

Neural mechanisms underlying fast face category and identity processing

by

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B.Sc., University of Victoria, 2014

M.Sc., University of Victoria, 2017

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We acknowledge and respect the ləkʷəŋən peoples on whose traditional territory the university stands and the Songhees, Esquimalt and W̱SÁNEĆ peoples whose historical relationships with the land continue to this day.

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Abstract

Given the ecological importance of face recognition, it is not surprising that the visual system is capable of processing faces with remarkable efficiency. When presented with a face, information is rapidly extracted to detect and categorize it as a face, followed by face-specific information such as age, gender, and identity. According to cognitive and neural models, the processes underlying face recognition encompass a sequence of steps that begin with a perceptual or visual analysis followed by more image-invariant and identity-selective representations. Importantly, it is only familiar faces for which we have acquired long-term face memories that reach the final stages of identity processing to permit robust, image-invariant behavioural recognition.

A key aspect of face processing is that it is fast and automatic. This can be said for both high-level categorization (i.e., detecting that a stimulus is a face) and for encoding at the identity-level. The purpose of these experiments was to use novel electrophysiological and psychophysical techniques to characterize these fast and automatic categorization processes. Experiment 1 and 2 used an implicit visual discrimination paradigm (fast periodic visual stimulation; FPVS) combined with electroencephalography (EEG) to isolate identity-specific neural responses to a personally familiar face, the own-face, and an unfamiliar stranger face. Experiment 1 showed that identity-specific responses recorded over the occipito-temporal region were stronger for a personally familiar face compared to the unfamiliar control identity, while the response to the own-face was even greater than to a personally familiar friend. In Experiment 2, identity-specific responses for a given identity were measured in participants both before and after real-world familiarization. As expected, the results showed a significant increase in the identity-specific response once participants became personally familiar with the test identities. In Experiment 3, we used saccadic eye movements to estimate the lower bounds of the speed of face categorization, and in particular to investigate the question of whether this categorization occurs during early feedforward processing. The results support the view that information needed to detect and selectively respond to face stimuli happens during the earliest visual processing. Collectively, these studies provide additional insight on the mechanisms underlying rapid and automatic face detection and face identity recognition.

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Chapter 1: General Introduction

Face processing is fast and efficient

Given the ecological importance of face recognition, it is not surprising that the visual system is capable of processing faces with remarkable efficiency. When presented with a face, information is rapidly extracted to detect and categorize it as a face, followed by face-specific information such as age, gender, and identity (Bentin et al., 1996; Dobs et al., 2019; Gobbini & Haxby, 2007; Haxby et al., 2000). Manual reaction times for face recognition have been observed to be as fast as 360-380 ms when recognising famous (Barragan-Jason et al., 2013; Besson et al., 2017) and personally familiar faces (Ramon et al., 2011). Saccadic choice tasks, where response times are based on how quickly a participant can fixate on a target identity, provide more precise estimates on the lower bounds for face recognition because they don't require the initiation and execution of a manual motor response (Crouzet et al., 2010; Kirchner & Thorpe, 2006). Using this approach, it has been found that faces can be detected in as little as 100 ms (Crouzet et al., 2010) and that, when presented with a familiar and unfamiliar face, a friend's face can be selected as quickly as 180 ms (Di Oleggio Castello & Gobbini, 2015). Given that it takes about 20-35 ms to generate an oculomotor response once a target is detected (Heeman et al., 2017; Schiller & Kendall, 2004), saccadic reaction times suggest that faces can be detected within 80 ms, while face identity can begin affecting behaviour within 145 ms. Indeed, recent work using multivariate pattern analysis has shown that familiar face identity is encoded incredibly fast, with neural signals carrying information about identity emerging as early as 100 ms after stimulus onset (Ambrus et al., 2019, 2021; Dobs et al., 2019).

According to cognitive and neural models, the processes underlying face recognition encompass a sequence of steps that begin with a perceptual or visual analysis followed by more image-invariant and identity-selective representations (Barragan-Jason et al., 2012, 2013; Besson et al., 2017; Bruce & Young, 1986; Burton, Bruce, et al., 1999; Young & Bruce, 2011). Inspired by neuropsychological findings, Bruce & Young's (1986) classic model indicated that there are a variety of face information "codes" at different levels of analysis; for example, prosopagnosic patients typically have intact category-level recognition for faces (i.e. being able to detect that a visual stimulus is a face) despite impairments in identity-level recognition (Bruyer et al., 1983; see also Busigny et al., 2010). Recently, Barragan-Jason and colleagues (Barragan-Jason et al., 2012, 2013; see also Besson et al., 2017) proposed a model of face processing based on Rosch's (1975) hierarchical model of object recognition, where levels of processing correspond to different levels of categorization and where the most specific, identity-level of categorization occurs at the final stage. This is

supported by the finding that reaction times become increasingly longer as the level of categorization becomes more specific: detecting a human face among animal faces requires at least 240 ms (Besson et al., 2017), detecting gender requires 280 ms (Barragan-Jason et al., 2012), and detecting a familiar identity among unfamiliar faces requires at least 350 ms (Barragan-Jason et al., 2013).

Neural models also support the view of a hierarchical processing pipeline for face recognition along the ventral visual stream, beginning with visual analysis in the primary visual cortex and involving areas up to the anterior temporal lobes for identity representation (Axelrod & Yovel, 2015; Duchaine & Yovel, 2015; Gobbini & Haxby, 2007; Haxby et al., 2000; Kovács, 2020; Kriegeskorte et al., 2007; Natu & O'Toole, 2011; Quiroga et al., 2005). And, consistent with the idea that different information is extracted along the hierarchy, recent magnetoencephalography (MEG) decoding work indicates that age and gender information is represented within 60-72 ms after image onset, followed by the emergence of a familiar identity representation by 91 ms (Dobs et al., 2019).

Finally, when considering a face processing hierarchy, face familiarity is critical because behavioural results show striking differences in the identification of familiar compared to unfamiliar faces (Bruce et al., 1999, 2001; Burton, Wilson, et al., 1999; Henderson et al., 2001; Jenkins et al., 2011; Kemp et al., 1997; Megreya & Mike Burton, 2007; White et al., 2014; Young & Burton, 2018). This has led to the view that identity processing for familiar, known faces is qualitatively different from identity processing for unfamiliar faces (Burton, 2013; R. A. Johnston & Edmonds, 2009; Megreya & Bindemann, 2018; Megreya & Burton, 2006; Young & Burton, 2018). In particular, identity processing of familiar faces is believed to be mediated by image-invariant face representations acquired through our perceptual and social experience with a particular individual (Burton et al., 2011; Ramon & Gobbini, 2018; Ritchie & Burton, 2017; Schwartz & Yovel, 2016, 2019) – a processing stage that is reached for familiar but not unfamiliar faces.

Face processing is automatic

As described above, early theoretical models of face recognition were heavily informed by clinical findings from prosopagnosic patients who had lost the ability to recognize familiar faces after brain trauma (Bruce & Young, 1986; Damasio et al., 1982; Ellis, 1986). Besides the finding that face detection is usually still intact (Bruyer et al., 1983; see also Busigny et al., 2010), evidence from skin conductance responses, EEG, and behavioural measures indicate that some patients retained the ability to recognize familiar faces at a covert level despite having no ability to overtly identify them (Bauer, 1984; De Haan et al., 1992; Tranel et al., 1995). This implicit recognition indicates that face recognition can proceed in the absence of conscious awareness. Consistent with dual-process theories

of automatic processing (Moors, 2016; Posner & Snyder, 1975; Shiffrin & Schneider, 1977), evidence from healthy adults also shows that face recognition can occur in the absence of attention or voluntary control (Fockert et al., 2001; Jenkins et al., 2002; P. Johnston et al., 2016; Lavie et al., 2003; Wiese et al., 2019, 2022; Yan et al., 2017; Young et al., 1986). Faces are therefore said to *automatically* activate internal representations (Dalski et al., 2021; Palermo & Rhodes, 2007; Young & Burton, 2018).

Automatic identity processing is best demonstrated in tasks where face identity is task-irrelevant. For example, famous faces presented as distractors alongside with task-relevant stimuli (e.g. printed names) can interfere with task performance when identity information is incongruent with the appropriate response (Fockert et al., 2001; Lavie et al., 2003; Young et al., 1986). This interference indicates that information from the face is automatically processed despite that participants are told to ignore the faces. More recently, Yan et al. (2017) found evidence for automatic identity processing by asking participants to make same/different judgements to sequentially presented face image pairs based on gender, race, expression or identity. Crucially, on half of the trials, the relevant dimension was given to participants before the images were presented (pre-cueing condition) and on the other half of the trials, the relevant dimension was given after the images were presented (post-cueing). For identity judgments, accuracy performance was superior in the pre-cueing than the post-cueing condition for unfamiliar faces, however, accuracy performance was equivalent in the pre- and post-cueing conditions for familiar faces. Thus, identity information appears to be processed even when task-relevance is unknown, but only when those faces activate a pre-existing face representation. Likewise, the neural responses believed to reflect the activation of those face representations are still observed when participants are instructed to actively conceal the recognition of a familiar face, consistent with the claim that identification processes are not under volitional control (Wiese et al., 2022).

A neural measure of implicit, automatic familiar face recognition

Over the past years, Rossion and colleagues (Jacques et al., 2016; Liu-Shuang et al., 2014; Rossion, 2014; Rossion et al., 2012, 2015; Zimmermann et al., 2019) have introduced a frequency-tagging approach for obtaining electrophysiological measures of implicit, automatic face processing. In an early application of this “fast periodic visual stimulation” (FPVS) technique to measure face categorization, Rossion et al. (2015) presented different face images as every 5th image within a 6 Hz stream of different non-face object images. During the visual stimulation sequence (which may be as short as 60 seconds), a black fixation cross presented over the image sequence flashed red at random intervals, and observers were asked to monitor and respond to each colour change.

When EEG data recorded during the visual stimulation is analyzed in the frequency domain, distinct responses are predicted to be observed at the base stimulation frequency of 6 Hz (and its harmonics) and the “oddball” frequency at which faces are presented (6 Hz / 5 images = 1.2 Hz and its harmonics). Experimental data confirmed this, with a 6 Hz response that was right lateralized in the occipitotemporal region, and a clear 1.2 Hz response that was right lateralized over more anterior occipitotemporal channels. Because the 1.2 Hz response can only be driven by the occurrence of face images at that same frequency, this oddball response provides a measure of the neural processes evoked each time the visual system categorizes the stimulus as a face. Given that images are presented only long enough for a single fixation (~166 ms per image at a 6 Hz frequency) and that the images themselves are task-irrelevant, the paradigm provides a measure of implicit and automatic processing.

A unique advantage of the FPVS technique is the ability to isolate responses elicited by a *specific* stimulus property while at the same time capturing responses that *generalize* across multiple images. In the face categorization task, any visual processing that is common across objects and faces will be evoked at the base 6 Hz frequency. General low-level processing is therefore not reflected in the 1.2 Hz oddball response (unless it is a low-level feature that is unique to faces). This allows the experimenter to isolate responses evoked by a specific stimulus property by presenting stimuli that possess the target property within a stream of images that share all features *except* the property of interest. And, because the oddball frequency reflects the periodic occurrence of stimuli with that target property, it indicates a response that generalizes over multiple stimuli rather than being image-specific.

Using this approach, experimenters have been able to characterize implicit and automatic face categorization (Jacques et al., 2016; Retter et al., 2020; Retter & Rossion, 2016; Rossion et al., 2015), word recognition (Lochy et al., 2015), object recognition (De Keyser et al., 2018; Jacques et al., 2016), subordinate-level object recognition (Hagen & Tanaka, 2019), semantic processing (Stothart et al., 2017; Volfart et al., 2021), the discrimination of individual faces (Dzhelyova et al., 2019; Liu-Shuang et al., 2014, 2016), holistic face processing (Boremanse et al., 2014), gender processing (Rekow et al., 2020), and facial expression recognition (Dzhelyova et al., 2019). Individual differences in automatic face discrimination have also been shown to correlate with scores on the Cambridge Face Memory Task (CFMT; Duchaine & Nakayama, 2006; Xu et al., 2017), thus establishing a link between individual variability in implicit face discrimination and overt face recognition performance. Most recently, identity-specific responses have been reported to demonstrate implicit and automatic familiar face recognition. This has been found for famous faces (Yan et al., 2020; Yan & Rossion, 2020; Zimmermann et al., 2019), and the work presented in

Chapter 2 and 3 extends these findings to personally familiar faces (Campbell et al., 2020) and personally familiarized faces (Campbell & Tanaka, 2021).

The test-retest reliability has been found to be high for both implicit face discrimination (Dzhelyova et al., 2019) and implicit face identification (Campbell & Tanaka, 2021). And, because image presentation is very brief, FPVS is useful for characterizing automatic face processing in individuals who might otherwise resort to alternative strategies, such as acquired prosopagnosics (Gao et al., 2018; Liu-Shuang et al., 2016) or individuals with autism spectrum disorder (Dwyer et al., 2018; Vettori et al., 2018, 2020).

Implicit, automatic face processing and eye movements

As described earlier, behavioural experiments have demonstrated the remarkable speed and efficiency with which humans process faces. Most of these have used a go/no-go categorization task (Barragan-Jason et al., 2013; Besson et al., 2017; Ramon et al., 2011; Rousselet et al., 2003; see also Thorpe et al., 1996) which requires observers to make a manual response when they detect the presence of a target among distractor images, such as an image of a human face among animal faces (Besson et al., 2017) or a familiar face among unfamiliar faces (Barragan-Jason et al., 2013; Besson et al., 2017; Ramon et al., 2011). Because these measures include both the time of visual processing and motor response, Kirchner and Thorpe (2006) proposed that oculomotor responses could provide a better estimate of the visual processing component because preparing a saccadic response takes only 20-35 ms (Heeman et al., 2017; Schiller & Kendall, 2004). Therefore, in saccadic choice tasks, two images are presented side-by-side and observers are asked to make a saccade as fast as possible to the side where the image from the target category appears (Crouzet et al., 2010; Guyonneau et al., 2006; Kirchner & Thorpe, 2006). Based on this approach, it was found that face categorization (detecting faces among object distractors) can occur within 100 ms (Crouzet et al., 2010) and that familiar face recognition (detecting personally familiar faces among unfamiliar distractors) can occur within 180 ms.

Interestingly, in both cases, the saccadic reaction times suggest that the preceding categorization process can be completed within 150 ms. The initial finding of face-selective eye-movements was especially meaningful because EEG responses differentiating target present and absent trials had been measured over the frontal cortex by 150 ms (Thorpe et al., 1996). The implication is that category information needed to trigger a saccadic movement must be extracted during the first feedforward pass of activation up the ventral visual pathway to prefrontal task circuits (Bullier, 2001; Lamme & Roelfsema, 2000; Ungerleider & Haxby, 1994). Critically, this feedforward stage is dominated by bottom-up processing (Bullier, 2001; Kreiman & Serre, 2020; Lamme, 2010), and is not sufficient for conscious perception, since visual awareness requires reentrant processing in the feedback

stage (Del Cul et al., 2007; Fahrenfort et al., 2007, 2017; Lamme, 2010; Lamme & Roelfsema, 2000). It therefore appears that selective eye movements during face detection and familiar face recognition are a result of early, automatic processing.

Overview of Research

The goal of the first two experiments (Chapter 2 and 3) was to examine processes related to the implicit and automatic face recognition of personally familiar faces using a frequency-tagging approach. Personally familiar faces were selected to examine identity representations that we acquire in the real-world for identities with whom we have extensive perceptual and semantic experience and that are socially-relevant. In the third experiment (Chapter 4), we tested the limits of automatic eye movements during a face detection task. In a novel saccadic choice task, target and distractor images were briefly presented followed by visual masking images to disrupt feedback processing, thereby suppressing conscious perception of the test images. The goal of this study was to determine whether eye movements to faces are elicited even in the absence of conscious experience, thus providing a strong test of implicit, automatic face detection.

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Chapter 2: Examining the neural correlates of implicit recognition of personally familiar faces

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Abstract

Previous studies have focused on the modulatory effects of face familiarity on different components of an event-related potential (ERP), but there is controversy in the literature regarding the precise component that reflects the process of identity recognition. This may be partly explained by limits to this waveform analysis approach, as waveforms elicited by the presentation of a face are likely to reflect a variety of different cognitive processes that overlap in time. Using fast periodic visual stimulation and EEG (FPVS-EEG), we directly measured the electrophysiological response reflecting identity-specific recognition after isolating it from responses attributable to low-level visual processing and face-selective processes that are not identity-specific. The observed response therefore provides a robust and objective measure of the recognition of a personally familiar face generated bilaterally in the occipito-temporal region. We tested the magnitude of this identity-specific response to three categories of familiarity: the own-face (high familiarity), a friend's face (moderate familiarity), and a stranger's face (no familiarity). We found the largest response to the participant's own-face, followed by an intermediate response to a highly personally familiar face, and the smallest response to an unfamiliar face. An additional response was observed over the posterior cortical midline for familiar faces only, consistent with theories that familiar identity recognition also triggers post-perceptual semantic processing.

A face can be categorized at multiple levels of abstraction such as gender, race, and age. However, the critical level in everyday face recognition is the identity level where the face is individuated as a specific identity. According to models of face recognition, face recognition first requires a structural representation of the visual input to be matched to identity-specific, image-invariant perceptual representations in long-term memory (originally termed a “face-recognition unit”, or FRU), which subsequently leads to the activation of even more abstract representations storing identity information, such as name and biographical information (Bruce & Young, 1986; Burton, Bruce & Hancock, 1999; Burton, Jenkins, & Schweinberger, 2011; Haxby, Hoffman, & Gobbini, 2000). The identity’s image-invariant representation is an important mediating mechanism in recognition because faces undergo constant change due to expression, head movement, and development. Past experience with specific faces demonstrate our reliance on identity-specific perceptual representations in face recognition: familiar faces can be recognized over different and even degraded images, while even small image changes can impair recognition of unfamiliar faces (e.g., Jenkins, White, Van Montfort, & Burton, 2011; Burton, Wilson, Cowan, & Bruce, 1999; Hancock, Bruce, & Burton, 2000; Watier & Collins, 2009; Ramon, Vizioli, Liu-Shuang, & Rossion, 2015).

Yet, despite its critical role in face recognition and large behavioural effects, a reliable neural marker corresponding to the activation of identity-specific representations has not been identified. As temporal resolution of EEG is required to study the neural dynamics of face recognition, previous studies have focused on the modulatory effects of familiarity on different event-related potential (ERP) components elicited by familiar and unfamiliar faces. Recently, a late, occipitotemporal component peaking at 400ms and lasting until 600ms post-stimulus has been shown to reliably differentiate between faces of varying familiarity (a “sustained familiarity effect” or “SFE”, Wiese et al., 2018). However, as speeded recognition tasks have found that familiar faces can be identified with response times as fast as 260 ms (Besson et al., 2017; see also Barragan-Jason, Cauchoix, & Barbeau, 2015; Ramon, Caharel, & Rossion, 2011), the perceptual representations that trigger these behavioural responses are likely to be accessed at a much earlier latency. These later components are therefore not likely to reflect the stage at which a robust face representation is activated.

A component that appears more closely related to memory processes is the N250. The amplitude of this ventral temporal negativity peaks with a latency of 230-330 ms and is enhanced to repeated presentations of face images (Begleiter, Porjesz, & Wang, 1995; Schweinberger, Pfütze, & Sommer, 1995; Pfütze, Sommer, & Schweinberger, 2002; Schweinberger, Huddy, & Burton, 2004; Neumann & Schweinberger, 2008; Neumann, Mohamed, & Schweinberger, 2011) and identities (Schweinberger, Pickering, Jentsch, Burton, & Kaufmann, 2002; Bindemann, Burton, Leuthold, & Schweinberger, 2008). Its

relation to perceptual learning is also shown in its sensitivity to newly learned faces (Andrews, Burton, Schweinberger, & Wiese, 2017; Kaufmann, Schweinberger, & Burton, 2008; Pierce et al., 2011; Tanaka, Curran, Porterfield, & Collins, 2006; Joyce & Kutas, 2005) and newly learned bird species (Scott, Tanaka, Sheinberg, & Curran, 2001) that elicit greater negativity at the N250. The N250 has commonly been interpreted to reflect the transient activation of individual face representations elicited by repeated exposure and learning (i.e., the activation of an FRU; c.f. Pfütze et al., 2002; Schweinberger & Burton, 2003; Pierce et al., 2011; Schweinberger & Neumann, 2016); however, it has also been said to more specifically reflect the facilitated access to post-perceptual representations (i.e., the activation of a PIN) due to strengthened input connection from the perceptual face representation rather than a change or activation of the perceptual representation itself (Schweinberger et al., 2002).

At the same time, there is now a large body of research suggesting that identity-sensitive perceptual representations are accessed before 250 ms post-stimulus. The N170 component peaks between 140-200ms in occipitotemporal regions and is the earliest component to distinguish between faces and non-face objects (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Rossion & Jacques, 2011). Although early studies found no difference in the N170 elicited by famous and non-famous faces (Bentin & Deouell, 2000; Eimer, 2000), a large proportion of studies support the view that this component is sensitive to face familiarity. First, compared to unfamiliar faces, famous faces often do not significantly alter the N170 elicited during passive viewing (Andrews et al., 2017; Gosling & Eimer, 2011; Anaki, Zion-Golumbic, & Bentin, 2007; Henson et al., 2003; Pfütze et al., 2002; Bentin & Deouell, 2000; Eimer, 2000; but see Jemel, Schuller, & Goffaux, 2010), but for a personally familiar face, the N170 is often enhanced (Caharel, Poiroux, Bernard, Thibault, Lalonde, & Rebaï, 2002; Caharel, Courtay, Bernard, Lalonde, & Rebaï, 2005; Herzmann, Schweinberger, Sommer, Jentsch, 2004; Wild-Wall, Dimigen, & Sommer, 2008; Keyes, Brady, Reilly, & Foxe, 2010; Caharel, Ramon, & Rossion, 2014; but see Tanaka et al., 2006; Pierce et al., 2011). This is consistent with the view that personally familiar faces have more robust representations (Tong & Nakayama, 1996; Carbon, 2008) and more efficient global processing (Ramon & Van Belle, 2016; Ramon et al., 2015; Ramon, 2015; Ellis, Shepherd, & Davies, 1979; Caharel, Fiori, Bernard, Lalonde, & Rebaï, 2006). Second, identity adaptation paradigms have demonstrated that the amplitude of the N170 is modulated by face identity (Jacques & Rossion, 2006; Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009; Caharel, Jacques, d'Arripe, Ramon, & Rossion, 2011; Johnston, Overall, Kaufman, Robinson, & Andrew, 2016) and that familiarity may further influence these modulatory effects (Caharel et al., 2011). Similarly, it has been found that the N170 is sensitive to identity priming of familiar but not unfamiliar faces (Jemel, Pisani, Calabria, Crommelinck, & Bruyer, 2003). Finally,

whole brain analysis of EEG associated with fast and accurate familiarity judgments has shown that face familiarity can be reliably decoded as early as 145 ms post stimulus (Barragan-Jason et al., 2015).

Although the effects of familiarity on the N170 are not consistently observed across all stimulus types and paradigms, collectively, the above findings indicate that identity recognition occurs fast enough to exert modulatory effects within 140-200ms post-stimulus. Consequently, the N250 might not reflect the identity-specific representation and may instead reflect additional learning or consolidation processes. And yet, the N170 presents the problem of not providing a reliable index of identity-processing. The difficulty in pinning down the precise stage of identity-processing may relate to limitations of the ERP approach of comparing average waveforms. First, the waveforms elicited by the presentation of face are likely to reflect a variety of different cognitive processes that may overlap in time. For example, in the 200-300ms post-stimulus time window, it has been suggested that the N250 enhancement to repeated faces (i.e., N250r) and the N250 enhancement to familiar or newly learned faces may reflect different learning mechanisms (c.f. Schweinberger & Neumann, 2016; Kaufmann et al., 2008), or that this negativity reflects a combination of both image-dependent and image-independent processes (Schweinberger et al., 2002). Likewise, the N170 may reflect multiple subprocesses in the occipito-temporal area given that it is sensitive to a range of cognitive factors and shows different response properties to different object categories (Rossion, Joyce, Cottrell, & Tarr, 2003). The discrepancy across studies could therefore be partly due to the signal related to the activation of an identity-specific representation being obscured by other visual and face processing signals in the waveform. Second, many image presentations are needed to increase signal-to-noise ratio in the average ERP waveform, but the components of interest are also sensitive to image repetition (N170: Caharel et al., 2009; Caharel et al., 2014; Kaufmann et al., 2009; N250: Kaufmann et al., 2009; SFE: Wiese et al., 2018). For example, Caharel et al. (2014) found that familiar faces showed an enhanced N170 compared to unfamiliar faces during the first block of testing (2 presentations of each image), but an increase in the N170 to unfamiliar faces in subsequent blocks eliminated this familiarity effect. These modulatory effects might not even be entirely attributable to learning or repetition, since Kauffman et al. (2008) also observed increased N170 and N250 amplitudes to unfamiliar faces over the duration of testing even though each identity was shown only once. This suggests that both ERP components are also likely to reflect general processes engaged by simply performing a face recognition task and highlights the limits of isolating specific processes using this approach.

The aim of the current study was to use frequency-tagging (via fast periodic visual stimulation, or FPVS) to isolate the neurophysiological response which reflects recognition of a specific identity, possibly by means of the activation of an identity-specific perceptual

representation in long-term memory. Through neural entrainment, frequency-tagging paradigms can be used to measure specific cognitive processes as neural responses to the stimulus of interest are evoked and quantifiable at the exact frequency of presentation (a steady-state visually-evoked potential; Rossion & Boremanse, 2011; Gentile & Rossion, 2014; for review, see Norcia, Appelbaum, Ales, Cottureau, & Rossion, 2015; Rossion, 2014). The distinct advantage is that signals from processes that overlap in the domain time can be isolated from each other using a dual-frequency paradigm (e.g., Regan & Cartwright, 1970; Tononi, Srinivasan, Russell, & Edelman, 1998; Liu-Shuang, Norcia, & Rossion, 2014; Rossion, Torfs, Jacques, & Liu-Shuang, 2015). This is accomplished by periodically presenting the stimuli of interest within a rapidly presented sequence of other base images. Neural responses associated with processes elicited by both the stimuli of interest and the base images to be entrained and measurable at the general stimulation frequency ($F1$), while the neural responses that are evoked exclusively by the stimuli of interest are only observed at the second, slower frequency at which they occur within the sequence ($F2$). For example, when presented in isolation, a single face image will generate several neural responses that overlap in time and can make it difficult to cleanly separate signals related to low- and mid-level visual processing from the high-level visual categorization processes. However, when inserted within a stream of object images, the responses associated with low-level visual processing and mid-level object perception of the face image are captured at the general stimulation frequency because they are also evoked by the object images, but the responses that are uniquely elicited by the faces are observed only at the face-specific frequency (Rossion et al., 2015). This effectively partials out the low- and mid-level processing signals from the high-level categorization signals.

Compared to an ERP waveform analysis, FPVS avoids the assumption that the only difference between the signal of the two different stimuli is the process of interest and instead seeks to decompose the response signal of a stimulus eliciting the process of interest. It also has the additional benefits of having both a higher signal-to-noise ratio (since noise does not occur periodically, it does not contaminate the periodic signal-of-interest in the predicted frequency bin) and, unlike the practice and expectation effects commonly observed in ERPs (Huang et al., 2017), FPVS responses have been shown to be immune to effects of expectation and temporal predictability (Quek & Rossion, 2017) despite the temporal repetition of the stimulation. FPVS may therefore be more sensitive to signals that are weak relative to strong general visual response signals.

Based on this logic, we aimed to isolate identity recognition responses by periodically presenting images of a particular identity within base images of different unfamiliar faces and investigate the effect of familiarity on this identity-specific response. Recently, Zimmerman and colleagues (2019) used a similar approach and observed clear identity-specific

responses (individual face recognition, or IFR) to famous faces interleaved with unfamiliar faces. They found that, averaged across participants, the celebrity rated as being the most familiar elicited the strongest identity-specific response, and the celebrity rated the least familiar elicited the weakest response. However, in a paradigm where the degree of familiarity for each identity is roughly equal across participants, comparing different levels of familiarity rests on response differences between one single most-familiar face and another single least-familiar face. Response differences could therefore reflect difference in familiarity as well as difference on other dimensions, such as distinctiveness or attractiveness (e.g., head size).

The current research extends these findings and directly compares the effect of familiarity on identity-specific responses by equating the stimuli (face identities) in each of three categories of personal familiarity: the own-face, a personally familiar friend, and an unfamiliar stranger. Exposure to one's own face is usually continuous and consistent; one study found that people spend an average of 41 minutes per day looking at themselves (Veale & Riley, 2001). By contrast, a visual survey of daily face exposure found that participants spent 12 minutes of each waking hour looking at other people's faces (Oruc, Shafai, Murthy, Lages, & Ton, 2019). Assuming a 16-hour day, this would amount to 192 minutes per day looking at other people's faces. The time spent looking at one's own face could therefore account for as much as 18% of the total "face time" (233 minutes). This exposure has been linked to the processing advantage of one's own-face: The own-face is often recognized faster than less familiar faces, such as friends (Sugiura et al., 2008; Keyes & Brady, 2010; Li, 2011), but not when compared to the recognition of highly familiar others such as parents or romantic partners (Kircher et al., 2001; Wang, Kitayama, & Han, 2011; Wang & Zheng, 2015), and a meta-analysis indicated that the effect size of the own-face advantage decreases as the own-face is compared to unfamiliar, famous familiar, and personally familiar faces (Bortolon & Raffard, 2018). These findings suggest that own-face recognition is supported by highly robust representations that are attributable to the extensive visual experience acquired for the own-face.

For the current study, participants were recruited in pairs. In the own-face condition, each observer was presented with their own face; in the friend-face condition, each observer was presented with the face of the friend; and in the unfamiliar stranger condition, each observer was presented with the face of another participant who was a stranger to them. Therefore, across the full experiment, the face of each participant was used in each familiarity condition. Because, at the group level, the same test identities were used in each condition, we controlled for any stimulus differences between familiarity conditions arising from test identities, and any response differences observed between conditions could be attributed to the level of observer familiarity with the test stimulus.

Twelve distinct images were used for each identity to ensure that the response generalized across different images of the face. Because personal familiarity is usually based on in-person interactions, we photographed each identity as they engaged in a social interaction with the experimenter to obtain images that capture the person's normal range of facial expression. Since this dimension of facial variability might be very idiosyncratic, our experience with a person's facial gestures may play an important role in how individual faces are represented in memory (Redfern & Benton, 2019). Although they do not capture the appearance variability that arises from changes in external features, age, and ambient conditions, they provide a different kind of expression variability than is commonly captured in normal photos and selfies. Most importantly, they may reflect a better likeness of the identity as they appear during real-life social interactions.

If representations based on greater visual experience generate a larger neural response, we predicted that the response magnitude to the own-face should be the greatest, followed by the response to the friend-face, and the response to the unfamiliar face should be the lowest. Alternatively, it is possible that identity-specific neural areas recruited during identification do not actually produce graded responses for more familiar faces. In this case, the identity-specific response observed for the friend-face and the own-face should not differ.

Method

Participants

Twelve participants (mean age = 21.3 ± 2.4 years, all Caucasian females) were recruited through advertisement in the University of Victoria's online psychology participant system and through friends of the experimenters. The experiment was described as a study on best friends, and candidates were requested to apply along with a good friend. Inclusion criteria were that the pairs were friends for a minimum of 6 months with at least weekly face-to-face contact. The sample consisted of six pairs of friends who reported having an average friendship of 2.6 years ($SD = 2.1$, range = 0.75-7) and, at the time of testing, interacted an average of 2.66 times per week ($SD = 1.8$, range = 0.5-6). Participants reported no brain injury or diagnosed learning disability. The experiment and consenting procedures were approved by the human research ethics committee of the University of Victoria.

Stimuli

Prior to the experimental test session, an experimenter conducted brief interviews with each participant individually that were video-recorded using a Canon EOS Rebel DSLR camera mounted on a tripod. The camera was repositioned throughout the interview to capture video of the seated participant from the front, the right angle, and the left angles. All

interviewees sat on the same chair in the same room during video recording, so that the background and lighting conditions did not differ across images. Still frame images (6 frontal, 3/4 right, 3/4 left) were randomly selected from the video footage to serve as the image set for each identity (12 images per identity). Using Adobe Lightroom, the images were cropped so that the face occupied roughly 80% of the image with the nose just below center and then resized to 350×350 pixels. This procedure was applied to the 6 identities who were not experimental participants in the study. The 72 images that were created from these 6 identities served as the image set used for the base stimuli described below (the unfamiliar base faces).

Procedure

After electrode cap placement, participants were seated at a table in front of a keyboard and LCD monitor. Visual stimulation consisted of four 70 s image sequences for each condition (own, friend, unfamiliar) and was presented using a custom MATLAB script (SinStim; e.g., Jacques et al., 2016) while the EEG was recorded. Breaks of about one minute were provided between each stimulation sequence, and the condition order was pseudorandomized for each participant. The total testing time was approximately 25 minutes.

Within each sequence, stimuli were presented at a constant rate of 6 Hz ($F1$ = the visual-stimulation frequency) via sinusoidal contrast modulation from 0%-100%. The image sequence was structured so that, depending on the condition, every 7th image was the participant's own face (own), their friend's face (friend), or the unfamiliar identity (stranger), and was drawn randomly from the own/friend/stranger set of images. All other images were randomly selected from the set of unfamiliar base faces; identity therefore varied at every image cycle. By contrast, the face of the own/friend/stranger appeared with a periodicity of $F1/7 \approx 0.86$ Hz ($F2$ = the identity-specific frequency).

The presentation of each stimulation sequence was as follows: 1) 2-5 s black fixation cross appeared on a gray background; 2) 2 s image sequence fade-in; 3) 63 s image sequence presentation; 4) 5 s image sequence fade-out; 5) 2 s black fixation cross on gray background (Figure 1). The fixation cross remained on the screen for the entire duration of the stimulation sequence and was positioned to appear over the center of the image. Across all face images, this roughly corresponded to the area just above the nose. Displayed on a monitor from a distance of 0.7 m, the stimuli subtended an angle of approximately 7 degrees of visual angle.

To maintain a steady point of fixation and attention during visual stimulation, participants were asked to engage in a fixation color change detection task during each sequence presentation (e.g., Liu-Shuang et al., 2014). At eight random time points in the

sequence, the color of the fixation cross changed briefly (200 ms) to red. Participants were told that face images would be presented rapidly on the screen with a black fixation cross in the middle of the screen and that their primary task was to press the spacebar on the computer keyboard every time they detected the color of the cross changed from black to red.

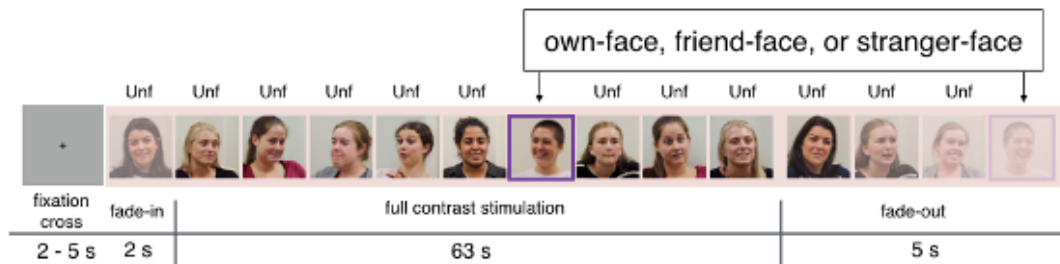


Figure 1. Visual stimulation sequence. The visual stimulation sequences consisted of face images contrast modulated at a rate of 6 Hz (each image cycle had a duration of ~167ms). Depending on the condition, every 7th image presented was either the participant's own face, the face of their friend, or the face of an unfamiliar stranger (another subject who was unfamiliar to the participant). The own-, friend-, or stranger-face therefore appeared at a rate of $6 \text{ Hz}/7 = 0.86 \text{ Hz}$. All other images were selected randomly from a set of faces that were unfamiliar to all participants. During visual stimulation, participants engaged in a fixation cross colour change detection task (not that required them to press the spacebar every time that a fixation cross superimposed in the middle of the screen changed from black to red. Fixation cross changes occurred 8 times at random intervals. Face images are shown here with permission from the participants/models.

EEG Acquisition

During each stimulation sequence, the electroencephalogram (EEG) was recorded using a montage of 42 electrode sites in accordance to the extended international 10-20 system (Jasper, 1958). Signals were acquired using Ag/AgCl ring electrodes mounted in a nylon electrode cap with an abrasive, conductive gel (EASYCAP GmbH, Herrsching-Breitbrunn, Germany). Signals were amplified by low-noise electrode differential amplifiers with a frequency response of DC 0.017–67.5 Hz (90 dB–octave roll off) and digitized at a rate of 250 samples per second. Digitized signals were recorded to disk using Brain Vision Recorder Software (Brainproducts, Munich, Germany). Impedances were kept below 20 k Ω . The EEG was recorded using the average reference.

EEG Analysis

Preprocessing

All EEG processing steps were carried out using the free software Letswave 6 (<https://github.com/NOCIONS/letswave6>) running on MATLAB (MathWorks). A Butterworth filter with cut-off values of 0.1-120 Hz and a slope of 24 dB/octet was applied to the data. Across participants, the continuously recorded EEG data for each stimulation sequence was segmented to include 2 seconds before and after the stimulation sequence. Channels which were artifact-prone across multiple trials (less than 5% of channels on average) were re-estimated using linear interpolation of the two nearest channels. Independent component analysis (ICA) was applied to the data for each stimulation sequence and a single component accounting for blink artifacts was removed. All EEG segments were re-referenced to a common average reference.

Frequency-domain analysis

The EEG for each sequence was re-segmented, beginning from sequence onset until approximately 64 s (before stimulus fade-out), to contain an integer number of 0.86 Hz cycles (55 cycles, 16035 time bins in total \approx 64 s). For every participant, the four segmented sequences within the own, friend, unfamiliar face conditions were averaged in the time-domain to reduce EEG activity that is not phase-locked to the stimulus. A Fast Fourier Transform (FFT) was then applied to the averaged segments to represent the data of each channel as a normalized amplitude spectrum (μ V) in the frequency domain with a frequency resolution of 0.0156 Hz (i.e., 1/64.14 s).

Harmonic selection

As responses are expected to be observed across multiple harmonics of the stimulation frequencies (see Rossion et al., 2015), we determined how many harmonics to include for the response analysis of each stimulation frequency (i.e., F1, F2) by pooling all channels and selecting harmonics based on their z-scores from the averaged spectra. The

procedure was as follows: 1) Within each condition, individual amplitude spectra were averaged across participants and all channels; 2) For responses at all frequencies of interest (i.e., $F1 = 6$ Hz, $F2 = 0.86$ Hz, and their harmonics), z-scores were computed as the difference between the amplitude at the frequency of interest and the mean amplitude of the local baseline divided by the standard deviation of local baseline (local baseline = 20 surrounding frequency bins, excluding the immediately adjacent bins and the bins containing the minimum and maximum response); 3) Using the z-scores as a stopping rule, the range of harmonics to include for each stimulation frequency was constrained to the highest number of consecutively significant harmonics observed in any one condition (e.g., $1F2$, $2F2$, $3F2$, etc., where each $z \geq 3.1$, $p < .001$, 1-tailed, i.e., signal > noise). For visual-stimulation responses, 8 significant harmonics were selected (up to $8F1 = 48$ Hz); for identity-specific responses, 10 significant harmonics were selected (up to $11F2 = 9.43$ Hz, but excluding $7F2 = 6.00$ Hz because it is confounded with the 6 Hz visual-stimulation frequency).

Baseline correction

To visualize the signal-to-noise ratio (SNR) across the frequency spectrum, a baseline-division correction was applied to the amplitude spectra using the same local baseline definition used for the z-score (Figure 2). For response quantification and scalp topographies, a baseline-subtraction correction was applied instead (Figure 3 and Figure 4).

Region-of-interest analysis

For each stimulation frequency, responses were quantified as the summed amplitude of the relevant amplitudes (the summed-harmonic responses) and the three channels with the maximum summed-harmonic response were used to define a region-of-interest (ROI). At the visual-stimulation frequency ($F1$), the channels of maximum response were P8, Oz, and PO8, and, with the addition of the left hemisphere homologues PO7 and P7, defined an occipital region. At the identity-specific frequency ($F2$), the channels of maximum response were P10, P8, and TP10, and, with the addition of the left hemisphere homologues P9, P7, and TP9, defined an occipito-temporal region. Then, for each condition, the visual-stimulation and identity-specific responses were quantified as the summed-harmonic response averaged across ROI channels. Repeated-measures ANOVA were conducted on baseline-corrected amplitudes for both the visual-stimulation and the identity-specific responses with condition (own, friend, stranger) as a within-subject factor. Mauchly's test for sphericity was performed and a Greenhouse-Geisser correction was applied whenever sphericity was violated. Pairwise comparisons were carried out using paired-sample t-tests with a Bonferroni-Holm correction for multiple comparisons.

The lateralization of the identity-specific response was defined based on the magnitude of the left and right channels of the occipito-temporal ROI and expressed as the lateralization index: $(R-L)/(R+L)$.

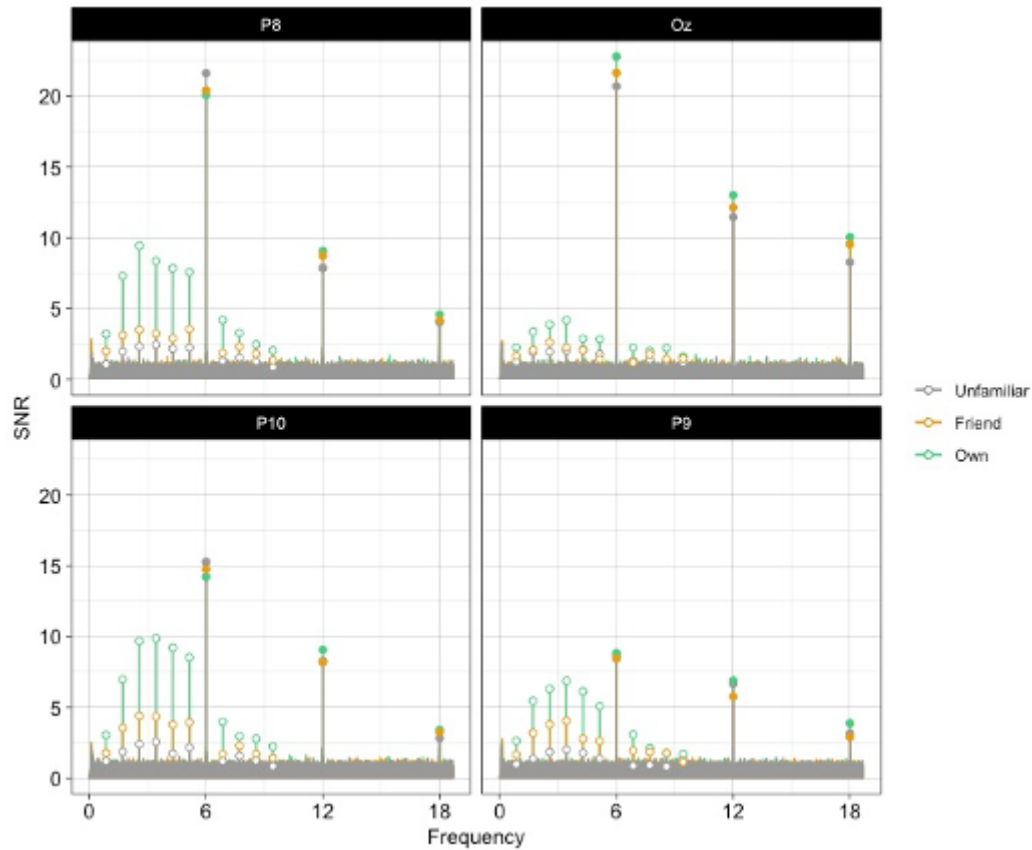


Figure 2. Signal-to-noise ratio within the frequency spectrum. The EEG amplitude spectra averaged across participants and conditions and represented as the signal-to-noise ratio at the channels of maximum response. At the visual stimulation frequency (6 Hz and its harmonics), SNR was highest in channel P8 and Oz. At the identity-specific frequency (0.86 Hz and its harmonics), SNR was highest in channel P10 (the homologous channel in the left hemisphere, P9, is also shown).

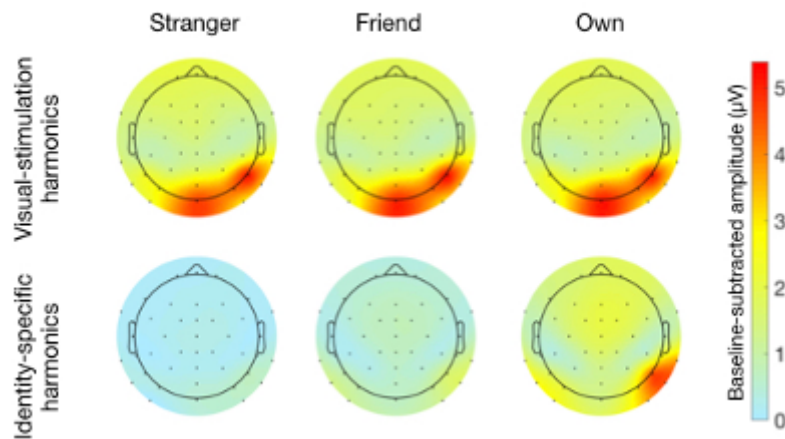


Figure 3. Scalp topographies of the group-averaged visual-stimulation and identity-specific response in each condition. Summed-harmonic response (baseline-subtracted amplitudes) at the identity-specific and visual stimulation frequency, averaged across all participants.

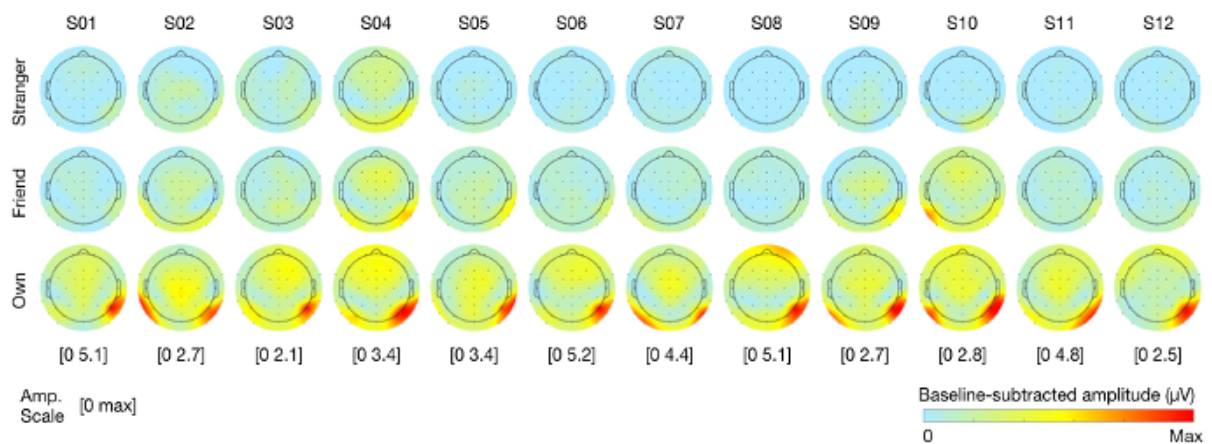


Figure 4. Scalp topographies of the identity-specific response for each participant and condition. Scalp distribution of each participant's identity-specific response to a stranger (top row), friend (middle row), and their own face (bottom row). The amplitude scale used for each participant is reported at the bottom of each subject's column.

Harmonic analysis

To examine the neural dynamics of the identity-specific response, we grand-averaged the individual baseline-subtracted spectra for each channel and computed their z-scores to compare the topography of significant neural responses of each harmonic. This was done for each condition separately.

Results

Fixation cross task

Response times (RT) were calculated relative to the onset of fixation cross color change and for responses recorded within 1500ms of the color change. Analyses were based on correct RTs. Accuracy for the color change detection task was close to ceiling in all three conditions (own: $M = 97.0\%$, $SD = 6.7\%$; friend: $M = 95.4\%$, $SD = 15.1\%$; stranger: $M = 94.9\%$, $SD = 10.3\%$; $F < 1$). There was no difference in reaction times across conditions (own: $M = 450$ ms, $SD = 63$ ms; friend: $M = 446$ ms, $SD = 92$ ms; stranger: $M = 448$ ms, $SD = 79$ ms; $F < 1$).

Frequency domain

The signal-to-noise ratio (SNR) of electrophysiological responses during FPVS are shown in Figure 2. Clear responses were visible at the visual-stimulation frequency ($1F1 = 6$ Hz) up to the 8th significant harmonic ($8F1 = 48$ Hz). Responses at these frequencies reflect the onset and offset of each visual stimulus in the sequence and therefore the processing that is common to all stimuli. These include responses elicited by low-level properties, such as color and spatial frequency, but also high-level properties: as each stimulus is the onset of a face, each stimulus would elicit a face categorization response and, as each stimulus is the onset of an identity, each stimulus would elicit a face individuation response. Consistent with this, SNR at 6 Hz and its harmonics was maximal in the medial occipital region (Oz; average SNR of 7.04) as well as the occipito-temporal region (P8; average SNR of 5.38).

Responses at the identity-specific frequency ($1F2 = 0.86$ Hz) were significant up to the 11th significant harmonic ($11F2 = 9.43$ Hz; Figure 2). Responses at these frequencies are driven by the onset of either the own, friend, or stranger face. However, responses elicited by these face images that are common to responses elicited by unfamiliar face images should be captured at the common presentation rate of 6 Hz and its harmonics (the visual-stimulation frequency). The responses at the identity-specific frequency (and its harmonics) therefore reflect any processing that is unique to the identity of the face images, such as the activation of an identity-specific face representation. As predicted, the SNR at 0.86 Hz and its harmonics was maximal in the occipito-temporal region (P10; average SNR of 3.50).

The scalp topography of the summed-harmonic responses averaged across participants for each condition and stimulation frequency are shown in Figure 3. Individual differences in the scalp distribution of the summed-harmonic identity-specific response are shown in Figure 4.

Identity-specific and visual-stimulation response analysis

For each stimulation frequency, we compared the summed-harmonic response across conditions in the regions-of-interest defined by the channels of maximum response. The identity condition had no effect on the magnitude of the visual-stimulation responses in the occipital region (P8/7, Oz, PO8/O7; own: $1.50 \pm 0.81 \mu\text{V}$; friend: $1.49 \pm 0.79 \mu\text{V}$; stranger: $1.48 \pm 0.74 \mu\text{V}$; $F < 1$). However, there was a main effect of identity on the magnitude of the identity-specific responses in the occipito-temporal region (P10/9, P8/7, TP10/9), $F(2, 22) = 86.12$, $p < .001$, $\eta^2 = 0.89$. Pairwise comparisons showed that the response to the friend-face ($0.94 \pm 0.50 \mu\text{V}$) was significantly greater than the response to the stranger-face ($0.31 \pm 0.32 \mu\text{V}$; $t(11) = 6.82$, $p = .001$), and the response to the own-face ($2.31 \pm 1.20 \mu\text{V}$) was significantly greater than both the friend, $t(11) = 8.54$, $p < .001$, and stranger, $t(11) = 10.18$, $p < .001$. In all participants, the magnitude of the identity-specific response in the occipito-temporal region was greater to the friend than the stranger, and the response to the own-face was greatest in magnitude (Figure 5).

The lateralization index of the identity-specific responses revealed that the occipito-temporal response was right lateralized in all three conditions (own: $M = 0.33$, $SD = 0.22$; friend: $M = 0.21$, $SD = 0.21$; stranger: $M = 0.42$, $SD = 0.40$) and was not significantly different across conditions, $F(2, 22) = 1.63$, $p = .22$ (Figure 6).

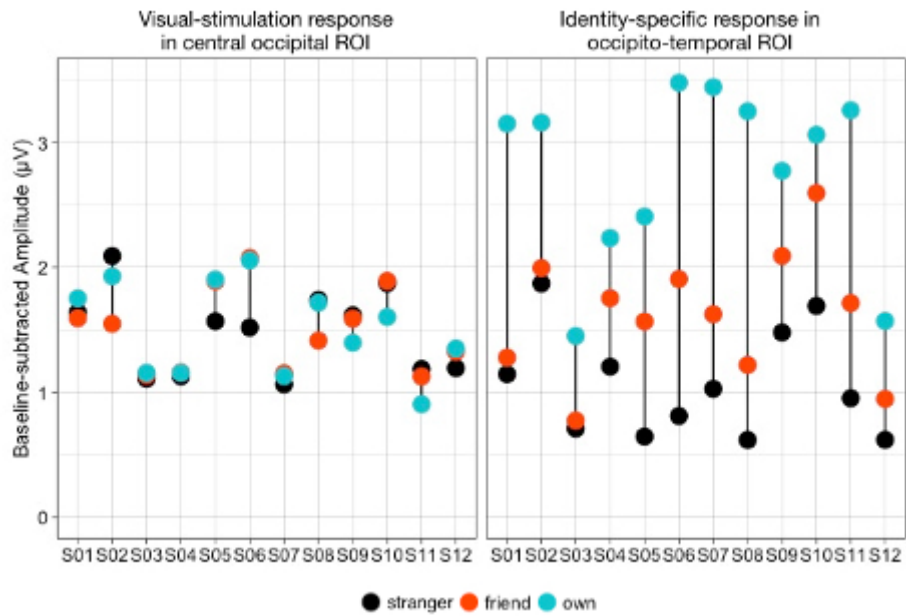


Figure 5. Summed-harmonic response for the visual-stimulation and identity-specific responses. Visual-stimulation and identity-specific responses for each condition and participant, quantified as the average summed-harmonic response of the channels of maximal response. For the visual-stimulation response, the channels P8, Oz, PO8, P7 and PO7 defined the occipital region of interest. For the identity-specific response, the channels P10, P8, TP10, P9, P7, and TP9 defined the occipito-temporal region of interest.

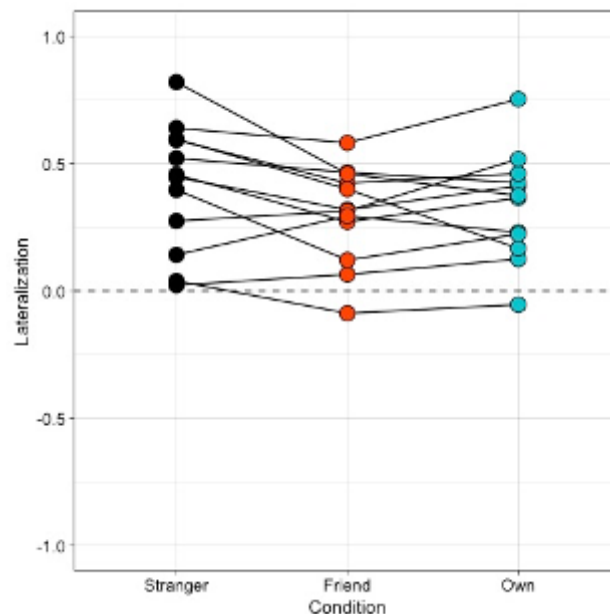


Figure 6. Lateralization indices for each participant and condition. The lateralization index for identity-specific responses in the occipito-temporal region. Expressed as $(R-L)/(R+L)$, based on magnitude of right and left hemisphere channel responses. Positive values indicate stronger right hemisphere response.

Harmonic analysis

At the first harmonic of the 6 Hz visual-stimulation frequency, the largest response was observed over the right occipito-temporal region. Higher harmonics (e.g., 12 Hz, 18 Hz, up to 48 Hz) were focused on the medial occipital channel Oz (Figure 7A). For all harmonics of the 0.86 Hz identity-specific frequency (0.86 Hz, 1.72 Hz, up to 9.43 Hz), the largest response was over the right occipito-temporal region (e.g., P10, P8, TP10). However, in the first harmonic (0.86 Hz), an additional response at the centro-parietal channels Pz and POz was observed in response to the own-face and friend-face, but not to the face of a stranger (Figure 7B). Importantly, this additional response is dissociable from the occipito-temporal response, since the occipito-temporal response increases in magnitude in subsequent harmonics while the centro-parietal response decreases (Figure 7B).

Individual responses at this first harmonic (0.86 Hz) were examined by calculating z-scores for each participant. A less conservative threshold of $z > 1.64$ ($p < .05$, one-tailed, signal > noise) was used for the participant-level as the 0.86 Hz response is located in a highly noisy area of the frequency spectrum. Significant responses were observed over the centro-parietal region (POz or Pz) in 8 of 12 participants for the friend condition and in 11 of 12 participants in the own-face condition (Figure 8). Pairwise comparison of the average amplitude of Pz and POz in the first harmonic (0.86 Hz) revealed a stronger response to the own-face ($0.23 \pm 0.15 \mu\text{V}$) compared to the friend-face ($0.08 \pm 0.12 \mu\text{V}$; $t(11) = 3.13$, $p = .01$).

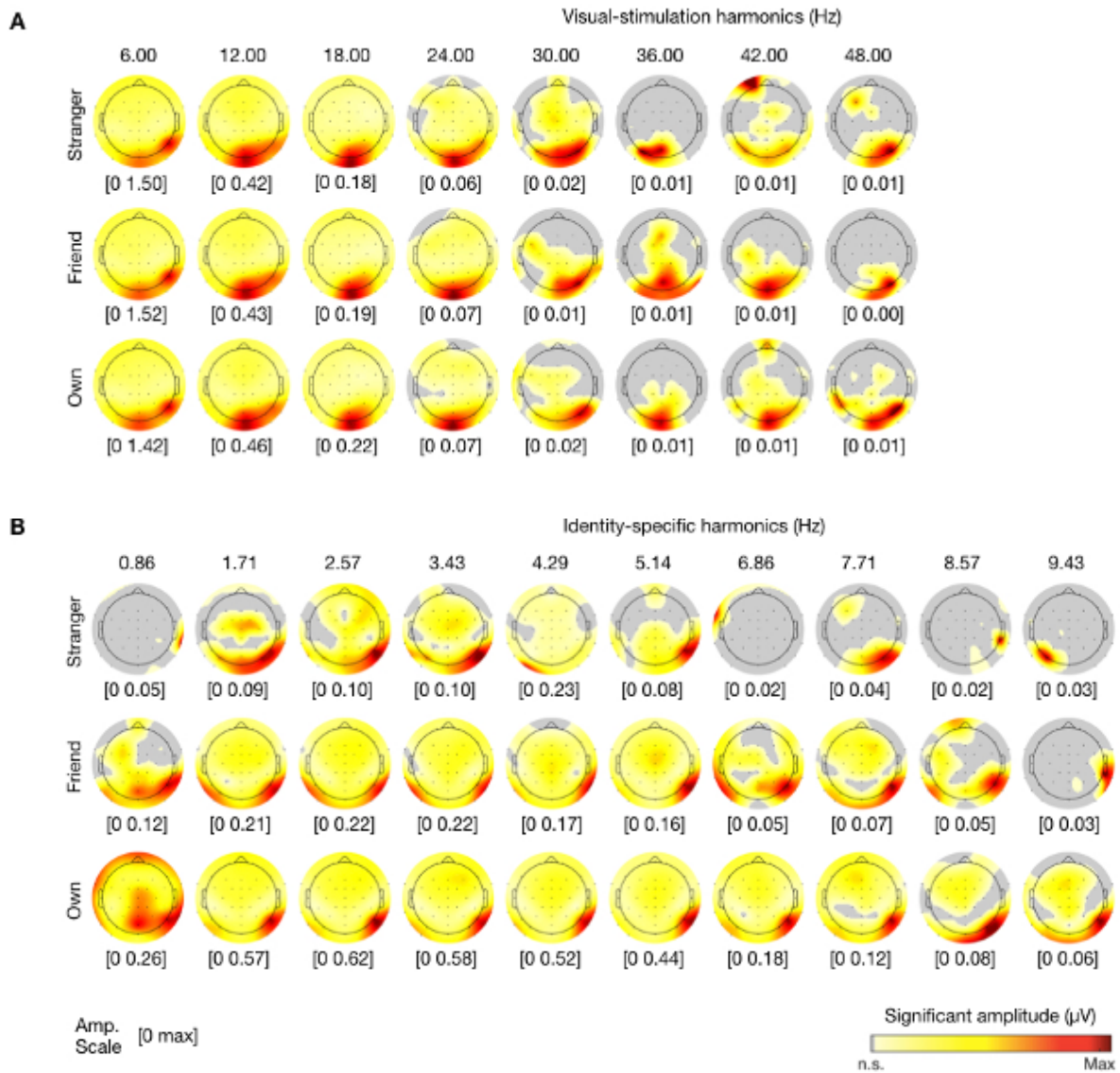


Figure 7. Scalp topographies of the significant harmonic responses. Scalp topography maps of significant grand-averaged EEG responses (baseline-subtracted) observed for each significant harmonic ($z > 3.1$, $p < .001$, 1-tailed) in each condition (own, friend, and stranger). The amplitude scale used for each harmonic is reported below each map. Gray indicates no significant response. A. Scalp topography of 8 significant visual-stimulation frequency harmonics. B. Scalp topography of 11 significant identity-specific frequency harmonics.

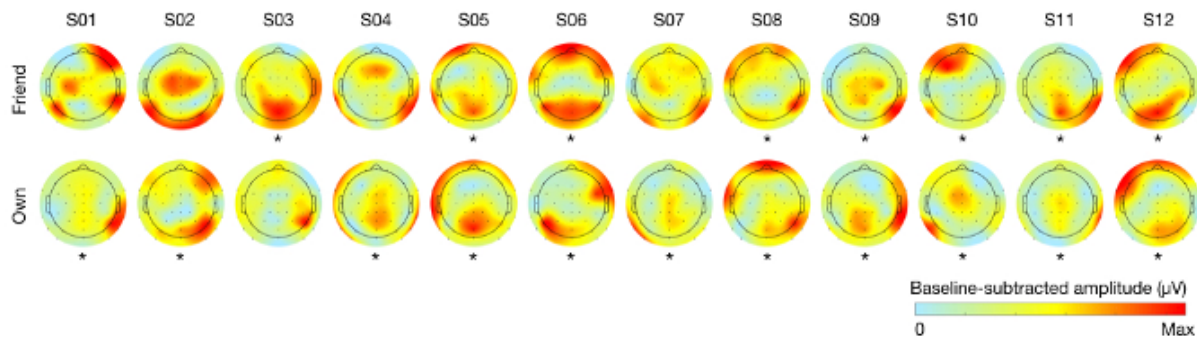


Figure 8. Scalp topographies of the first harmonic of 0.86 Hz identity-specific response. Subject scalp topography maps of baseline-corrected EEG responses observed at the first harmonic of the identity-specific frequency (0.86 Hz) in the friend- and own-face conditions. Subjects showing a significant response over the centro-parietal channels (POz or Pz, $z > 1.64$, $p < .05$, 1-tailed) are indicated by an asterisk.

Discussion

Using a fast periodic visual stimulation paradigm (e.g., Liu-Shuang et al., 2014; Rossion et al., 2015), we sought to measure the neurophysiological response signals related to image-invariant face identification. This was achieved by periodically presenting either the participant's own face, the face of their friend, or the face of a stranger within a sequence of unfamiliar face images. This presentation technique splits the neural response evoked by the identity of interest (own, friend, or stranger) into two separate response frequencies. Although these specific identities are presented at 0.86 Hz, the low-level visual and general face categorization responses evoked by these images are also evoked by the other unfamiliar face images in the stimulation sequences, and this leads these responses to entrain to and be observed at the 6 Hz visual stimulation frequency. The response that remains observable at the 0.86 Hz identity-specific frequency therefore reflects the isolated response of any population of neurons that are specifically responsive to the own, friend, or stranger face. Compared to previous ERP studies which have been limited to waveform-subtraction analysis to indirectly measure processes specific to familiar faces (e.g., Herzmann et al., 2004; Caharel et al., 2005; Sui, Zhu, & Han, 2006; Wild-Wall et al., 2008; Keyes et al., 2010; Caharel et al., 2014; Barragan-Jason et al., 2015; Andrews et al., 2017; Wiese et al., 2019; Alzueta et al., 2019), the fast periodic visual stimulation technique allows identity-specific processes to be measured directly because they are parsed from other identity-general processes and objectively because they are observed at the exact frequency predicted by the presentation frequency.

The 6 Hz response was maximal over medial-occipital and occipito-temporal regions. This is consistent with the observations made in previous FPVS-EEG studies using

sequences of objects (Rossion et al., 2015; Jacques et al., 2016; Retter & Rossion, 2016) and faces (Liu-Shuang et al., 2014; Xu et al., 2017; Dzhelyova et al., 2019) and the prediction that this response reflects low-level visual processing in early visual areas and face-selective processes in high-level visual areas. As predicted, the familiarity condition had no effect on the scalp distribution or the magnitude of this response. The similarity of the general stimulation response across the own-, friend-, and stranger-face conditions indicates that, beyond identity-processing, the overall neural response did not differ across testing conditions. In other words, having seen or potentially expecting to see an image of a familiar face did not have an effect on how images in the test sequences were processed.

By contrast, the 0.86 Hz response that was expected to reflect identity-specific processes was strongest over the right occipito-temporal channels and the magnitude varied according to personal familiarity: responses were greatest to the participant's own face, followed by the friend's face, and were smallest to the stranger's face.

Notably, a stranger's face interleaved in other unfamiliar faces elicited a weaker yet significant response. A smaller response for an unfamiliar face compared to a familiar face is consistent with behavioural studies showing reduced identity recognition of an unfamiliar face across different images (Hancock et al., 2001; Jenkins et al., 2011). However, because images of each identity were taken on the same day, it's possible that part of the signal observed at the 0.86 Hz frequency reflects image regularities due to clothing and external features such as hair.

The topography of the 0.86 Hz identity-specific response was similar across conditions at both the group and individual level (Figures 3 and 4) and is consistent with the topography of several identity-sensitive ERP components (e.g., Caharel et al., 2014; Gosling & Eimer, 2011; Pierce et al., 2011) and face individuation responses measured with FPVS (Zimmerman et al., 2019; Dzhelyova et al., 2019; Vettori, Dzhelyova, Jacques, & Rossion, 2018; Dwyer, Xu, & Tanaka, 2018; Xu et al., 2017; Liu-Shuang et al., 2014). We also found that the identity-specific response was right lateralized for all participants and in all conditions (Figure 4), and that the degree of this lateralization did not differ across categories of familiarity. The fact that lateralization did not change highlights that greater familiarity elicited a stronger response in both the right and left occipito-temporal regions. This is consistent with previous studies showing an increased bilateral response to familiar faces or to the own-face, and even reduced lateralization to more familiar faces (Keyes et al., 2010; Taylor et al., 2009), but that the response remains stronger in the right hemisphere compared to the left (Ma & Han, 2012; Keyes et al., 2010; Taylor et al., 2009; Pierce et al., 2011; Tanaka et al., 2006; Gobbini et al., 2004; Rossion, Schiltz, & Crommelinck, 2003; Sugiura et al., 2008).

When the harmonics of the visual-stimulation and identity-specific response were examined individually, we observed systematic changes in the scalp distribution of the response across harmonics. In the first harmonic of the 6 Hz visual-stimulation response, we observed a right lateral occipito-temporal response, but in the higher harmonics, we observed mostly medial occipital responses. This dissociation of the harmonic scalp topographies is typical of fast periodic presentation of faces and objects (Zimmerman et al., 2019; Xu et al., 2017; Jacques et al., 2016; Gentile & Rossion, 2014; Rossion et al., 2015) and suggests that low-level visual processes reflected by activity in the medial occipital cortex are captured at higher frequencies, while higher-level visual processes (e.g., shape-related processes, face individuation) in the lateral occipital cortex are captured at lower frequencies. This is consistent with the general finding that the frequency of maximal response decreases when moving up in the ventral visual stream (Hawken, Shapley, & Grosf, 1996; McKeef, Remus, & Tong, 2007; Gauthier, Eger, Hesselman, Giraud, & Kleinsschmidt, 2012).

Similarly, we observed a distinct scalp topography in the first harmonic of the 0.86 Hz identity-specific response where there was a strong response over the posterior midline cortex in addition to the right occipito-temporal cortex for familiar faces (own, friend) but not the stranger face. In the same way that low- and high-level visual processes are captured in different harmonics of the general visual-stimulation frequency, it is possible that certain processes elicited by familiar faces are subtended by regions that respond only at very low frequencies (in this case, below 1 Hz) but not at higher frequencies. For example, functional neuroimaging studies show that areas of the cortical midline are sensitive to face familiarity, with the precuneus and posterior cingulate being consistently reported to respond more strongly to personally familiar (Taylor et al., 2009; Gobbini & Haxby, 2007), famous (Avidan & Berhmann, 2009; Eger, Schweinberger, Dolan, & Henson, 2005; Leveroni et al., 2000), and learned faces (Gobbini & Haxby, 2006; Kosaka et al., 2003; Leveroni, Seidenberg, Mayer, Mead, Binder, & Rao, 2000) relative to unfamiliar faces, with personally familiar faces evoking a larger response compared to famous faces (Gobbini, Leibenluft, Santiago, & Haxby, 2004). Additionally, the precuneus has been reported to respond differentially to the own-face compared to less familiar faces (Platek & Kemp, 2009; Devue et al., 2007; Kircher et al., 2000, 2001; Platek, Keenan, Gallup Jr., & Mohamed, 2004; Platek et al., 2006; Sugiura et al., 2000, 2005) and, using pattern-based analyses, the precuneus has also been shown to contain representations useful for the classification of familiar compared to unfamiliar faces (Natu & O'Toole, 2015; di Oleggio Castello, Halchenko, Guntapalli, Gors, & Gobbini, 2017), with the dorsal region playing a larger role in identity-specific representations (di Oleggio Castello et al., 2017). Conversely, participants with congenital prosopagnosia fail to show a selective response in the precuneus and posterior cingulate cortex to famous

faces compared to unfamiliar faces demonstrated in healthy controls (Avidan & Behrmann, 2009). Functionally, this area is generally linked to the retrieval of long-term episodic and autobiographical memory (Burgess, Maguire, Spiers, & O'Keefe, 2001; Ishai et al., 2000; Fletcher, Frith, Baker, Shallice, Frackowiak, & Dolan, 1995; Gorno-Tempini et al., 1998) and, as it is responsive to familiar identity stimuli across sensory modalities (Nakamura et al., 2001; Shah et al., 2001), may reflect post-perceptual person knowledge processing (Gobbini & Haxby, 2006, 2007). In line with the view that recognition of personally familiar individuals entails both visual recognition and semantic retrieval of person knowledge (Gobbini & Haxby, 2007; for review, see Ramon & Gobbini, 2018), it is possible that the posterior midline response reflects post-perceptual person recognition processes while the higher harmonics reflect the perceptual face representations of the familiar face.

A limitation of the current study is that the degree of familiarity might vary between participant pairs (e.g., one pair might be more familiar with each other than another pair) and even within pairs (e.g., one friend might be more familiar with their partner than vice versa). Second, although processing advantages for the own-face have been linked to high visual experience for the own-face compared to other familiar faces (Bortolon & Raffard, 2018), the ratio of exposure to the own-face compared to a personally familiar friend has not been quantified and future work should also attempt to control for variability of familiarity between categories. Finally, the responses observed in both the current study and Zimmerman et al. (2019) may reflect a general face familiarity signal in addition to the identity-specific response which could differentially impact the lateralization of less familiar (famous) or highly familiar faces (Denkova, Botzung, & Manning, 2006). In future studies, a general face familiarity signal could be inferred by comparing the response to the exact same familiar face identity when interleaved in other familiar faces relative to when it is interleaved in unfamiliar faces.

In conclusion, we used fast periodic visual stimulation to isolate electrophysiological responses reflecting image-invariant identity recognition processes elicited by a personally familiar face from general visual and face individuation processing. These identity-specific responses were observed bilaterally over the occipito-temporal cortex but were stronger in the right hemisphere and greater in magnitude for more familiar faces. Only familiar faces evoked an additional response in a posterior midline in the first harmonic of the identity-specific response, adding further evidence that this region is involved in personally familiar face processing, even during rapid and implicit recognition.

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**Chapter 3: Examining the neural correlates of implicit recognition of newly
familiarized faces**

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Abstract

Humans can readily and effortlessly learn new faces encountered in the social environment. As a face transitions from unfamiliar to familiar, the ability to generalize across different images of the same person increases substantially. Fast periodic visual stimulation and EEG (FPVS-EEG) was used to isolate identity-specific responses that generalize across different images of the same person from low-level visual processing and face-general processes that aren't identity-specific. We observed these signals emerge and increase in magnitude as a group of strangers became lab mates ($N = 9$). The neural response to an unfamiliar identity that remained unfamiliar did not change. Comparison of the response to the newly familiarized face to a highly overlearned face (the own-face) showed that this identity-specific signal was modulated by level of familiarity. The study presents the first examination of identity-specific processing changes as they occur *in situ* from normal, everyday face experience.

Faces are ubiquitous to the human visual experience. A recent visual diary study found that we spend 20% of the day looking at faces and encounter about 255 different individuals each day (Oruc et al., 2019), while the total number of faces that a person will know has been estimated to be 5000 on average (Jenkins et al., 2018). This extensive experience has been said to give rise to a visual expertise for faces (Carey, 1992; Diamond & Carey, 1986) that supports the constant demand for discriminating and individuating all those faces in our day-to-day environment and for recognizing the identities of the faces we know. This is consistent with studies showing robust recognition of well-known faces from almost any image, even when they are degraded (Burton et al., 1999; Lander et al., 2001), distorted (Bindemann et al., 2008; Hole et al., 2002), or partially occluded (Brunas et al., 1990; Johnston et al., 1996). By contrast, an unfamiliar face is more difficult to recognize as the same person across different photos (Bruce et al., 2001; Burton et al., 2010), where within-person variability (i.e., changes in appearance) is often confused for between-person variability (i.e., different identities; Adini et al., 1997; Jenkins et al., 2011). This discrepancy between the highly efficient recognition of familiar faces and the fallibility of unfamiliar face recognition has led some to claim that we are only experts for recognizing faces we know, and not for the generic recognition of any face identity (Young & Burton, 2018).

An alternative view is that our expertise for face recognition is not for the perception of identity per se, but in the ability to readily learn a new face so that unfamiliar faces quickly and easily become familiar (Rossion, 2014). In daily life, faces are usually learned without explicit efforts to encode the faces of new acquaintances. Subsequent recognition requires the ability to overcome within-person variability of the appearance of an individual face due to changes to the environment or to the face itself (Burton, 2013; Jenkins et al., 2011). Face learning is therefore especially impressive given that individual faces have been found to vary along idiosyncratic dimensions (Burton et al., 2016), meaning that learning to tolerate the variability of one identity does not transfer to other identities (Dowsett et al., 2016). Instead, recognizing a familiar face is thought to depend on an image-invariant representation that is identity-specific and that is robust to within-person variability (Bruce & Young, 1986; Burton et al., 2011; Kramer et al., 2018), and that invariance is acquired through experience with an identity's variability (Baker et al., 2017; Burton et al., 2016; Dowsett et al., 2016; Murphy et al., 2015; Ritchie & Burton, 2017).

If familiar face recognition is mediated by accessing a stable face representation, this activation should be measurable by comparing the neural processing of an unfamiliar face as it transitions to familiar. The goal of the experiment was to measure the neural changes that occur during everyday, real-world experience by tracking the face representations that emerged when a group of strangers became lab mates. Whereas many studies have examined changes in neural processing for experimentally learned faces (e.g., Pierce et al.,

2011; Verosky et al., 2020; Zimmermann & Eimer, 2013), there is currently no research that examines how face recognition changes as a result of learning a new face “in the wild” through normal social interaction and under naturalistic viewing conditions (but see Ambrus et al., 2021 where participants interacted with confederates). Here we had a unique opportunity to measure neural responses amongst personally familiar lab mates, first before familiarization (i.e., before meeting) and again after 2 months of real-world familiarization in an actual social setting. This ecological factor may have substantial consequences for face identity processing, since the recognition of personally familiar faces can involve increased perceptual, semantic, affective, and lexical processing compared to faces that are only visually familiar, famous, or experimentally learned (Ramon & Gobbini, 2018). Most importantly, it captures our natural “expertise” for acquiring highly stable face representations without any deliberate encoding effort.

We used fast periodic visual stimulation (FPVS) to parse identity-specific processing signals from signals related to general face processing, face individuation, and low-level visual processes (Campbell et al., 2020; Yan et al., 2020; Zimmermann et al., 2019). Familiarized faces were presented at a predetermined presentation frequency (i.e., 0.86 Hz) to evoke brain responses at the exact frequency of presentation and associated harmonics. The major advantage of this approach is that the familiarized face response can be decomposed into two separate frequencies to isolate the identity-specific response. By presenting images of a familiarized face within a stream of other faces that are matched on all dimensions except the one of interest (e.g., identity), the neurophysiological responses elicited by these other dimensions are siphoned into this higher face presentation frequency (e.g., 6 Hz); what remains at the slower presentation frequency of the familiarized face images (e.g., 0.86 Hz) is the response related to the identity of the familiarized face.

Previously, we found that the magnitude of identity-specific responses to personally familiar faces may index the relative familiarity of pre-familiarised faces (Campbell et al., 2020). Responses related to identity processing of the face of a well-known friend were stronger than an unfamiliar face, but identity-specific responses elicited by the own-face were, on average, 2.5 times greater than those elicited by the friend’s face. Own-face recognition is often faster compared to less familiar faces, and own-face processing advantages have been attributed to the extreme familiarity with one’s own face (Bortolon & Raffard, 2018; Devue et al., 2009; Devue & Brédart, 2008). The response magnitude associated with identity processing may therefore provide an index of face familiarity.

Here, we tracked the effect of personal familiarity on changes in the magnitude of an identity-specific response. Changes in face processing were measured by comparing identity-specific responses to images of an assigned lab partner pre-familiarisation and at two months post-familiarization. The key prediction was that real-world face learning would

cause changes to identity-specific processing that would not be observed for a novel face that remained unfamiliar at both test times. We also contrasted the response to a newly learned face against a highly overlearned face by comparing it to the response obtained for the participant's own face. We therefore predicted that the own-face response would remain stronger than the response to the newly familiarized face.

Method

Participants

Participants were ten undergraduate students from the University of Victoria who were recruited as research assistants to join the lab as part of an undergraduate research course. Each participant was partnered with another student (their "new friend") whom they had not met and who was unfamiliar to them. EEG data from one participant was not included due to a technical recording issue but who remained partnered with another participant. The remaining nine participants (8 female) had a mean age of 21.4 years ($SD = 1.5$ years). The experiment and consenting procedures were approved by the human research ethics committee of the University of Victoria.

Power Analysis

FPVS provides a very high signal-to-noise ratio (SNR) compared to normal ERP techniques because presenting the visual stimuli at a specific frequency leads to the response to be concentrated within narrow frequency bins of the EEG bandwidth (Regan, 1989; Rossion, 2014). Responses of interest are therefore relatively immune to artifacts because they are isolated from broadband EEG noise. This sensitivity makes FPVS especially well-suited for measuring effects in single patient cases (Liu-Shuang et al., 2016), individual participants (Xu et al., 2017; Yan & Rossion, 2020) and from small samples of special populations (Dwyer et al., 2018; Hagen & Tanaka, 2019). Because the main goal of the study was to examine face learning in an ecologically-relevant social setting, the size of our sample was constrained by the number of new student researcher assistants who join our research lab each year. Using this group as our naturalistic sample also ensured that the quality, duration and frequency of social interactions between our participants were roughly the same.

To ensure that we had adequate power to detect familiarization effects, a power analysis was conducted based on previously reported effect sizes. The appropriate sample size for a given level of power depends on the size of the effect, and previous work has shown that familiarity effects on FPVS face-identity responses are very strong (Campbell et al., 2020; Zimmermann et al., 2019). We used effect sizes reported for responses to the own-face and a personally familiar face relative to an unfamiliar face (Campbell et al., 2020)

to determine the statistical power ($1 - \beta$) of the planned sample ($n = 9$) using a dependent t-test. Effect sizes were adjusted to account for publication bias and uncertainty using the correction procedure designed by Anderson et al. (2017) and implemented in the R BUCSS package (Anderson & Kelley, 2020). This procedure uses the previously reported t-statistic and sample size to adjust the noncentrality parameter. The adjusted noncentrality parameter (based on a t-value of 6.82, $n = 12$, $d = 1.97$ reported by Campbell et al., 2020) used to determine statistical power to detect responses to a personally familiar face using a dependent t-test was 3.796. The adjusted noncentrality parameter (based on a t-value of 10.18, $n = 12$, $d = 2.94$ reported by Campbell et al., 2020) used to determine statistical power to detect responses to the own-face using a dependent t-test was 6.175. To correct for publication bias, we specified a prior alpha-level of .05 (i.e., the assumed statistical significance necessary for publishing in the field). To correct for uncertainty, we specified an assurance level of 0.95 (i.e., the proportion of times that power will be at or above the desired level, if the experiment were to be reproduced many times). The alpha-level for the planned study was set at .05. Using this conservative approach, our power analysis showed that we had 80% power to detect personally familiar face effects and 99% power to detect own-face effects with an $n = 9$.

Stimuli

Prior to the experimental test session, an experimenter conducted brief interviews with each participant individually that were video-recorded using a Canon EOS Rebel DSLR camera mounted on a tripod. The camera was repositioned throughout the interview to capture video of the seated participant from the front, the right angle, and the left angles. Stimuli were created this way to obtain images that varied in viewing angle and to capture natural rather than posed expressions.

All interviewees sat on the same chair during video recording.¹ Still frame images (6 frontal, 3/4 right, 3/4 left) were randomly selected from the video frames to serve as the image set for each identity (12 images per identity). Using Adobe Lightroom, images were cropped so that the face occupied roughly 80% of the image with the nose just below center and then resized to 350 x 350 pixels.

Stranger faces

The same procedure was used to obtain images of 10 individuals who were not participants in the study or the research lab. Each participant was assigned a “stranger” that was matched to their “new friend” in gender and general description (e.g. hair color, skin

¹ We did observe a small but significant difference in the image luminance between the participant faces compared to the stranger and base faces. This difference was due to slight lighting variations that were unexpected. However, since these stimulus qualities were present at both pre-post-test, they would not contribute to any change in response between test times.

complexion) and served as a control identity that remained unfamiliar at both testing times. Consequently, 1 male and 8 female identities were used to match the gender of participant faces used in the new friend and own-face condition.

Unfamiliar base faces

The same procedure was used to obtain images of 12 individuals who were not participants in the study or the research lab. The images of these identities were used for the unfamiliar base face stimuli (6 identities in each set, all female²). One set was used for the unfamiliar base faces in the pre-familiarization test and the other set was used for the unfamiliar base faces in the post-familiarization test. This was done to ensure that the base faces at the second testing time were completely unfamiliar to participants. The set used for pre- post-familiarization was counterbalanced across participants.

The same set of images (own, new friend, stranger) were used at both testing times.

Procedure

Each participant was partnered with another incoming student in the research lab. Each week, students met for a two hour lab meeting and a two hour research meeting to work on a joint lab research project with their assigned partner (the “new friend”). In the first “pre-familiarization” test time, participants were tested before meeting their assigned partner, and in the second “post-familiarization” test time, participants were tested after ~8 weeks of working with the partner in the lab. In both test sessions, participants were seated at a table in front of a keyboard and LCD monitor.

As shown in Figure 1, visual stimulation consisted of four 70 s image sequences for each condition (own, new friend, stranger) and was presented using a custom MATLAB script (SinStim; Jacques et al., 2016). In each sequence, images were presented at a constant rate of 6 Hz ($F1$ = the base-stimulation frequency). The image sequence was structured so that, depending on the condition, every 7th image was the participant’s own face (own-face condition), the face of their assigned partner (new friend condition), or an unfamiliar stranger face (stranger condition), and were drawn randomly from the images of the relevant identity. All other images were randomly selected from the set of unfamiliar base faces. Identity therefore varied at every image cycle, but the face of the own/new friend/stranger appeared with a periodicity of $F1/7 \approx 0.86$ Hz ($F2$ = the identity-specific

² We used female base faces because all but one participant was female. In test conditions where a male face was presented at 0.85 Hz, it is possible that the 0.85 Hz response also reflects a gender discrimination response (Rekow et al., 2020). However, this gender discrimination response would be present in both pre- post-test measurements, so could not account for an increase between test sessions. Also, since the stranger faces were matched by gender, any influence of a gender discrimination response would be present in all three identity conditions and would not bias any one identity response condition.

frequency). All other images were randomly selected from the set of unfamiliar base faces; identity therefore varied at every image cycle.

The presentation of each stimulation sequence was as follows:

1. 2-5 s black fixation cross appeared on a gray background;
2. 2 s image sequence fade-in;
3. 63 s image sequence presentation;
4. 5 s image sequence fade-out;
5. 2 s black fixation cross on gray background (Figure 1).

The fixation cross remained on the screen for the entire duration of the stimulation sequence and was positioned to appear over the center of the image. Across all face images, this roughly corresponded to the area just above the nose. Displayed on a monitor from a distance of 0.7 m, the stimuli subtended an angle of approximately 7 degrees of visual angle. To maintain a steady point of fixation and attention during visual stimulation, participants were asked to engage in a fixation colour change detection task during each sequence presentation (e.g., Liu-Shuang et al., 2016). At eight random time points in the sequence, the colour of the fixation cross changed briefly (200 ms) to red. Participants were told that face images would be presented rapidly on the screen with a black fixation cross in the middle of the screen and that their primary task was to press the spacebar on the computer keyboard every time they detected the colour of the cross changed from black to red.

During each stimulation sequence, the electroencephalogram (EEG) was recorded using a montage of 42 electrode sites in accordance with the extended international 10-20 system (Jasper, 1958). Signals were acquired using Ag/AgCl ring electrodes mounted in a nylon electrode cap with an abrasive, conductive gel (EASYCAP GmbH, Herrsching-Breitbrunn, Germany). Signals were amplified by low-noise electrode differential amplifiers with a frequency response of DC 0.017–67.5 Hz (90 dB–octave roll off) and digitized at a rate of 250 samples per second. Digitized signals were recorded to disk using Brain Vision Recorder Software (Brainproducts, Munich, Germany). Impedances were kept below 20 k Ω . The EEG was recorded using the average reference.

Breaks of about one minute were provided between each stimulation sequence, and the condition order was pseudorandomized for each participant. The testing time for each test session was approximately 25 minutes.

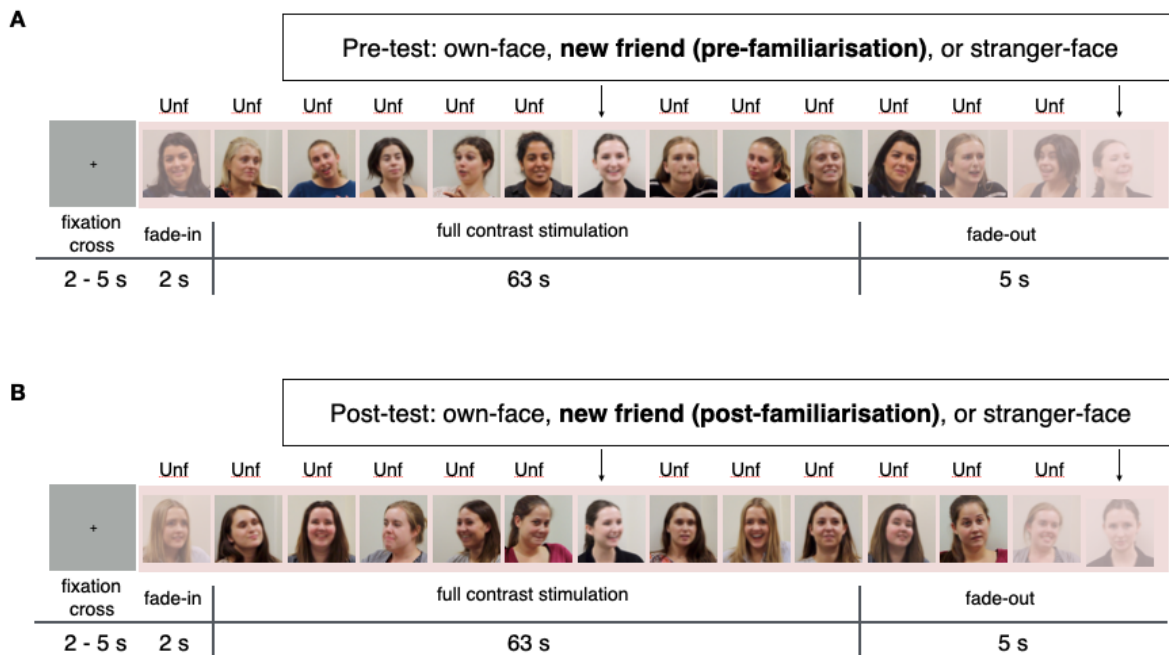


Figure 1. The visual stimulation sequences at the pre-familiarisation (A) and post-familiarisation (B) test sessions consisted of face images contrast modulated at a rate of 6 Hz (each image cycle had a duration of ~167ms). Depending on the condition, every 7th image presented was either the participant's own face, the face of the to-be-familiarised new friend, or the face of an unfamiliar stranger (another subject who was unfamiliar to the participant). The own, new friend, or stranger-face therefore appeared at a rate of $6 \text{ Hz}/7 = 0.86 \text{ Hz}$. All other images were selected randomly from a set of faces that were unfamiliar to all participants. Identities used for the base face stimuli at post-familiarisation were novel to ensure unfamiliarity; the set of base face identities used for pre-familiarisation and post-familiarisation were counterbalanced across participants. During visual stimulation, participants engaged in a fixation cross colour change detection task (not shown) that required them to press the spacebar every time that a fixation cross superimposed in the middle of the screen changed from black to red. Fixation cross changes occurred 8 times at random intervals. Face images are shown here with permission from the participants/models.

EEG Analysis

All EEG processing steps were carried out using the free software Letswave 6 (<https://github.com/NOCIONS/letswave6>) running on MATLAB (MathWorks). A Butterworth filter with cut-off values of 0.1-100 Hz and a slope of 24 dB/octave was applied to the data. Data of participants who blinked more than 10 times during any of the stimulation sequences within a recording session were corrected by applying ICA to the data from each stimulation sequence and removing a single component accounting for blink artifacts (mean number of blinks across participants and recording sessions = 9.5, SD = 6.8). ANOVA of the number of blinks showed no significant difference between identity conditions, $p = .080$ (mean number of blinks within the own-face condition = 8.9, SD = 7.2; mean number of blinks within the new friend condition = 9.5, SD = 7.0; mean number of blinks within the stranger condition = 10.0, SD = 6.5).

Channels which were artifact-prone across multiple trials (less than 1% of channels on average) were re-estimated using linear interpolation of the two nearest channels. All EEG segments were re-referenced to a common average reference.

The EEG for each sequence was re-segmented, beginning from sequence onset until approximately 64 s (before stimulus fade-out), to contain an integer number of 0.86 Hz cycles (55 cycles, 16035 time bins in total ≈ 64 s). For every participant during the pre-post-familiarization testing sessions, the four segmented sequences within the own, new friend, and stranger face conditions were averaged in the time-domain to reduce EEG activity that is not phase-locked to the stimulus. A Fast Fourier Transform (FFT) was then applied to the averaged segments to represent the data of each channel as a normalized amplitude spectrum (μV) in the frequency domain with a frequency resolution of 0.0156 Hz (i.e., 1/64.14 s).

As responses are expected to be observed across multiple harmonics of the stimulation frequencies, we assessed harmonics of each stimulation frequency (i.e., F1, F2) based on z-scores. The procedure was as follows: 1) Within each condition and test session, individual amplitude spectra were averaged across participants and all channels; 2) At each harmonic, z-scores were computed as the difference between the amplitude at the frequency of interest and the mean amplitude of the local baseline divided by the standard deviation of local baseline (local baseline = 20 surrounding frequency bins, excluding the immediately adjacent bins and the bins containing the minimum and maximum response); 3) Using the z-scores as a stopping rule, the range of harmonics was constrained to the highest number of consecutively significant harmonics observed in any one condition (e.g., 1F2, 2F2, 3F2, etc., where each $z \geq 3.1$, $p < .001$, 1-tailed, i.e., signal > noise).

Responses were significant up to the 6th harmonic for the 6 Hz base-stimulation response (i.e., $6F1 = 36$ Hz), and up to the 12th harmonics for the 0.86 Hz identity-specific response (i.e., $12F2 = 10.29$ Hz, but excluding the 6 Hz harmonic that overlapped with the base-stimulation frequency). For each stimulation frequency ($F1$, $F2$), the same number of harmonics were used for quantifying responses in each identity condition.

A baseline-subtraction correction was applied to the amplitude spectra using the same local baseline definition used for the z-score. For each stimulation frequency, responses were quantified as the sum of the baseline-corrected amplitudes across significant harmonics.

Base-stimulation Response (6 Hz)

The 6 Hz response was quantified as the average summed-harmonic response in the channels of maximum response: Oz, POz, PO8 and the left hemisphere homologue PO7. These defined a *medial-occipital* (MO) region.

Given that we did not have predictions for effects in the base-stimulation responses (6 Hz), response differences across identity conditions and time were tested using repeated-measures ANOVA with condition (own, new friend, stranger) and time (pre-post-familiarization) as within-subject factors. Mauchly's test for sphericity was performed and a Greenhouse-Geisser correction was applied whenever sphericity was violated. Effects of condition and time were also assessed by computing the Bayes factor favoring either a model that included the effect of interest or a model that excluded that effect. All Bayes factors were generated using the R BayesFactor package (Morey & Rouder, 2018) using default priors. We interpreted Bayes factors (BF) according to the modified guidelines of Jeffreys (1961), whereby a BF of 3 is taken as positive support for an outcome (Raftery, 1995; Lee & Wagenmakers, 2013).

Identity-specific Response (0.86 Hz)

The 0.86 Hz identity-specific response was quantified as the average summed-harmonic response in the channels of maximum response (averaged across all identity conditions): P10, PO10, PO8 and the left hemisphere homologues P9, PO9, and PO7. These defined an *occipito-temporal* (OT) region; the same region-of-interest was used for quantifying the identity-specific response for all conditions.

Because it was our goal to observe face familiarization that occurs spontaneously in the real-world, the sample size was determined by the actual group size in a real-world social setting: a psychology research lab. However, the trade-off of this ecological validity is statistical power. Although increasing the number of participants would increase statistical power, it would disturb the critical element of a real-world social setting for capturing face familiarization *in situ*.

To maximize power, our main analysis relied on three planned comparisons:

1. response to the stranger face would not change between sessions;
2. response to the new friend face, which transitions from unfamiliar to familiar between test sessions, would show a significant increase in response;
3. response to the own-face would not change between sessions.

Uncorrected paired-samples t-tests were used to test for a significant increase in the response to the face of the assigned lab partner (“new friend”), the stranger face, and the own-face across test sessions. To increase the credibility of our findings, Bayesian tests were conducted to quantify the evidence for and against the hypothesis that an effect was present, and responses were examined at the individual level to corroborate the group-level effects.

We then determined the significance of the 0.86 Hz identity-specific responses for individual participants. This was done for each condition and test time by summing the raw amplitude spectra containing the relevant 0.86 Hz harmonics and their local baselines (i.e., 20 surrounding frequency bins) and calculating z-scores to quantify the response relative to EEG noise in surrounding frequency bins.

Statistical significance of each participant’s response change to the familiarized new friend face was assessed using single case t-tests with one-tailed significance thresholds (Crawford et al., 2010; see Liu-Shuang et al., 2016). Here, each participant was treated as a single case, and their difference score (of summed-harmonic responses) for the familiarized new friend face was compared against difference scores in the control group, which in this case was the differences scores of all participants for the unfamiliarised stranger face. The procedure was repeated to evaluate any changes to the own-face response (two-tailed).

To examine differences between identity conditions, multiple comparisons (Bonferroni-Holm corrected) were conducted to compare response magnitudes across identity conditions in each test session.

Between and within-session reliability

We examined the test-retest reliability and the split-half reliability (i.e., internal consistency) of the 6 Hz base-stimulation and 0.86 Hz identity-specific responses using the intraclass correlation coefficient (ICC). This provides a measure of the absolute agreement between measurements. Since the ICC is defined by the proportion of the total variance due to between-subject variance, values can range between 0 and 1, with higher values indicating more consistency within-subjects (Koo & Li, 2016; Shrout & Fleiss, 1979). For each identity condition, split-half reliability was assessed by comparing the mean responses evoked in the first (first two stimulation sequences) and second halves (third and fourth stimulation sequences) of a test session.

ICC estimates and their 95% confidence intervals were calculated for both the 6 Hz and 0.86 Hz responses for each identity condition and ROI using the R psych package (Revelle, 2019) based on an absolute agreement, 2-way mixed effects model. As there are no definitive standards for acceptable reliability using ICC (Koo & Li, 2016), we interpreted ICC using the same conservative guidelines recently used to evaluate the FPVS face individuation response (Dzhelyova et al., 2019): Within-subject reliability was interpreted as poor (ICC < 0.40), moderate (ICC 0.41-0.59), good (ICC 0.60-0.74), or excellent (ICC > 0.75).

Results

Behavioural Data

Accuracy for the color change detection task was close to ceiling across all three conditions and test times ($M = 96.6\%$, $SD = 5.9\%$), and a repeated measures ANOVA found no effects of identity (own, new friend, stranger; $F(2, 16) = 1.41$, $p = .27$, $\eta^2p = .15$), or time (pre- post-familiarization; $F(1, 8) = 0.31$, $p = .59$, $\eta^2p = .04$), and no interaction, $F(2, 16) = 1.23$, $p = .32$, $\eta^2p = .13$.

Response times (RT; $M = 439$ ms, $SD = 70$ ms) were calculated relative to the onset of fixation cross color change and for responses recorded within 1500 ms of the color change. A repeated measures ANOVA found no effects of identity (own, new friend, stranger; $F(2, 16) = 1.00$, $p = .39$, $\eta^2p = .11$), or time (pre- post-familiarization; $F(1, 8) < .01$, $p = .99$, $\eta^2p < .01$), or interaction, $F(2, 16) = 1.23$, $p = .32$, $\eta^2p = .13$.

EEG Data

Distinct peaks were observed in the frequency domain at the exact stimulation frequencies and their associated harmonics. Figure 2 shows the grand-averaged EEG amplitude spectra (baseline-corrected using a signal-to-noise subtraction) during visual stimulation pooled across all channels. Scalp topography of the group-averaged and individual response changes (post minus pre) for each identity condition and stimulation frequency is shown in Figures 3 and 4, respectively. Figure 5 shows the average 6 Hz and 0.86 Hz summed-harmonic responses for each identity and test time in the relevant ROIs. Figure 6 shows the 6 and 0.86 Hz summed-harmonic responses for individual participants, with post-familiarization responses plotted against the pre-familiarisation response.

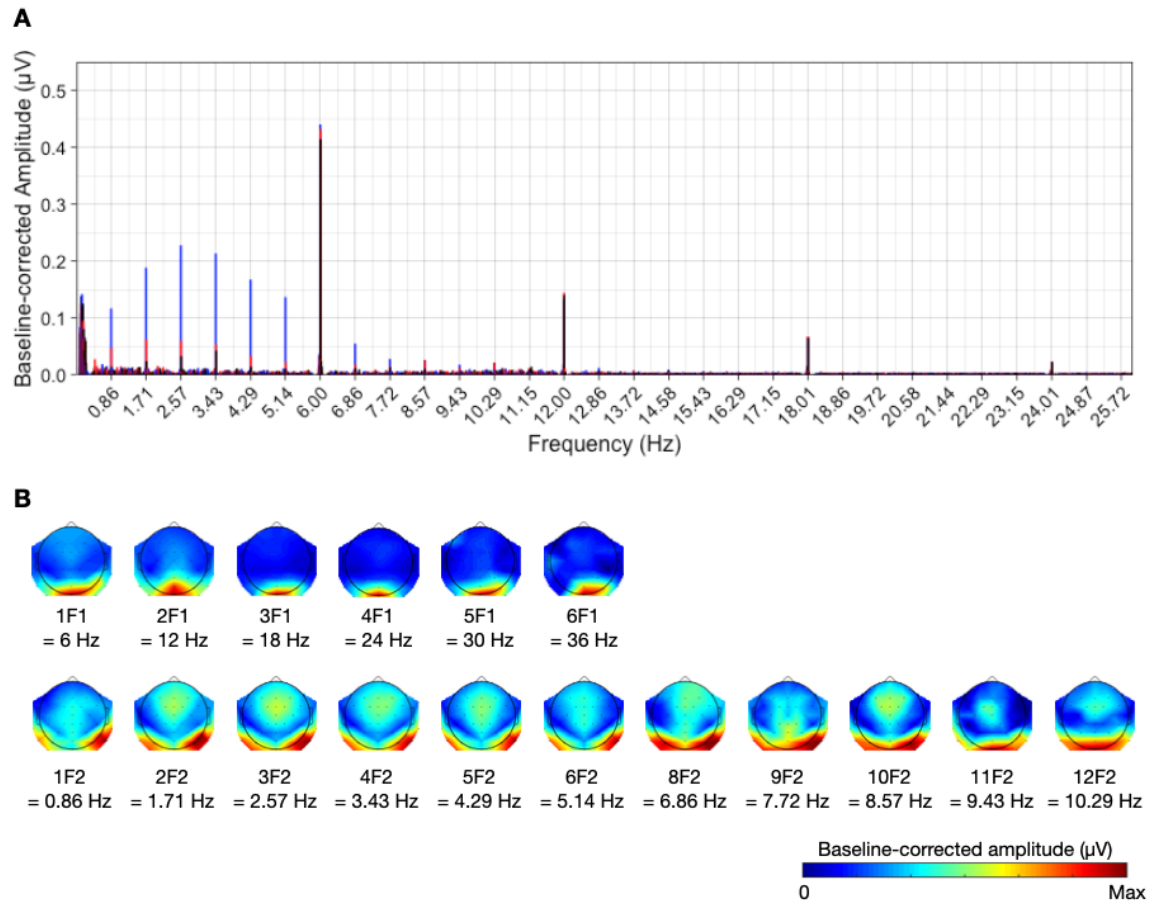


Figure 2. (A) Grand-averaged EEG amplitudes across the frequency spectrum, averaged across all conditions and channels. Clear responses were observed at the base visual stimulation frequency (6 Hz and its harmonics) and the identity-specific frequency (0.86 Hz and its harmonics). (B) Scalp topographies of significant harmonics for each stimulation frequency. Responses at the 6 Hz frequency were significant up to the 6th harmonic (36 Hz; only the first four harmonics are shown in the spectrum). Responses at the 0.86 Hz frequency were significant up to the 12th harmonic (the 7th harmonic that overlaps with the 6 Hz component was excluded). For each stimulation frequency, responses were quantified as the sum of the baseline-corrected amplitudes across significant harmonics.

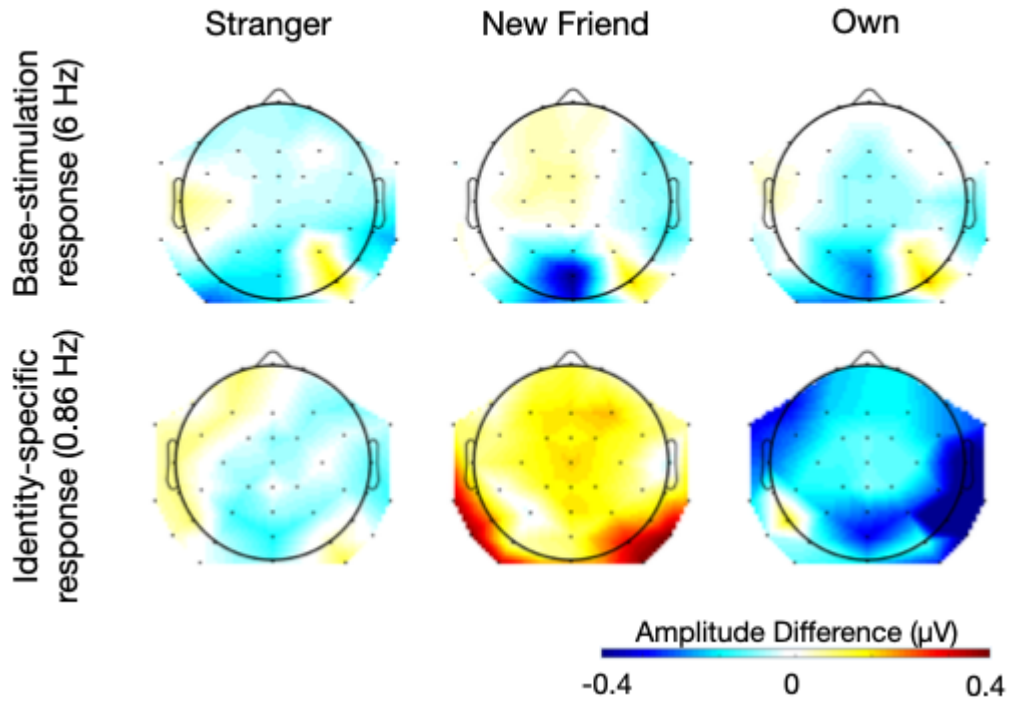


Figure 3. Scalp distribution of the group-averaged change in response (post minus pre) of the summed-harmonic responses at base-stimulation and identity-specific frequency. Scale is based on maximum response increase independent of condition.

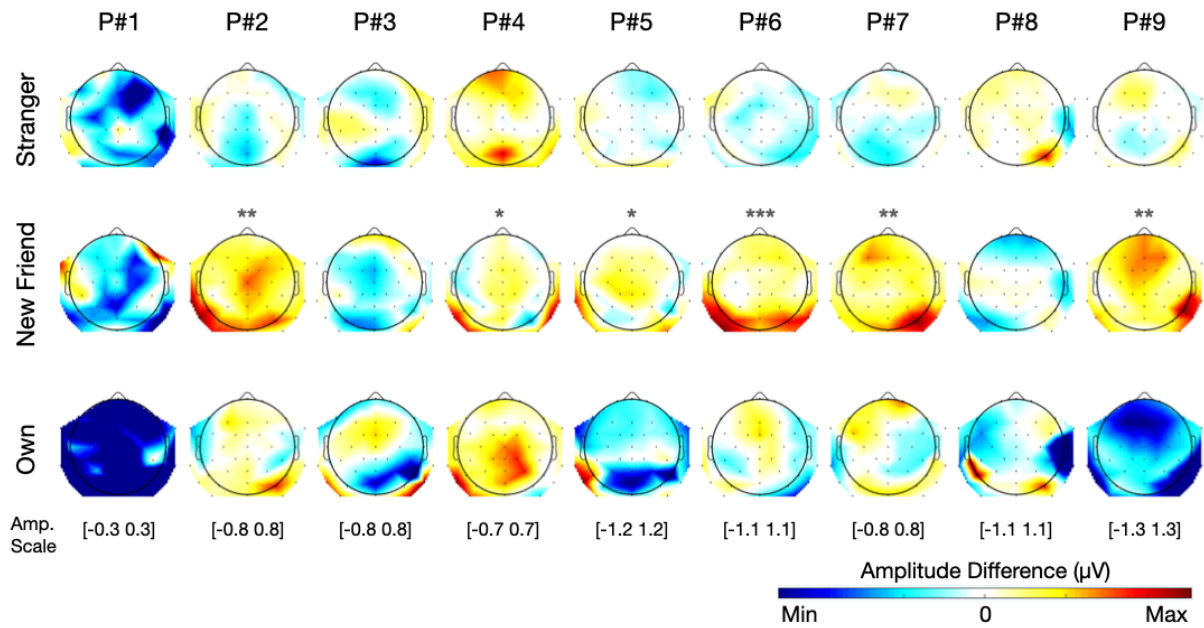


Figure 4. Scalp distribution of each subject's change in identity-specific response (post minus pre) to an unfamiliar stranger face (top row), the new friend's face (middle row), and their own face (bottom row). Scale is based on maximum response increase for each participant independent of condition and is reported at the bottom of each subject's column. Asterisks indicate a significant increase in the 0.86 Hz response to the new friend face in the occipito-temporal ROI (P10/P9, PO10/PO9, PO8/PO7). * $p < .05$, ** $p < .01$, *** $p < .001$.

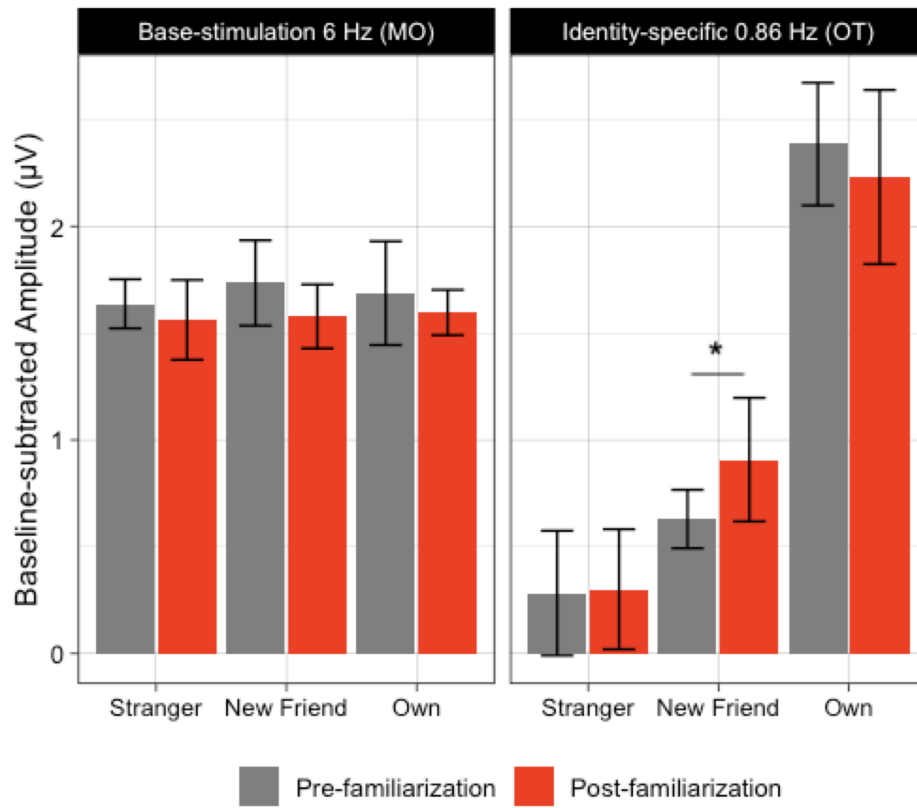


Figure 5. Group-averaged summed-harmonic responses for the base visual-stimulation responses (6 Hz) and identity-specific responses (0.86 Hz) for each face category and test time. Error bars represent within-subject standard error (Cousineau, 2005). * $p < .05$, one-tailed.

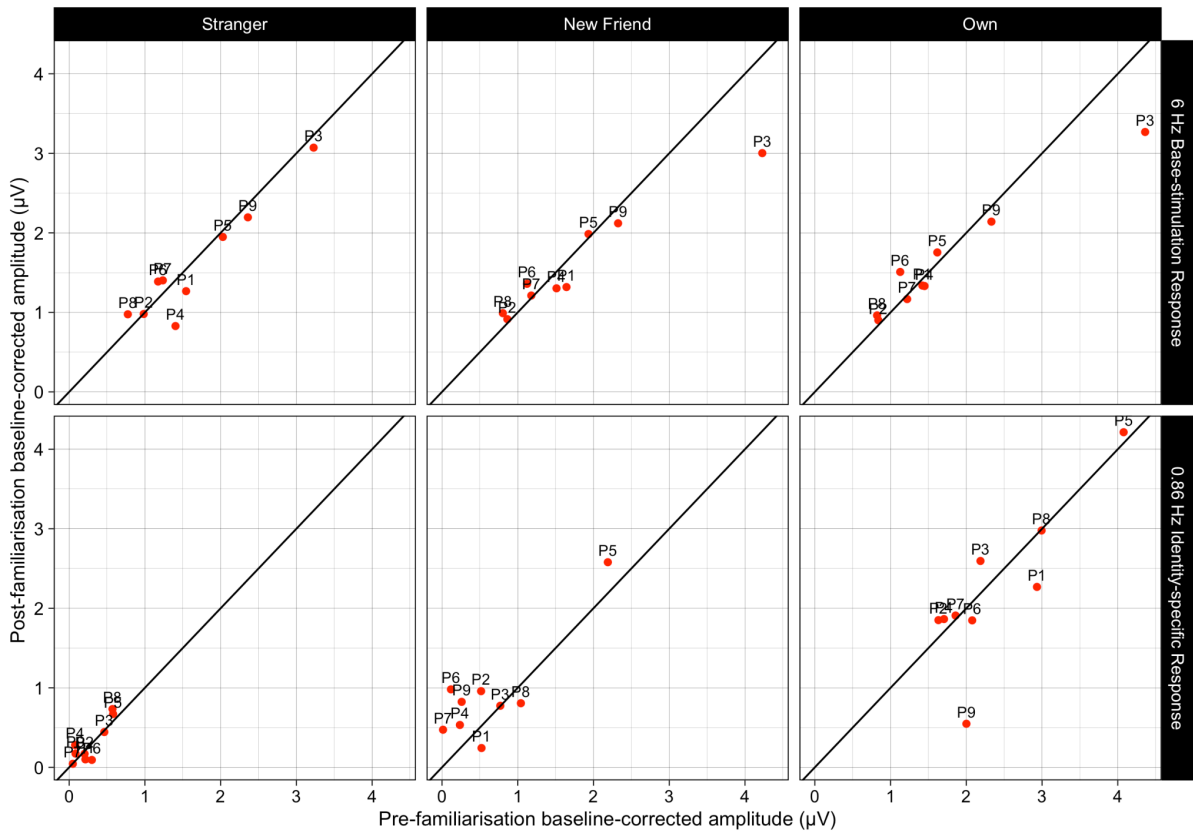


Figure 6. Post-familiarisation responses are plotted against the pre-familiarisation responses for each participant, identity condition, and response frequency. Each point represents a participant's summed-harmonic response for the particular frequency, with points above the diagonal line representing participants whose response at the second test time was larger than the response observed at the first test time.

Base-stimulation responses

At the 6 Hz base-stimulation frequency, ANOVA of the summed-harmonic response in the medial occipital region (MO: Oz, POz, PO8/PO7) showed no effects of identity, time, and no interaction. A Bayesian analysis with identity and time as within-subjects factors showed no effect of condition ($BF = 5.3$ in favor of the null hypothesis), time ($BF = 1.3$ in favor of the null hypothesis), or interaction ($BF = 4.6$ in favor of the null hypothesis).

Identity-specific responses: Pre vs. post-familiarization

At the 0.86 Hz identity-specific frequency, planned comparison of responses to the face of the assigned lab partner (“new friend”) showed a significant increase in the response post-familiarization compared to pre-familiarisation (pre M : 0.63 μ V, $SD = 0.67$ μ V; post M : 0.91 μ V, $SD = 0.67$ μ V; $t(8) = 2.21$, $p = .029$, $d = 0.74$, 95% CI [-0.03, 1.55], one-tailed). Bayesian analysis indicated moderate evidence against the null hypothesis: specifically, $BF_{+0} = 3.1$, meaning that the data are approximately 3.1 times more likely to occur under the alternative hypothesis (i.e., post > pre) than under the null hypothesis (i.e., post not greater than pre).

When the response to the new friend was examined in the right (P10, PO10, PO8) and left (P9, PO9, PO7) channels separately, the response increase was significant in the right hemisphere (pre M : 0.66 μ V, $SD = 0.63$ μ V; post M : 0.99 μ V, $SD = 0.64$ μ V; $t(8) = 2.85$, $p = .012$, $d = 0.94$, 95% CI [-0.13, 1.81], one-tailed) and Bayesian analysis showed moderate evidence in favor of an effect ($BF_{+0} = 6.5$). The response increase was not significant in the left hemisphere (pre M : 0.60 μ V, $SD = 0.72$ μ V; post M : 0.83 μ V, $SD = 0.74$ μ V; $t(8) = 1.46$, $p = .091$, $d = 0.49$, 95% CI [-0.23, 1.24], one-tailed), although the corresponding Bayes factor indicated anecdotal evidence in favour of an effect ($BF_{+0} = 1.3$).

Planned comparison of the identity-specific responses to the stranger face showed no change in response between test times, (pre M : 0.28 μ V, $SD = 0.21$ μ V; post M : 0.30 μ V, $SD = 0.26$ μ V; $t(8) = 0.41$, $p = .670$, $d = 0.14$, 95% CI [-0.55, 0.84], two-tailed). The corresponding Bayes factor ($BF_{0+} = 2.9$) indicated anecdotal evidence in favour of the null hypothesis. Comparison of responses in the right hemisphere were consistent with the null hypothesis (pre M : 0.30 μ V, $SD = 0.23$ μ V; post M : 0.34 μ V, $SD = 0.35$ μ V; $t(8) = 0.59$, $p = .571$, $d = 0.20$, 95% CI [-0.50, 0.90], two-tailed; $BF_{0+} = 2.7$), as were those in the left hemisphere (pre M : 0.27 μ V, $SD = 0.22$ μ V; post M : 0.27 μ V, $SD = 0.21$ μ V; $t(8) = 0.13$, $p = .900$, $d = -0.04$, 95% CI [-0.74, 0.65], two-tailed; $BF_{0+} = 3.1$).

Planned comparison of the identity-specific responses to the own-face showed no change in response between test times, (pre M : 2.38 μ V, $SD = 0.80$ μ V; post M : 2.23 μ V, $SD = 1.00$ μ V; $t(8) = 0.80$, $p = .445$, $d = -0.27$, 95% CI [-0.98, 0.43], two-tailed; $BF_{0+} = 2.4$). Comparison of responses in the right hemisphere were consistent with the null hypothesis (pre M : 2.68 μ V, $SD = 0.85$ μ V; post M : 2.44 μ V, $SD = 1.15$ μ V; $t(8) = 0.93$, $p = .381$, $d =$

-0.31, 95% CI [-1.03, 0.39], two-tailed; $BF_{0+} = 2.2$), as were those in the left hemisphere (pre M : 2.09 μV , $SD = 0.94 \mu V$; post M : 2.02 μV , $SD = 1.07 \mu V$; $t(8) = 0.43$, $p = .673$, $d = -0.31$, 95% CI [-1.03, 0.39], two-tailed, $BF_{0+} = 2.9$).

As shown in Figure 7, presentation of the own-face generated clear identity-specific responses in all participants: in both test sessions, the occipito-temporal 0.86 Hz response was significant for all 9 participants ($z > 3.1$, $p < .001$, one-tailed). Pre-familiarization, the assigned partner face elicited a significant response in 5 participants (P1, P2, P3, P5, P8); after familiarization, all but one participant (P2, P3, P4, P5, P6, P7, P8) showed a significant response to the new friend face. By comparison, the unfamiliar stranger face elicited significant responses in the same 3 (P3, P5, P8) participants in the first and second test session, respectively.

Single-case t-tests (one-tailed) showed that the response difference between pre-post-familiarization for the new friend significantly exceeded that observed for the stranger faces in 6 participants: P2, $t(8) = 3.08$, $p = .008$; P4, $t(8) = 2.02$, $p = .039$; P5, $t(8) = 2.70$, $p = .014$; P6, $t(8) = 6.13$, $p < .001$; P7, $t(8) = 3.20$, $p = .006$; and P9, $t(8) = 3.96$, $p = .002$. Three participants failed to show an increased response to the new friend: P1, $t(8) = 2.16$, $p = .097$; P3, $t(8) = 0.10$, $p = .538$; and P8, $t(8) = 1.84$, $p = .098$. Statistically significant response increases are indicated in Figure 7. For responses to the own-face, single-case t-tests (two-tailed) showed a change in response in 3 participants: P1, $t(8) = 4.95$, $p = .001$, and P9, $t(8) = 10.68$, $p < .001$, showed a decrease in response; P3, $t(8) = 2.83$, $p = .022$, showed an increase in response.

Identity-specific responses: Comparing own, newly-familiarized, and stranger faces

Comparison of identity-specific responses across identity conditions at each test time was conducted using two-tailed paired-sample t-tests (Bonferroni-Holm corrected). Pre-familiarisation, the difference between the stranger face and the unfamiliarised new friend face was not significant, $t(8) = 2.03$, $p = .077$, $d = 0.68$, 95% CI [-0.07, 1.47], $BF_{0+} = 0.75$, however the own-face response was greater than both the unfamiliarized new friend face, $t(8) = 13.94$, $p < .001$, $d = 4.65$, 95% CI [2.46, 7.38], $BF_{+0} = 20159$, and the stranger face, $t(8) = 9.57$, $p < .001$, $d = 3.19$, 95% CI [1.60, 5.13], $BF_{+0} = 1728$. post-familiarization, the response to the newly familiarized friend face was significantly greater than the stranger face, $t(8) = 3.23$, $p = .012$, $d = 1.08$, 95% CI [0.24, 2.01], $BF_{+0} = 5.5$, yet the response to the own-face remained stronger than both the familiarized new friend face, $t(8) = 5.28$, $p < .001$, $d = 1.76$, 95% CI [0.71, 2.98], $BF_{+0} = 52$, and the stranger face, $t(8) = 7.02$, $p < .001$, $d = 2.34$, 95% CI [1.09, 3.84], $BF_{+0} = 258$.

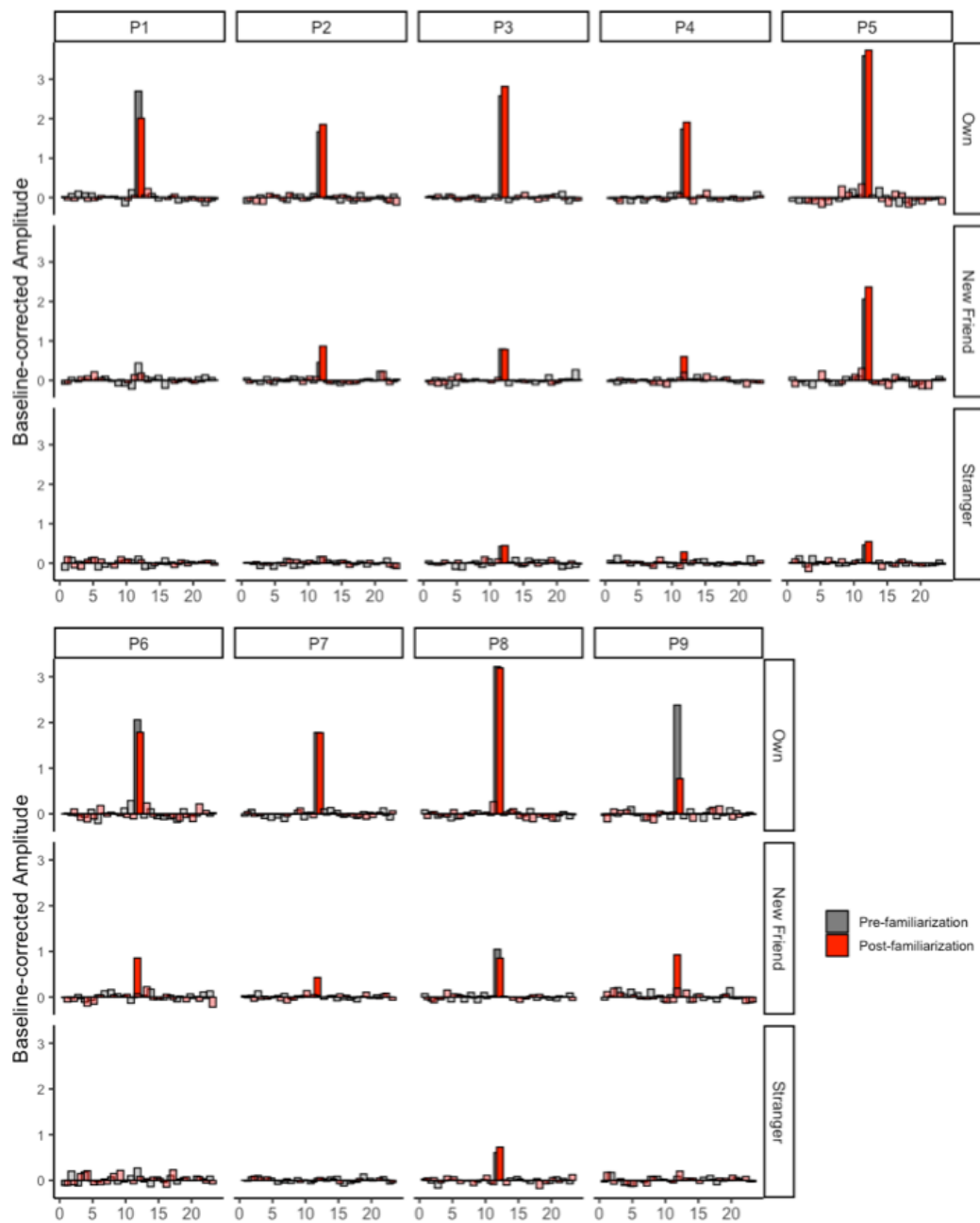


Figure 7. Bar graphs of the identity-specific response observed for each participant and condition. Bars represent the summed amplitudes of the relevant 0.86 Hz harmonics and their surrounding frequency bins, averaged over all channels in the left and right OT ROIs. Each subplot shows 21 frequency bins, with the bin containing the summed 0.86 Hz harmonics in the middle and their 10 neighboring frequency bins on each side. The unit of the x-axis is arbitrary. Pre-familiarisation responses are shown in gray bars and post-familiarisation responses are shown in red. Overlapping bars have been jittered for visibility. Significant responses ($z > 3.1$, $p < .001$, one-tailed) are shown as solid bars. Significant

Between and within-session reliability

Test-retest reliability indices are shown in Table 1. The 6 Hz base base-stimulation response had excellent overall within-subject reliability (ICC values ranged from .87-.94, p 's < .001). The reliability of the 0.86 Hz response was also excellent across all three identity conditions, with subject scores being the most consistent in the stranger face condition (ICC = .86, p < .001, 95% CI [0.60, 0.96]), followed by the own-face (ICC = .80, p = .002, [0.48, 0.94]), and the the new friend (ICC = .79, p = .001, [0.37, 0.93]). The split-half reliability was also excellent. Across test sessions and identity conditions, split-half reliability showed nearly perfect internal consistency for both the 6 Hz base-stimulus response (ICC = .98, p < .001, 95% CI = [.97 .99]) and the 0.86 Hz identity-specific response (ICC = .96, p < .001, 95% CI = [.93 .97]).

Table 1. Intraclass correlation coefficients (ICC) for accessing test-retest reliability of base-stimulation and identity-specific responses.

	Base-stimulation response (6 Hz)		Identity-specific response (0.86 Hz)	
	ROI	ICC	ROI	ICC
Stranger	MO	0.94 [0.83, 0.98] ***	OT	0.86 [0.60, 0.96] ***
New Friend	MO	0.87 [0.64, 0.96] ***	OT	0.79 [0.37, 0.93] **
Own	MO	0.91 [0.73, 0.97] ***	OT	0.80 [0.48, 0.94] **

Note: 95% confidence intervals in parentheses. MO = medial occipital region (Oz, POz, PO8, PO7). OT = occipito-temporal region (P10/P9, PO10/PO9, PO8/PO7). Within-subject reliability was interpreted as poor (ICC < 0.40), moderate (ICC 0.41-0.59), good (ICC 0.60-0.74), or excellent (ICC > 0.75).

* p < .05, ** p < .01, *** p < .001

Discussion

Results confirmed the predictions and indicated that learning a new face “in the wild” was associated with an increased identity-specific response. The critical control condition for this response change was the stranger identity that remained unfamiliar to participants, and for this control identity we did not observe an increase in response. At the individual level, significant identity-specific responses to the newly familiarized face were observed in 8 of 9 participants, whereas the stranger face evoked significant responses in only 3 participants. When compared to changes observed for the unfamiliar stranger face, 6 of 9 participants showed a significant increase in the magnitude of the identity-specific response to the new friend face after familiarization. This suggests that the real-world face learning that occurred in the 2 months between test sessions caused a neural change, such that brief (~166 ms) presentations of the same face images that were once unfamiliar to the participants evoked stronger neural responses after real-world familiarization. Importantly, this response was elicited automatically, since face identity was task irrelevant and attention was directed to another target (the fixation cross) superimposed on the face stimulus. In addition, post-hoc analysis of this response increase suggests that increased magnitude is more prominent in the right hemisphere, and future studies with larger samples would be helpful for replicating this effect and understanding whether this reflects a group-level effect or individual differences in hemispheric specialization.

We also found that the identity-specific responses might index the relative familiarity of a face. Although newly familiarized faces evoked stronger responses than unfamiliar faces, the own-face response was still 2.5 times larger on average than the newly learned face. By comparison, the only ERP component that can distinguish less familiar faces from more familiar faces emerges about 400 ms post-stimulus (Wiese et al., 2019) and is therefore too late to account for perceptual processes underlying the fast recognition of familiar faces.

These results provide the first demonstration of transformations in the neural response to faces as a result of real-world familiarization in a real-world social context. Participants were told that they were participating in a study about face recognition as part of their research experience, but were not aware of the research question or that their familiarization with their assigned lab partner was the key “manipulation” until after the study. These results extend previous studies of identity-specific processing of famous (Yan et al., 2020; Zimmerman et al., 2019) and personally familiar faces (Campbell et al., 2020). Notably, we replicate the finding that implicit recognition of the a friend’s face is associated with a stronger occipito-temporal response than an unfamiliar face, and that the response to

the own-face is that is at least twice as great in amplitude than the response elicited by another personally familiar face (Campbell et al., 2020).

Our findings conflict with those from a recent study by Ambrus et al. (2021) that examined how representations of face familiarity and identity changed as a result of perceptual, media, or personal familiarization. Using representational similarity analysis, they found that both media and personal familiarization led to clear representations of face familiarity, but the identity representations remained the same even after personal familiarization. One explanation for this difference might be due to the limited familiarity for even the personally familiar faces in their experiment, since familiarization consisted of three 1-hour conversations with a research assistant. By comparison, the identity representations we tracked in both the current and previous study reflect identities that are also socially-relevant, since they share either a personal (Campbell et al., 2020) or a working relationship. Experimental work on face learning has shown that socially-relevant, conceptual information can be even more important than perceptual information (Schwartz & Yovel, 2016; Schwartz & Yovel, 2019), so future studies might investigate the role of social information during personal familiarization. The identity representations measured here also reflect extensive familiarization that would expose participants to the familiarized faces on different days and in different environments (in and outside the lab). Previous research on face learning has shown that increasing the within-person variability of a face during learning leads to much more robust identity recognition (Ritchie & Burton, 2017), so it is also possible that the limited variability in a single in-person encounter was not strong enough to induce detectable changes to the identity representations. Finally, our ability to observe post-familiarization changes to an identity-specific response might be due to the increased sensitivity obtained by using a frequency-tagging approach to isolate the activation of an identity representation. By periodically presenting the familiarized faces within a stream of other faces identities, the neurophysiological response associated with general face processing, face individuation, and low-level processing are siphoned off at the base-stimulation frequency, leaving responses that are uniquely elicited by the familiarized face identities observable at their presentation frequency (Yan et al., 2020; Zimmermann et al., 2019). The former are reflected in the scalp distribution of the 6 Hz response, where response was highest over medial-occipital regions and did not vary according to the identity category of the face inserted at the 0.86 Hz frequency. The response that remained at the 0.86 Hz frequency at which the stranger, new friend, or own-face was presented should reflect the population of neurons that are specifically responsive to that face identity and that support the ability to generalize across different images of that face.

Unfamiliar face individuation measured using FPVS has already been shown to have high test-retest reliability for both amplitude and spatial distribution (Dzhelyova et al., 2019),

and our study provides evidence that this stability extends to individual face recognition responses. Given that we expect measurement consistency for the same subject under the same conditions, responses to the stranger and own-face are the most relevant because their familiarity status did not change between test sessions. The 0.86 Hz response to the stranger face had the highest intraclass correlation, but, because it is unfamiliar to participants, this response likely reflects low-level image and face features and not identity recognition. More importantly, responses to the own-face also had excellent within-subject stability in the identity-specific responses evoked 2 months apart. Additionally, unlike many ERP components which have been found to be sensitive to image repetition (Caharel et al., 2009, 2014; Kaufmann et al., 2009; Wiese et al., 2019), the split-half reliability was near perfect within test sessions for both the 6 Hz base-stimulation response and the 0.86 Hz identity-specific response. This suggests that responses evoked in a FPVS paradigm may be better protected from image repetition effects and learning during tests.

A limitation of the current paradigm is that it remains unknown to what extent the element of social interaction contributed to the development and magnitude of the observed identity recognition responses. The condition of the unfamiliar stranger face served as a control comparison for stimulus exposure effects and test time to ensure that increases in the identity recognition responses post-familiarization were not likely to be spontaneous or a result of prior exposure to the test stimuli. Future studies could attempt to determine the relevant contribution of visual exposure and social interaction by including another set of identities that are viewed with the same temporal regularity but with whom the participants have no interactions.

Second, although we were able to examine neural response changes arising from faces learned in the real-world and with all their natural variability (at least within 2 months time), we had less control over the exact quality and quantity of exposure during the “familiarization” phase. Exposure among partners all exceeded a certain threshold based on weekly meetings and in-lab work, but it is not possible to know to what extent exposure differences account for variability in the post-familiarization response (e.g., whether students spent time together socially outside of the lab). There is also a question as to whether behavioural differences measured in a standardized face recognition test could account for the variability in the post-familiarization response. Previous studies have found a modest correlation between standardised behavioural measures of face recognition and the neural responses measured using FPVS with a face discrimination paradigm (Xu et al., 2017). However, future research should examine whether variability in behavioural measures of face learning and memory correspond to neural response changes to face identity after familiarization.

Third, it is unknown what proportion of the identity-specific responses measured here reflect a general familiarity signal. Recently, a common familiarity response was shown to be evoked by different identities, indicating that familiar faces share a common neural network that is not identity-specific (Yan & Rossion, 2020). This could be tested in subsequent experiments by embedding a familiar identity within a stream of other familiar faces, so that the general dimension of face familiarity is also siphoned into the higher base-stimulation frequency.

Finally, photos of each identity were obtained on the same day and therefore had less within-person variability compared to social media images or personal photo collections (e.g., Jenkins et al., 2011). However, personal photos and selfies are often highly posed and can be a biased representation (White et al., 2016). Our stimuli captured a range of spontaneous and idiosyncratic facial expressions as they appeared during a real-life interaction, and therefore may more closely match how they are represented in memory (Redfern & Benton, 2019). However, future studies would benefit from increasing the within-person variability across images to provide a stronger test of the generalisability of the identity-specific response over highly variable images.

In conclusion, the human brain readily and effortlessly learns new faces that are regularly encountered in the social environment. Here, we documented changes in identity processing as a face transitions from being an unfamiliar person to a familiar person in the real-world. Critically, this biological marker shows that normal, everyday experiences and social interactions transform the neural network to increase perceptual sensitivity and responsiveness to a familiar face identity.

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Chapter 4: Accurate and rapid saccadic responses to subliminal face images

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Abstract

Saccadic choice tasks use eye movements as a response method, typically in a two-alternative forced choice task where observers are asked to saccade as quickly as possible to an image of a pre-specified target category. Saccadic reaction times provide more precise estimates on the lower bounds for face recognition because the initiation and execution of eye movements is faster than for manual hand responses. Using this approach, it has been found that faces can be detected in as little as 100 ms (Crouzet et al., 2010, *JoV*). When taking into account the time needed to execute eye movements, this finding suggests that faces can be detected in as little as 80 ms. It has therefore been suggested that face detection must occur during the first feedforward sweep of activation, since this latency leaves little time for feedback processing. In the current experiment, we tested this hypothesis using backward masking – a technique shown to primarily disrupt feedback processing while leaving feedforward activation mostly intact. We show that saccades to human faces are as fast under moderate (50 ms SOA) and strong (8 ms SOA) masking conditions as they are in an effectively unmasked condition (400 ms SOA). We also found that the fastest saccades tended to be directed to faces, even when houses were the targets and when images were moderately masked. Finally, we observed remarkable response accuracy for face and house detection, even when participants indicated having no visual experience of the test images. These results provide evidence for the view that face-selective mechanisms are faster than those for object-selection, that the bias for face detection is automatic, and that selection is based on feedforward representations that precede conscious perception.

Previous research has shown that saccadic eye movements towards faces can be elicited as quickly as 100 ms after image onset (Crouzet et al., 2010; Crouzet & Thorpe, 2011; Di Oleggio Castello & Gobbini, 2015; Honey et al., 2008). Rapid face detection is demonstrated in saccadic choice tasks, where two images are presented side-by-side of different objects and participants are instructed to fixate as quickly as possible on a target from a prespecified category, such as an animal (Guyonneau et al., 2006; Kirchner & Thorpe, 2006). In these tasks, it has been shown that saccadic eye movements towards face targets are highly accurate (typically around 90%) and faster compared to eye movements directed towards non-face objects, such as animals and vehicles (Crouzet et al., 2010; Crouzet & Thorpe, 2011). In fact, the fastest saccades (elicited within 150 ms of image onset) tend to be directed towards faces, even when they are not the intended target (Experiment 2, Crouzet et al., 2010; Fletcher-Watson et al., 2008), suggesting a strong bias towards human faces that generates especially fast saccadic responses.

Given that oculomotor responses take around 20-35 ms to generate (Heeman et al., 2017; Schiller & Kendall, 2004), the saccadic reaction times suggest that faces can be detected in as little as 80 ms. Visual processing can be roughly divided into two stages of processing: early, bottom-up processing carried by feedforward activation during the first 150 ms, followed by a later stage of "reentrant" processing carried by feedback activation (Felleman & Van Essen, 1991; Kreiman & Serre, 2020; Lamme & Roelfsema, 2000; Martin et al., 2019; Ungerleider & Haxby, 1994; VanRullen & Thorpe, 2001). Ultra-fast saccadic latencies place strong constraints on models of face detection, since they imply that face selectivity can be accomplished before the completion of the first feedforward pass through the ventral processing stream. Critically, it leaves little time for feedback connections to exert an effect on visual processing (Lamme & Roelfsema, 2000). It has therefore been claimed that eye movements towards faces are triggered by visual face cues extracted during early feedforward processing (Crouzet et al., 2010; Crouzet & Thorpe, 2011; Honey et al., 2008).

Computational (Riesenhuber & Poggio, 2002; Serre et al., 2007) and neural (Cauchoix et al., 2016; DiCarlo et al., 2012; Hong et al., 2016; Liu et al., 2002; VanRullen & Thorpe, 2002) models also indicate that feedforward processing may be sufficient to perform object categorization at very fast latencies, although it is thought to depend on coarse representations that are differentiated by low-level visual statistics (Crouzet & Thorpe, 2011; Honey et al., 2008; VanRullen, 2006) rather than high-level, semantic representations (but see Hershler & Hochstein, 2006). For example, in a saccadic choice task in which object category was task-irrelevant, Honey et al. (2008) found a bias to saccade towards faces relative to vehicles even when images were completely phase-scrambled. This suggests that amplitude spectrum information, which still remains after phase-scrambling, is an informative cue that can drive rapid saccades towards faces (see also Gaspar & Rousselet, 2009;

Wichmann et al., 2010). In a follow-up study, Crouzet & Thorpe (2011) showed that normalizing amplitude spectrum information across face and vehicle images significantly reduced saccadic accuracy and reaction time to face targets, but had no effect on saccadic movements towards vehicles. Thus, amplitude information seems important for the early selectivity mechanisms for faces. However, saccadic accuracy and speed remained higher for faces over vehicles, indicating that phase information is still the most important factor for this rapid response.

Given that eye movements towards faces appear to be executed based on coarse representations encoded during the feedforward sweep, it should be theoretically possible to observe selective eye-movements even when feedback processing is interrupted. One way that this may be accomplished is by presenting a second stimulus shortly after an initial target image to create an effect known as backward masking (Breitmeyer & Ogmen, 2000, 2006). Perceptual visibility of the initial target image is reduced as the stimulus onset asynchrony (SOA) between the target and masking image is decreased, and at a very short SOA (usually below 50 ms), backward masking can render a stimulus completely invisible (Bacon-Macé et al., 2005; Del Cul et al., 2007; Fahrenfort et al., 2007, 2017; Martin et al., 2019). Importantly, this effect has been attributed to a disruption to feedback processing. Electrophysiological data from primates (Cauchoix et al., 2016; Kovacs et al., 1995; Lamme et al., 2002) and humans (Bacon-Macé et al., 2005; Del Cul et al., 2007; Fahrenfort et al., 2007, 2017; Harris et al., 2011; Martin et al., 2019) support the view that backward masking largely disrupts feedback processing while leaving feedforward processing mostly intact. For example, Fahrenfort et al. (2007) found that masking visual targets had no effect on early occipito-temporal electrophysiological responses observed at approximately 110 ms post-stimulus, but it abolished a later occipito-temporal response occurring from 180-305 ms. Masking also reduced target detection to chance performance. This is consistent with the current understanding that visual awareness of a stimulus critically depends on recurrent processing in the feedback period (Boehler et al., 2008; Camprodon et al., 2010; Del Cul et al., 2007; Fahrenfort et al., 2017; Haynes et al., 2005; Koivisto et al., 2011, 2016; Lamme, 2010; Lamme et al., 2000; Lamme & Roelfsema, 2000; Martin et al., 2019; Pascual-Leone & Walsh, 2001; Ro et al., 2003).³

More recently, Martin et al. (2019) examined the nature of the neural interference between two successive stimuli with varying intervals between target images. When target images (animal images) were presented approximately 400 ms apart, each stimulus evoked a distinct pattern of EEG activation in posterior channels corresponding to an early

³ While recurrent processing may be necessary for conscious perception, recurrent processing has been observed in the absence of conscious perception, indicating that it is not sufficient (Fahrenfort et al., 2017).

feedforward response 150 ms post-stimulus and a later feedback response 230 ms post-stimulus. However, when the interval between the two targets was reduced, there was an increased overlap between the feedback processing of the first target and the feedforward processing of the second, and a greater cost to the behavioral detection of the first target compared to the second. Critically, this interference was reduced when targets were presented in different halves of the visual field to segregate their neural responses in separate hemispheres. These results reveal how feedback processing of the initial image “crashes into” the incoming feedforward signal from the mask and are consistent with an interruption theory of backward masking (Bridgeman, 1980; Di Lollo et al., 2000; Fahrenfort et al., 2007, 2017; Kovács et al., 1995; Lamme et al., 2002). Accordingly, the technique of backward masking has been said to be particularly useful for emphasizing bottom-up processing (Kreiman & Serre, 2020) and to “isolate between feed-forward dominated versus recurrent processing” (Serre et al., 2007).

In the current study, we tested the hypothesis that feedforward activation from face images would be sufficient to elicit fast saccadic responses towards faces in a saccadic choice task (Crouzet et al., 2010; Kirchner & Thorpe, 2006). Backward masking was used to interrupt feedback processing and to constrain visual processing of the test images to the initial feedforward pass. Given that semantic information is primarily carried by phase information (Oppenheim & Lim, 1981) and the earlier finding that phase information is the main driver of ultra-rapid face selective responses (Crouzet & Thorpe, 2011), we used phase-scrambles of the test images themselves as masking stimuli. Three target-mask SOA conditions were examined: 8 ms, 50 ms, and 400 ms. The 8 ms SOA was chosen because pilot testing showed that visual awareness of the test images was almost entirely suppressed; this SOA therefore allowed us to test the hypothesis that feedforward activation of a face image is sufficient to elicit a saccadic response towards it, even in the absence of conscious perception. However, based on previous findings of the timing of feedforward and feedback processing in posterior occipito-temporal areas, we predicted that feedforward processing of the mask would maximally interfere with the feedback processing of the target at an SOA of 50 ms. At this SOA, the feedforward activation elicited by the mask should occur 150-200 after the onset of the target image, thus putting it within the time period when long-range feedback connections are being established for target processing (Fahrenfort et al., 2007; Martin et al., 2019). This SOA allowed us to test the hypothesis that ultra-rapid saccades may be generated even when there is strong neural interference between the target images and the mask, but without completely suppressing visual awareness. Finally, we examined saccadic responses with a target-mask SOA of 400 ms. In this condition, we sought to replicate the image presentation conditions used in the original study by Crouzet et

al. (2010) within our masking paradigm to serve as a control condition, given that test images are effectively not masked at such a long SOA.

In addition to recording eye movements during the target detection tasks, we also asked participants to manually indicate on which side of the screen the target appeared. This provided an objective measure of target detection and allowed us to examine whether participants can report target location with and without conscious perception. Lastly, participants were asked to provide a subjective visibility rating on each trial to examine the extent to which target-mask SOA affected conscious perception and to confirm whether selective eye movements towards faces (and potentially houses) could be executed independent of subjective perceptual experience.

Under viewing conditions that were comparable to the original study by Crouzet et al. (2010), we replicated the saccadic response profile for faces when they were targets as well as when they were distractors. These saccadic responses were both faster than for house targets and harder to control. Critically, we observed the same saccadic response profile for face targets when they were masked with a moderate 50 ms target-mask SOA and a strong 8 ms target-mask SOA. The results support an early face-selective mechanism that is capable of escaping the effects of backward masking and is consistent with coarse feedforward face representations.

Methods

Participants

Twelve participants were recruited from our university's psychology research participation pool. Six participants were excluded from the final sample (see exclusion criteria below) and were replaced with another 6 participants. Exclusions were based on abnormal saccade behaviour in the 400 ms target-mask SOA condition for face detection. Three were excluded based on a median saccadic reaction time over 600 ms (i.e. failing to make eye movements when images were presented for 400 ms) and three were excluded based on saccadic response accuracy below 75%. For the final sample, ages ranged from 19-31 years of age ($M = 23.8$, $SD = 3.6$). 11 participants self-reported as female and 1 self-reported as male, and all had normal or corrected-to-normal vision.

Stimuli

We used a total of 100 grayscale photographic images taken from an existing database of natural scene images (Rossion et al., 2015) with either a face (50 images) or a house (50 images) appearing in the center, but which differed in terms of size, viewpoint, lighting, and background. Images had been normalized for mean pixel luminance and

root-mean-square contrast. Scrambled versions of the images had also been created by replacing the phase of each image by random coefficients. For masking stimuli, we created a composite image of the scrambled versions of the target images for each particular trial. All image modifications were done using MATLAB. Presented at a distance of 80 cm, the stimuli subtended approximately 14° of visual angle and were presented so that the center of the image was 4° horizontally away from the center of the screen. Images were presented on a gray background. For each participant, we randomly generated 50 image pairs with one face image and one house image in each pair.

Apparatus

Participants viewed the stimuli in a dimly lit room with their head in a chin rest to constrain head movements and maintain a viewing distance of 80 cm. Stimuli were displayed on a 25" Dell Alienware (AW2521HF) gaming monitor with the screen resolution set to 1920 × 1080 pixels and a refresh rate of 240 Hz. The experiment was written in MATLAB, using the Psychophysics Toolbox 3 extension (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

Procedure

The experiment was divided into two halves, starting with either a face detection task (faces as targets, houses as distractors) or the house detection task (houses as targets, faces as distractors).

The detection tasks combined a 2AFC saccadic choice response, a manual response, and a perceptual awareness rating (Figure 1). We used the Perceptual Awareness Scale (Ramsøy & Overgaard, 2004) as a purely introspective measure to examine the quality of participants' conscious perception of the test stimuli on each trial. This 4-point scale includes (1) No experience, (2) Brief glimpse, (3) Almost clear image, (4) Absolutely clear image, and has been shown to have correspondence to performance compared to other measures of visual awareness, including confidence ratings (Sandberg et al., 2010). Each trial consisted of the following:

1. A central fixation cross appeared for 800-1200 ms.
2. After a 200 ms gap, an image pair was displayed left and right of the screen center for either 8 ms, 50 ms, or 400 ms.
3. Images were replaced by the phase-scrambled composite of each image in the image pair for 300 ms.
4. Instructions appeared to prompt participants to manually indicate which side of the screen the target appeared using the F and J keys on the keyboard (until response).

5. Instructions appeared to prompt participants to manually rate their perceptual experience using the top number keys 1, 2, 3, or 4 on the keyboard (until response).

Participants were told that their main task was to look as quickly and as accurately as possible to the side containing the face (face detection task) or house (house detection task). To reduce conflicts in motor response planning, participants were told that manual response speed was not important and that they could not respond until after the masking stimuli were removed from the screen and the manual response probe was presented. Each trial was followed by a 1000 ms black intertrial interval. For each detection task, each participant performed 6 blocks of 50 trials.

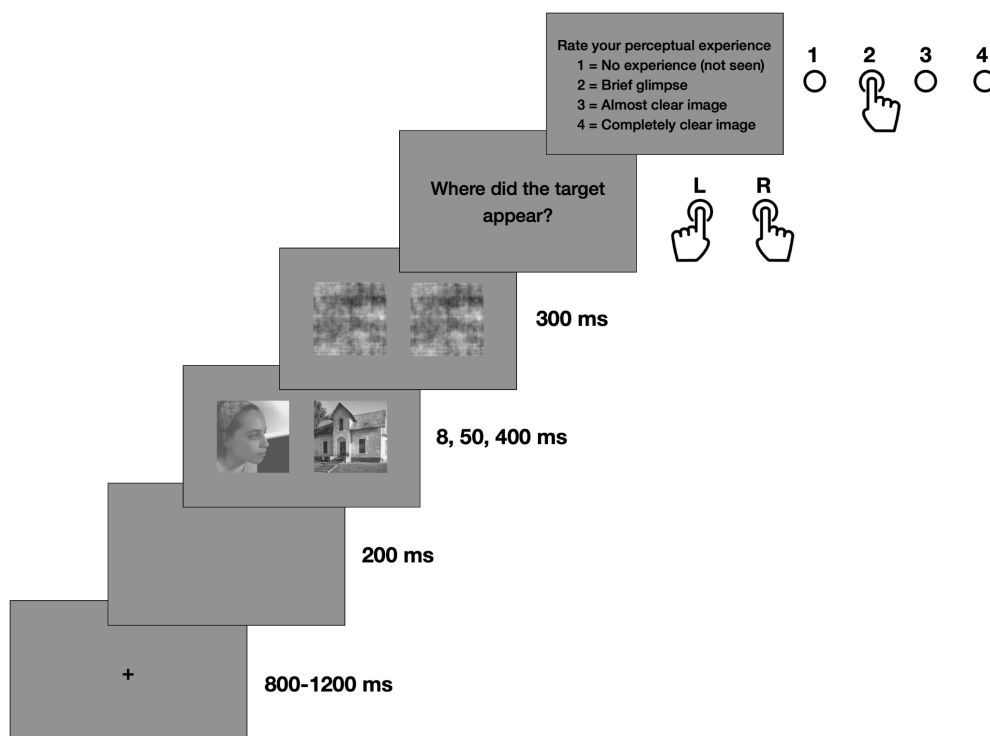


Figure 1. On each trial, a fixation cross appeared for 800-1200 ms, followed by a 200 ms interval, then the target and distractor images appeared for either 8, 50, or 400 ms. A masking image was presented immediately after for 300 ms. Participants were then prompted to indicate by manual response where they saw the target image and to rate their perceptual experience.

Eye Movement Recording

Eye movements were recorded with an SR Research EyeLink 1000 system (SR Research, Osgoode, ON) at a sampling rate of 2000 Hz using a 35mm lens and 940 nm infrared illuminator. Saccade detection was performed offline using EyeLink's built-in algorithm with standard cognitive thresholds for velocity ($30^\circ / \text{s}$), acceleration ($8000^\circ / \text{s}^2$), and motion (0.1°). For each trial, the onset of the first saccade after stimulus onset before the manual response probe was considered as the saccadic reaction time (SRT). Trials with saccades onsets faster than 70 ms were considered as anticipatory responses and discarded. A 9-point calibration was performed before each detection task.

Data analysis

Minimum saccadic reaction times (SRT) were determined by dividing the SRT distribution for each task and SOA condition into 10 ms time bins (i.e., the 100 ms bin contained latencies from 100 ms to 109 ms) and performing a chi-square test to determine whether it contained significantly more correct than incorrect responses ($p < .05$). Saccades were considered accurate if they were directed towards the intended target. If 5 consecutive bins were found to be significantly accurate, the first was considered to correspond to the minimum reaction time. Minimum SRT were obtained from the SRT distributions pooled across all observers.

We also created cumulative accuracy curves to examine the time-course of saccadic accuracy for each task and SOA condition. For each time point, the accumulated accuracy was calculated based on the proportion of correct responses for all saccades up to that SRT value. The curves therefore indicate how accuracy depends on response speed. 95% confidence intervals were obtained through bootstrap ($n = 500$). Since this measurement is very noisy for the first time-points, curves are shown from 110 ms for face detection and 180 ms for house detection (i.e., beginning 10 ms before reliably accurate saccadic responses in the 400 ms SOA condition for each task).

Results

The main result from the experiment was that participants were fast and accurate to saccade to faces even with very strong masking. The effect of the target-mask SOA on subjective visibility was first examined using a 2 x 2 repeated-measures ANOVA of the perceptual awareness ratings. This showed a main effect of target-mask SOA, $F(2, 22) = 120.03$, $p < .001$, $\eta^2 = .83$, and post-hoc tests showed that ratings significantly differed between all target-mask SOA conditions (all $p < .001$, Bonferroni-Holm corrected). As shown in Figure 2, the perceptual ratings indicate that the masking technique was effective in reducing the subjective visibility of the target images: on the majority of trials, participants

reported a “brief glimpse” in the 50 ms SOA condition ($M = 2.39$ [2.36, 2.40] 95% bootstrap confidence interval) and “no visual experience” in the 8 ms SOA condition ($M = 1.58$ [1.56, 1.61]). These were both significantly lower than ratings in the 400 ms SOA condition, which was intended to approximate natural viewing conditions, and for which participants reported “completely clear” perceptual awareness of the test images on the majority of trials ($M = 3.48$ [3.45, 3.50]). Surprisingly, visibility was not entirely abolished in the 8 ms SOA condition, as participants reported experiencing a brief glimpse of the images (rating 2) on 54%-41% of trials during the face and house detection tasks, respectively (see Figure 3).

Backward masking significantly reduced the rate of saccadic response (Figure 4). A 2×2 repeated-measures ANOVA indicated a main effect of target-mask SOA, $F(2, 18) = 86.2$, $p < .001$, $\eta^2 = .76$, with significant differences between all conditions (all $p < .05$, Bonferroni-Holm corrected). Saccades were observed on 74% of trials ($n = 1782$) in the 400 ms SOA conditions, but on only 19% ($n = 455$) and 10% ($n = 206$) of trials in the 50 ms and 8 ms SOA conditions, respectively. Pairwise comparisons of the average perceptual awareness rating for trials with and without saccades did not indicate any significant difference in visibility for trials on which a saccade was recorded (Wilcoxon signed-rank tests, all $ps > .10$).

Manual response accuracy across all conditions was very high (Table 1), with accuracy ranging from 98-99% for both face and house detection in the 50 ms SOA and 100 ms SOA conditions. Manual response accuracy was also significantly above chance in the 8 ms SOA conditions for both face ($M = 84.1\%$) and house ($M = 83.5\%$) detection as indicated by Wilcoxon signed-rank tests (both $p < .001$). Surprisingly, detection remained above chance for trials on which participants provided a rating of 1 (i.e. no visual experience) for both face (69.4% [62.7 78.5], $p = .003$) and house (75.3% [69.1 81.6], $p < .001$) detection. A 2×2 repeated-measures ANOVA of indicated a main effect of target-mask SOA on accuracy, $F(2, 22) = 42.97$, $p < .001$, $\eta^2 = .66$, and post-hoc tests showed that accuracy in the 8 ms condition was reliably different from accuracy in the two other condition (both $p < .001$, Bonferroni-Holm corrected).

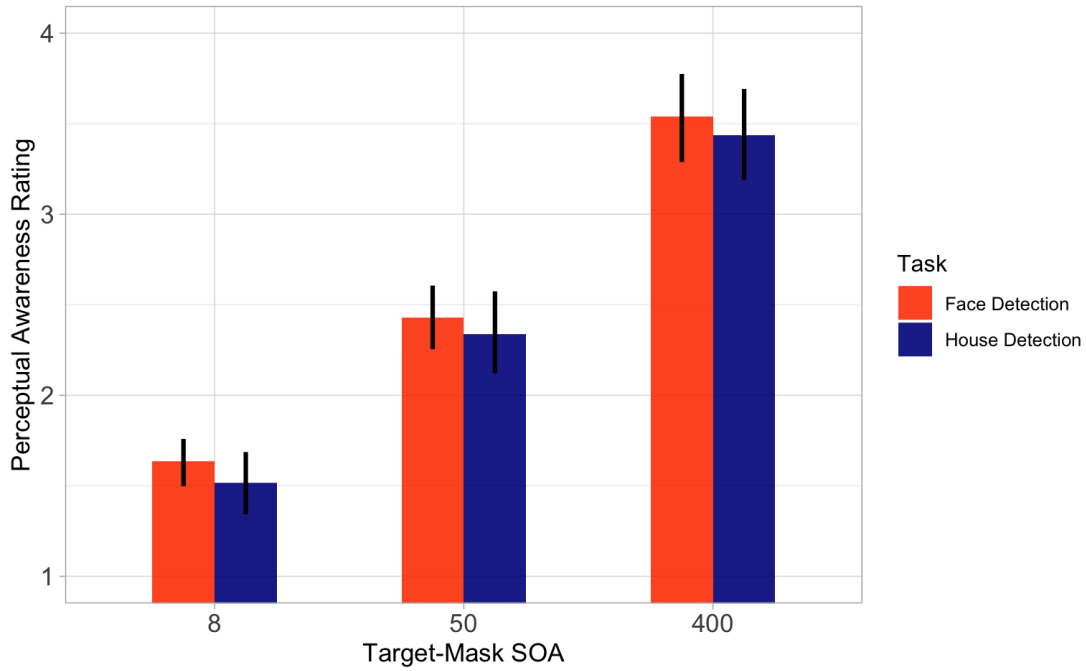


Figure 2. Average ratings on the Perceptual Awareness Scale for each condition and task (1 = No experience, 2 = Brief glimpse, 3 = Almost clear image, 4 = Absolutely clear image) based on participant responses collected on each trial.

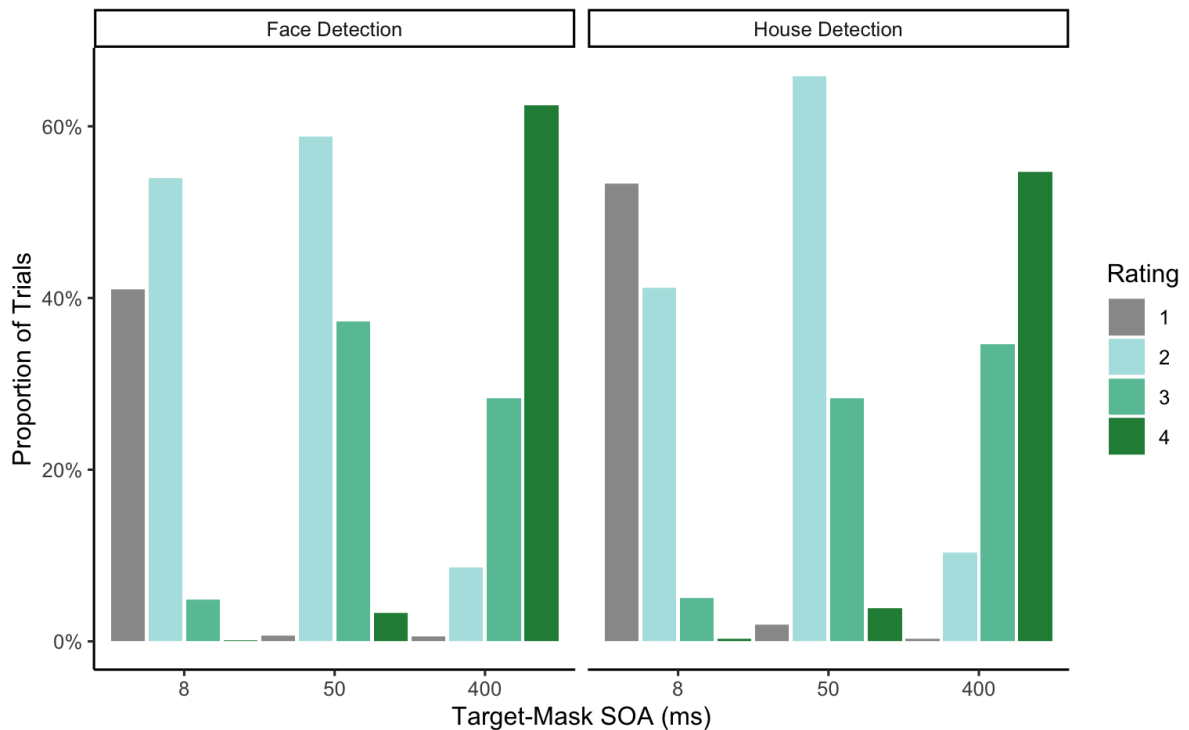


Figure 3. Distribution of responses on the Perceptual Awareness Scale for target-mask SOA condition and for each task.

Table 1. Mean saccadic accuracy and 95% bootstrapped confidence intervals for each task and target-mask SOA.

Task	SOA	Manual accuracy (%)	Saccadic accuracy (%)	Minimum SRT (ms)	Median SRT
Face detection	400 ms	99.1 [96.8 99.7]	95.7 [94.4 97.0]	120 [110 120]	177 [175 180]
	50 ms	98.9 [97.4 99.5]	86.1 [81.9 90.0]	130 [120 160]	278 [270 286]
	8 ms	84.1 [80.7 88.4]	83.3 [76.5 89.4]	140 [120 150]	255 [232 268]
House detection	400 ms	99.4 [98.8 99.7]	82.7 [80.2 85.0]	190 [180 200]	235 [230 241]
	50 ms	99.5 [98.9 99.8]	78.4 [73.0 83.8]	250 [205 280]	303 [290 314]
	8 ms	83.5 [77.2 88.9]	63.5 [54.1 75.7]	290 [195 300]	246 [216 267]

The main purpose of our study was to investigate whether the fast and accurate evoked by faces under normal viewing conditions could escape the disruptive effects of backward masking. Given that data was limited at the observer level, we first examined trial data pooled across observers to obtain more reliable estimates of saccadic accuracy and reaction times (Table 1). Average accuracy for the two masking conditions were compared against the 95% bootstrapped confidence interval of the unmasked condition (see Figure 4). Face detection accuracy in both the 50 ms (86.1% [81.9 90.0]) and 8 ms (83.3% [76.5 89.4]) conditions was lower than accuracy in the 400 ms (95.7% [94.4 97.0]) condition, although accuracy remained well above chance even with strong masking. For house detection, only the 8 ms (63.5% [54.1 75.7]) SOA condition was reliably different in saccadic accuracy from the 400 ms (82.7% [80.2 85.0]) condition, although accuracy also remained above chance. As shown in Figure 4, saccadic response to faces was reliably more accurate in both the unmasked 400 ms SOA condition and the strongly masked 8 ms SOA.

Estimates of minimum saccadic reaction time (SRT) for each SOA condition and task were obtained from reaction time distributions of trial data pooled across observers (Table 1). The minimum SRT represents the first 10 ms time bin in which the cumulative number of correct responses is significantly greater than the number of incorrect responses (chi-square test). We again compared minimum SRT values based on the 95% bootstrapped confidence intervals for data pooled across all observers. As shown in Figure 5, the minimum SRT for face detection remained fast across all target-mask SOA conditions, as the minimum SRT for the 8 ms (140 ms [120 150]) and 50 ms (130 ms [120 160]) conditions were not reliably different from the minimum SRT obtained in the 400 ms (120 ms [110 130]) condition. By contrast, the minimum SRT for house detection was reliably slower in both the 50 ms (250 ms [205 280]) and 8 ms (290 ms [195 300]) SOA conditions compared to the 400 ms condition (190 ms [180 200]).

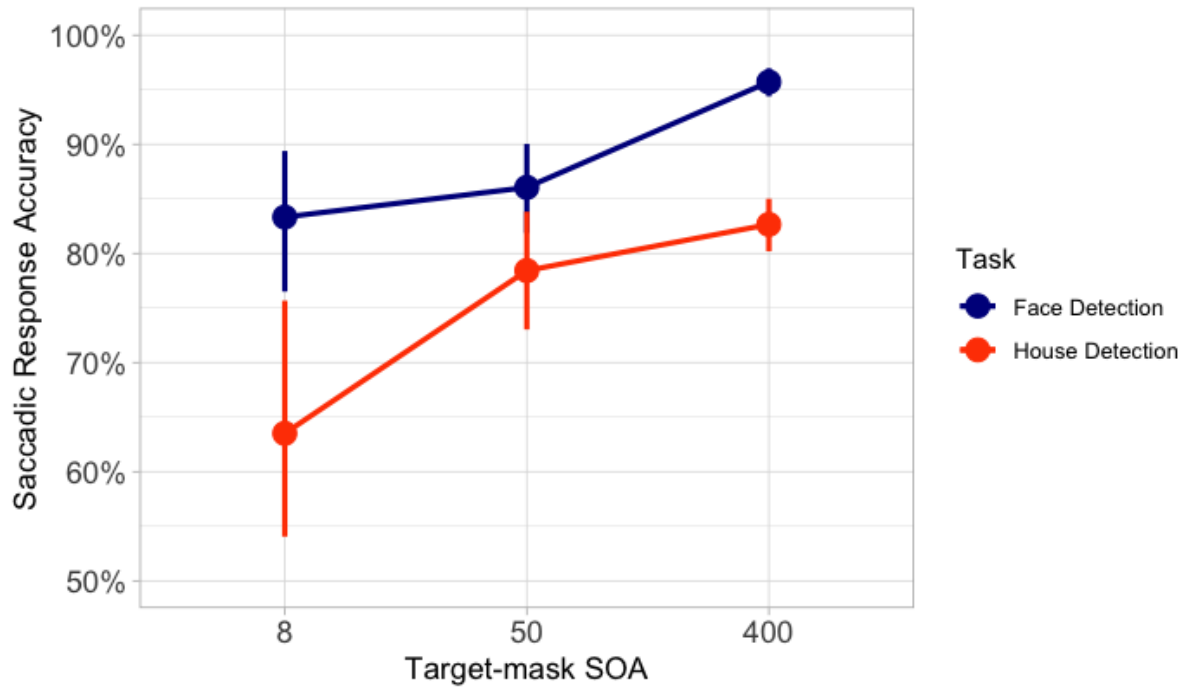


Figure 4. Mean saccadic accuracy for each target-mask SOA and task. Error bars represent 95% bootstrapped confidence intervals.

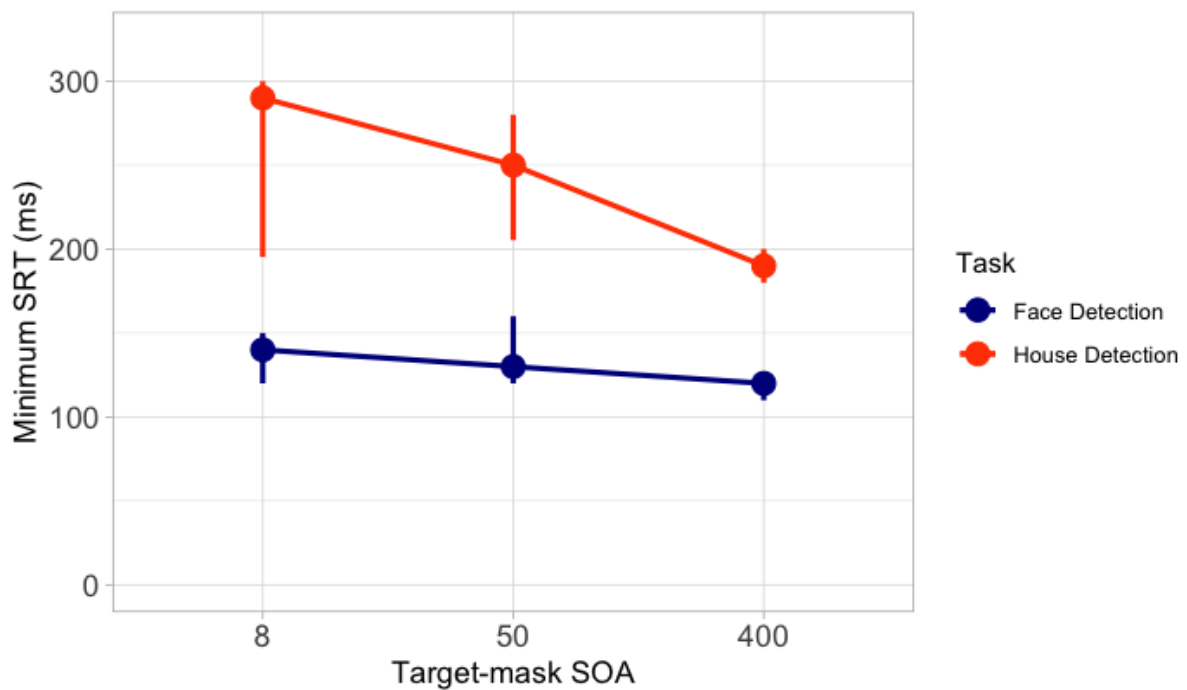


Figure 5. Minimum saccadic reaction time (SRT) for each target-mask SOA and task. Error bars represent 95% bootstrapped confidence intervals.

The reaction time distributions for correct and incorrect responses in each task are shown in Figure 6. Clear differences can be seen for saccadic responses to face and house in the 400 ms condition (Figure 6, top row). For faces, most saccadic responses were initiated within 100-250 ms, but for houses, the distribution is shifted and spread over approximately 150-300 ms. It is also clear that the fastest saccades tend to be directed towards faces, regardless of the task: in the face detection task, the earliest saccades are directed towards the face targets with almost none towards the house distractors, and in the house detection task, the earliest saccades are directed towards the face distractors with relatively fewer towards the correct house targets. The difference in the proportion of saccades to targets over distractors represents an underlying selectivity mechanism that mediates eye movements towards an intended target, and the emergence of this selectivity earlier in the distribution for face detection supports the idea of a different, faster mechanism for face categorization.

The time from the earliest face-selective saccades at 120 ms to the earliest house-selective saccades at 190 ms (i.e., when face distractors no longer out-compete house targets) suggests that saccades to faces initiated between 120-190 ms may arise from fast and automatic detection processes. This provides a time window of interest when examining the SRT distributions of the 50 ms and 8 ms SOA conditions for fast, feedforward face detection. As shown in Figure 6b.1 and 6c.1, the earliest face-selective responses occur within this time frame for both masking conditions (130 ms in the 50 ms SOA condition and 140 ms in the 8 ms condition), as indicated by the early difference in the number of correct saccades to face targets and incorrect saccades to house distractors. For house detection, there again appears to be an early bias towards face distractors within 120-190 ms in the 50 ms masking condition, followed by later selectivity for houses at 250 ms. In the 8 ms SOA condition, saccade direction appears to be at chance for house detection until 290 ms when saccades to house targets significantly outnumber saccades to face targets. Overall, the SRT distributions are consistent with the hypothesis of an early face-selective mechanism that supports more rapid and more accurate detection of faces compared to objects from a non-face category.

Finally, we examined the cumulative accuracy distributions for each task and condition (Figure 7) to compare the response accuracy based on the time that the response was made. Each point on these curves represents the proportion of correct responses for all saccades up to that time point. In Figure 7a, the accuracy curve for face detection in the 50 ms condition is shifted downward relative to the accuracy curve for the 400 ms condition. This indicates that masking with a 50 ms SOA affected overall saccadic accuracy, but that the onset of accurate saccadic response (i.e., the point at which accuracy reliably surpasses 50%) remained the same. This is consistent with the minimum SRT estimations described

above. The accuracy curve for the 8 ms SOA condition shows that saccades that were elicited in this condition tended to be accurate, especially true for the fastest saccades, and cumulative accuracy (represented at tail end of the distribution) was comparable to that observed in the 50 ms SOA condition.

The pattern of results for house detection is visibly different (Figure 7b). The accuracy curve for house detection in the 50 ms condition is shifted rightward relative to the accuracy curve for the 400 ms condition. This shows that masking at 50 ms SOA delayed the onset of accurate saccadic responses and is consistent with the slower minimum SRT found for the 50 ms SOA. Unlike the responses for face targets, the accuracy curve for the 8 ms SOA condition shows that saccades that were elicited in this condition tended to be inaccurate, and cumulative accuracy was less comparable to that of the 50 ms condition.

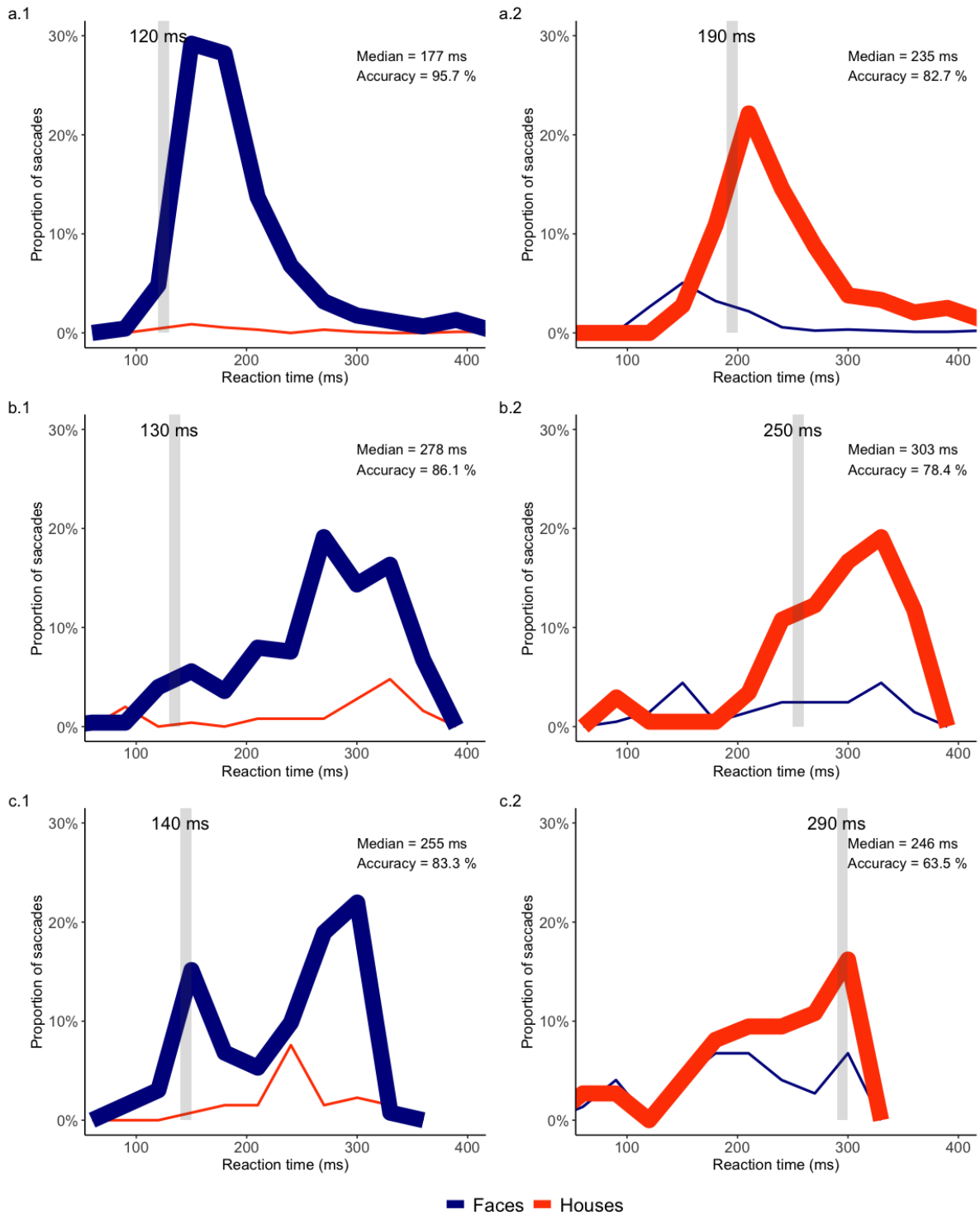


Figure 6. Distributions of saccadic reaction time pooled across observers when the task is to saccade toward faces (left column) or house (right column) in the 400 ms (top row), 50 ms (middle row) and 8 ms (bottom row) target-mask SOA conditions. Correct responses are plotted in thick lines and incorrect responses are plotted in thin lines.

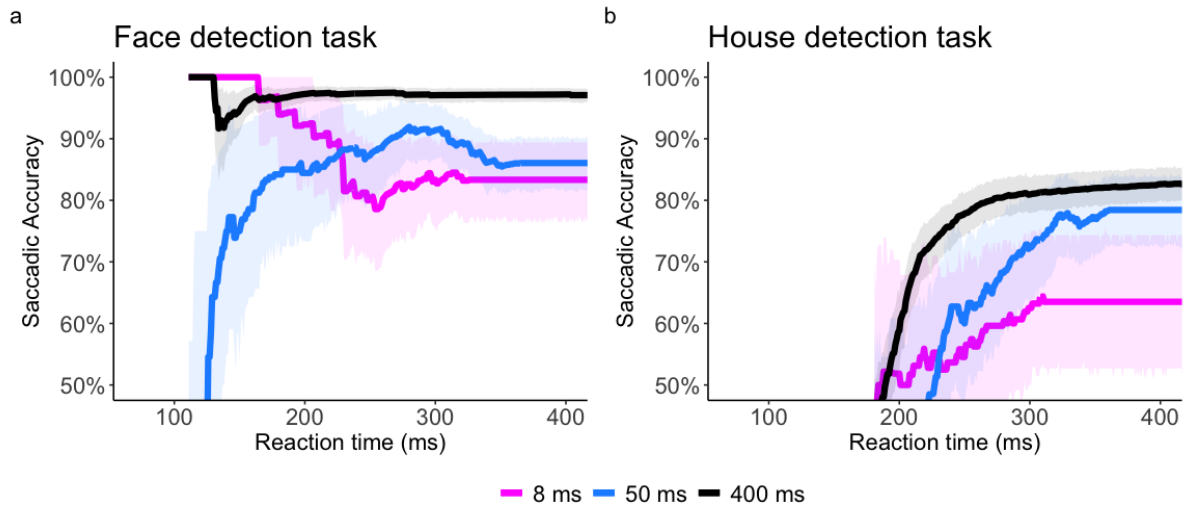


Figure 7. Cumulative accuracy curves were obtained from the SRT distributions for correct and incorrect responses for each task and condition, pooled across all observers. The shaded areas correspond to 95% bootstrapped confidence intervals. For each time point, the accumulated accuracy represents how accuracy depends on response speed. Since this measurement is very noisy for the first time-points, curves are shown from 110 ms for face detection and 180 ms for house detection (i.e. beginning 10 ms before reliably accurate saccadic responses in the 400 ms SOA condition for each task).

Discussion

In the current study, we replicated and extended the classic finding of ultra-rapid saccades towards faces using a backward masking procedure that was intended to disrupt feedback processing and conscious perception. We used two levels of masking: a moderate masking condition with a 50 ms target-mask SOA and a strong masking condition with 8 ms target-mask SOA. Perceptual awareness ratings confirmed that masking reduced subjective visibility, with participants reporting only a brief glimpse on the majority of trials with a 50 ms SOA, yet manual responses showed that categorization was still at ceiling. Thus, even with reduced visibility, sufficient information was available for accurate categorization. Perceptual awareness was not completely abolished in the stronger 8 ms SOA masking condition, but test images were reported to be invisible on roughly half the trials. Despite this substantial loss of visibility, accuracy remained remarkably high for both face and house detection, and even when observers reported no visual experience. This suggests that, even with extremely limited stimulus exposure and little-to-no conscious perception, the representations underlying category detection and response selection were still encoded.

The main finding was that ultra-rapid saccades towards faces were observed even with strong backward masking and reduced visibility. First, we replicated the pattern of results observed when test stimuli were presented for 400 ms. The minimum RT (the earliest saccade latency for above chance accuracy) for faces was between 120-130 ms, which is within the 100-135 ms range observed in previous studies (Crouzet et al., 2010; Di Oleggio Castello & Gobbini, 2015). Under masking conditions, the minimum RT ranged from 130-150 ms, although these estimates were not reliably different from the minimum RT obtained in the 400 ms condition. Crucially, these early saccades were highly accurate, with almost none of the saccades in the early SRT distribution directed towards houses. In other words, saccades made within 150 ms were highly selective for faces and were fast enough to escape the effects of backward masking. To the extent that backward masking disproportionately affects feedback and recurrent processing (Bacon-Macé et al., 2005; Cauchoix et al., 2016; Fahrenfort et al., 2007, 2017), the results are consistent with early face selectivity during the feedforward sweep.

The minimum RT for houses was between 190-200 ms, which is similar to the 170-200 ms range observed for vehicles when faces are distractors (Crouzet et al., 2010). Notably, we observed the same bias for the earliest saccades to move towards the face distractors in both the 400 ms and 50 ms SOA conditions. This provides further evidence that the fastest saccades are both selective for faces and automatic. Unlike saccadic responses to faces, backward masking affected the latency of accurate saccades towards houses. This was most evident in the rightward shift of the cumulative accuracy curve for the

50 ms SOA condition and the overall low accuracy in the 8 ms SOA condition. Compared to faces, it seems that the representations that drive selection for a non-face object category are more dependent on the recurrent processing that is disrupted by backward masking.

Although it did not impede categorization, backward masking significantly reduced the number of saccades that observers made during the task. One possible explanation for this is that the rapid stimulus offset and masking image onset could have disrupted the initiation of saccadic eye movements. To our knowledge, only one other study has incorporated backward masking into a saccadic detection task in which observers responded to simple “X” and “O” shapes with a 7 ms target-mask SOA, but saccadic responses were observed on over 90% of trials (Crouzet et al., 2014). This indicates that it is theoretically possible to initiate a saccade despite rapid stimulus presentation, at least with very simple stimuli. However, an important difference in their study was that the target appeared at varying locations and amongst a number of distractors, and so the task involved a visual search component that may not be possible to perform without eye movements. By contrast, the target and distractor location is predictable in the standard 2AFC saccadic choice task used here, and maintaining a point of fixation may be advantageous when stimulus exposure is so limited. It may also be that participants are more likely to prioritize a manual response when it is part of the stimulus response procedure (which it has not been in previous studies), despite instructions to fixate on the target. Fewer saccadic responses may therefore be due to a combination of visual and task factors. However, as manual response accuracy (especially for faces) indicates that stimulus category was still being accurately encoded, the saccadic responses that we *did* capture likely reflect those underlying category representations.

Overall, the current results contribute to recent evidence for several ways that the visual system may be specialized for fast-tracking face detection. First, neuroimaging and psychophysical findings indicate that face-selective processing begins before the ventral visual stream. Subcortical structures such as the amygdala have been shown to have robust face-selective responses, and connective pathways link these structures to areas of the cortical face network (Mende-Siedleck et al., 2013). Data from psychophysical paradigms also indicate that face perception is influenced by processing that occurs before the cortical level (Gabay, Burlingham, et al., 2014; Gabay, Nestor, et al., 2014). Campana et al. (2020) have also found converging evidence from eye-tracking, EEG, and fMRI to support face-selective responses in V1/V2 within 40 ms of image onset. They propose that such representations could potentially access a “shortcut” in the visual hierarchy to the circuits for initiating fast motor responses via connections from early visual areas to the superior colliculus (Sherman, 2016). Ultra-rapid and involuntary saccades to faces may therefore

arise from both subcortical specialization for face processing as well cortical shortcuts that allow face information to be quickly passed to circuits for motor response.

Behaviourally, the current study also contributes to the evidence for motor responses in the absence of conscious report. In the saccadic response measure, we observed a similar saccadic response profile for clearly visible faces as we did for faces with little-to-no visibility. In the manual response measure, we found remarkably high accuracy even when observers reported no conscious perception for both faces and houses (although it's possible that the presence of the face was used to guide responses in the house detection task). This suggests that fast feedforward representations are sufficient to activate motor regions and form a decision-variable in the frontal cortex before the onset of conscious perception (Freedman et al., 2003; Thorpe et al., 1996; VanRullen & Thorpe, 2001). Future work in human observers is needed to better understand how coarse visual representations activate saccadic responses, but at least one study found that undetected (masked) stimuli elicited EEG responses associated with motor response preparation and influenced subsequent behavioural response (Dehaene et al., 1998). In primates, single-unit recording of neurons in the frontal eye field (FEF) involved in transforming visual signals into motor commands were activated by both detected and undetected (masked) shape targets (Thompson & Schall, 1999). Although the FEF response was stronger for detected targets, the activation of the FEF without overt detection is consistent with our saccadic data.

The current work replicates and extends the seminal finding of ultra-fast saccades to faces by testing the hypothesis that face-selective saccadic responses would be evoked even under strong backward masking. Our findings not only support the claim that face-selective saccades are mediated by coarse feedforward representations, but they also demonstrate a capacity for accurate response selection in the absence of perceptual awareness. Overall, these findings reveal more about the role of unconscious processing and early visual processing in eye movements and response selection for faces and potentially other biologically-relevant stimuli.

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Chapter 5: General Discussion

The main purpose of this research was to better understand the neural mechanisms that underlie fast and automatic face processing. My work showed that rapidly presented, task-irrelevant images of a familiar face evokes a neural response that is recorded over the occipito-temporal region. I observed these responses for personally familiar faces that were either newly familiar, highly familiar, or the participant's own-face, and in a visual stimulation paradigm in which participants were engaged in an orthogonal colour detection task. Thus, the responses we observed were automatic, since they were not dependent on attention or under volitional control, and implicit, since the cognitive recognition process is implied from the neural response and not dependent on an explicit behavioural response. Moreover, since we extracted responses from the frequency domain, the use of fast periodic visual stimulation yields a response that necessarily generalizes across multiple images of the same identity rather than a response evoked by a single image. Any neural activity related to the structural encoding or pictorial cues of any given image would not be captured in the identity-specific neural response, unless it is a structural representation that is invariant to superficial image differences. This is analogous to the computational nature of face recognition itself, since theoretical accounts emphasize the importance of the visual system to tolerate (and therefore discount) the image variability that is unrelated to the face itself and to generate a response that generalizes across different encounters with the same face (Hancock et al., 2000; Kramer et al., 2017; Young & Burton, 2017, 2018). The identity-specific FPVS response that is isolated from the image-specific response is therefore well-aligned with the concept of an abstract face representation and which is hypothesized to underlie familiar face recognition (Bruce & Young, 1986; Young & Burton, 2017).

Given that FPVS responses are elicited automatically and without necessitating the explicit perceptual awareness of the category of each image, these responses may reflect the same processes that mediate the covert recognition responses observed in prosopagnosics (Bauer, 1984; De Haan et al., 1992; Tranel et al., 1995). Like rapid serial visual presentation paradigms (Potter, 2012; Potter et al., 2014; Potter & Levy, 1969), the stimuli in FPVS are presented briefly and within a continuous stream of images such that each image is both forward and backward masked (Retter et al., 2018). This temporally limits the availability of visual information for each image and, as was discussed in Chapter 4, emphasizes bottom-up processing and limits recurrent processing. As such, FPVS responses should primarily reflect feedforward processing, and leads to the question of whether automatic identity processing occurs as a result of the coarse representations activated during the first feedforward sweep. This would be consistent with the finding that

familiar face identification occurs involuntarily (Jenkins et al., 2002; Yan et al., 2017; Young et al., 1986), even when there is active intent to conceal it (Wiese et al., 2022), since feedforward processing occurs before conscious perception (Del Cul et al., 2007; Lamme, 2010; Lamme & Roelfsema, 2000). It is also consistent with the finding that observers can reliably saccade towards familiar faces (when unfamiliar faces are distractors) within 180 ms (Di Oleggio Castello & Gobbini, 2015). Taking into account the time needed to execute eye movements (see Chapter 4), this indicates that identity information is available for behavioural response in as little as 145 ms and with little time for long-range feedback processing (Lamme & Roelfsema, 2000; Martin et al., 2019; Thorpe et al., 1996). Future research that directly investigates the contribution of feedforward and feedback processing in automatic identity processing would provide a richer understanding of how face representations are accessed and may reveal informative differences between familiar and unfamiliar face processing.

Although feedforward and feedback processing dynamics are routinely discussed in the object recognition and computational modeling literature (Cauchoix et al., 2016; Kreiman & Serre, 2020; Serre et al., 2007; Thorpe et al., 1996), they are rarely considered in the context of face processing. Interestingly, the known timing of these distinct modes of processing would predict that the two event-related potential (ERP) components that are most commonly linked to face identification occur in different stages. As discussed in Chapter 2 and 3, effects of familiarity are often, but not always, found in the N170 (for recent review, see Caharel & Rossion, 2021), a component with an onset of about 150 ms and a peak amplitude of about 170 ms (Bentin et al., 1996; Rossion & Jacques, 2012). This timing would align with the first feedforward sweep, before it terminates in the frontal cortex between 150-200 ms post-stimulus onset (Lamme & Roelfsema, 2000; Thorpe et al., 1996; Vanrullen, 2008; VanRullen & Thorpe, 2001). However, differences between familiar and unfamiliar faces are more consistently found in the N250 component, which is usually measured at the same channels as the N170 but occurs in the later 200-300 ms time range (Kaufmann et al., 2009; Schweinberger et al., 1995; Schweinberger & Neumann, 2016; Tanaka et al., 2006). This would place the N250 in the later stage of recurrent processing, which is characterized by both long-range feedback activation and local recurrent processing (Lamme & Roelfsema, 2000). Whether the N170 or N250 reflects the activation of a face identity representation has been a matter of debate, but it might also be that the former reflects an initial feedforward activation of an identity representation while the latter reflects a reactivation (or elaboration) of that representation during recurrent processing. It may also be the case that the initial representation of identity is very coarse, which would explain why only the most familiar or well-learned face representations would be discernible from those for unfamiliar faces at the N170 (Caharel & Rossion, 2021). Again, contextualizing these

face-selective responses within a broader framework of brain dynamics may shed light on how face identity is represented and how information from other cognitive systems (such as semantic memory and affective systems) get integrated with visual processing signals.

In conclusion, the current work extends our understanding of the mechanisms that support the rapid detection and identification of faces. The speed at which face stimuli are categorized and identified has been a major focus of research in face processing, and our findings support the view that this rapid processing is also characterized by its automaticity, even at the limits of perceptual awareness.

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