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Revealing the neural time-course of direct gaze processing via spatial frequency manipulation of faces

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ABSTRACT

Direct gaze is a powerful social cue signalling the attention of another person toward oneself. Here we investigated the relevance of low spatial frequency (LSF) and high spatial frequency (HSF) in facial cues for direct gaze processing. We identified two distinct peaks in the ERP response, the N170 and N240 components. These two components were related to different stimulus conditions and influenced by different spatial frequencies. In particular, larger N170 and N240 amplitudes were observed for direct gaze than for averted gaze, but only in the N240 component was this effect modulated by spatial frequency, where it was reliant in LSF information. By contrast, larger N170 and N240 components were observed for faces than for non-facial stimuli, but this effect was only modulated by spatial frequency in the N170 component, where it relied on HSF information. The present study highlights the existence of two functionally distinct components related to direct gaze processing.

1. Introduction

Rapid and accurate perception of eye-gaze direction is an essential social function which permits the understanding of another's allocation of attention. Direct eye-gaze, in particular, signals when the attention of another is directed towards oneself and is therefore crucial for human social interaction throughout development to adulthood (Kleinke, 1986). In line with its importance, a number of visual search studies have suggested that direct gaze is a more salient visual cue than other gaze directions (Doi, Ueda, & Shinohara, 2009; Senju, Hasegawa, & Tojo, 2005; von Grünau & Anston, 1995), a phenomenon termed the stare-in-the-crowd effect. This faster orienting towards faces with direct gaze, compared with averted gaze, has further been shown in express saccades (saccades occurring under 130 ms), supporting the very early processing of gaze information (Mares, Smith, Johnson, & Senju, 2016). Accordingly, neural responses as observed through event related potentials (ERP) have shown that direct gaze is differentiated from averted gaze in early components such as the P100 (Berchio et al., 2016; Conty, Dezecache, Hugueville, & Grèzes, 2012).

The importance of different spatial frequency bands for the fast processing of direct gaze remains, however, poorly understood. It has been proposed that coarser information, meaning low spatial frequencies (LSF), are important for fast object processing by activating faster magnocellular pathways reliant on this type of visual information (Bar, 2003, 2004). Early processing and detection of direct gaze in particular, has been suggested to rely on LSF information (Senju & Johnson, 2009). However, different studies have yielded very mixed results regarding the spatial frequencies that support gaze processing. The importance of LSF, for gaze processing has been shown in a gaze cueing paradigm (de Jong, van Engeland, & Kemner, 2008). de Jong et al. (2008) found a N200 ERP component effect, in neurotypical participants, for gaze cueing validity in which larger N200 amplitudes were observed for faces containing only LSF information compared with faces containing only more detailed high spatial frequency (HSF) information. This pattern was reversed for participants with autism spectrum disorders (ASD). Similarly, newborns, who lack sensitivity to HSFs (Norcia, Tyler, & Hamer, 1990) and rely on LSF for face recognition (de Heering et al., 2008), are sensitive to gaze information, looking longer towards faces with direct gaze than towards faces with averted gaze (Farroni, Csibra, Simion, & Johnson, 2002).

On the other hand, it is not clear how the critical spatial frequency bandwidths for gaze processing change throughout development, with HSF information being critical for the explicit discrimination between leftwards and rightwards gaze directions in adults (Vida & Maurer, 2015). Furthermore, early neural differentiation between direct and averted gaze has only been observed for broad spatial frequency, while no effects of gaze direction were found for stimulus displayed only with high or low spatial frequency information (Burra, Kerzel, & George,

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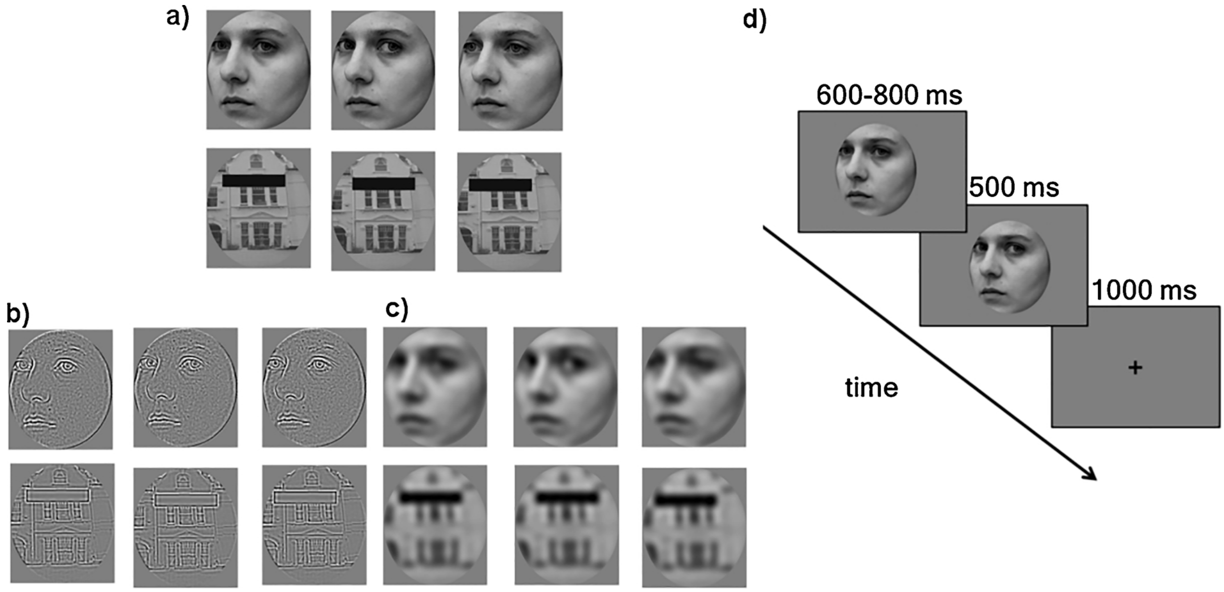

Fig. 1. Examples of face and building stimuli in a) BSF, b) HSF and c) LSF. d) Schematics of the procedure.

2016).

Thus, the present study aims to analyse the contribution of LSF and HSF for direct gaze processing in an adapted version of a task that has previously shown to lead to enhanced processing of direct gaze, both at neural and behavioural levels (Conty, N'Diaye, Tijus, & George, 2007). The ERP paradigm used by Conty et al. (2007) has previously shown a larger N170 component for dynamically presented direct gaze in comparison with averted gaze, which was accompanied by a better recognition of direct gaze. Several studies have shown the face selective N170 component, an early negativity occurring over lateral occipito-temporal brain regions, is routinely and robustly associated with face perception and encoding (e.g. Bentin, Allison, Puce, Perez, & McCarthy, 1996; Itier & Taylor, 2004) and is sensitive to dynamic gaze motion (Conty et al., 2007; Latinus et al., 2015; Puce, Smith, & Allison, 2000).

ERP studies analysing LSF and HSF modulation of the N170/M170 in face processing, using different tasks, have found mixed results. While some studies have reported no differences in this component between stimuli containing HSF or LSF information (Holmes, Winston, & Eimer, 2005; Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005), other studies have reported either an advantage for stimuli containing only LSF information (Goffaux, Gauthier, & Rossion, 2003; Halit, de Haan, Schyns, & Johnson, 2006; Vlamings, Goffaux, & Kemner, 2009) or for stimuli containing only HSF information (Hsiao, Hsieh, Lin, & Chang, 2005; Nakashima et al., 2008). Task dependent effects have been observed to modulate N170 amplitudes to specific bandwidths of spatial frequency in faces (Goffaux, Jemel, Jacques, Rossion, & Schyns, 2003). Similarly, the use of different spatial frequency bands has been shown to be task dependent in a previous behavioural study (Schyns & Oliva, 1999). Thus, to try to avoid a direct impact of task, the present study only asked participants to detect a rarely occurring target to keep participants attentive.

Original images of faces with direct and averted gaze were filtered to create stimuli presenting high, low and broad (unfiltered) spatial frequencies. Furthermore, matched conditions were created with pictures of buildings, which allowed for the dissociation between general motion processing and eye gaze processing. As a secondary question, the current study also allowed us to analyse separately the impact of HSF and LSF information on the ERP components associated with facial motion compared to non-facial motion, and those associated with different direction of gaze shift.

2. Methods

2.1. Participants

Fifteen participants (10 female, between 21 and 48 years old, mean age: 33.13 years) were tested. They were right handed, with normal or corrected to normal vision. All participants signed a written informed consent form and were paid a small sum or received course credits for their participation. The study was approved by the ethical committee of the Department of Psychological Sciences, Birkbeck College, University of London.

2.2. Stimuli

Twenty-four greyscale digitized photographs were used as stimuli, 12 of which were of faces (6 male and 6 female) and the other 12 were of buildings. Faces had neutral expressions and were cropped to exclude external features such as hair. A similar oval cropping was used for the building stimuli. Faces with direct and averted (30° of centre, counterbalanced between right and left) gaze directions were included (see George et al., 2001 for details about the stimuli generation process). Faces were presented oriented to the left and to the right (30°), to avoid a symmetry confound. To be able to simulate a change in gaze direction, a morphed version of direct and averted gaze was created to establish a common baseline for both conditions (eye-gaze at approximately 15°). Similarly, a black bar was inserted in building images either centred, deviated to the left or to the right or morphed between them (Fig. 1a). This control was used to account for differences in the perception of motion to the centre or towards the periphery. HSF (Fig. 1b) and LSF (Fig. 1c) versions of all images were created by applying a high (above 24 cycles per stimuli) and low (below 8 cycles per stimuli) pass filter. Second order Butterworth filters were used to filter stimuli, using an in house Matlab script (The Mathworks, Natick, MA). The selected spatial frequency cut-offs per image and filtering were similar to the ones used by Schyns and Oliva (1999). These spatial frequency cut-offs are outside the mid-range spatial frequencies considered crucial for face recognitions (8–16 Hz) and have been previously used in other ERP studies tackling the spatial frequency information used for face processing (Halit, de Haan, & Johnson, 2003). Images without any filtering were also presented (BSF). Mean luminance and root mean square contrast (RMS) were equalized between all conditions. RMS has been shown to be the best index for perceived