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The relationship between stimulus repetitions and fulfilled expectations

Mareike Grotheer[a,b], Gyula Kovács[a,b,c,*]

[a] Department of Cognitive Neuroscience, Institute of Psychology, Friedrich Schiller University Jena, 07743 Jena, Germany
[b] DFG Research Unit Person Perception, Friedrich Schiller University Jena, 07743 Jena, Germany
[c] Department of Cognitive Science, Budapest University of Technology and Economics, 1111 Budapest, Hungary

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ABSTRACT

Several neuroimaging studies showed that fulfilled expectations increase the magnitude of repetition suppression (RS) in the face-selective visual cortex. However, previous fMRI studies did not allow a distinction between the reductions of the response due to stimulus repetitions and fulfilled expectations (expectation suppression, ES). In most prior studies repetitions and expectations were not independent from each other as repetitions occurred more often when they were expected and less often when they were not expected, thereby confounding RS with ES. To overcome this confound, we presented pairs of female and male faces that were either repeating or alternating with an overall probability of 50–50%. Orthogonally to this, the gender of the first face in each pair signaled with 75% accuracy whether repetitions or alternations were more likely to occur. We found significant RS in the FFA, the OFA and the LO. In addition, these areas showed a reduction of the response for expected when compared to surprising trials. Moreover, the effects of RS and ES were always additive rather than interactive in our ROIs. This implies that stimulus repetition and fulfilled expectations can be dissociated from one another in terms of their effects on the neural responses.

1. Introduction

One of the most intensively studied finding of cognitive neurosciences is the fact that the repetition of a stimulus induces a reduced neuronal response in comparison to its first presentation (for review see Grill-Spector et al., 2006). This phenomenon termed as repetition suppression (RS; Henson, 2003) or fMRI adaptation (fMRIa) is a commonly applied method to determine the stimulus selectivity of neuronal regions (Malach, 2012). Similarly, other studies found that the occurrence of an expected when compared to a surprising event leads to a reduced neuronal activity as well; a phenomenon recently termed as expectation suppression (ES; Todorovic and de Lange, 2012).

In an influential study Summerfield et al. (2008) used a mixed fMRI design to combine RS with ES. Subjects were presented with pairs of images which could either show the same (repetition trial; RepT) or different faces (alternation trial, AltT). Crucially however, repetition probability was not random during the experiment: stimulus pairs were presented in blocks that alternated between high (75%) or low (25%) repetition probabilities. Hence, the design contained blocks in which repetitions were frequent and therefore expected (RepB) or rare and surprising (AltB). Summerfield et al. (2008) observed an enhancement of the repetition suppression in the fusiform face area (FFA; Kanwisher et al., 1997) in those blocks in which repetitions were frequent, as compared to blocks with less frequent repetitions, and explained their results in the context of the predictive coding model (PC; Rao and Ballard, 1999). This model proposes a hierarchical structure of the visual cortex in which the different processing stages are interconnected with both feed-forward and feed-back connections. This setup allows higher-order regions to send predictions about the sensory input to lower-level areas which return the prediction error, i.e. the mismatch between received predictions and sensory input. In this model the brain is portrayed as a “Bayesian inference machine” which only needs to code the surprising, unpredictable inputs, thereby making neuronal processing faster and more efficient (Friston, 2005, 2010; Friston and Kiebel, 2009). According to Summerfield et al. (2008) RS represents the reduction in neuronal coding intensity when stimuli become expected. The findings of Summerfield et al. (2008) were well replicated for faces (Grotheer et al., 2014; Kovács et al., 2012, 2013; Larsson and Smith, 2012) as well as for stimuli of high expertise (Grotheer and Kovács, 2014) in both fMRI and EEG (Summerfield et al., 2011) experiments. Still it

* Corresponding author at: Institute of Psychology, Friedrich Schiller University Jena, Leutragraben 1, 07743 Jena, Germany.
E-mail address: gyula.kovacs@uni-jena.de (G. Kovács).

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should be noted that an effect of expectation on repetition suppression is dependent on the stimulus material used, as it is not found for objects and unfamiliar characters (Grotheer and Kovács, 2014; Kaliukhovich and Vogels, 2011; Kovács et al., 2013; but see Mayrhauser et al., 2014). One disadvantage of the usually applied mixed-design is that it makes repetition events more or less likely by manipulating their probability over many trials within a given block. As a consequence, in the blocks with higher numbers of repetitions RepT are expected, while in blocks with less likely repetitions AltT are expected. In other words stimulus repetitions and their expectations are not independent factors but rather covary in accordance with the probabilities of the blocks. Therefore, such designs where repetition probabilities over several trials are used to form expectations of the upcoming events do not allow the independent testing of ES and RS effects.

Perceptual expectations of a given stimulus can, however, also be evoked on a trial-by-trial basis by associating them with a preceding schematic cue (Egner et al., 2010) or with another, leading image (Meyer and Olson, 2011). For example, Egner et al. (2010) used colored frames that predicted the category of the subsequent image, which either depicted a face or a house. They found that stimulus expectations and surprise determine the activity of the FFA together. Similar to this logic, the first stimulus of a pair itself can already predict repetitions or alternations in a paradigm testing repetition suppression as well. Indeed, in a recent MEG study, Todorovic and de Lange (2012) applied such a paradigm allowing the independent manipulation of RS and ES. Authors presented subjects with pairs of tones, which could either be identical (i.e. have the same pitch) or different. Orthogonally to this the first tone in each pair functioned as a cue and signaled whether repetition or alternation was likely to occur (with 75% accuracy), thereby controlling the expectations of the subjects. Authors found an early (40–60 ms) reduction of the MEG signal due to stimulus repetitions and a late (100–200 ms) signal reduction due to fulfilled expectations. Most importantly, at no point in time did RS and ES interact with each other, suggesting the independence of the two effects.

Here we exploited the fact that the first, leading stimulus of a pair can serve as the predictor of repetitions/alternations and tested if RS and ES show similar independence in the visual modality as well. We used an fMRI event-related design with pairs of faces, where the two stimuli could either be identical (Repetition Trial-Rep) or different (Alternation Trial-Alt). Orthogonally to this, the gender of the first face in each pair signaled with 75% accuracy whether repetition or alternation was more likely to occur. Fig. 1 illustrates schematically how repetition and expectation might affect neural responses in such a paradigm. First, it is possible that expectation has no effect on the neural responses at all (A) (Kaliukhovich and Vogels, 2011; Kovács et al., 2013). Second (B), repetition suppression can be enhanced for expected, repeated stimuli leading to an interaction of RS and ES, as suggested by the prior experiments with very familiar stimuli (Grotheer and Kovács, 2014; Kovács et al., 2012, 2013; Larsson and Smith, 2012; Summerfield et al., 2008, 2011). Finally, the similar reduction/enhancement of the expected/unexpected stimuli similarly for both the repeated and alternating stimulus pairs (C) would suggest the independence of RS and ES processes (Todorovic and de Lange, 2012).

To briefly anticipate our results, we found significant RS and ES in the FFA and the occipital face area (OFA; Gauthier et al., 2000) and significant RS and a marginally significant ES in the caudal-dorsal part of the lateral occipital complex (LO; Grill-Spector et al., 1999; Malach et al., 1995). Most importantly, no interaction of the two effects was found suggesting that repetition suppression is independent from expectation suppression in the ventral visual stream.

2. Material and methods

2.1. Participants

Twenty-seven healthy volunteers participated in the experiment. None of the subjects reported any neurological or psychiatric illnesses. 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 Jena. Two subjects had to be excluded from the study due to excessive head-movement (i.e. translation/rotation of >7 mm/deg or clearly visible movement artifacts in the anatomical image) during the recording and one subject failed to perform the experimental task properly (performance of $<55\%$ in the third run). Therefore the presented results are based on the data of 24 participants (8 male; 2 left-handed, mean age ($\pm$SD): 23 (3.3) years).

2.2. Stimulation and procedure

Stimulus presentation was controlled via Matlab R2013a (The MathWorks, Natick, MA, USA), using Psychtoolbox (Version 3.0.9).

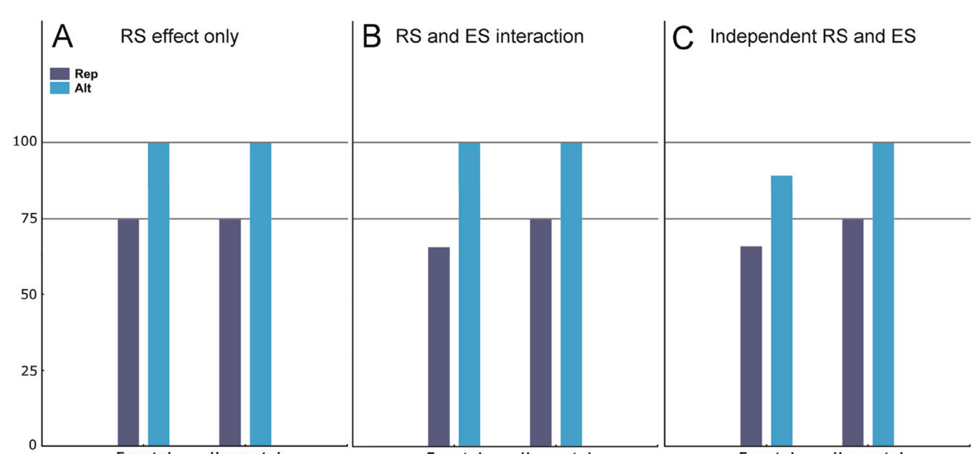

Fig. 1. Schematic illustrations of how repetitions and expectations might affect neural responses. Hypothetical fMRI responses are depicted separately for repeating and alternating faces under conditions of fulfilled and violated expectations. (A) Repetition suppression is independent of expectations. (B) Repetition suppression is enhanced for expected repetitions, leading to an interaction of RS and ES. (C) Responses are independently reduced for expected and repeated stimuli.