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Electrophysiological correlates of visual adaptation and sensory competition

Gyula Kovács [a,b,c,*], Márta Zimmer [b], Gregor Volberg [d], Iulia Lavric [d], Bruno Rossion [e,f]

[a] Institute of Psychology, Friedrich-Schiller-University of Jena, Leutragraben 1, 07743 Jena, Germany
[b] Department of Cognitive Science, Budapest University of Technology and Economics, Budapest, Hungary
[c] DFG Research Unit Person Perception, Friedrich-Schiller-University of Jena, Germany
[d] Institute of Psychology, University of Regensburg, Regensburg, Germany
[e] Institute of Psychology, Université catholique de Louvain, Belgium
[f] Institute of Neuroscience, Université catholique de Louvain, Belgium

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ABSTRACT

The face-sensitive evoked N170 component of the event related potential (ERP) is reduced if another face is presented before when compared to the previous presentation of a low-level control stimulus (phase-scrambled face). This effect is thought to reflect category-specific adaptation processes. Similarly, presenting two faces concurrently also reduces the N170, suggesting that stimuli compete for neural representations in the occipito-temporal cortex as early as 170 ms. Here we compared the ERPs obtained for two faces or for a face and a phase-scrambled face in three different conditions: (1) a first stimulus (S1) followed by a second one (S2), similarly to previous adaptation paradigms; (2) S1 remaining on screen when S2 appeared, as previously used in studies of competition; (3) or S1 and S2 having simultaneous onset and offset as well. We found a significant and stimulus specific reduction of the N170 in both conditions where the onset of S1 preceded the onset of S2. In contrast, simultaneous presentation of the two stimuli had no specific effect on the ERPs at least until 200 ms post-stimulus onset. This suggests either that competition does not lead to early repetition suppression or that the absence of a larger N170 response to two simultaneously presented face stimuli compared to a single stimulus reflects competition between overlapping representations. Overall, our results show that the asynchronous presentation of S1 and S2 is critical to observe stimulus specific reduction of the N170, presumably reflecting adaptation-related processes.

1. Introduction

In every-day life, objects are rarely seen alone, against a uniform background. Still, this is how visual stimuli are presented in most experiments. Recently, the fact that multiple stimuli interact with each other in the visual field has received increasing attention. It has been shown that simultaneously presented multiple stimuli interact with each other in a competitive and mutually suppressive way (Duncan, 1996; for a review see Beck and Kastner (2008)). Theories of sensory competition suggest that the processing capacity of simultaneously presented multiple stimuli within the receptive field of a given neuron is limited, presumably due to these mutually suppressive interactions. Further, it has been suggested that competition among stimuli can be biased by attention in such a way that if attention is directed towards one of the stimuli, the mutually competitive effects are reduced (Kastner, De Weerd, Desimone, & Ungerleider, 1998; Recanzone, Wurtz, & Schwartz, 1997; Reynolds, Chelazzi, & Desimone, 1999). Indeed, signs of this biased competition have been already found in several visual areas using extracellular single-cell recording techniques in macaques (Britten & Heuer, 1999; Miller, Gochin, & Gross, 1993; Missal, Vogels, & Orban, 1997; Recanzone et al., 1997; Reynolds et al., 1999; Snowden, Treue, Erickson, & Andersen, 1991) as well as functional magnetic resonance imaging (fMRI) in humans (Axelrod & Yovel, 2011; Beck & Kastner, 2005, 2007, 2008; Gentile & Jansma, 2010; Kastner, De Weerd, Pinsk, Elizondo, Desimone, & Ungerleider, 2001; Macevoy & Epstein, 2009; McMains & Kastner, 2010, 2011; Reddy & Kanwisher, 2007; Reddy, Kanwisher, & VanRullen, 2009).

As of today, only a few electrophysiological studies in humans examined the temporal development of the competition effects among high-level visual stimuli. Jacques and Rossion (2004, 2006) used event related potential (ERP) recordings to study competition between faces. They found that the amplitude of the face-related N170 component (Bentin, Allison, Puce, Perez, & McCarthy, 1996; for a

* Corresponding author at: Institute of Psychology, Friedrich-Schiller-University of Jena, Leutragraben 1, 07743 Jena, Germany. Tel.: +49 3641945936.
E-mail address: gyula.kovacs@uni-jena.de (G. Kovács).

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review see Rossion and Jacques (2011)) to a target face was reduced if a distractor face was present next to the target face, in comparison to a condition in which the distractor was a phase-scrambled face stimulus. This stimulus specific reduction of the N170 amplitude suggests that the simultaneously presented faces compete for the neural resources. Later, the same authors provided evidence for the dissociation of this sensory competition effect from the effect of spatial attention, which took place at an earlier P1 component and was additive to the sensory competition effect on the N170 (Jacques & Rossion, 2007). In a more recent study a similar reduction of the N170 ERP component was found for inverted faces and larger competition effects were found between two inverted faces than between upright and inverted faces or between faces and objects (Sadeh & Yovel, 2010). Altogether these results suggest that sensory competition affects the neural processing of faces already at a relatively early stage and is presumably due to bottom-up mechanisms.

Recently however Gentile and Jansma (2012) questioned these conclusions. These authors presented pairs of similar or dissimilar faces simultaneously. Subjects had to attend either to one of the faces and to perform a match-to-sample task or ignore both faces and perform a bar-width discrimination task in the center of the screen. They reasoned that similar faces, sharing neural representations in the ventral stream (Gilaie-Dotan & Malach, 2006; Leopold, Bondar, & Giese, 2006; Young & Yamane, 1992) would results in higher competition effects than dissimilar faces, which are encoded by separate populations. However, according to theories of biased competition this competition effect should only be present if the stimuli are unattended (Kastner et al., 1998; Recanzone et al., 1997; Reynolds et al., 1999), a result confirmed by a previous fMRI study (Gentile & Jansma, 2010). Surprisingly, Gentile and Jansma (2012) found similar N170 amplitudes for similar and dissimilar faces, suggesting that no competition effects take place at this time-window. The earliest competition effect started significantly later; at around 230 ms post-stimulus onset while the effect of attentional task was even more delayed, corresponding to the N2b ERP component, occurring at around 280 ms (Lange, Wijers, Mulder, & Mulder, 1998).

However, there is an important difference between the studies that found competition effects on the face-related N170, and those that did not. On the one hand studies that showed N170 amplitude reductions presented the context stimulus (S1) first. Then, only after a few hundreds of milliseconds, the second, target image (S2) appeared on the screen next to S1 (Jacques & Rossion, 2004, 2006, 2007; Sadeh & Yovel, 2010). Hence S1 and S2 appeared sequentially, one after the other and then remained on screen simultaneously for a few hundreds of milliseconds. On the other hand, the study that failed to show N170 amplitude reduction presented the context (S1) and target (S2) stimuli simultaneously: the short presentation of a blank screen was followed by a pair of faces presented for 500 ms (Gentile & Jansma, 2012). It is very tempting to suggest that this difference in trial structure accounts for the discrepant results regarding the temporal development of competitive interactions. Support for such an explanation comes from ERP studies in which the same, or similar, stimuli are presented successively. In such studies, a face stimulus, the adapter, is presented (in the range of a few hundreds to few thousands milliseconds) and then disappears for a variable time-period before the target face appears. Following the initial study of Kovács, Zimmer, Bankó, Harza, Antal, and Vidnyánszky (2006), such studies showed reductions of the N170 component or its corresponding magneto-encephalographic (MEG) component (M170) when the adapter stimulus is a face when compared to non-face objects or phase-scrambled face stimuli (Harris & Nakayama, 2007, 2008; Henson, Rylands, Ross, Vuilleumeir, & Rugg, 2004; Kloth, Schweinberger, & Kovács, 2010; Kovács, Zimmer, Harza, Antal, & Vidnyánszky, 2005; Kovács et al., 2006; Kovács, Zimmer, Harza, & Vidnyánszky, 2007; Nemrodov & Itier, 2012; Privman et al., 2011). Collectively, these studies suggested that the adapter stimulus reduces the target-related neural activation, a phenomenon called repetition suppression, adaptation, or habituation (for a review see Grill-Spector, Henson, and Martin (2006)). If the adapter activates similar or overlapping neural populations as the target stimulus (such as in the case of face adapter) this repetition suppression will be larger than when the adapter is a non-face or noise image. This difference is, in turn, manifest in the electromagnetic signal as an adapter-specific reduction of component amplitude.

In the present study, our goal was to compare the effect attributed to sensory competition to the effect attributed to adaptation, using the same set of stimuli in the same participants, in order to potentially integrate the findings of these different studies in a more coherent framework. Moreover, we aimed at testing the hypothesis that the lack of effect on the N170 in the study of Gentile and Jansma (2010) was due to the simultaneous presentation mode which, unlike in the successive presentation paradigms, does not allow a clear separation of the response to each of the face stimuli. To do so, we used the same stimuli and setup but varying the onset asynchrony of S1 and S2 within the same subjects.

2. Materials and methods

2.1. Subjects

Fifteen naïve, healthy volunteers (nine females) participated in the experiment (median age = 22.5 years, SD = 6 years; min = 20; max = 38). They all had normal or corrected-to-normal vision (evaluated by a questionnaire, filled out by the subjects), had no previous history of any neurological or ophthalmologic diseases,

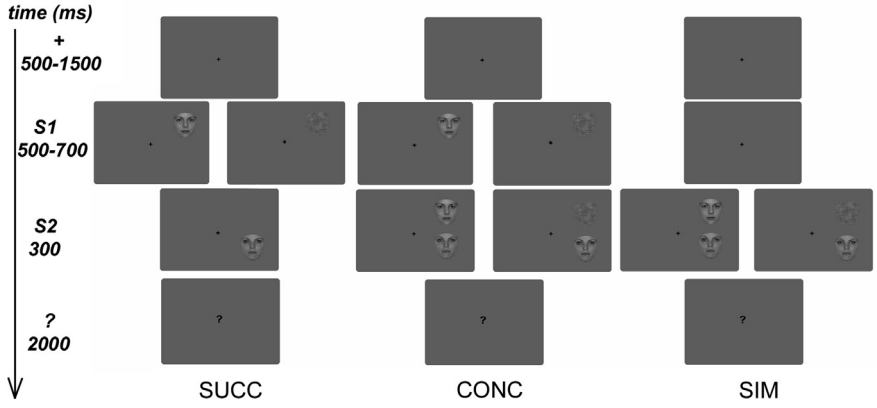

Fig. 1. Schematic sequence of the three conditions. SUCC: S1 (adapter) could be a face or a phase-scrambled face. S2 (target) appeared together with the offset of S1. Its position was always on the same side as that of S1, 2° below it. CONC: the onset of S1 is identical to that in the SUCC but it remains on screen together with S2 as well, just like in SIM. SIM: S1 and S2 had a simultaneous onset and offset. Stimuli could be either on the right (illustrated) or left of the fixation spot randomly.