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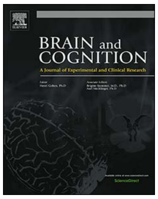

When noise is beneficial for sensory encoding: Noise adaptation can improve face processing

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ABSTRACT

The presence of noise usually impairs the processing of a stimulus. Here, we studied the effects of noise on face processing and show, for the first time, that adaptation to noise patterns has beneficial effects on face perception. We used noiseless faces that were either surrounded by random noise or presented on a uniform background as stimuli. In addition, the faces were either preceded by noise adaptors or not. Moreover, we varied the statistics of the noise so that its spectral slope either matched that of the faces or it was steeper or shallower. Results of parallel ERP recordings showed that the background noise reduces the amplitude of the face-evoked N170, indicating less intensive face processing. Adaptation to a noise pattern, however, led to reduced P1 and enhanced N170 amplitudes as well as to a better behavioral performance in two of the three noise conditions. This effect was also augmented by the presence of background noise around the target stimuli. Additionally, the spectral slope of the noise pattern affected the size of the P1, N170 and P2 amplitudes. We reason that the observed effects are due to the selective adaptation of noise-sensitive neurons present in the face-processing cortical areas, which may enhance the signal-to-noise-ratio.

1. Introduction

When visual noise is added to face images, their processing is usually affected negatively leading to impaired behavioral performance (e.g., Bankó, Gál, Körtvélyes, Kovács, & Vidnyánszky, 2011; Németh, Kovács, Vakli, Kovács, & Zimmer, 2014; Rousselet, Pernet, Bennett, & Sekuler, 2008; Schneider, DeLong, & Busey, 2007). Studies focusing on the neurophysiological correlates of face processing showed that the amplitudes of early event-related potential (ERP) components are modulated by such added noise. Most significantly, the face-encoding N170, a negative component that peaks around 170 ms after stimulus onset, is reduced by the presence of noise in face images (note that reduced N170 refers to the amplitude, thus to less negative values, situated closer to the isoelectric line, throughout the manuscript; Jemel et al., 2003; Rousselet et al., 2008). These studies suggested that the extraction of face information from noisy stimuli occurs in this early time-window. Furthermore, the later P2 component is enhanced by noisy face stimuli (Bankó et al., 2011). The changes in ERP components, especially those in the P2 time window, were thought to reflect the enhanced activation of noise processing neurons in the lateral occipital complex (LOC; Bankó et al., 2011). The P1, the earliest extra-striate component following face presentation, is usually sensitive to low-level image properties (e.g., Tanskanen, Näsänen, Montez, Päällysaho, & Hari, 2005). Its sensitivity to noise was, however, not consistently observed (Bankó et al., 2011; Jemel et al., 2003; Schneider et al., 2007). Taken together, enhancing the level of visual noise leads to altered face-sensitive ERPs (reduced N170 and enhanced P2 amplitudes) which are usually accompanied by behavioral impairments of face perception.

Besides adding visual noise to the stimulus, another way to render its perception difficult is to surround it by another, irrelevant stimulus. We know from a number of prior studies that multiple stimuli presented within the visual field compete for neural representations in the visual cortex (for a review see Beck & Kastner, 2009; Duncan, 1996). It has

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Abbreviations: slope, spectral slope; ERP, event-related potential; FFA, fusiform face area; LOC, lateral occipital cortex; LSF, low spatial frequency; HSF, high spatial frequency; EEG, electroencephalogram; NN, noise-noise condition; NU, noise-uniform condition; UN, uniform-noise condition; UU, uniform-uniform-condition; *matching*, matching slope condition; *steeper*, steeper slope condition; *shallower*, shallower slope condition; OFA, occipital face area

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been suggested that stimuli that are simultaneously presented within the receptive field of a neuron, mutually suppress each other's processing, thereby limiting its sensory processing capacity. Recent neuroimaging studies showed signals of such sensory competitions for low-level stimuli in early visual cortical areas (Beck & Kastner, 2005; Kastner, De Weerd, Desimone, & Ungerleider, 1998) as well as for faces in the fusiform face area (FFA) and LOC of the human brain (Nagy, Greenlee, & Kovács, 2011).

The goal of the current study was to test whether and how visual noise surrounding a clear image of a face interacts with the processing of the face. Effects of sensory competition are expected to be strong when the neural correlates of the simultaneously presented stimuli are overlapping. A recent study, comparing typical competition and adaptation paradigms for faces, emphasized the role of adaptation-related processes during the asynchronous presentation of competing stimuli (Kovács, Zimmer, Volberg, Lavric, & Rossion, 2013). Therefore, to investigate the common or separate neural representations of noise and face images, we further studied the effect of adaptation to noise on the processing of subsequently presented faces. Since prolonged adaptation induces stronger aftereffects (Leopold, Rhodes, Müller, & Jeffery, 2005), we decided to use a top-up adaptation paradigm which is used extensively in the literature to test high-level configural aftereffects (e.g., Fang, Murray, Kersten, & He, 2005; Furl, van Rijsbergen, Treves, & Dolan, 2007; Webster & Maclin, 1999). The prolonged presentation of noise patterns is assumed to reduce neural activity during face processing only if noise patterns and face images share common neural representations. As suggested by the study of Wu, Xu, Dayan, and Qian (2009), the similarity between noise and face stimuli might influence this cross-adaptation effect. To investigate the dependence of the competition effect on the low-level similarity of the noise and face images, we introduced noise patterns with different statistical properties.

Images of natural scenes share common statistical properties, to which the visual system is evolutionary adapted (Olshausen & Field, 1996; Simoncelli & Olshausen, 2001). For example, when the radially averaged Fourier power is bi-logarithmically plotted as the function of spatial frequency, the slope of the curve equals approximately -2 for natural images (Burton & Moorhead, 1987; Koch, Denzler, & Redies, 2010; Ruderman & Bialek, 1994). The slope of this curve is referred to as spectral slope (henceforth *slope*). In contrast to natural scenes, face images possess relatively more power in the low spatial frequencies (LSF) leading to a steeper *slope* of around -3 (Keil, 2008; Redies, Hänisch, Blickhan, & Denzler, 2007). Current studies suggest that *slope* information is diagnostic in the sense that faces can be detected fast by using the power spectrum information of the images (Crouzet & Thorpe, 2011; Honey, Kirchner, & VanRullen, 2008; Rossion & Caharel, 2011). Based on the described findings, we used noise images which either possessed a *slope* that matched that of the face images or deviated from that in a shallower or steeper direction.

Overall, in the present study we aimed at investigating the behavioral and neurophysiological effects of the competition between noise and face stimuli, the adaptation to noise, the interaction of competition and adaptation, and the influence of statistical similarity of noise and face images on these effects. We hypothesized that the competition between the background noise pattern and face image should manifest itself in a reduction of the N170 ERP component. Furthermore, we were also interested to see how the addition of background noise affects the P2 component, which is also related to noisy stimulus processing. We hypothesized that the effects of competition are larger when a face is surrounded by noise with a *slope* that matched that of the face in comparison to a *slope* that deviates from that. Adaptation to noise patterns was expected to modulate the face-sensitive ERP components, especially when the noise patterns had a *slope* that matched that of the face image. The expected adaptation effects include a reduction of the N170, which is assumed to reflect less intense face encoding after adaptation (cf., Amihai, Deouell, & Bentin, 2011; Kovács et al., 2006, 2013; Mercure, Cohen Kadosh, & Johnson, 2011).

The expected changes in mean amplitudes of the investigated ERP components might not only be caused by amplitude changes in the single trials but also by a varying peak latency jitter across trials (Navajas, Ahmadi, & Quian Quiroga, 2013; Regan, 1989; Rossion & Jacques, 2011). For example, peak latency jitter explains at least a part of the N170 amplitude differences in response to intact and phase-scrambled faces in prosopagnosic compared to neurotypical participants (Németh, Zimmer, Schweinberger, Vakli, & Kovács, 2014). To further understand the mechanisms behind the expected changes in amplitude, we additionally analyzed the inter-trial variance of peak latencies.

2. Materials and methods

2.1. Participants

We recorded the electroencephalogram (EEG) from 28 healthy subjects. Five of them were excluded from the analysis because their EEG data were of low quality and resulted in less than 40 artifact-free trials per condition. Another participant was excluded from the analysis because of low performance (under 60% correct in 6 conditions). The remaining 22 participants (1 male; 1 left-handed; 18–29 years old, mean age 21.3) had normal or corrected-to-normal vision. Participants gave their written consent and received either partial course credits or a monetary reimbursement. The study conformed to the Declaration of Helsinki and was approved by the Ethics Committee of Jena University Hospital.

2.2. Stimuli

Faces were presented in four different conditions (adaptation yes/no and background noise yes/no) with three different noise categories (*shallower*, *matching* and *steeper slopes*; Fig. 1 and Table 1).

2.2.1. Face images

We used 100 images of the FACES database (Ebner, Riediger, & Lindenberger, 2010) depicting 100 different individuals with a neutral expression as stimuli. Twenty-five faces belonged to each of the following categories young women (19–30 years old), young men (20–30 years old), middle-aged women (45–50 years old) and middle-aged men (39–55 years old). Face images were gray-scaled and resized by bicubic interpolation to 512 × 512 pixels. External features (background, neck and hair) were covered by an oval mask. The luminance histogram of the foregrounds (i.e., the faces) of these images was matched using the SHINE toolbox for Matlab (The MathWorks Inc., Natick, MA; 'histMatch' function optimized using SSIM) (Willenbockel et al., 2010). Next, the slope of the curve in the log-log plot of Fourier power and spatial frequency (i.e., the *slope*) was calculated in the frequency range between 10 and 255 cycles/image, as described elsewhere (e.g., Menzel, Hayn-Leichsenring, Langner, Wiese, & Redies, 2015). The *slope* of all face images was set to their average (-3.02) using a custom-written Python-based algorithm. Therefore, a pivot point was defined as the log-center of the x-axis (the SFs) and the amplitude at this point was calculated. Then, the amplitudes for the frequencies between 10 and 255 cycles/image were adjusted according to the new *slope*. With these new data points, a power spectrum was calculated and combined with the reconstructed phase-spectrum. To create the image, pixel values that were outside the range of 0 and 255 were assigned to 0 or 255, respectively.

Finally, the foregrounds (i.e., the faces) of these images were cut out, resulting in oval images. Spot measurements of the faces' luminance from the observer's point of view revealed an average of 10.1 cd/m^2.