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Temporal frequency tuning of cortical face-sensitive areas for individual face perception

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In a highly dynamic visual environment the human brain needs to rapidly differentiate complex visual patterns, such as faces. Here, we defined the temporal frequency tuning of cortical face-sensitive areas for face discrimination. Six observers were tested with functional magnetic resonance imaging (fMRI) when the same or different faces were presented in blocks at 11 frequency rates (ranging from 1 to 12 Hz). We observed a larger fMRI response for different than same faces – the repetition suppression/adaptation effect – across all stimulation frequency rates. Most importantly, the magnitude of the repetition suppression effect showed a typical Gaussian-shaped tuning function, peaking on average at 6 Hz for all face-sensitive areas of the ventral occipito-temporal cortex, including the fusiform and occipital "face areas" (FFA and OFA), as well as the superior temporal sulcus. This effect was due both to a maximal response to different faces in a range of 3 to 6 Hz and to a sharp drop of the blood oxygen level dependent (BOLD) signal from 6 Hz onward when the same face was repeated during a block. These observations complement recent scalp EEG observations (Alonso-Prieto et al., 2013), indicating that the cortical face network can discriminate each individual face when these successive faces are presented every 160–170 ms. They also suggest that a relatively fast 6 Hz rate may be needed to isolate the contribution of high-level face perception processes during behavioral discrimination tasks. Finally, these findings carry important practical implications, allowing investigators to optimize the stimulation frequency rates for observing the largest repetition suppression effects to faces and other visual forms in the occipito-temporal cortex.

Introduction

In everyday life the human brain is constantly presented with many different faces (e.g., when walking in a crowd). It is able to differentiate these faces very rapidly, even when they have never been seen before (i.e., unfamiliar faces). Neuroimaging studies have investigated individual face discrimination by taking advantage of the phenomenon of repetition suppression, also called fMRI adaptation (Grill-Spector and Malach, 2001; Grill-Spector et al., 2006). Specifically, the reduction of the fMRI signal for repeated compared to different faces in the fusiform gyrus, and more posteriorly in the lateral occipital complex, points to the involvement of face-sensitive areas in individual face discrimination (e.g., Davies-Thompson et al., 2009; Gauthier et al., 2000; Grill-Spector and Malach, 2001; Grill-Spector et al., 1999).

In the present study, we investigated the temporal rate at which individual faces can be discriminated in functional brain areas that respond more to pictures of faces than nonface objects ("face-sensitive areas", Haxby et al., 2000; Puce et al., 1995; Sergent et al., 1992). This issue is important because humans live in a highly dynamic visual world in which they are exposed to many different faces within a short timeframe, or even simultaneously. Therefore, being able to rapidly individualize faces may be critical for adequate social interactions. Moreover, face-sensitive areas along the cortical visual hierarchy may have different temporal frequency tuning functions, which may shed light on their respective contribution to face perception.

Most neuroimaging studies that have addressed the issue of temporal frequency tuning have used low-level stimuli such as flickering pattern-flashes (Pastor et al., 2003), checkerboards (Fox and Raichle, 1984, 1985), gratings (Muthukumaraswamy and Singh, 2008; Singh et al., 2000) or chromatic versus achromatic simple stimuli (D'Souza et al., 2011; Liu and Wandell, 2005; Mullen et al., 2010). Using object shapes, Mukamel et al. (2004) reported a significant but relatively lower signal increase in high-level as compared to low-level areas when the stimulation rate of face and house stimuli increased from

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1 Hz to 4 Hz. Above 4–5 Hz, a decline of temporal frequency tuning to faces in category-sensitive high-level visual areas such as the "fusiform face area" (FFA, Kanwisher et al., 1997) has been reported in two studies (Gauthier et al., 2012; McKeeff et al., 2007).

Here, the temporal frequency tuning of individual face discrimination was investigated by studying the repetition suppression effect across many stimulation frequency rates. To our knowledge, the frequency tuning of repetition suppression has never been determined, whether low-level or high-level visual stimuli are concerned. Specifically, we measured fMRI responses to face stimuli presented at multiple frequency rates (1–12 Hz) in two conditions of interest, namely repetition of the exact same face during a block or different faces, and we computed the response difference between these two conditions. We focused our investigation on the whole set of face-sensitive areas identified in an independent whole-brain functional face localizer (Rossion et al., 2012). In line with independent results obtained with scalp electroencephalogram (EEG) concerning both frequency tuning (Alonso-Prieto et al., 2013) and the time course of individual face repetition effects (Jacques et al., 2007), we hypothesized a maximal neural adaptation effect at 6 Hz on average, expecting a decrease of the peak of the frequency tuning function along the cortical hierarchy of face-sensitive areas.

Methods

Subjects

Six healthy volunteers (4 females) with normal visual acuity participated in the main experiment and performed two fMRI sessions. Due to the large amount of different points sampled in the parametric design (11 frequencies × same/different faces, see *Procedure*) and to the specific hypotheses about the tuning function of the responses to multiple temporal frequencies (see *Introduction*), a rather limited number of participants was tested in two fMRI sessions. All participants were undergraduate students (mean age = 23.5 +/ −2.3) recruited at Maastricht University. Their participation was compensated with cash money. After the explanation of the procedures, participants signed an informed consent form. The ethical committee of the faculty (Ethical Committee Psychology, ECP) approved the study.

Stimuli

The stimuli consisted of 18 different faces (males in the first 2 runs and females in the remaining 3 runs). In 2 runs (out of 5) we used a set of face pictures from the Tubingen Max Planck Institute (MPI) database of laser-scanned (Cyberware TM) heads. For the remaining 3 runs, faces were selected from a large set of pictures used in a recent behavioral study (Laguesse et al., 2012). The pictures were in color, they were all taken under similar lightning with neutral facial expressions and they were additionally equalized in luminance. Faces were presented on a light-gray background and were unfamiliar to the participants.

Procedure

Face stimuli were presented in blocks and were repeated with a variable stimulation rate ranging from 1 Hz (1 face per second) to 12 Hz (12 faces per second = one face every 83.33 ms). Specifically, faces were presented at 11 different frequencies: 1, 2, 3, 4, 5, 6, 6.66, 7.5, 8.57, 10, and 12 Hz. These rates were selected to cover a wide range of stimulation frequencies with a fine-grained sampling, and were constrained by the refresh rate of the stimulation monitor (i.e., 60 Hz/frequency rate = integer). Faces were presented according to a sinusoidal contrast-modulation function, i.e., every cycle started with a gray background changing sinusoidally into a face stimulus, which reached its full contrast at half a cycle (Fig. 1.c, see Rossion and Boremanse, 2011). Compared to a boxcar ON/OFF function, the sinusoidal function makes the face stimulus appear and disappear more smoothly, and has been successfully used in recent EEG studies to elicit robust periodic visual responses to faces (Rossion and Boremanse, 2011). Specifically, the first sample of a cycle consisted of a face with 0% contrast, at half a cycle the face was presented at full contrast and the last sample was again a 0% contrast stimulus. It follows that for high frequency rates, the number of samples per cycle is smaller compared to low frequency rates. However, as a face is clearly visible at 30–35% of contrast, even at 12 Hz (5 samples per cycle at a 60 Hz refresh rate of the monitor) there are 4 consecutive samples at which the face is visible (40%–80%–80%–40%). Therefore, it is reasonable to assume that also for very high frequencies, most of the samples per cycle represented "perceivable" faces. The stimuli were delivered in Matlab (the Mathworks) via a custom-made application (SinStim) whose timing accuracy was verified by an oscilloscope and validated by the frequency spectrum analysis of a similar EEG study.

The faces in a block were either identical (same) or different from each other (Fig. 1.b). In each block where the same face was presented repeatedly, the program selected one of the 18 faces, randomly. In the blocks of different faces, all of the 18 faces were presented in random order, with the constraint that a given face was never presented twice consecutively. Thus, the complete design consisted of a total of 22 conditions: 11 frequencies × same/different faces (Fig. 1.a). An automatic algorithm ensured that the order of those conditions was randomized for every run.

The participants performed 5 runs in total (spread over two fMRI recording sessions to include the functional localizer runs, see the next section, *Localization of face-sensitive areas*), each consisting of 22 blocks (one block per condition). A run started with a blank screen lasting for 18 s after which the first block-condition was presented. A single block lasted for 27 s and it was followed by a resting period of 9 s. During a block of faces the participant was instructed to attend to a black cross that was positioned at the level of the nasion of the face (roughly corresponding to the center of the screen). In order to keep the participants' attention high and constant during a block of faces, they were asked to press a response key when the black cross turned red (between 2 and 3 times during a block and in a random position within the block). Moreover, in order to eliminate low-level repetition suppression effects, the faces changed randomly in size (88–112% of a base face) at every cycle. A base face size subtended approximately 9.1° (height) × 6.3° (width) of visual angle (8.0°× 5.5°–10.2° × 7.0°) and was aligned with the center of the screen. The participants were not made aware of any of the manipulations described. The entire session lasted approximately 60 min.

Localization of face-sensitive areas

An independent functional localizer, fully described in a recent study (Rossion et al., 2012), was used to localize the face-sensitive areas in each individual brain. This localizer consisted of 4 different categories of stimuli photographs: faces, cars, scrambled faces and scrambled cars. The original photographs of the face stimuli were edited to eliminate external features (e.g., hair). Both the face and car categories consisted of 43 different stimuli (22 of the 43 faces were female), they were presented in color, in frontal view and embedded in a gray rectangle. Scrambled faces and scrambled cars were made by applying a Fourier phase randomization procedure. This algorithm replaces the phase spectrum related to the Fourier transformation of the face and car stimuli with random values while keeping the amplitude spectrum of the image unaltered (Nasanen, 1999). This procedure degrades completely category-related information and yields images that preserve the global low-level properties of the original image (luminance, contrast, spectral energy, etc.). The pictures of the 4 categories of stimuli subtended equal shape, size and contrast against background.

The participants performed 3 runs, each lasting for 11 min. The 4 different categories of stimuli were presented in blocks. In a single run 6 blocks were presented per category, for a total of 24 blocks. Each block lasted for 18 s and 24 stimuli were presented in each block (no resting