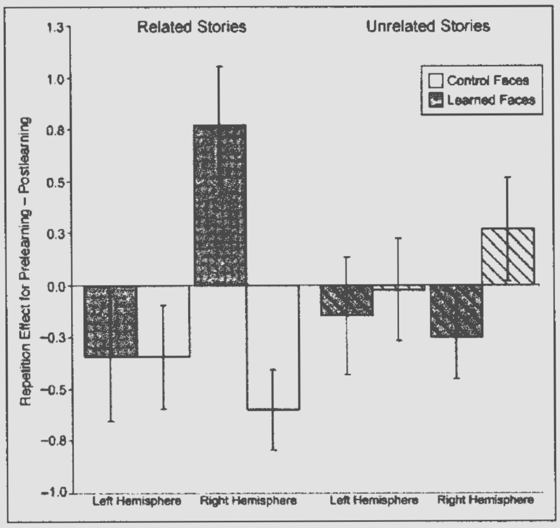

Figure 2. The difference in left and right hemisphere N170 repetition effect between pre- and postlearning sessions for learned and control faces in the related and unrelated story conditions (e.g., subtract the postlearning repetition effect from the prelearning repetition effect for each condition). A positive value indicates a reduction in the N170 repetition effect following learning, whereas a negative value indicates an enhancement in the N170 repetition effect following learning. The right hemisphere N170 repetition effect was reduced after learning faces with related stories. Error bars reflect standard error.

objects). ERPs were recorded before and after learning, and we were interested in learning-induced changes in the N170, an ERP component primarily implicated in perceptual face processing (Carmel & Bentin, 2002; Sagiv & Bentin, 2001; Eimer, 2000b; Bentin et al., 1996). We expected a change in the N170 repetition effect, which is characterized by a reduction in the N170 amplitude following immediate presentations of the same face (Heisz et al., 2006a, 2006b; Itier & Taylor, 2002, 2004; Guillaume & Tiberghien, 2001; Campanella et al., 2000; George, Evans, et al., 1997; George, Jemel, et al., 1997). The N170 repetition effect is observed for unfamiliar faces but not familiar faces (Henson et al., 2003; Caharel et al., 2002; Schweinberger, Pickering, Burton, et al., 2002; Schweinberger, Pickering, Jentzsch, et al., 2002), therefore we expected the repetition effect to be reduced or eliminated following face learning. We hypothesized that the N170 repetition effect reflects perceptual identity processing as the primary mode used to recognizing unfamiliar faces. In contrast, processing of familiar faces is further supported by semantic knowledge about the person, which leads to identity processing at a later stage, thus eliminating the N170 repetition effect for familiar faces. To test this, we compared the N170 repetition effect elicited after learning faces with semantically related stories versus learning faces with unrelated stories. As predicted, the N170 repetition effect was affected by as little as 5 days of experience with a particular face. The N170 repetition effect was eliminated by associating previously novel faces with a rich semantic context in the form of stories, whereas no change was observed in the N170 repetition effect after learning faces with unrelated stories.

Previous studies using famous faces reported comparable lack of the N170 repetition effect (Henson et al., 2003; Caharel et al., 2002; Schweinberger, Pickering, Burton, et al., 2002; Schweinberger, Pickering, Jentzsch, et al., 2002) and when unfamiliar faces were used in similar paradigms the N170 repetition effect was observed (Heisz et al., 2006a, 2006b; Itier & Taylor, 2002, 2004; Guillaume & Tiberghien, 2001; Campanella et al., 2000; George, Jemel, et al., 1997). In the present study, prior to face learning, all faces were unfamiliar and elicited the N170 repetition effect. After a mere 5 days of learning the faces with related stories, the N170 repetition effect was eliminated over the right hemisphere (P8), mimicking that observed for famous faces. These results suggest that perceptual processing as reflected by the N170 repetition effect is modulated by familiarity.

Some studies fail to show any N170 repetition effect for familiar faces (Henson et al., 2003; Schweinberger, Pickering, Jentzsch, et al., 2002; Eimer, 2000a), yet we continue to show the N170 repetition effect at P7 (left hemisphere) for the related story faces. One possibility for this difference may be that we are observing a transition from unfamiliar to familiar face processing, which may require more experience to reach the level of familiarity of the well-known faces used in these other studies, and that this transition from unfamiliar to familiar begins with processing changes in right hemisphere face areas. Indeed, the left hemisphere represents faces in an image-independent manner (Cooper, Harvey, Lavidor & Schweinberger, 2007), a form of facial representation supported by a high level of familiarity (Eger, Schweinberger, Dolan, & Henson, 2005). Our results suggest a special role for the right hemisphere in acquisition of face familiarity.

Although personal information was acquired for faces learned with related stories, the simple visual repetition of faces over the 5 days may have been an important factor in the elimination of the N170 repetition effect. Previous studies using famous faces to investigating the N170 repetition effect were unable to control for this important variable (Henson et al., 2003; Caharel et al., 2002; Schweinberger, Pickering, Burton, et al., 2002; Schweinberger, Pickering, Jentzsch, et al., 2002). To determine the extent to which semantic knowledge and visual repetition were contributing to the change in the N170 repetition effect, we repeated the experiment using stories that were not related to the person; across five consecutive days, subjects viewed the faces while listening to stories about rocks and other inanimate objects. This created a situation in which faces were familiarized through simple visual repetition, but were not personally related to any semantic information. Unlike learning faces with related stories, learning faces with unrelated stories caused no change in the N170 repetition effect. Although the faces in both learning paradigms were seen equally for 5 days, it was the person-related semantic information associated with the faces, and not simply the visual repetition, that produced the reduction in the N170 repetition effect. In other words, knowing information about a person changed the way their face was processed at a perceptual level.

Our results fit well with the previous studies demonstrating behavioral differences between familiar and unfamiliar faces processing. Familiar faces are processed faster and more accurately than unfamiliar faces (Burton, Bruce, et al., 1999; Burton, Wilson, et al., 1999; Klatzky & Forrest, 1984; Bruce, 1982; Ellis et al., 1979). Moreover, we rely on different facial information to identify familiar and unfamiliar faces, focusing more on the eyes and eye region when identifying familiar faces and scanning the entire face image when identifying unfamiliar faces (Heisz & Shore, 2008; Althoff & Cohen, 1999). These processing differences are consistent with the change in perceptual processing which we observe at the N170. Acquiring semantic knowledge associated with a face eliminated the N170 repetition effect. We purport this change is the result of top-down processes involving rich networks of semantic information that modulate perceptual processing of familiar faces, ultimately leading to a more robust representation of facial identity. Akin to the face recognition units of the face recognition model (Burton, Bruce, et al., 1999; Burton et al., 1990; Bruce & Young, 1986), the N170 may be the premier stage in which face processing depends on familiarity. Although this is earlier than previously reported (e.g., Joyce & Kutas, 2005), our data suggest that the perceptual stage of face processing as reflected by the N170 depends on the existence of person-specific semantic information associated with the particular face.

In conclusion, associating semantic information with a previously novel face changes the way we process that face at a perceptual level. This is the first article to demonstrate a dynamic change from novel to familiar, adding critical understanding to the processing changes in face recognition following learning. This article highlights the importance of the learning paradigm used to induce familiarization; familiarization achieved through simple visual repetition of a face is not sufficient to change the N170 repetition effect. However, familiarization achieved through visual repetition and rich semantic stories about the face is sufficient to bring about the change in the N170 repetition effect. The latter is more comparable to real-world person learning.

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Chapter 4

ERP evidence for semantic retrieval associated with familiar faces and incongruent parts

Jennifer J. Heisz & Judith M. Shedden

2.1 Preamble

Early perceptual N170 processes are involved in unfamiliar face recognition as revealed by repetition priming. However, such perceptual-based recognition processes are reduced once a face is associated with relevant semantic information.

In Chapter 4, I assessed the link between N170 perceptual processes and N400 semantic processes. I tested this by creating a composite face made of familiar halves; when a composite was processed holistically it was perceived to be novel. Since identity processing reflected by the N170 seems to be based on holistic matching (Jacques & Rossion, 2009), we expected our composite faces to elicit typical N170 repetition effects. However, the familiar parts of the composite engaged in semantic-based processes reflected by the N400 and the novel whole of the composite failed to elicit N170 repetition priming. These results suggest that semantic processes modify early perceptual processes. Furthermore, these results suggest that typical recognition processes can be engaged by partial familiar face information even in the presence of incongruent perceptual information.

ERP EVIDENCE FOR SEMANTIC RETRIEVAL ASSOCIATED WITH FAMILIAR FACES AND INCONGRUOUS PARTS

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Running head: Familiar faces with incongruous parts

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Abstract

Partial familiar face information is sufficient for the retrieval of semantically related information even in the face of incongruous perceptual information. We created 40 composite faces by halving each familiar face, aligning the top half of one familiar person's face and the bottom half of a different familiar person's face. Thus, novel faces were constructed from familiar parts. We recorded ERPs to both the original familiar faces (familiar parts, familiar wholes) and the composite faces (familiar parts, novel whole) as participants performed a 1-back identity-matching task. Familiar part information was enough to produce the N400 response, activating associated semantic information. Furthermore, the incongruent information that makes the face novel surprisingly did not produce the N170 repetition effect. We suggest that late semantic processes modulate early perceptual processes, and discuss the implications this has for familiar versus unfamiliar face processing.

Prior representation of a complex visual stimulus (e.g., object, face) modifies subsequent processing of that same stimulus and this is generally referred to as repetition priming. Repetition priming not only improves the speed and accuracy of stimulus categorization but also modulates neural processing (for review, see Grill-Spector, Henson & Martin, 2006). Much research has been devoted to detailing repetition priming of facial stimuli, with particular interest in the extent to which a prime face is processed and the stage of processing modulated by such prior representation.

Faces are complex visual stimuli with many different perceptual cues to identity. Individual variation in the contour of a face, the size and shape of features (e.g., eyes, nose, mouth) and the spacing between features could be used for identification (for review, see Maurer, Le Grand & Mondloch, 2002). However, recognition seems to rely on the integration of each of these face parts into a coherent unit or holistic representation (Farah, Wilson, Drain & Tanaka, 1998; Sergent, 1984; Tanaka & Farah, 1993). The most convincing behavioral evidence for this comes from the composite face effect (Hole, 1994; Hole, George, & Dunsmore, 1999; Young, Hellawell & Hay, 1987). Aligning the top half of one face with the bottom-half of another face creates a composite face; the same top half of a face is perceived as different when aligned with different bottom halves and this is known as the composite face illusion (Rossion, 2008b).

Early perceptual representation of a face is reflected by the event-related potential (ERP) N170 component, occurring between 150 ms and 180 ms post-face onset over occipiotemporoparietal cortex. The N170 is thought to be an index of basic-level categorization or face detection, involving the encoding of global face shape (i.e., first-order relations; George, Jemel, Fiori, Chaby & Renault, 2005; Latinus & Taylor, 2005; Rossion & Jacques, 2008; Zion-Golumbic & Bentin, 2007) and internal face features (e.g., eyes; Bentin, Allison, Puce, Perez & McCarthy, 1996; Harris & Nakayama, 2008; Itier, Alain, Sedore & McIntosh, 2007; Schyns, Jentzsch, Johnson, Schweinberger & Gosselin, 2003; Zion-Golumbie & Bentin, 2007). In addition, the N170 is sensitive to face repetition. Immediate repetition of the same face results in a less negative N170 amplitude response (Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009; Campanella et al., 2000; George, Jemel, Fiori, & Renault, 1997; Guillaume & Tiberghien, 2001; Heisz & Shedden, 2009; Heisz, Watter, & Shedden, 2006a, 2006b; Jaques, d'Arripe, & Rossion, 2007; Jemel, Pisani, Calabria, Crommelinck & Bruyer, 2003; Itier & Taylor, 2002, 2004). This is observed across different images of the same individual (Caharel et al., 2009; Campanella et al., 2000; Guillaume & Tiberghien, 2001), suggesting sensitivity to the individual face.

To determine whether the N170 represents faces holistically rather than by parts, Jacques & Rossion (2009) measured the N170 response during an adaptation paradigm of the composite illusion. An adapting stimulus was presented followed by a test stimulus; adapting and test stimuli were the same composite face, different composite faces, or composite faces with the same top half but different bottom halves (able to induce the composite face illusion). A less negative N170 amplitude response was observed for test faces that were preceded by the same composite face versus a different composite face, replicating the typical N170 repetition effect seen for natural face images. More importantly, there was no adaptation (reduction) in the N170 amplitude when participant experienced the composite face illusion—the test face had the same top half as the adapting face but the top halves were perceived as different because they were aligned with different bottom halves. This result demonstrates that the N170 response to repeated faces is the result of holistic-based matching between incoming perceptual face information and preexisting perceptual representation of the preceding face stimulus. Such a finding may suggest that early perceptual representation of an individual face is holistic and not based on independent features. However, it is important to note that Jacques & Rossion (2009) used composites of unfamiliar faces and it is possible that these results will not generalize to familiar face processing.

Indeed, face familiarity seems to modify the way in which a face is processed. Behaviorally, familiar faces are recognized faster and more accurately than unfamiliar faces (Burton, Wilson, Cowen, & Bruce, 1999; Bruce, 1982; Ellis, Shepherd, & Davies, 1979; Klatzky & Forrest, 1984; Young, Hay, McWeeny, Flude & Ellis, 1985) even when image quality is poor (Burton et al., 1999) and image context is variable (i.e., changes in viewpoint; Bruce, 1982). Moreover, the scanning of familiar faces is more efficient: when viewing a familiar face we tend to scan fewer and more informative regions than when viewing an unfamiliar face (Althoff & Cohen, 1999; Heisz & Shore, 2008).

Familiarity also leads to a shift of default categorization from basic level (e.g., human face) to individual level (e.g., Bob; Anaki & Bentin, 2009; Tanaka, 2001). This shift to individual level seems to interfere with basic and superordinate (e.g., living) processing; categorization by these more general levels is slower and less accurate for familiar faces than unfamiliar faces (Anaki & Bentin, 2009). Critically, familiar and unfamiliar objects produced the same kind of shift to individual-level processing and the same interference with basic and superordinate processing, suggesting that categorization is modified by associated semantic information and not specific to expertise with faces or objects (Anaki & Bentin, 2009).

Early perceptual face processing is also modified by associated semantic information. Repetition priming at the N170 is reduced in response to faces associated with semantic information (Heisz & Shedden, 2009). Moreover, highly familiar or famous faces fail to show repetition priming at the N170 (Schweinberger, Pickering, Burton & Kaufmann, 2002; Schweinberger, Pickering, Jentzsch, Burton & Kaufmann, 2002). Instead, repetition priming of familiar faces is seen at a later stage in processing reflected by the ERP N400 component, occurring approximately 400 ms post-stimulus onset over centroparietal cortex. Familiar faces elicit more negative N400 amplitudes (Bentin & Deouell, 2000; Eimer, 2000) and larger repetition priming effects than unfamiliar faces (Barrett, Rugg, & Perrett, 1988; Eimer, 2000;Engst, Matin-Loeches & Sommer, 2006; Herzmann, Schweinberger, Sommer & Jentzsch, 2004; Schweinberger, Pfütze & Sommer, 1995; Schweinberger, Pickering, Burton, et al., 2002).

Moreover, the N400 is sensitive to the structural integrity between a familiar face and its stored perceptual representation. When target eyes are presented following a familiar prime face with eyes blurred-out or occluded, the N400 is smaller in response to target eyes that match the prime face, even though most of the cues to identity of the prime face come from featural and configural information other than the eyes (Jemel, George, Chaby, Fiori & Renault, 1999; Jemel, George, Olivares, Fiori & Renault, 1999). This suggests that the stored representations reflected by the N400 can be activated by a subset of recognizable features of a familiar face. However, the N400 response may have been affected by holistic processing of the prime face, which included several global cues (e.g., global face shape and configural arrangement of internal and external features such as nose, mouth, and hair). Therefore it is unclear whether the stored representations reflected by the N400 are being activated via holistic or part-based processing. Furthermore, Jemel and colleagues did not measure N170 priming and therefore it is unclear whether the N170 repetition effect is produced by partial familiar face information.

In the present study, familiar face parts were presented with incongruous information so that a face would be perceived as novel if processed holistically. We created 40 composite faces by halving each familiar face, aligning the top half of one familiar person's face and the bottom half of a different familiar person's face (Figure 1). Thus, novel faces were constructed from familiar parts. We recorded ERPs to both the original familiar faces (familiar parts, familiar wholes) and the composite faces (familiar parts, novel whole) as participants performed a 1-back identity-matching task (Figure 1). We were particularly interested in whether composites would be processed as familiar faces (driven by the familiar parts) and produce N400 effects. We were also interested in whether semantic processes reflected by the N400 would affect early perceptual processes reflected by the N170. If the semantic and perceptual processes are linked then semantic networks activated by familiar face parts may modulate perceptual processing. Even though the N170 should be sensitive to the novelty of the whole face information (Jacques & Rossion, 2009), the composites may fail to produce the N170 repetition effect because the familiar parts engage in sufficient semantic retrieval to modulate the N170 response.

Experiment 1

Our main goal was to examine familiar face processing which we present in Experiment 2, but first we ran Experiment 1 to verify that our composite face manipulation would elicit the same processing as seen for natural face images. We created 40 composite faces by halving each unfamiliar face, aligning the top half of one unfamiliar face and the bottom half of a different unfamiliar face (as shown in Figure 1 for familiar face). We observed a less negative N170 amplitude response for composite faces that were preceded by the same composite face versus a different composite face, suggesting that our composite stimuli were processed as typical unfamiliar faces.

Method

Participants

Thirty-two students (23 female; mean age 19 years ± 2 years SD) at McMaster University participated for course credit. All were Caucasian and reported normal or corrected-to-normal vision. One student (female) produced an anomalous positive going peak during the time window of the N170 (mean peak amplitude +7.513 at 174 ms) and absence of an identifiable P1-N1 morphology therefore, to avoid potential artifact this participant was excluded from further analysis. All procedures complied with the Canadian tri-council policy on ethics as approved by the McMaster Ethics Research Board.

Apparatus & stimuli

Stimulus presentation and manual response measurement were controlled by Presentation experimental software (Version 11, www.neuro-bs.com), running on a Pentium 4 Computer under Windows XP operating system. The stimuli were displayed on a 17-inch color CRT display at a resolution of 1280 x 1024 and frame refresh rate of 85 Hz. Participants were seated 80 cm from the display and the experiment was run in a dimly lit room.

The face stimuli consisted of 40 images of unfamiliar Caucasians (20 male) obtained via the worldwide web. All images captured the front of the face, with a neutral or smiling expression, without glasses. Images were cropped to include hair but exclude background, and converted to grayscale. All images were resized to equate height, width, and resolution.

Using Adobe Photoshop (Version 7.0) and Adobe Illustrator (Version 9.0), composite faces were created from the adopted stimuli by dividing the face images in half at the base of the nasal bridge. Based on likeness of original images and the naturalness of the resulting composite images, the top and bottom halves of the same facial image were paired with the bottom and top halves of a second facial image. We created 40 composite face images by centering the top and bottom halves so that the nasal bridge of each half was in line. Facial images were presented at the center of the display on a white background, with mean visual angle of 5 degrees wide and 4 degrees high.

Figure 1 about here

Procedure

The experiment consisted of 240 trials: a block of 120 trials consisting of composite faces and a block of 120 trials consisting of original faces (block order was counterbalanced across participant). The 40 composite faces were randomly split in half; during the first 60 trials of the composite face block, half of the faces were presented once and the other half of the faces were presented twice successively, with the order of presentation randomized. Presentation delivery was reversed during the next 60 trials of the composite face block. In total, each of the 40 composite faces was presented three times, once as a single and once as a repetition. The same procedure was applied with original face presentation, such that each of the 40 original faces was presented three times during the original face block, once as a single and once as a repetition. Each trial began with a fixation point presented for 1000 ms followed by a facial image presented until manual response. Participants were instructed to determine if the current face was the same as or different from the previous face by pressing 1 or 2 on the number pad for same and different responses respectfully (response buttons were counterbalanced across subjects). Both speed and accuracy were emphasized.

Electrophysiology

The ActiveTwo Biosemi electrode system was used to record continuous electroencephalographic (EEG) activity from 128 Ag/AgCl scalp electrodes plus four addition electrodes placed at the outer canthi and just below each eye for recording horizontal and vertical eye movements. Two additional electrodes, common mode sense (CMS) active electrode and driven right leg (DRL) passive electrode were also used. These electrodes replace the "ground" electrodes used in conventional systems (http://www.biosemi.com/faq/cms&drl.htm). Because the BioSemi system is an active electrode system there is no conventional reference electrode; a monopolar signal is stored for each active electrode and all rereferencing is done in software after acquisition. The continuous signal was acquired with an open pass-band from DC to 150 Hz and digitized at 512 Hz. The signal was bandpass filtered off-line at 0.1 to 30 Hz and rereferenced to a common average reference.

ERP averaging and analysis were performed using EEProbe software (ANT, www.antsoftware.nl). EEG and EOG artifacts were removed using a +/-35 μV deviation over 200 ms intervals on all electrodes. Blink artifacts were selected manually and corrected by a subtraction of VEOG propagation factors via a regression algorithm on EOG components (using EEProbe signal processing software). A 1000 ms recorded EEG epoch, including 100 ms pre-stimulus baseline and 900 ms interval following stimulus onset, was chosen for ERP averaging. ERP waveforms were then averaged separately for each electrode for each experimental condition.

N170. ERP analysis of the N170 component focused on an occipitotemporoparietal region of interest, which exhibited maximal N170 amplitude. A set of twelve electrodes were assessed, six electrodes from each of left and right hemispheres. Electrode locations corresponding to locations defined by the 10-20 system: P7/P8, a pair of electrodes slightly inferior to P7/P8, PO7/PO8, a pair of electrodes slightly inferior to PO7/PO8, O1/O2, a pair of electrodes slightly inferior to O1/O2. These electrode locations were similar to those used by Jacques and Rossion (2009). The peak amplitude of the N170 component was isolated using a time window ranging from 120 to 210 ms, obtained via inspection of the grand average waveform.

N400. ERP analysis of the N400 component focused on a parietal region of interest, which exhibited maximal N400 amplitude. Two midline electrodes were assessed corresponding to locations defined by the 10-20 system: Pz and an electrode slightly superior to Pz. The mean amplitude of the N400 component was isolated using a time window ranging from 340 to 400 ms, obtained via inspection of the grand average waveform.

Results and discussion

Behavioral response

Regardless of face type, responses were faster for faces preceded by the same face (740 ms ± 40 ms SEM) than faces preceded by a different face (849 ms ± 42 ms SEM). Responses were generally accurate (93.5% ± 3% SEM) and unaffected by the treatment conditions. These results were supported by two separate two-way repeated measures analysis of variance (ANOVA) conducted on mean response time for correct trials and mean accuracy with factors face type (composite, original) and repetition (preceded by the same face, preceded by a different face). For response time, the main effect of repetition was significant [$F(1,30) = 6.187, p < .05, \eta_p^2 = .17$]. There were no significant main effects or interactions of response accuracy.

N170

Figure 2 (top panel) depicts grand average morphology of the N170 ERP component. Figure 3 (left panel) depicts the magnitude of the N170 repetition effect in response to unfamiliar faces and composites made of unfamiliar face halves. The magnitude of the repetition effect was calculated by subtracting the peak N170 amplitude of faces preceded by a different face from that of faces preceded by the same face and thus, a positive value is indicative of repetition priming. Both original and composite faces showed repetition priming at the N170 over the right hemisphere, with less negative amplitudes for faces preceded by the same face than faces preceded by a different face. Neither face type produced the N170 repetition effect over the left hemisphere. These observations were supported by three-way repeated measures ANOVA conducted on the N170 peak amplitude with factors of hemisphere (left, right), face type (composite, original) and repetition (preceded by the same face, preceded by a different face). The two-way interaction between hemisphere and repetition was significant [$F(1,30) = 5.953, p < .05, \eta_p^2 = .17$]. No other effects or interactions were observed.

Figures 2 and 3 about here

N400

Figure 4 (left panel) depicts grand average waveforms over parietal cortex in response to unfamiliar faces and composites made of unfamiliar face halves. As observed by previous studies (e.g., Bentin & Deouell, 2000), there was no negative deflection during the time window used to assess the N400 (340 ms to 400 ms). This result is not too surprising given that unfamiliar faces are not associated with semantic information and therefore are not likely to engage in semantic associative processing.

Figure 4 about here

In Experiment 1, we observed repetition priming at the N170 for composite faces preceded by the same composite face versus a different composite face. This replicates some of the findings reported by Jacques and Rossion (2009) who also tested composite stimuli of unfamiliar faces. More importantly, our composite faces elicited the typical N170 repetition effect seen for natural unfamiliar face images, confirming that typical face processing is not disrupted by our composite face manipulation.

Experiment 2

Our main goal was to examine familiar face processing. We recorded ERPs to both the original familiar faces (familiar parts, familiar wholes) and composite faces made of familiar parts (familiar parts, novel whole) as participants performed a 1-back identity-matching task (Figure 1). This design allows us to ask whether semantic processes reflected by the N400 affect early perceptual processes reflected by the N170. If semantic retrieval by familiar parts of the composite face modulates the N170 then we will not observed the typical N170 repetition effect to the unfamiliar whole. To verify that the composite faces with incongruous parts are being treated as novel wholes, which would be expected to show a N170 repetition effect (Jacques & Rossion, 2009), we measured the composite face effect to show that incongruent parts disrupt naming of the top half when the parts are aligned but not when they are misaligned (results presented in method section).

Method

Details of the method were identical to Experiment 1 but with a different set of participants and different stimuli.

Participants

Thirty-one students (23 female; mean age 18 years ± 2 years SD) at McMaster University participated for course credit. All were Caucasian and reported normal or corrected-to-normal vision. Fifteen students who participated in Experiment 1 were recruited to participate in Experiment 2 (experiment order was counterbalanced across participant). The data from these 15 participants was used in a whole-brain analysis to directly compare unfamiliar face priming in Experiment 1 with familiar face priming in Experiment 2. All procedures complied with the Canadian tri-council policy on ethics as approved by the McMaster Ethics Research Board.

Stimuli

The face stimuli consisted of 40 images of current Caucasian celebrities (20 male; mostly movie stars) obtained via the worldwide web. All images captured the front of the face, with a neutral or smiling expression, without glasses. Images were cropped to include hair but exclude background, and converted to grayscale. All images were resized to equate height, width, and resolution. To assess familiarity, participants were asked to name each of the faces at the end of the experiment. Mean accuracy of face naming was 80% ± 3% SEM. Only those faces that were accurately named by the participants were included in the following analyses.

Using Adobe Photoshop (Version 7.0) and Adobe Illustrator (Version 9.0), composite faces were created from the adopted stimuli by dividing the face images in half at the base of the nasal bridge. Based on likeness of original images and the naturalness of the resulting composite images, the top and bottom halves of the same facial image were paired with the bottom and top halves of a second facial image. We created 40 composite face images by centering the top and bottom halves so that the nasal bridge of each half was in line. See Figure 1 for examples of the composite faces used in this experiment.

To establish that our composite stimuli were being processed holistically we ran a pilot study to examine the composite face effect. The top half of one familiar person's face was paired with the bottom half of another familiar person's face and the two halves were either aligned (as depicted in Figure 1) or misaligned (i.e., top and bottom halves horizontally displaced). Participants (N = 15, 13 female, mean age of 18 ± 1 year SD) were asked to name the familiar person represented by the top half of the face (as in

Young et al., 1987) and were slower and less accurate when the two halves were aligned than when the two halves were misaligned. These observations were supported by separate *t* tests conducted on the mean response time for correct trials [$t(14) = 2.878$, $p < .05$] and accuracy [$t(14) = -3.545$, $p = .003$] of aligned versus misaligned composite faces. Response time for aligned, 3310 ms ± 110 ms S.E.M. versus misaligned, 2930 ms ± 65 ms S.E.M., and accuracy for aligned, 52% ± 2% S.E.M. versus misaligned, 64% ± 1% S.E.M.

Results and discussion

Behavioral responses

Regardless of face type, responses were faster for face preceded by the same face (724 ms ± 45 ms SEM) than faces preceded by a different face (893 ms ± 69 ms SEM). Responses were generally accurate (96.5% ± .7% SEM) and unaffected by the treatment conditions. These results were supported by two separate two-way repeated measures ANOVAs conducted on mean response time for correct trials and mean accuracy with factors face type (composite, original) and repetition (preceded by the same face, preceded by a different face). For response time, the main effect of repetition was significant [$F(1,30) = 11.335$, $p < .01$, $\eta_p^2 = .27$]. There were no significant effects or interactions with accuracy.

N170

Figure 2 (bottom panel) depicts grand average morphology of the N170 ERP component. Figure 3 (right panel) depicts the magnitude of the N170 repetition effect for familiar original and composite faces. The magnitude of the repetition effect was calculated by subtracting the peak N170 amplitude of faces preceded by a different face from that of faces preceded by the same face and thus, a positive value is indicative of repetition priming. Neither original nor composite faces showed repetition priming at the N170. These observations were supported by a three-way repeated measures ANOVA conducted on the N170 peak amplitude with factors of hemisphere (left, right), face type (composite, original) and repetition (preceded by the same face, preceded by a different face). There were no significant main effects and interactions. Critically, the two-way interaction between hemisphere and repetition was not significant [$F(1,30) = .333, p =$ n.s.].

N400

Figure 4 (right panel) depicts grand average waveforms of the N400 ERP component in response to familiar faces and composites made of familiar face halves. Both original and composite faces elicited an N400 of similar morphology as revealed by the amplitude response to faces preceded by a different face. This suggests that partial information was sufficient to activate semantic processing. Although the amplitude response to faces preceded by the same face was more positive for original faces than composite faces, it is unclear whether this difference reflects processing of the N400 or processing of the broad positive going P3 component that occurred within the same time-window. These observations were supported by three-way repeated measures ANOVA conducted on the N400 mean amplitude with factors of hemisphere (left, right), face type (composite, original) and repetition (preceded by the same face, preceded by a different face). The main effects of face type [$F(1,30) = 4.205, p < .05, \eta_p^2 = .12$] and repetition [$F(1,30) = 153.658, p < .001, \eta_p^2 = .84$] were significant, as was the two-way interaction of face type and repetition [$F(1,30) = 7.686, p < .01, \eta_p^2 = .20$]. Simple main effects revealed repetition priming for both original [$F(1,30) = 109.910, p <.001, \eta_p^2 = .77$] and composite faces [$F(1,30) = 98.911, p <.001, \eta_p^2 = .77$]. Face type (composite vs. original) affected the N400 amplitude of faces preceded by the same face [$F(1,30) = 8.963, p <.01, \eta_p^2 = .23$] but did not affect the N400 amplitude of faces preceded by a different face [$F(1,30) = .113, p =$ n.s.].

Whole brain analysis

To further investigate the lack of N170 repetition priming for familiar faces and composites made of familiar face parts, we directly compared unfamiliar face priming in Experiment 1 with familiar face priming in Experiment 2. We were particularly interested in identifying potential top-down modifiers of the N170 response revealed by repetition priming of familiar faces at more anterior sites but around the same time as the N170 peak amplitude. We calculated participants' mean repetition effect for Experiment 1 stimuli and Experiment 2 stimuli at each time point between 90 ms and 225 ms. To better localize region-specific activity, ERPs waveforms of electrodes over the right hemisphere were transformed into 4 region-specific source waveforms via inverse spatial filtering (Scherg, Ille, Bornfleth & Berg, 2002); regions represented by the source waveforms included temporal-parietal, parietal, central, and frontal regions. We focused on the right hemisphere because our unfamiliar face stimuli only elicited N170 repetition priming over the right hemisphere. Percentile bootstrap method (Wilcox, 2005) was used to assess statistical significance of each data point by sampling the mean repetition effect from participants with replacement. This process was repeated 999 times to create a distribution of bootstrapped estimates of the mean repetition effect. We then computed 96% confidence intervals for each data point and data points were considered to show significant repetition effects if confidence intervals did not include zero.

Figure 5 depicts statistically significant ($p < .04$) repetition priming for familiar and unfamiliar faces at time points around the peak of the N170 across the entire right hemisphere. Even though familiar faces and composites made of familiar halves failed to produce the N170 repetition effect, they did produce repetition priming over frontal and central regions prior to (90 ms to 150ms) the N170 peak amplitude. Such repetition priming at anterior sites may indicate top-down modulation of the N170 repetition priming effect that is usually reflected at temporal-parietal sites and may contribute to the lack of this effect for familiar faces. In contrast, unfamiliar faces produced the N170 repetition effect over temporal-parietal regions around 150 ms. Unfamiliar faces also produced repetition priming over frontal regions but a slightly later time than familiar faces. Unfamiliar faces failed to produce repetition priming over central regions.

Figure 5 about here

In Experiment 2, both original familiar faces and composite faces made of familiar parts elicited an N400 response of similar morphology and of equally large amplitude to non-repeat faces. These results suggest that partial familiar face information was sufficient to activate semantic processing. Moreover, neither original nor composite faces showed repetition priming at the N170. It is surprising that the incongruent information of our composite stimuli produced a novel whole which disrupted face naming (see pilot study described in the methods section of Experiment 2) but did not elicit the N170 repetition effect of unfamiliar faces. In Experiment 1, we showed that composites made of unfamiliar parts elicited the same ERP responses as natural unfamiliar face images. Therefore, the lack of N170 repetition effect seen for composites made of familiar parts cannot be a result of our composite manipulation. The only difference between the composite made of familiar parts and the stimuli of Experiment 1 is that the composites made of familiar parts elicit engagement of semantic processes. Thus, semantic processes may modify the N170 response by reducing repetition priming at perceptual stages. Right frontal and central regions that are engaged just prior 150 ms (Figure 5) may mediate such top-down modulation of the N170 response to familiar faces.

General Discussion

We created a set of composite faces by aligning the top half of one familiar person's face and the bottom half of a different familiar person's face (Figure 1). Although there is some familiarity from the parts, the incongruent information produces a novel whole. We ran a pilot study to test the composite face effect on our stimuli (described in the methods section of Experiment 2). Participants had more difficulty identifying the top half of the face when aligned with an incongruent bottom half than when the halves were misaligned. This suggests that there is interference from the incongruent information when the face is processed holistically and that the aligned composite face is perceived as a novel face. Although face naming was disrupted, it is unclear whether the incongruent information affects ERP component processes specific for unfamiliar and familiar face processing. ERPs can provide insight into the time course of perceptual and semantic processing of faces.

We recorded ERPs to original familiar faces and novel composite faces made of familiar parts. Participants performed a 1-back identity-matching task (Figure 1) during which they were not required to name the face but to match successive images. Our main question was whether we would observe N400 effects for the composites made of familiar but incongruous parts, and if so, whether semantic processes reflected by the N400 would modulate the N170 repetition effect as might be expected if semantic and perceptual processes are linked. Indeed, familiar part information was enough to produce the N400 response, which may reflect activation of associated semantic processes. Furthermore, the incongruent information that makes the whole face novel did not produce the N170 repetition effect. Together these results suggest that late semantic processes modulate early perceptual representations.

Our results provide important mechanistic detail regarding how a face is processed and how such processes differ for known individuals. In general, familiar faces seem to rely less on holistic information than unfamiliar faces. Our results demonstrate that partial familiar face information is sufficient for typical familiar face processing. A critical difference between familiar and unfamiliar faces is that familiar faces are associated with a rich network of person-specific information. Different aspects of a person act as effective retrieval cues resulting in superior recognition of highly familiar individuals (for relevant models, see Bruce & Young, 1986; Burton, Bruce & Johnston, 1990; Burton, Bruce & Handcock, 1999). Moreover, associating a face with rich information also allows for a more abstract, conceptual representation of the individual. For example, identity matching of familiar faces is likely done by name (e.g., "I just saw Paul Ekman") rather than by facial structure. Indeed, N400 semantic-based processes seem to reflect such abstract representation: N400 priming occurs when a familiar face follows its name (Pickering & Schweinberger, 2003) or a familiar face follows the face of a related individual (Schweinberger et al., 1995).

Semantic information associated with a familiar face also represents a memory for the face image itself. Jemel and colleagues showed N400 priming for eyes that matched the familiar prime face even when the eyes of the prime face were blocked-out (Jemel, George, Chaby et al., 1999; Jemel, George, Olivares et al., 1999). This may be why we see familiar face processing at the N400 for our composite stimuli made of familiar parts. Part of a familiar face likely cues the retrieval of store memories of the matching face image. These stored representations may help to fill in the missing structural detail, overriding the contribution from the incongruous half of the face. Although there seems to be some interference from the incongruous whole during naming tasks (as seen in our pilot study), the ERP measures suggest that retrieved semantic information plays an important role.

Such semantic-based structural representations at the N400 may mean less work for earlier perceptual process. Indeed, our results suggest a link between N400 and N170 processes as our composites made of familiar parts failed produced the N1

70 repetition effect despite the novelty of the whole. Semantic processes likely feed back into early perceptual areas via top-down pathways. If there is enough structural detail from stored information to do the task then there is no need for additional perceptual processing. Frontal regions (Figure 5) may play a role in coordinating the retrieval of pre-existing information from memory with the encoding of additional perceptual information (Leveroni et al., 2000; Summerfield et al., 2006). Indeed, functional magnetic resonance imaging (fMRI) studies report greater activation of frontal regions by familiar faces compared to unfamiliar faces (Leveroni et al., 2000; Platek et al., 2006) and there tends to be greater right frontal activity during tasks that require detailed identity discrimination among faces of equal familiarity (Jiang, Haxby, Martin, Ungerleider & Parasuraman, 2000; Rotshtein, Henson, Treves, Driver, & Dolan, 2005). Moreover, the pre-perceptual (i.e., pre-N170) timing of the activity we observed over frontal regions is consistent with the timing of frontal activity during top-down modulation of object perception (Bar et al., 2006). With our composite stimuli, frontal regions may inhibit the processing of incongruent perceptual information to allow for semantic information associated with the parts to be retrieved.

Given all this semantic support and top-down control, there is little need to establish a robust perceptual representation of familiar faces and thus, there is no N170 repetition priming for repeated faces. In contrast, unfamiliar faces have little or no semantic support. Moreover, a new face has never been seen before so it must be fully encoded. We know that N170 processes are involved in pulling out structural face information (e.g., Sagiv & Bentin, 2001). Such structural information is thought to be used to build-up a holistic structural bases that can be used for facial identity processing (Jacques & Rossion, 2009). The structural representation of a new face is established upon initial exposure. When the face is immediately repeated there is some savings in perceptual processing and this is revealed in the N170 repetition priming.

In conclusion, familiar face recognition is supported by rich person-specific detail of stored memories that can be accessed with very little facial information. As a result, perceptual representation is less important for familiar faces than unfamiliar faces. Moreover, retrieval of semantically related information during processing of familiar faces occurs even in the face of incongruous perceptual information.

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Figure 1.A depiction of the composite stimuli made of familiar halves (stimuli of Experiment 2) in the 1-back identity-matching task. Composite stimuli made of unfamiliar halves (stimuli of Experiment 1) were constructed in the same way.

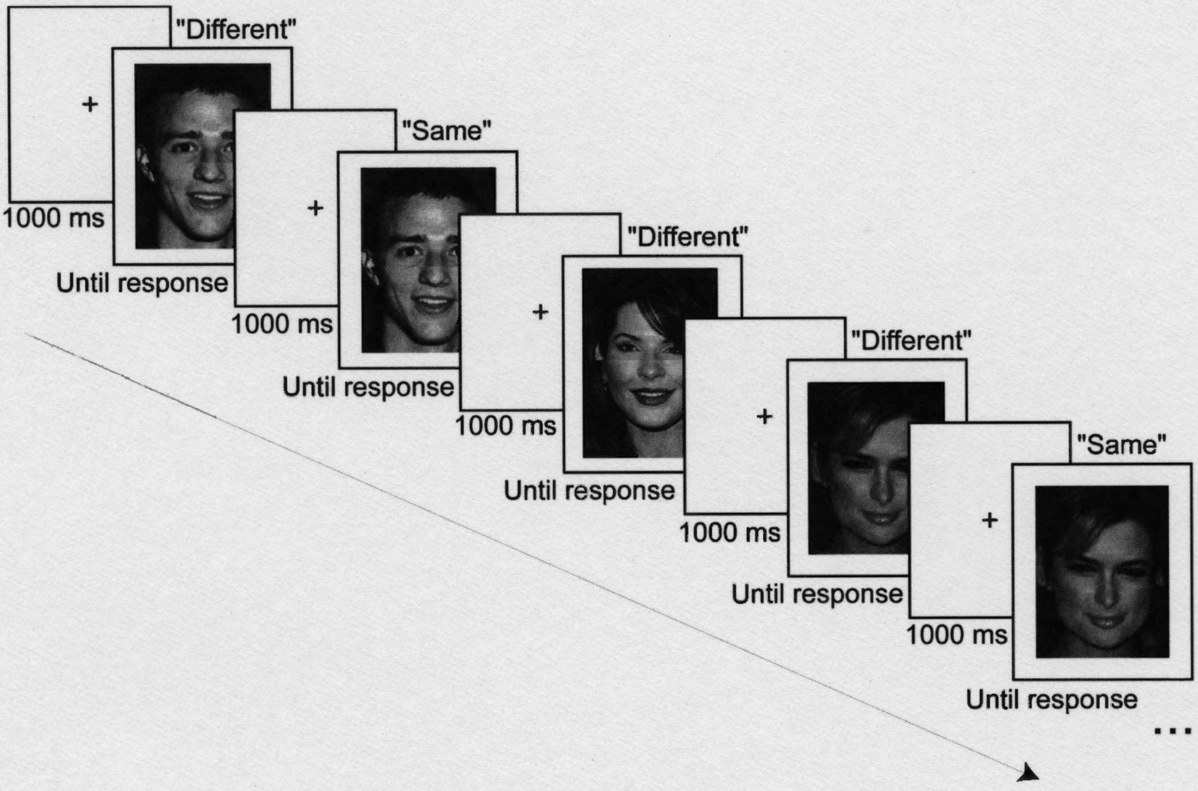


Figure 2.Grand average waveforms of the N170 ERP component in response to stimuli of Experiment 1(unfamiliar faces and composites made of unfamiliar parts) and stimuli of Experiment 2 (familiar faces and composites made of familiar parts) at temporal-parietal sites over right and left hemispheres.

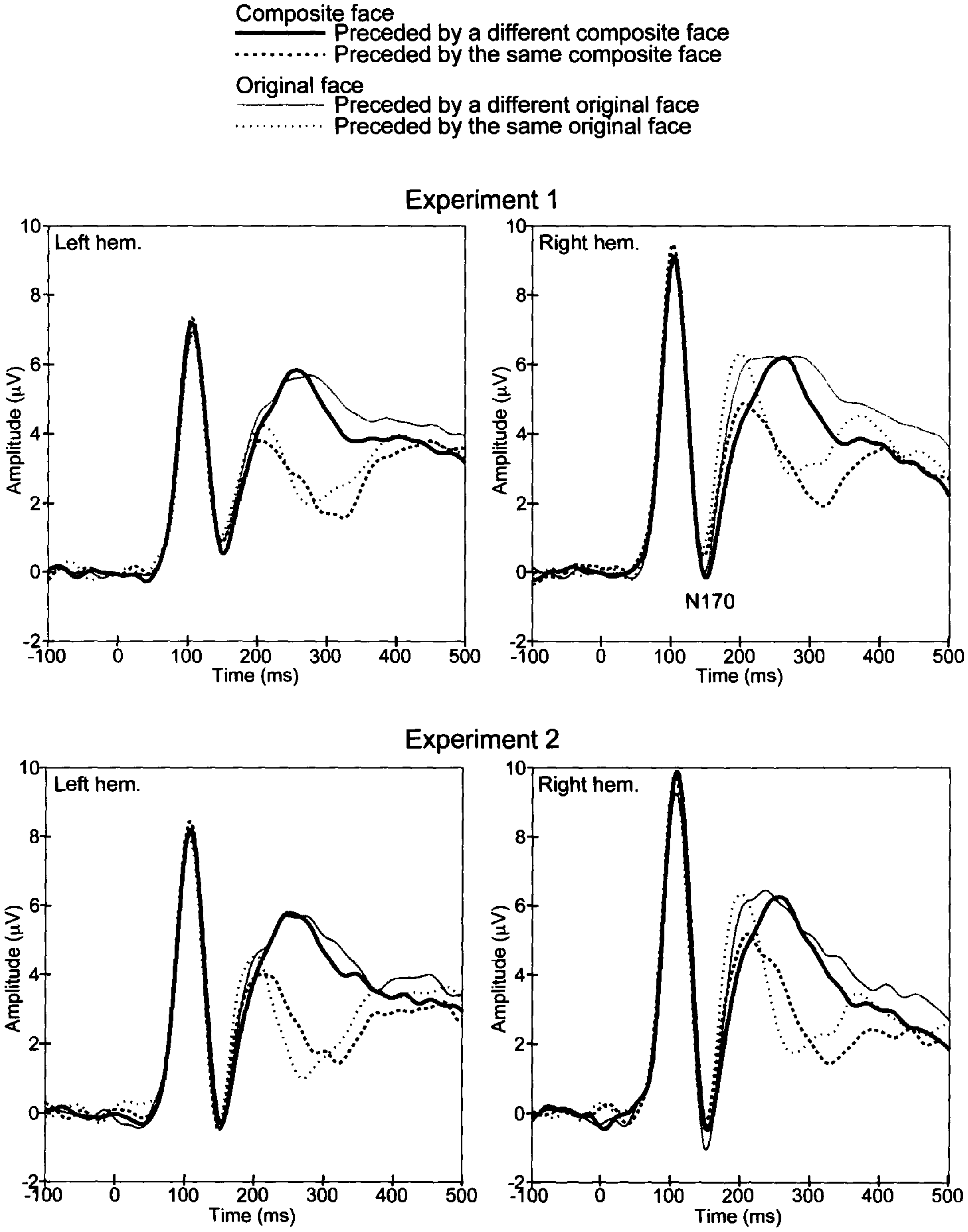


Figure 3.The magnitude of the N170 repetition effect (faces preceded by the same face subtracted from faces preceded by a different face) for stimuli of Experiment 1 (unfamiliar faces and composites made of unfamiliar parts) and stimuli of Experiment 2 (familiar faces and composites made of familiar parts) at temporal-parietal sites over right and left hemispheres. Only unfamiliar faces and composites made of unfamiliar faces produced N170 repetition effect over the right hemisphere. Error bars depict standard errors corrected for repeated measures.

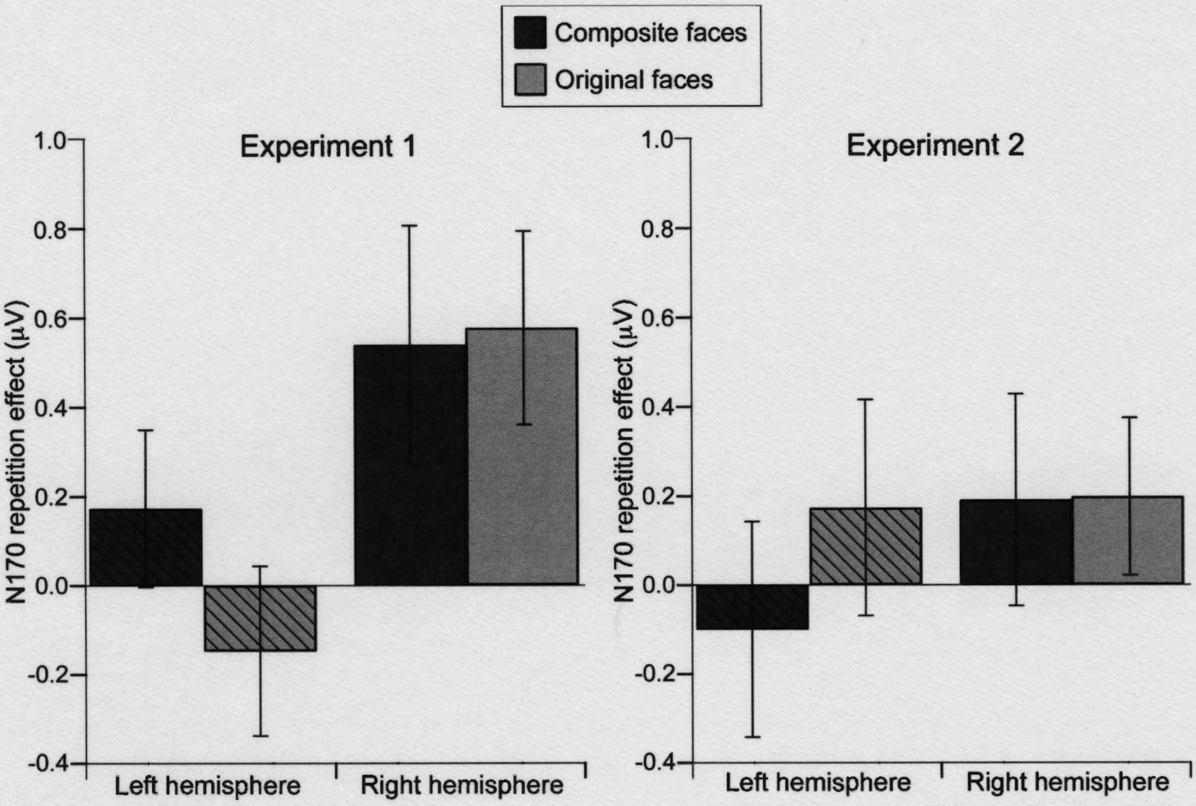


Figure 4.Grand average waveforms of the N400 ERP component in response stimuli of Experiment 1 (unfamiliar faces and composites made of unfamiliar parts) and stimuli of Experiment 2 (familiar faces and composites made of familiar parts) faces at parietal sites over the midline. Only familiar faces and composites made of familiar faces produced the N400 response. Repetition priming at the N400 seems confounded with the broad positive-going waveform.

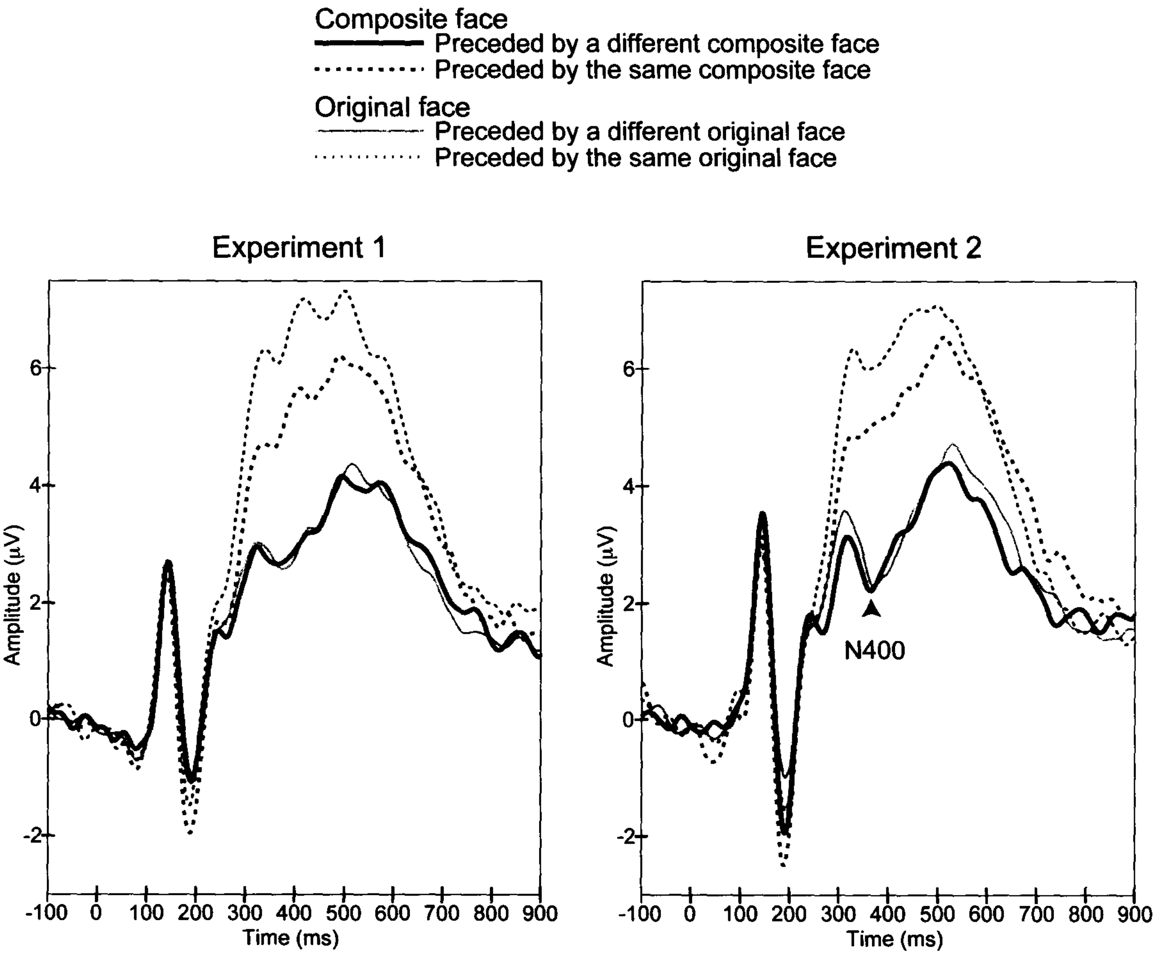
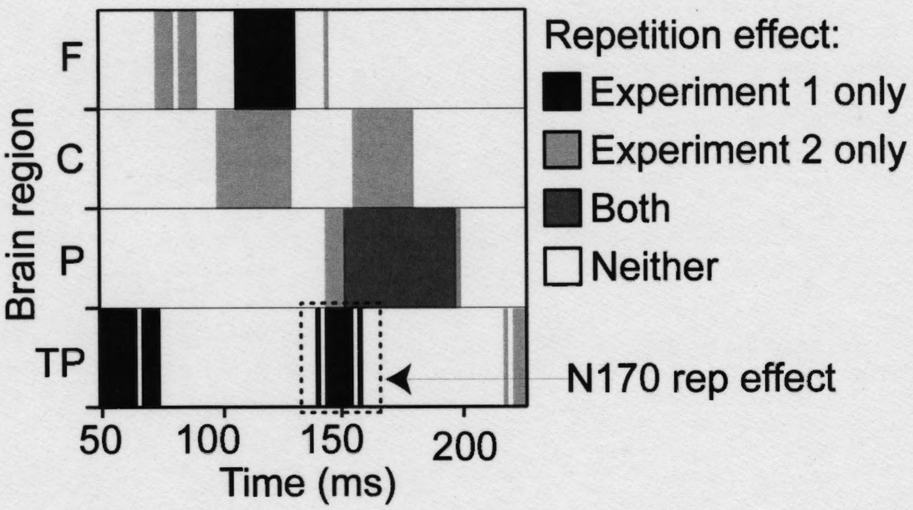


Figure 5. Repetition effects for stimuli of Experiment 1(unfamiliar faces and composites made of unfamiliar parts) and stimuli of Experiment 2 (familiar faces and composites made of familiar parts) at time points around the peak of the N170 (~150 ms) across the entire right hemisphere. Brain regions correspond to Temporal-parietal (TP), Parietal (P), Central (C), and Frontal (F) regions. Statistical significance of $p < .04$ is depicted.



Chapter 5

Discussion

Accurate face recognition is central to developing and maintaining social relationships. Most of us are remarkably good at face recognition, demonstrated by our superior recognition for highly familiar faces and our ability to recognize new faces even after a single exposure. Although semantic processes support familiar face recognition, when I began my thesis it is unclear what processes mediate unfamiliar face recognition. The main objective of my thesis was to identify unique neural mechanisms underlying familiar versus unfamiliar face recognition and to detail how these mechanisms change as a result of learning. I used event-related potentials (ERPs) to assess the stages of face processing affected by familiarity.

Many differences exist between familiar and unfamiliar face processing. Recognition is faster and more accurate for familiar than unfamiliar faces (Burton, Wilson, Cowen, & Bruce, 1999; Bruce, 1982; Ellis, Shepherd, & Davies, 1979; Klatzky & Forrest, 1984; Young, Hay, McWeeny, Flude & Ellis, 1985). Part-based facial identity cues (i.e., eyes) are sufficient for familiar but not unfamiliar face recognition (O'Donnell & Bruce, 2001). We scan familiar and unfamiliar faces differently; when viewing unfamiliar faces we tend to scan the entire face image, whereas when viewing familiar faces we tend to focus on the eyes and eye region (Althoff & Cohen, 1999; Heisz & Shore, 2008). Compared to familiar faces, unfamiliar faces elicit greater activation in occipital and fusiform face areas (Rossion, Schiltz, & Crommelinck, 2003). Furthermore, prosopagnosia (i.e., the inability to recognize faces) can affect familiar but not unfamiliar face recognition, and vice versa (Malone, Morris, Kay & Levin, 1982).

A critical distinction between familiar and unfamiliar faces is that familiar faces are associated with rich semantic information. According to the current face recognition model (Bruce & Young, 1986; Burton, Bruce & Johnston, 1990; Burton, Bruce & Handcock, 1999), various aspects of a person (e.g., name, occupation, marital status) can be used to retrieve associated information resulting in superior recognition of highly familiar individuals. Specifically, view-invariant face recognition units (FRU) represent the perceptual properties of a face. The FRU of familiar faces are linked via recurrent connection with person identity nodes (PINs) that represent person-specific semantic information and can be activated by different aspects of the person. PINs are thought to mediate familiar face recognition. In contrast, unfamiliar faces are associated with little or no semantic information and thus, recognition may be based primarily on perceptual processes.

Unique mechanistic details of familiar and unfamiliar face recognition may emerge from differential processing at perceptual and semantic stages. Perceptual and semantic stages involved in face processing have been isolated using ERPs. ERP N170 component reflects early perceptual face processes and ERP N400 component reflects semantic processes. Familiar face recognition is mediated by semantic processing reflected by the N400. Yet, little research has considered the N170 as a marker for unfamiliar face recognition. This is mostly because initial studies failed to observe N170 differences for familiar versus unfamiliar faces (Eimer, 2000; Bentin & Deouell, 2000).

However in these studies, each face was only presented once (i.e., no repeats), and face repetition may be needed to elicit perceptual-based identity matching.

Indeed, face repetition reveals N170 priming. In general, repetition effects provide important information about the nature of representation at that particular stage of processing (Grill-Spector, Henson, & Martin, 2006). With face processing specifically, N170 repetition effects are seen for unfamiliar faces (Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009; Campanella et al., 2000; George, Jemel, Fiori, & Renault, 1997; Guillaume & Tiberghien, 2001; Heisz & Shedden, 2009; Heisz, Watter, & Shedden, 2006a, 2006b; Jaques, d'Arripe, & Rossion, 2007; Itier & Taylor, 2002, 2004) but not for familiar faces (Heisz & Shedden, submitted; Schweinberger, Pickering, Burton & Kaufmann, 2002; Schweinberger, Pickering, Jentzsch, Burton & Kaufmann, 2002). Although these results point to the N170 as a marker of unfamiliar face recognition, at the time I began my thesis identity processing at the N170 was still largely discounted.

My thesis sought to develop the idea that early perceptual processes reflected by the N170 may be a mechanism for unfamiliar face recognition. In Chapter 2, I assessed the automaticity (i.e., processing that is spontaneously or without intention) of unfamiliar face recognition at the N170 (Heisz, Watter, & Shedden, 2006b). I tested this by making face identity task irrelevant. I also tested the specificity of N170 repetition priming by contrasting upright versus inverted face processing. N170 repetition priming was seen for upright faces only, suggesting that N170 processes mediate automatic identity processing of unfamiliar faces. We originally thought different task demands explained why Itier and Taylor (2002, 2004) found N170 repetition effects for inverted faces whereas we did not; however since publication of Heisz, Watter and Shedden (2006b), Jacques, d'Arripe, and Rossion (2007) have also failed to observed N170 repetition priming for inverted face repetition even when identity was task relevant. Thus, task demands do not seem to explain this discrepancy. Further work is needed to tease apart this discrepancy.

In Chapter 3, I assessed whether semantic learning modifies the N170 response (Heisz & Shedden, 2009). I tested this using a five-day learning paradigm, whereby one group of participants learned faces with person-specific semantic information and another group of participants learned faces with irrelevant information. ERPs were recorded on Day 1 (when all faces were unfamiliar) and Day 5 (after learning). Only faces learned with person-specific information showed a reduction in the N170 repetition effect, suggesting that N170 identity processes mediate face recognition in the absence of semantic information.

In Chapter 4, I assessed the link between N170 perceptual processes and N400 semantic processes (Heisz & Shedden, submitted). I tested this by creating a composite face made of familiar halves; when a composite was processed holistically it was perceived to be novel. Since identity processing reflected by the N170 seems to be based on holistic matching (Jacques & Rossion, 2009), we expected our composite faces to elicit typical N170 repetition effects. However, the novel whole of the composite faces failed to elicit N170 repetition priming. Instead, the familiar parts of the composite were enough to activate semantic-based processes reflected by the N400. Although we did not test this directly, the familiarity effect seen for composite faces might be determined by the familiarity of the top half. This makes sense given that the eyes carry important information for identity (Gosselin & Schyns, 2001; Sekuler et al., 2004). To test this, we would create two new sets of composite stimuli: one set with famous top halves and non-famous bottom halves, the other set with non-famous top halves and famous bottom halves. I would predict a larger familiarity effect for the composites with a famous top half only than composites with a famous bottom half only. Regardless of whether the composite face results are driven by the top or bottom half, semantic processes seem to modify early perceptual processes. Furthermore, these results suggest that typical recognition processes can be engaged by partial familiar face information even in the presence of incongruent perceptual information.

In the following section, I propose mechanistic details that account for the data and map those details onto Bruce and Young's (1986) face recognition model. I conclude this section by pointing to future methodological considerations.

5.1 Mechanistic details of face recognition

ERP N170 component processes play a critical role in face processing. The N170 is a direct measure of postsynaptic activity that occurs approximately 170 ms post-stimulus onset and has maximal scalp distribution over bilateral occipiotemporal cortex. Based on this scalp distribution, the N170 is thought to reflect multiple generators of the fusiform gyrus, the superior temporal sulcus, and the lateral temporal cortex (e.g., Corrigan et al., 2009). From single cell recordings in monkeys (see Desimone, 1991, for review), we can postulate that some cells within these regions (of humans) may represent faces in a distributed fashion. For example, the magnitude of each face cell's response may depend on the physical characteristics of the particular face image. When a face is presented, the populations of cells selective for its particular characteristics are engaged. This results in a dipole potential measurable at the scalp, observed at the N170 component.

Although N170 processes reflect the encoding of physical face characteristics (Bentin, Allison, Puce, Perez, & McCarthy, 1996; George, Jemel, Fiori, Chaby & Renault, 2005; Harris & Nakayama, 2008; Itier, Alain, Sedore & McIntosh, 2007; Latinus & Taylor, 2005; Rossion & Jacques, 2008; Schyns, Jentzsch, Johnson, Schweinberger & Gosselin, 2003; Zion-Golumbie & Bentin, 2007), the N170 is also sensitive to unfamiliar face repetition. Immediate repetition of the same unfamiliar face reduces the N170 amplitude response (Caharel et al., 2009; Campanella et al., 2000; George et al., 1997; Guillaume & Tiberghien, 2001; Heisz & Shedden, 2009; Heisz et al., 2006a, 2006b; Jaques et al., 2007; Itier & Taylor, 2002, 2004). This is seen across different images of the same unfamiliar individual (Caharel et al., 2009; Campanella et al., 2000; Guillaume & Tiberghien, 2001), suggesting that the N170 repetition effect is not just the result of repeating exactly the same image (pixel priming) but rather has something to do with repeating the particular face.

Critically, the N170 repetition effect provides a potential mechanism for unfamiliar face recognition based on neural perceptual priming. When the same face is repeated, the cells selective for its particular characteristics are re-engaged. Because they have just been activated, these cells are primed and may require reduced postsynaptic input to respond. This leads to a reduced dipole potential at the scalp, as revealed by the N170 repetition effect. In contrast, when a new face is presented, an entirely new set of generators will respond because of its unique facial characteristics. This leads to a large dipole potential at the scalp and the N170 amplitude does not differ compared to the previous trial.

Whole face selective cells may be particularly affected by repetition priming. Results from a recent ERP study show N170 repetition priming for whole face repetition but not for partial face repetition (Jacques & Rossion, 2009). This suggests that whole face representation may be particularly important for unfamiliar face recognition. Indeed, holistic information is thought to be more generalizable across different images of the same individual than part-based information (Robbins & McKone, 2003). Furthermore, unfamiliar face recognition is disrupted by whole face manipulations (Hole, 1994; Hole, George & Dunsmore, 1999; Yin, 1969).

Such N170 repetition effects by holistic-based matching may help to explain why inverted faces fail to elicit the N170 repetition effect when face identity is not task relevant (Heisz et al., 2006b). Inversion may impede our ability to automatically establish accurate whole face representations. Such variability would make it more difficult to match incoming face information with preexisting representations. When an inverted face is repeated, the same whole face selective cells may not be reactivated. Instead, new cells may fire and thus, fail to produce the N170 repetition effect.

While the idea of neural perceptual priming explains most of the data, it does not account for the release from adaptation (no reduction) seen when the same face is consecutively presented three or four times at the same (attended) location (Heisz et al., 2006a, 2006b). Nor does it account for lack of N170 repetition priming for faces learned with semantic information (Heisz & Shedden, 2009) or highly familiar faces (Heisz & Shedden, submitted; Schweinberger, Pickering, Burton et al., 2002; Schweinberger, Pickering, Jentzsch et al., 2002). In these cases (especially the latter ones), top-down processes may be recruited, and such activity may mask any perceptual priming.

Our understanding of familiar face recognition may benefit from the ideas of Barsalou and colleagues (2003) who proposed a general neural mechanism, in which conceptual knowledge is grounded in perceptual systems. Specifically, participants may be able to achieve a more robust representation of a familiar face by linking it to semantic knowledge. When a familiar face is presented, the populations of cells selective for its particular characteristics are engaged to produce the N170 component. In turn, this may lead to the activation of conjunctive cells that are selective for semantic information associated with the particular face. Back-propagation of semantic information may partially reactivate the earlier sensory representation. According to Barsalou and colleagues (2003) such partial reactivation may contain distortions. Consequently, such distortions may cause different face-selective cells to fire. If face repetition coincides with such top-down (somewhat distorted) reactivation then (even with perceptual priming) there may be overall more neural activity and thus, no N170 repetition priming.

Based on these ideas, we propose that the N170 response may be activated by input from bottom-up (structural) and top-down (semantic). Importantly, top-down semantic input may elicit an equivalent N170 amplitude response as bottom-up structural input. The N170 is modulated by bottom-up input and priming occurs when this information is repeated. The N170 is also modulated by top-down semantic information but there is less repetition of this information; as activation spreads across associated semantic networks, new information is retrieved and the semantic input to the N170 continues, possibly stimulating new cells each time the face is repeated.

Indeed, semantic information is thought to play an important role in face recognition processes. Heisz and Shedden (submitted) demonstrated this by examining the ERPs in response to composites made of familiar parts. Familiar part information was enough to produce the N400 semantic response and surprisingly, the incongruent information that makes the whole face novel did not produce the N170 repetition effect. This suggests that semantic processes reflected by the N400 modulate early perceptual processes reflected by the N170. In addition, learning faces with semantically relevant information reduces N170 repetition priming (Heisz & Shedden, 2009), pointing to a direct link between semantic information and early perceptual processing.

Although in Heisz et al. (2006a, 2006b) unfamiliar faces were merely repeated three or four times without semantic information, participants may have (with minimal mental effort) come up with their own stories (or mnemonic) about the faces. This is common in real world face learning situations; people often relate new faces to preexisting representations (e.g., “That person reminds me of Brad Pitt”). Associating a face with semantic information may allow for more elaborate encoding by establishing different retrieval cues associated with the particular face memory. By this, one might expect that any contextual information (not necessarily person specific) may be sufficient to reduce perceptual-based face recognition processes (e.g., “I always see that person on the bus”). Although Heisz and Shedden (2009) failed to find a reduced N170 repetition priming effect when faces were learned with non-person related stories, these stories failed to provide a particular context that could be associated with the face. The continually changing context of the non-person related information made it difficult for participants to link any particular semantic information with the face image. Furthermore, participants were required to evaluate the unrelated information, which may have prevented them from generating any of their own stories about the faces.

Associating semantic information with a face seems to allow for a more abstract, conceptual representation of the individual. For example, identity matching of familiar faces has a strong contribution from top-down processes such as identification by name (e.g., "I just saw Paul Ekman") or other contextually relevant information rather than by facial structure alone (as is required by unfamiliar face identity matching). Likewise, N400 priming is not only seen when the same familiar face is repeated (Barrett, Rugg, & Perrett, 1988; Eimer, 2000; Engst, Matin-Loeches & Sommer, 2006; Herzmann, Schweinberger, Sommer & Jentzsch, 2004; Schweinberger, Pfütze & Sommer, 1995; Schweinberger, Pickering, Burton, et al., 2002) but also when a familiar face follows its name (Pickering & Schweinberger, 2003) or the face of a related individual (Schweinberger et al., 1995).

Highly familiar faces are not only associated with semantic information but also with a rich memory for the face image itself. Like other stored information, access to stored structural representations seems to be mediated by N400 processes. For example, N400 priming occurs when target eyes match the familiar prime face even when the eyes of the prime face are blocked-out (Jemel, George, Chaby, Fiori, & Renault, 1999; Jemel, George, Olivares, Fiori, & Renault, 1999). This helps to explain why part-based information is sufficient for familiar face recognition (Heisz & Shedden, submitted; O'Donnell & Bruce, 2001) and why familiar face recognition is highly accurate under poor viewing conditions (Burton et al., 1999). Part of a familiar face may cue the retrieval of stored memories of the face image and these stored representations may help to fill in the missing structural detail.

Semantic processes (involving both abstract and structural representation) may feed back into early perceptual areas via top-down pathways. If there is enough person-specific detail from stored information to do the task then there is no need for additional perceptual processing. Frontal regions may mediate such top-down processing by coordinating memory retrieval with perceptual encoding (Leveroni et al., 2000; Summerfield et al., 2006). fMRI studies support this by showing greater activation of frontal regions by familiar faces compared to unfamiliar faces (Leveroni et al., 2000; Platek et al., 2006) and greater right frontal activity during tasks that require detailed identity discrimination among faces of equal familiarity (Jiang, Haxby, Martin, Ungerleider & Parasuraman, 2000; Rotshtein, Henson, Treves, Driver, & Dolan, 2005). Similarly, emotional processing of the amygdala feeds back to modulate the vigilance with which we process faces (Gobbini & Haxby, 2007). fMRI studies demonstrate this by showing greater activation of the amygdala in response to unfamiliar faces (or strangers) compared familiar faces (Dubois et al., 1999; Gobbini, Leibenluft, Santiago, & Haxby, 2004; Schwartz et al., 2003).

Taken together, the current knowledge of face recognition processes (reviewed in Section 1: Introduction), my dissertation data, and my proposed mechanistic details of face recognition map onto Bruce and Young's (1986) functional model of face recognition with some modifications. In Figure 5.1 I have detailed my proposed modification of Bruce & Young's model with respect to the stages of processing reflected by N170, N250, and N400 components. First, I propose that the two separate stages of "Structural Encoding" and "Face Recognition Unit (FRU)" be combined into one stage of structural face identity encoding, involved in processing (featural and holistic) aspects of an individual face that make it unique. Further, I propose that N170 processes reflect this structural face identity encoding stage.

Second, I propose to include a new stage of visually derived semantic encoding. Bruce and Young (1986) discussed this stage in their paper but did not include it in their model. Visually derived semantic encoding is defined as readily formed associations based on the physical characteristics of the face, such as age, sex, race, attractiveness, trustworthiness, or intelligence. Different from identity-specific semantic coding (reflected by N400 processes), a visually derived semantic code is dependent the physical image and can be easily established for new and visually learned faces. Furthermore, this form of encoding is not face-specific and can be established for non-face stimuli. I propose that N250 processes reflect visually derived semantic coding. Finally, I propose that these three stages: structural face encoding (N170), visually derived semantic processing (N250) and identity-specific semantic processing (N400), are all linked with each other via recurrent pathways to allow for both bottom-up and top-down modulation.

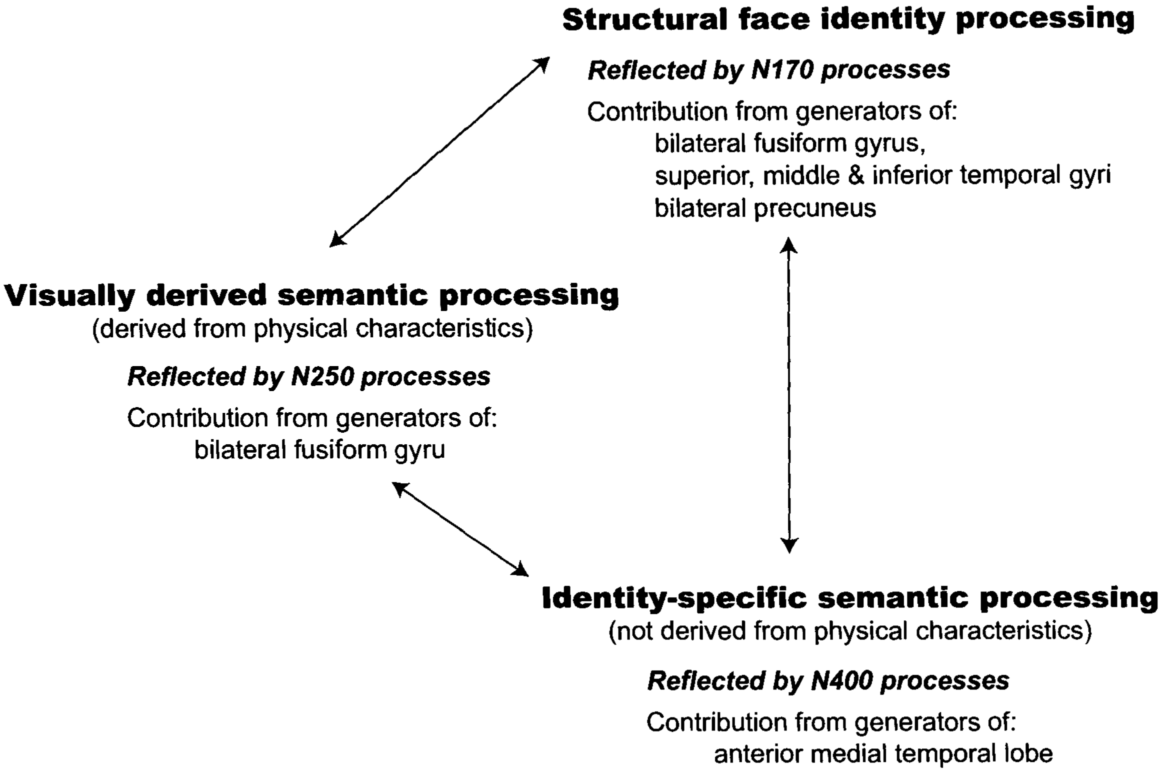


Figure 5.1. Proposed stages of face recognition depicting the main processes reflected by N170, N250 and N400 components.

In summary, I have described the unique neural mechanisms that underlie familiar and unfamiliar face processing. Unfamiliar face recognition is mediated by early perceptual processes and reflected by N170 repetition priming. Once a face is associated with sufficient semantic information, the recognition process shifts to a later semantic stage reflected by the N400 and such semantic processes can modulate early perceptual processes via top-down processes.

Despite these very important differences, both familiar and unfamiliar face recognition seem to rely on right hemisphere processes for recognition. N170 face effects tend to be larger over the right hemisphere than the left hemisphere (Heisz & Shedden, submitted; Rossion, Joyce, Cottrell, & Tarr, 2003). Right occipital and right fusiform face areas are modulated by face familiarity (Rossion et al., 2003). Furthermore, prosopagnosia can result from lesions to the right hemisphere only (see Barton, 2008, for recent review). Although it is not entirely clear why the right hemisphere is preferentially engaged for face processing, there is some evidence to suggest that the right hemisphere may be specialized in globally directed attention (Fink et al., 1996). This type of attention may be particularly important for holistic face processing, which seems to be involved in both familiar and unfamiliar face processing (Hole, 1994; Scapinello & Yarmey, 1970; Yarmey, 1971; Young, Hellawell & Hay, 1987). Indeed, the right hemisphere seems particularly sensitive to changes in facial configuration, whereas the left hemisphere seems particularly sensitive to changes in facial features (Scott & Nelson, 2006). By this, one might predict the left hemisphere to be more sensitivity to manipulations involving familiar faces.

5.2 Methodological and future considerations

There are methodological points to consider when evaluating the present studies. First, there are some limitations to using ERP as a measure of brain activity. Although ERP is a direct measure of neural activity with precise temporal resolution, it is extremely difficult to localize the source of ERP activity. Even with dipole source modeling, inferring dipole source(s) from voltage patterns can still be highly erroneous. To overcome this limitation and provide a more complete picture of brain activity it is important to combine ERP with fMRI techniques. From this, we may learn new information about the neural structures contributing to face-related ERP components. For example, we may find that decreased activity in fusiform and occipital face areas correlates with specific changes in repetition priming at the early perceptual N170 component.

Second, there are some limitations to using the classic approach when evaluating ERPs. By this I am referring to the evaluation of ERP peak components by focusing on the subset of electrodes that show maximal voltage change. A main benefit to using the classic approach is for comparability with previous studies. Moreover, particular ERP components have been linked to specific psychological processes and can be used to answer focused psychological questions. The focus of the thesis is on the N170 and N400 effects. The N250 has also been linked to identity processing but is task dependent. We were originally interested in face recognition processes that are task independent. For that reason we focused on the N170 responses and future work will more thoroughly explore N250 responses. In addition, there are many new ways to analyze ERP data (thanks to advancements in computing power) and these new tools may help to provide a better picture of whole brain activity. For example, the bootstrapping technique I used in Chapter 4 provided a better picture of whole brain activity around the time of the N170 peak component. Another way to assess whole brain activity is to measure brain signal variability (Costa, Goldberger & Peng, 2002). I plan to use this technique to further explore my data. Because of our rich experience with a familiar face, I expect that the associated brain signal may be more variable (maybe at certain ventral visual regions) than that associated with an unfamiliar face.

5.3 Conclusions

My thesis work has developed and tested hypotheses about the neural mechanisms that subtend familiar and unfamiliar face recognition. Unfamiliar face recognition is mediated by N170 processes and revealed by repetition effects. As an unfamiliar face becomes well known, its recognition processes become supported by a later semantic stage reflected by the N400 and such semantic processes seem to modulate early perceptual processes. This knowledge has advanced our understanding of face processing at cognitive and neural levels.

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