



Repetition probability effects for inverted faces



Mareike Grotheer^{a,b}, Petra Hermann^d, Zoltán Vidnyánszky^{c,e}, Gyula Kovács^{a,b,c,*}

^a Institute of Psychology, Friedrich-Schiller-University of Jena, Am Steiger 3, 07743 Jena, Germany

^b DFG Research Unit Person Perception, Friedrich-Schiller-University of Jena, Leutragraben 1, 07743 Jena, Germany

^c Department of Cognitive Science, Budapest University of Technology and Economics, Műgyetem rkp. 3, 1111 Budapest, Hungary

^d Faculty of Information Technology and Bionics, Pázmány Péter Catholic University, Práter str. 50/A, 1083 Budapest, Hungary

^e Brain Imaging Centre, Research Centre for Natural Sciences, Hungarian Academy of Sciences, Magyar tudósok körútja 2, 1117 Budapest, Hungary

ARTICLE INFO

Article history:

Accepted 3 August 2014

Available online 11 August 2014

Keywords:

Repetition suppression

Faces

Inversion

Prediction

Expectation

ABSTRACT

It has been shown, that the repetition related reduction of the blood-oxygen level dependent (BOLD) signal is modulated by the probability of repetitions (P(rep)) for faces (Summerfield et al., 2008), providing support for the predictive coding (PC) model of visual perception (Rao and Ballard, 1999). However, the stage of face processing where repetition suppression (RS) is modulated by P(rep) is still unclear. Face inversion is known to interrupt higher level configural/holistic face processing steps and if modulation of RS by P(rep) takes place at these stages of face processing, P(rep) effects are expected to be reduced for inverted when compared to upright faces. Therefore, here we aimed at investigating whether P(rep) effects on RS observed for face stimuli originate at the higher-level configural/holistic stages of face processing by comparing these effects for upright and inverted faces. Similarly to previous studies, we manipulated P(rep) for pairs of stimuli in individual blocks of fMRI recordings. This manipulation significantly influenced repetition suppression in the posterior FFA, the OFA and the LO, independently of stimulus orientation. Our results thus reveal that RS in the ventral visual stream is modulated by P(rep) even in the case of face inversion and hence strongly compromised configural/holistic face processing. An additional whole-brain analysis could not identify any areas where the modulatory effect of probability was orientation specific either. These findings imply that P(rep) effects on RS might originate from the earlier stages of face processing.

© 2014 Elsevier Inc. All rights reserved.

Introduction

A large body of experiments found, using various electrophysiological and neuroimaging techniques, that the neural activity decreases as a given stimulus is repeated (Grill-Spector et al., 2006; Gross et al., 1967, 1969; Henson and Rugg, 2003; Krekelberg et al., 2006; Schacter et al., 2004; Wiggs and Martin, 1998). The neural mechanisms of this reduced neural activity (denoted as repetition suppression (RS)) for repeated stimuli when compared to non-repeated ones are unclear as of today. While one explanation suggests that RS is related to the local alteration of the synaptic inputs/spike frequency of the neurons (De Baene and Vogels, 2010; Kohn and Movshon, 2003; Priebe et al., 2002; Sawamura et al., 2006), the theory of predictive coding (PC) suggests the involvement of top-down connections in determining RS. In the PC approach of visual processing Rao and Ballard (1999) proposed that hierarchically higher areas send predictions about sensory input to lower level areas via strong feedback connections. Lower level areas

then, in turn, compute the differences (or discrepancies) between the top-down predictions and the actual sensory input. This discrepancy or residual prediction error signal (ε) is then forwarded to higher areas to re-estimate and update the predictions. The more closely a top-down prediction matches the incoming sensory input, the smaller the feed-forward ε is, which maximizes the “efficiency” of the CNS in the sense that the neural activity evoked by predicted stimuli is less than that evoked by novel and hence unexpected stimuli (Friston and Kiebel, 2009). According to PC accounts RS reflects the reduction of ε during subsequent bottom-up/top-down processing iterations within a hierarchical system (Kveraga et al., 2007): repeating a stimulus (or adapting to it) leads to its increased expectation and recalibrates the predictions such that the adapted stimulus evokes reduced ε , which leads to RS in an area.

Indeed, in recent years a large body of direct evidence emerged that supports the PC explanation of RS. The first was Summerfield et al. (2008) who, using functional magnetic resonance imaging (fMRI), showed that the repetition probability (P(rep)) of a stimulus determines the degree of RS: the neuroimaging marker of RS, the fMRI adaptation (fMRIa) of the blood oxygenation level-dependent (BOLD) signal, was significantly larger in the fusiform face area (FFA) in blocks with high P(rep) of face stimuli than in blocks where repetitions were less frequent. This suggests that the modulation of P(rep) allows the

* Corresponding author at: Institute of Psychology, Friedrich-Schiller-University of Jena, Am Steiger 3, 07743 Jena, Germany.

E-mail addresses: mareike.grotheer@uni-jena.de (M. Grotheer), hermann.petra@gmail.com (P. Hermann), vidnyanszky.zoltan@gmail.com (Z. Vidnyánszky), gyula.kovacs@uni-jena.de (G. Kovács).

subjects to build and modify expectations whether stimulus repetition is likely to occur in a given block or not and that expectation of repetition reduces the BOLD signal further. Later, several studies replicated these results for human faces. Larsson and Smith (2012) found that P(rep) influences fMRIa in several visual areas, provided that the subjects attended the face stimuli. Kovács et al. (2012) showed that P(rep) influenced fMRIa equally for overlapping and non-overlapping peripheral stimulus arrangements in the FFA and the occipital face area (OFA). In an EEG study Summerfield et al. (2011) added the factor of stability/volatility to their previous design in a way that the probabilities of repetition and alternation changed in every 10 (volatile) or only in every 30–40 trials (stable). They found that P(rep) affected RS only during the stable periods, suggesting that the rate of change of probability of repetitions plays a significant role in determining the magnitude of RS. Egner et al. (2010) used a cueing paradigm to manipulate perceptual expectation while varying stimulus features (faces or houses) and found that the two factors interacted, whereby expectation determined the feature selectivity of FFA, a result that is most efficiently explained by PC models. Altogether, these neuroimaging and electrophysiological studies suggest that the attenuated neural response for repeated stimuli is a direct neural correlate of reduced ϵ of the bottom-up and top-down representations, as suggested by the predictive coding models of neural functions (Friston, 2005). Note however, that the role of stimulus expectation in generating RS for non-face stimuli has been directly called into question by some recent studies (Grotheer and Kovács, 2014; Kaliukhovich and Vogels, 2011; Kovács et al., 2013; but for a different conclusion see Mayrhauser et al., 2014). First of all, Kaliukhovich and Vogels (2011), using single-cell recordings in macaque monkeys, found no effect of P(rep) on RS. Similarly, Kovács et al. (2013) showed an effect of stimulus expectation for faces but not for chairs and other every-day objects. Finally, Grotheer and Kovács (2014) found that P(rep) affects RS only for stimuli of expertise. The current study aimed at elucidating this unexpected category specificity of the P(rep) effect on fMRIa.

Most theoretical accounts of face perception agree that faces differ from other visual stimuli in their processing in the sense that, as a result of extensive every-day expertise (Bukach et al., 2006), they undergo relatively little decomposition into component parts (Farah et al., 1998). Instead, information across the spatial relations of facial features are integrated into a holistic unit, gestalt or global representation that is more than the combined sum of individual features (Maurer et al., 2002). These configural and/or holistic processes¹ are specific, higher-level mechanisms of the encoding of upright faces and other categories of high expertise (Gauthier and Tarr, 2002; Rossion, 2008). Whether earlier steps, responsible for the structural description of facial features or relatively later, configural/holistic stages of face processing are affected by P(rep) is unclear as of today. One possibility is that the extensive experience we have with faces leads to enhanced configural/holistic processing of stimuli (Bukach et al., 2006), which, in turn, gives rise to the P(rep) effects. In other words, theoretically it is possible that only the configural/holistic processing stages, which are specific for faces, are affected by P(rep) and that this explains the face specificity of these probability effects (Kaliukhovich and Vogels, 2011; Kovács et al., 2013).

Experimentally, configural/holistic processing is measured by tasks such as the whole-part task, showing the superiority of wholes over parts (Tanaka and Farah, 1993), the composite task (Young et al., 1987) and the face inversion effect (FIE; Yin, 1969). FIE is an observation that a 180° in-plane rotation impairs recognition significantly more for faces than for non-face objects. Most current studies suggest that since inversion preserves the low-level features of faces, the FIE is attributed

to the interruption of higher-level processes such as the configural processing of spatial relationships of object parts as well as the face specific holistic processing (Rossion and Gauthier, 2002; Rossion, 2008; but see Yovel and Kanwisher, 2004 for another conclusion). Therefore, it seems that inversion leads to qualitatively different processing of stimuli belonging to categories of high expertise, such as faces. In line with this specificity, recent behavioral electrophysiological and neuroimaging results suggest that the visual system processes inverted faces more similarly to non-face objects than to upright faces (Haxby et al., 1999; Kloth et al., 2013; Rosburg et al., 2010; Rossion et al., 2000).

Therefore, we reasoned that if the face-specificity of P(rep) effects is due to the unique (holistic/configural) processing steps of an upright face then stimulus inversion, a manipulation that interrupts these processing steps, should interfere with the modulatory effects of P(rep) as well. However, if inversion does not affect P(rep) modulations of RS, the face-specificity of this effect can't be explained by the holistic/configural face processing steps.

Materials and methods

Subjects

Thirty healthy volunteers (8 male; 2 left-handed; mean age (\pm SD): 22.8 (3.2) years) participated in the experiment. All subjects had normal or corrected to normal vision and gave informed written consent in accordance with the protocols approved by the Ethical Committee of the Friedrich-Schiller-University of Jena. One subject had to be excluded from the study due to technical difficulties in the acquisition of the data, while in three subjects the regions of interests could not be identified reliably. Therefore the present results are based on the data of 26 subjects.

Stimulation and procedure

The experimental design of the current study was similar to that of Summerfield et al. (2008) and to that of Kovács et al. (2012), with the exception that the face stimuli were presented in two different orientations (Fig. 1A). 240 gray-scale, digital photos of full-frontal Caucasian faces, similar to the face stimuli of Kovács et al. (2012, 2013), were fit behind a circular mask (diameter = 5.5°) and either presented upright (UPR), or inverted (INV) in different runs of fMRI recordings. No stimulus occurred in more than one trial during each run. Stimuli were placed in the center of the screen on a uniform grey background. They were presented for 250 ms each pairwise, separated by an inter-stimulus interval that varied between 400 and 600 ms and followed randomly by a 1 or 2 s long inter-trial interval. The first stimulus (S1) was either identical to (Repetition Trial, RepT) or different from the second stimulus (S2) (Alternation Trial, AltT). All stimuli were presented with 2.75° visual angle in non-target trials; target stimuli were reduced in size by 54%. To reduce local feature adaptation the size of either S1 or S2 (chosen randomly) was reduced by 18%. Stimuli were back-projected via an LCD video projector (NEC GT 1150, NEC Deutschland GmbH, Ismaning, Germany, with modified lens for short focal point) onto a translucent circular screen, placed inside the scanner bore. Presentation was controlled via Matlab R2013a (The MathWorks, Natick, MA, USA), using Psychtoolbox (Version 3.0.9). In addition to the different trial types, two different types of blocks were presented to the subjects (Fig. 1B). In the Repetition Blocks (RepB) 75% of the non-target trials were RepT while 25% were AltT. In the Alternation Blocks (AltB) 75% of the non-target trials were AltT and 25% were RepT. With the exception of the first four trials of each block, which always consisted out of the more frequent trial type of that specific block (RepT in RepB and AltT in AltB), RepT and AltT were presented randomly within the blocks. In addition, 20% of all trials were target trials, whereas target trials could be AltT or RepT with the same relative probability. Hence, overall, Alternation Blocks contained 70% AltT and 30% RepT and Repetition Blocks

¹ Please note that the terms holistic and configural processing are sometimes used interchangeably in the literature. Here, following the terminology of Tanaka and Gordon (2011), we refer to both those processing steps that require the estimation of metric distances (configural) or the integration of featural/configural information of a face into a global percept (holistic; Sergent, 1984).

Download English Version:

<https://daneshyari.com/en/article/6025990>

Download Persian Version:

<https://daneshyari.com/article/6025990>

[Daneshyari.com](https://daneshyari.com)