

# Electrophysiological correlates of visual adaptation and sensory competition



Gyula Kovács<sup>a,b,c,\*</sup>, Márta Zimmer<sup>b</sup>, Gregor Volberg<sup>d</sup>, Iulia Lavric<sup>d</sup>, Bruno Rossion<sup>e,f</sup>

<sup>a</sup> Institute of Psychology, Friedrich-Schiller-University of Jena, Leutragraben 1, 07743 Jena, Germany

<sup>b</sup> Department of Cognitive Science, Budapest University of Technology and Economics, Budapest, Hungary

<sup>c</sup> DFG Research Unit Person Perception, Friedrich-Schiller-University of Jena, Germany

<sup>d</sup> Institute of Psychology, University of Regensburg, Regensburg, Germany

<sup>e</sup> Institute of Psychology, Université catholique de Louvain, Belgium

<sup>f</sup> Institute of Neuroscience, Université catholique de Louvain, Belgium

## ARTICLE INFO

### Article history:

Received 27 November 2012

Received in revised form

12 April 2013

Accepted 23 April 2013

Available online 3 May 2013

### Keywords:

Face perception

ERP

N170

Adaptation

Competition

## 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.

© 2013 Elsevier Ltd. All rights reserved.

## 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](mailto:gyula.kovacs@uni-jena.de) (G. Kovács).

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 result 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

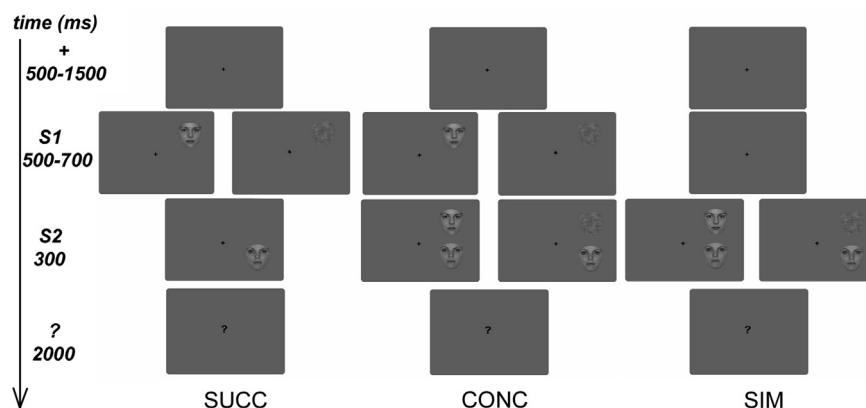
by a pair of faces presented for 500 ms (Gentile & Jansma, 2012). It is very tempting to suggest that this difference in trial structure accounts for the discrepant results regarding the temporal development of competitive interactions. Support for such an explanation comes from ERP studies in which 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, Vuilleumier, & 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.

they were not under medication and gave written informed consent in accordance with the protocols approved by the Ethical Committee of the University of Regensburg. The study conformed to the Declaration of Helsinki. Two subjects were excluded from the analysis of the behavioral data due to technical problems.

## 2.2. Stimuli

We used 50 full-front gray-scale neutral female face images (Set A—FACE). They were fit behind a mask eliminating all external features of the face (hair, ears, or the contour of the face, see Fig. 1). The luminance of the stimuli was equated for the whole set of pictures. A second set of stimuli (Set B—NOISE) was created by Fourier phase randomization of the face stimuli. These images were created by an algorithm (Nasanen, 1999) that replaces the phase spectrum with random values (ranging from 0° to 360°), leaving the low-level visual properties of the image intact, while removing shape information. All images subtended  $2.8 \times 3.7^\circ$  of visual angle. They were presented on the periphery on a uniform gray background (luminance 13 cd/m<sup>2</sup>), either on the right or on the left visual field, their closest point of the face being at  $5^\circ$  from the central fixation point (on a 19 in. monitor,  $1024 \times 768$  pixel resolution, 60 Hz vertical refresh rate, with a viewing distance of 63 cm maintained through the use of a chinrest). Each stimulus was presented twice in each block.

Each trial included the presentation of two stimuli, S1 and S2 (Fig. 1). Three different conditions were presented in separate blocks. (1) *Successive condition* (SUCC) in which S1 preceded S2 and disappeared at its onset (similar to the paradigm of Kovács et al. (2006)). (2) *Concurrent condition* (CONC) in which S1 preceded S2 but both remained on screen (e.g. different onset of the stimuli but simultaneous offset of them, identical to the paradigm of Jacques and Rossion (2004)). Note that in SUCC and CONC the stimulus onset asynchrony (SOA) of S1 and S2 was identical and only the offset of S1 was different. (3) *Simultaneous condition* (SIM) in which S1 and S2 were presented simultaneously and remained on screen for the same time. S1 could either be a face (S1<sub>face</sub>) or a noise (S1<sub>noise</sub>) stimulus and was presented in the upper half of the visual field, either in the left or in the right side, randomly. S2 was always a face stimulus and appeared in the lower half of the same visual field as S1 (note that in case of SUCC and CONC conditions S1 and S2 refer also to the sequence of stimulation while in case of SIM it merely signals the two simultaneously presented stimuli). In all three conditions, within a block, the left or right location of S1 was random.

## 2.3. Task and procedure

In each trial of SUCC or CONC first a fixation cross was presented for a random interval (between 500 and 1500 ms), then S1 was presented either in the upper left or right visual field, for an interval ranging from 500 to 700 ms. This was followed by S2 below (the distance between the closest points of the two faces was  $2^\circ$ ) S1 for 300 ms, and finally a question mark, presented centrally for 2000 ms (Fig. 1). In the SIM the fixation cross was presented for a longer time period, ranging from 1000 to 2200 ms, followed by the simultaneous presentation of S1 and S2 for 300 ms. Subjects were instructed to fixate on the center of the screen during the entire trial and to perform a detection task. Targets were faces from Set A, but presented upside-down and appeared randomly in about 12% of the trials. Subjects' task was to press a button as fast and as accurate as possible when the target face appeared on the screen. The target could be presented either as S1 or S2, randomly. Considering the increased amplitude and latency values of the N170 elicited by inverted faces (e.g., Bentin et al., 1996; Eimer, 2000; Rossion et al., 1999; Rossion et al., 2000) the trials in which this target face appeared were excluded from the EEG analyses. All software was written in MATLAB 2009b (Mathworks Inc.), using Psychtoolbox 3.0.8 for Windows (Pelli, 1997). In all three blocks (3; SUCC, CONC, SIM) we presented 400 trials (2 [type of S1, S1<sub>face</sub> or S1<sub>noise</sub>]  $\times$  50 [number of stimuli]  $\times$  2 [visual field]  $\times$  2 [number of repetition]). The recording session lasted approximately 80 min (3  $\times$  20 min with short breaks among blocks).

## 2.4. Electrophysiological recordings

EEG was recorded via 62 Ag/AgCl equidistant electrodes mounted in an elastic cap (EasyCap, Herrsching-Breitbrunn, Germany) and placed according to the international 10/10 System (Chatrian, Lettich, & Nelson, 1985). To control the eye movement artifacts, the horizontal EOG was recorded from an electrode placed on the outer canthus of the left eye. All channels were referenced to FCz channel online and later digitally transformed to a common averaged reference. The ground was placed on Iz electrode position. All input impedances were kept below 5 k $\Omega$ . EEG was digitized at a 500 Hz sampling rate with an analog bandpass of 0.016–100 Hz.

## 2.5. Behavioral data analysis

Accuracy and response times were collected during the experiment. Since accuracy was at ceiling, only response times for correct response trials were used

for further analysis. Accuracy and mean correct response times were analyzed with repeated-measures ANOVA with condition (3) as within-subject factors. The Greenhouse-Geisser correction was applied to correct for possible violations of sphericity. Post-hoc *t*-tests were computed using Tukey HSD tests.

## 2.6. ERP data analysis

A digital 0.53 Hz 12 dB/octave Butterworth zero phase high-pass filter was used to remove DC shifts, and a 50 Hz notch filter was applied to minimize line-noise artifacts. Finally, a 12 dB/octave low-pass filter with a cut-off frequency of 25 Hz was applied. Trials that contained voltage fluctuations exceeding  $\pm 100$  mV, or eye blinks exceeding  $\pm 50$  mV were rejected. The EEG was segmented offline (Brain VisionAnalyzer, ver1.05, Brain Products GmbH, Munich, Germany) into 1100 ms long trials using a 100 ms pre-S2-stimulus interval. After cleaning the ERP data there were 66% (median; min: 57%; max: 78%), 67% (median; min: 57%; max: 79%) and 67% (median; min: 56%; max: 81%) of the recorded segments in the SUCC, CONC and SIM conditions, respectively (note that 12% of the segments were always excluded from the analysis due to the presence of the target). ERPs were averaged separately for each subject, condition and channel separately. ERPs were synchronized to the onset of S2 in the SUCC and CONC and to the simultaneous appearance of stimuli in SIM. Subjects' ERPs were averaged to compute the grand average for visualization. Statistical analysis was performed on early visual components (P100, N170 and P2 components) of the grand average ERP waveform. The peak amplitude and latency of the individual averaged ERPs was extracted using a semiautomatic detection algorithm that identified the global maxima separately for each selected channels in a specific time window. P100 was defined as a main positive deflection at around 100 ms, N170 was defined as a negative component at around 170 ms after stimulus onset, and P2 as a second positive component at around 250 ms. For the P100 components the occipital sites, corresponding to PO1/PO2 electrode positions were used, while the N170 component was measured at posterior-occipito-temporal sites, corresponding to the P5/P7/PO7 (left hemisphere, LH) and P6/P8/PO8 (right hemisphere, RH) electrode positions. P2 signals were measured at occipital/parieto-occipital sites, corresponding to the PO1/P5/P7/PO7 (left hemisphere, LH) and PO2/P6/P8/PO8 (right hemisphere, RH) channels. After averaging, the individual peak amplitudes were measured for each subject and each condition using a  $\pm 40$  ms window centered on the maximum of the grand average. The latencies of the ERP components were measured at the site of the peak amplitude.

Both amplitude and latency values were entered into a four or five-way repeated-measures ANOVA with condition (3; SUCC, CONC, SIM), type of S1 (2; S1<sub>face</sub>, S1<sub>noise</sub>), visual field (2; LVF, RVF), hemisphere (2; LH, RH) and electrode as within-subject factors in case of N170 (3) or P2 (4) ERP components. The Greenhouse-Geisser correction was applied to counteract the possible violation of sphericity. Post-hoc *t*-statistics were performed by Fisher's least significant difference tests.

## 3. Results

### 3.1. Behavioral results

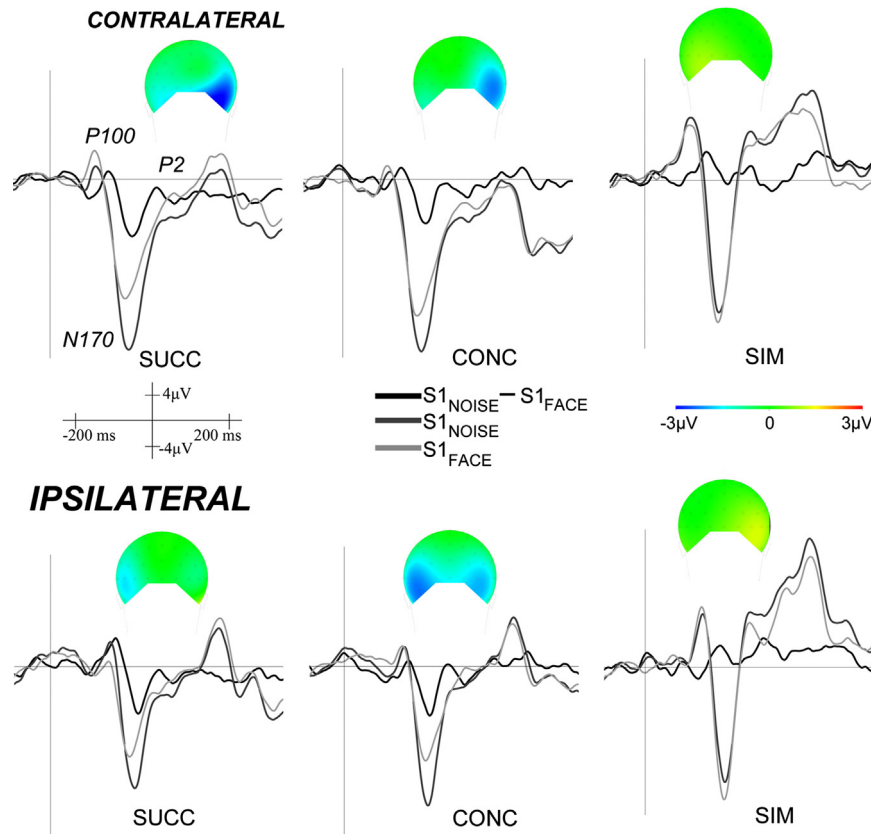
Subjects performed the task almost at ceiling in all conditions (mean: 92%, min and max 73% and 99%, respectively). One-way repeated-measures ANOVA showed no significant main effect of condition with regard to response times ( $F(2,24)=1.05$ ,  $p=0.37$ ).

### 3.2. ERP results

S2 stimuli evoked ERPs with clearly identifiable P100, N170 and P2 components measured at occipito-temporal sites. Fig. 2 shows the grand average ERPs displayed between  $-100$  and  $600$  ms at a representative occipito-temporal sites (PO8) for contralateral and ipsilateral S2 presentations and for S1<sub>face</sub> and S1<sub>noise</sub> contexts (see also Supplementary Fig. S1A).

#### 3.2.1. P100

We observed significantly larger P100 amplitudes for the SIM when compared to the other two conditions (Fig. 3A, see also Supplementary Fig. S1B; main effect of condition:  $F(2,28)=8.4$ ,  $p=0.001$ ,  $\eta_p^2=0.37$ ). P100 was also larger for the contralateral vs. the ipsilateral hemifield (main effect of hemifield:  $F(1,14)=10.3$ ,  $p=0.006$ ,  $\eta_p^2=0.43$ ), but mostly in the SIM condition (interaction of hemifield and condition:  $F(2,28)=8.4$ ,  $p=0.001$ ,  $\eta_p^2=0.38$ ). No



**Fig. 2.** Sample grand average event-related potentials from PO8 for contralateral (left visual field) and ipsilateral (right visual field) presentations in SUCC, CONC and SIM for  $S1_{noise}$  (dark gray) and  $S1_{face}$  (light gray). Black lines represent the difference wave of  $S1_{noise} - S1_{face}$ . Insets represent the topographical maps (back view of the head) depicting the scalp distribution of the  $S1_{noise} - S1_{face}$  differential activity (180–225 ms time-window).

other effects were significant, so that the  $S1$  context had no effect on the P100 amplitude (Fig. 3B).

The latency of the P100 component (Fig. 3C) showed slightly different pattern. While it was significantly shorter for the contralateral than for the ipsilateral hemifield (main effect of *hemifield*:  $F(1,14)=34.3$ ,  $p=0.00004$ ,  $\eta_p^2=0.71$ ) it was also shorter for the  $S1_{face}$  when compared to  $S1_{noise}$  condition (main effect:  $F(1,14)=8.5$ ,  $p=0.01$ ,  $\eta_p^2=0.38$ ; see also Fig. 3D), but mostly for the ipsilateral visual hemifield (interaction of *type of  $S1$*  and *hemifield*:  $F(1,14)=8.7$ ,  $p=0.01$ ,  $\eta_p^2=0.38$ ).

### 3.2.2. N170

We observed a main effect of *electrode* for the N170 amplitude ( $F(2,28)=6.4$ ,  $p=0.008$ ,  $\eta_p^2=0.31$ ), due to the lower amplitude over P5/P6 than over the other two sites. However, since none of the interactions were significant with the factor *electrode* we merged the results across this factor for further analysis. Fig. 4A presents the N170 amplitude data for the two hemispheres and ipsi- and contralateral stimulus presentation separately. We observed significantly lower N170 amplitude when a stimulus was presented after or together with  $S1_{face}$  when compared to a  $S1_{noise}$  (main effect of *type of  $S1$* :  $F(1,14)=33.1$ ,  $p=0.0001$ ,  $\eta_p^2=0.70$ ; Fig. 4B, see also Supplementary Fig. S1C), supporting prior results (Jacques & Rossion, 2004; Kovács et al., 2006) and suggesting stimulus specific interactions (in the form of adaptation or competition) of  $S1$  and  $S2$ . This effect, however, was only present in the SUCC and CONC, but not in the SIM condition, as reflected by the significant interaction of  $S1$  with *condition* ( $F(2,28)=14.1$ ,  $p=0.00014$ ,  $\eta_p^2=0.50$ ). In fact the three way *condition*  $\times$  *visual hemifield*  $\times$  *type of  $S1$*  interaction ( $F(2,28)=8.34$ ,  $p=0.0048$ ,  $\eta_p^2=0.37$ )

as well as the post-hoc tests suggest that the effect is smaller for ipsilateral presentations and it is even reversed for the ipsilateral SIM condition: the N170 amplitude was somewhat larger for the  $S1_{face}$  condition when compared to  $S1_{noise}$  (Fisher's post-hoc test:  $p=0.07$  for both hemispheres). This suggests that  $S1$  interacts with the  $S2$  face in a stimulus specific and negative manner, but only if the two stimuli are presented subsequently.

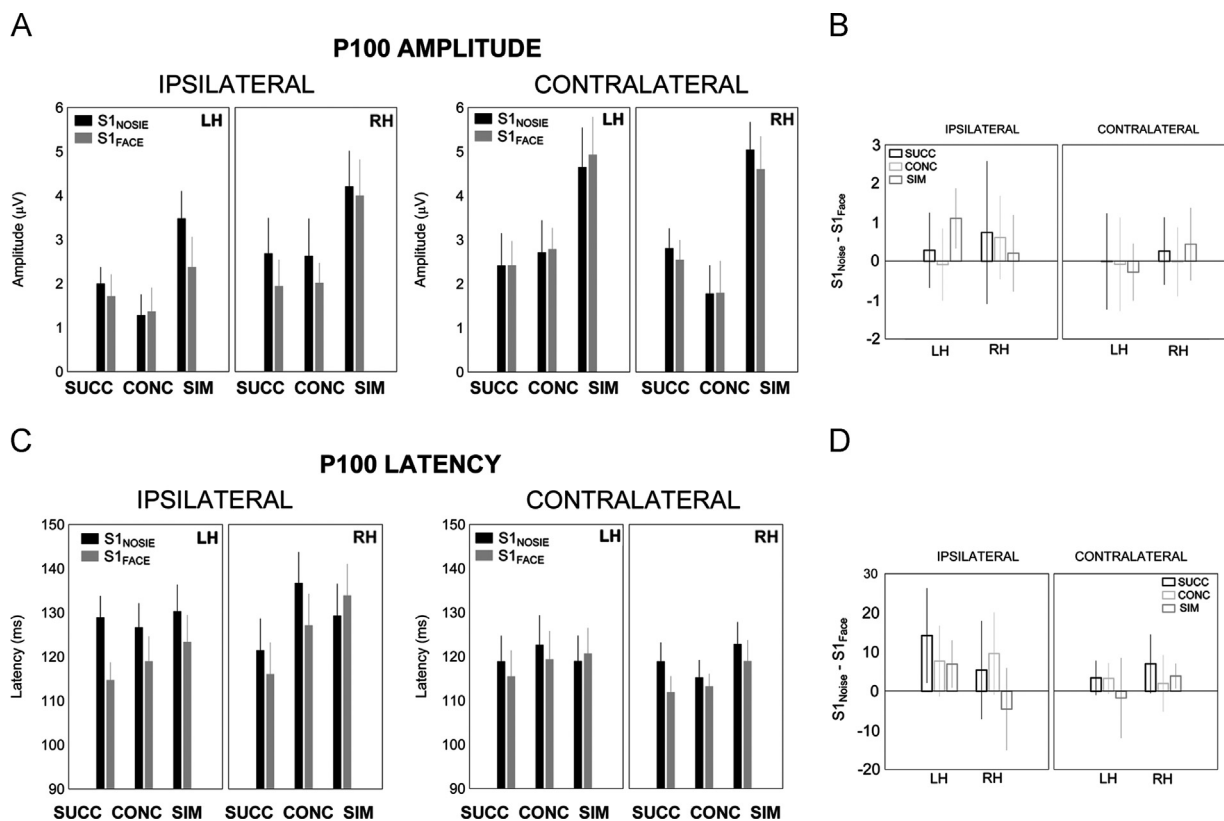
In addition, N170 showed a significant effect of visual hemifield in the sense that it was larger for contralateral than for ipsilateral presentations (main effect of ipsi- contralateral presentation:  $F(1,14)=48.4$ ,  $p=0.000007$ ,  $\eta_p^2=0.77$ ) and for the right when compared to the left hemisphere (main effect of hemisphere:  $F(1,14)=27.2$ ,  $p=0.0001$ ,  $\eta_p^2=0.66$ ), a result similar to the findings of prior studies (Kovács et al., 2005, 2007).

The latency of the N170 ERP component was significantly shorter for  $S1_{face}$  when compared to  $S1_{noise}$  (Fig. 4C and D; main effect of  $S1$ :  $F(1,14)=31.2$ ,  $p=0.00007$ ,  $\eta_p^2=0.69$ ). It was also shorter for contralateral than ipsilateral hemifields (main effect of *hemifield*:  $F(1,14)=56.1$ ,  $p=0.000003$ ,  $\eta_p^2=0.80$ ) and in the SIM when compared to the other two conditions (main effect of *condition*:  $F(2,28)=4.9$ ,  $p=0.01$ ,  $\eta_p^2=0.26$ ).

### 3.2.3. P2

Similarly to what we have observed for P100, the amplitude of P2 was also the largest for the SIM condition (Fig. 5A, see also Supplementary Fig. S1D; main effect of *condition*:  $F(2,28)=53.9$ ,  $p=0.00001$ ,  $\eta_p^2=0.79$ ). P2 was also smaller for contralateral visual hemifields when compared to ipsilateral, but only in the SUCC and CONC conditions (interaction of *condition* with *hemifield*:  $F(2,28)=$





**Fig. 3.** Average ( $\pm$  SE) amplitude (A) and latency (C) values of the P100 components for the two hemispheres (LH and RH), two visual hemifields (ipsilateral and contralateral), SUCC, CONC and SIM conditions and S1<sub>noise</sub> (black) and S1<sub>face</sub> (gray) separately. B and D represent the average ( $\pm$  95% confidence intervals) for the S1<sub>noise</sub> - S1<sub>face</sub> comparisons performed for each condition, hemisphere and hemifield separately. SUCC—black, CONC—light gray, and SIM—dark gray.

10.7,  $p=0.0003$ ,  $\eta_p^2=0.43$ ). The three way interaction of *condition*  $\times$  *hemifield*  $\times$  *type of S1* suggests that the difference between the two hemifields in the SUCC and CONC conditions was smaller for S1<sub>noise</sub> than for S1<sub>face</sub> conditions ( $F(2,28)=3.5$ ,  $p=0.048$ ,  $\eta_p^2=0.19$ ; Fig. 5B). Furthermore, the main effect of *hemisphere* ( $F(1,14)=7.3$ ,  $p=0.044$ ,  $\eta_p^2=0.34$ ) suggested that P2 was smaller over the right than over the left hemisphere.

Reflecting the largest P2 amplitude in SIM, the latency of P2 was the shortest in that condition (Fig. 5C; main effect of *condition*:  $F(2,28)=3.4$ ,  $p=0.047$ ,  $\eta_p^2=0.19$ ). In addition to that only the *condition*  $\times$  *hemisphere*  $\times$  *type of S1* three-way interaction was significant ( $F(2,28)=6.9$ ,  $p=0.0006$ ,  $\eta_p^2=0.33$ ) showing that P2 latencies are longer over the RH than over the LH, specially in the CONC condition with S1<sub>noise</sub>.

Altogether the ERP results suggest that the most significant effects of S1 were found in the time-window corresponding to the N170 ERP component and that these effects strongly depended on the temporal relationship of S1 and S2 presentations: the S1 effect disappeared if the two stimuli were presented simultaneously. In contrast to this, both P1 and P2 components showed a strong dependence on the experimental condition, being the largest in SIM, although this effect was independent of the nature of S1.

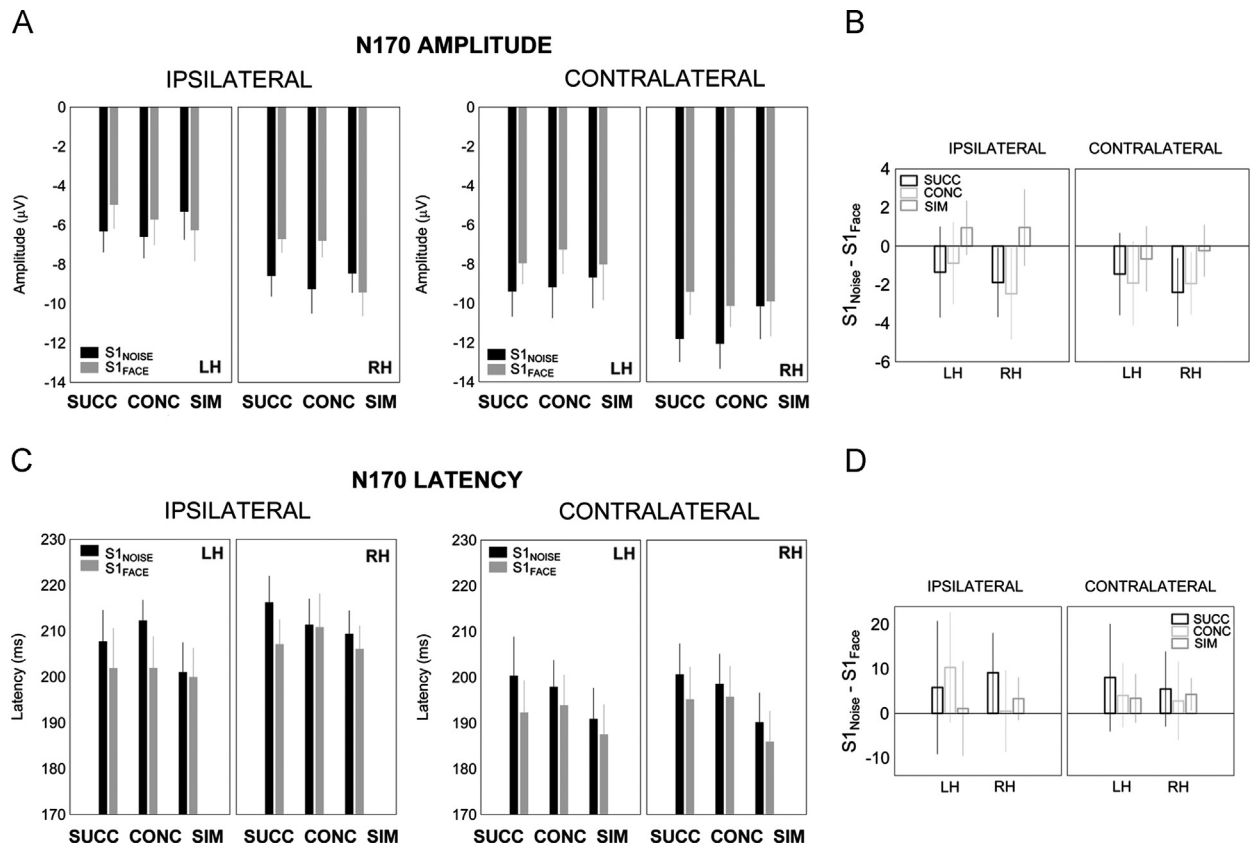
#### 4. Discussion

In line with previous observations (e.g., Jacques & Rossion, 2004; Kovács et al., 2006), we found that the presentation of a stimulus modifies the ERP elicited by a subsequent stimulus in a time-window corresponding to N170, while simultaneous presentation of the exact

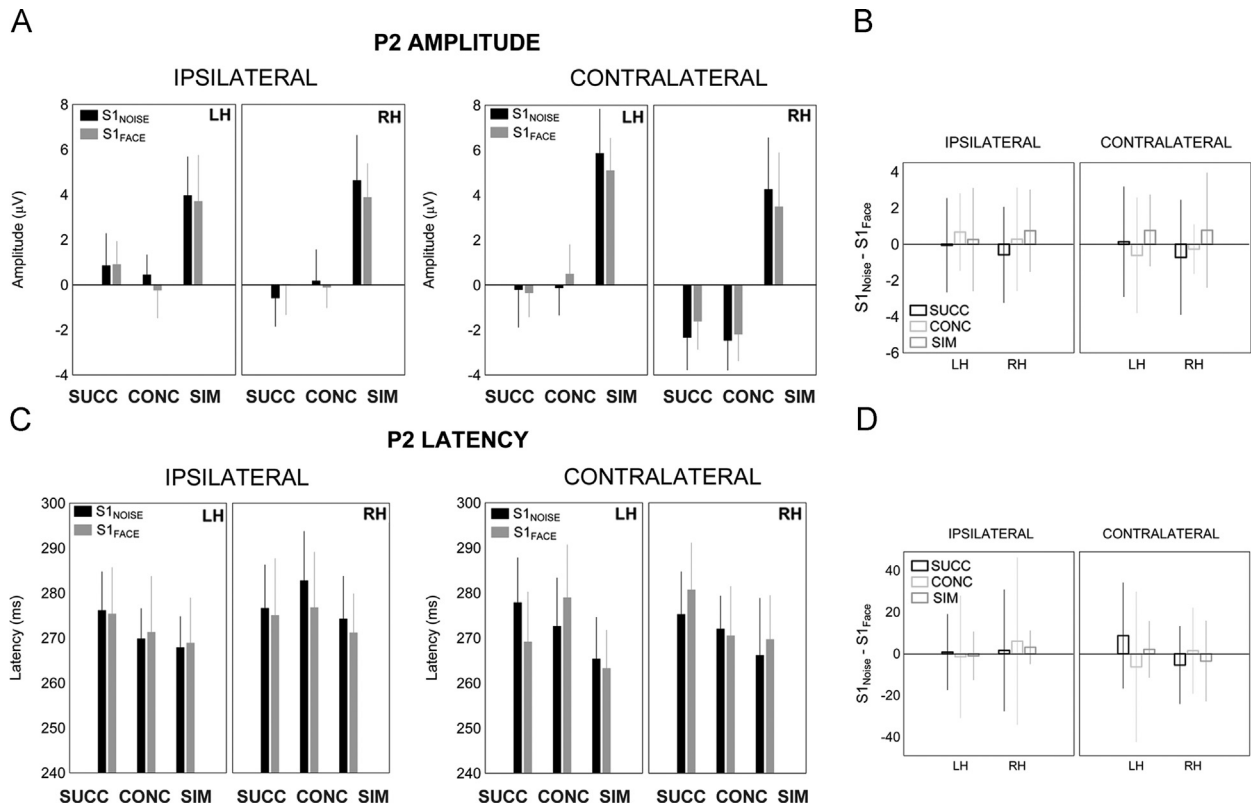
same two stimuli has no specific effect on the early parts of ERP, at least until 200 ms post-stimulus onset (Gentile & Jansma, 2010).

##### 4.1. Similarities of SUCC and CONC conditions

Previous results of sensory competition and adaptation experiments suggest that when S1 precedes the presentation of S2, a significant reduction of the face-evoked N170 is observed (Eimer, Kiss, & Nicholas, 2010; Jacques & Rossion, 2004, 2006, 2007; Kovács et al., 2006, 2007; Sadeh & Yovel, 2010; Zimmer & Kovács, 2011). This reduction is larger when S1 is a full face compared to a phase-randomized face, suggesting that high-level visual mechanisms drive this early modulation of the ERP (Kloth et al., 2010; see also Rossion, Kung, and Tarr (2004) and Rossion, Collins, Goffaux, and Curran (2007) for face-evoked N170 reduction when preceded by an object of expertise). The present results support this conclusion: we observed significantly reduced N170 amplitudes in our SUCC and CONC conditions with S1<sub>face</sub> when compared to S1<sub>noise</sub>. Most importantly, this amplitude reduction of N170 was not different in the SUCC and CONC, two conditions that differed from each other regarding the temporal relationship of S1 offset and S2 onset times. While the onset of S1 preceded the onset of S2 in both conditions, it remained on the screen together with S2 in CONC but disappeared at the onset of S2 in SUCC. The similar N170 modulation of the two conditions suggests that it is determined by the asynchronous prior occurrence of S1 while the presence or absence of simultaneous S1 presentation with S2 does not affect it. This argues strongly for a commonality of the mechanism driving N170 amplitude modulations when two stimuli are presented. In addition, neither the P100 nor the P2 component showed any difference between SUCC and CONC



**Fig. 4.** Average ( $\pm$  SE) amplitude (A) and latency (C) values of the N170 components for the two hemispheres (LH and RH), two visual hemifields (ipsilateral and contralateral), SUCC, CONC and SIM conditions and S1<sub>noise</sub> (black) and S1<sub>face</sub> (gray) separately. B and D represent the average ( $\pm$  95% confidence intervals) for the S1<sub>noise</sub>–S1<sub>face</sub> comparisons performed for each condition, hemisphere and hemifield separately. SUCC—black, CONC—light gray, and SIM—dark gray.



**Fig. 5.** Average ( $\pm$  SE) amplitude (A) and latency (C) values of the P2 components for the two hemispheres (LH and RH), two visual hemifields (ipsilateral and contralateral), SUCC, CONC and SIM conditions and S1<sub>noise</sub> (black) and S1<sub>face</sub> (gray) separately. B and D represent the average ( $\pm$  95% confidence intervals) for the S1<sub>noise</sub>–S1<sub>face</sub> comparisons performed for each condition, hemisphere and hemifield separately. SUCC—black, CONC—light gray, and SIM—dark gray.

conditions, suggesting that the offset of S1 has little effect on the early ERP components generally. Moreover, the S1 context had no significant effect on the P100 and P2 components either. This result is in correspondence with what previous competition studies found regarding P100, using a very similar design to our CONC condition (Jacques & Rossion, 2004, 2006, 2007). It is worth to note, however, that a previous adaptation study found a moderate increase of P100 component for peripheral faces when S1 (the adapter) was a face when compared to when it was a noise image (Kovács et al., 2007). The longer SOA of that study (1000 ms SOA with 500 ms S1 exposition time) when compared to the present paradigm (500 ms SOA, being identical to the S1 exposition time) might explain this difference.

The implication of these observations is that the phenomena described as sensory competition in one set of studies (Jacques & Rossion, 2004, 2006, 2007) and adaptation in another set of studies (Kovács et al., 2005, 2006, 2007) appear to reflect the same mechanisms.

#### 4.2. Differences of SIM condition from SUCC and CONC

When S1 and S2 appeared synchronously (SIM), we observed strong differences in the ERP between this and the other two conditions where the onset of S1 and S2 was asynchronous. First and above all, context had no effect on the P100, N170 and P2 ERP components in the sense that  $S1_{\text{face}}$  and  $S1_{\text{noise}}$  elicited very similar potentials in SIM.

This result is in line with observations of the Gentile and Jansma (2012) study, which used similar or dissimilar face-pairs and found similar ERPs until 250 ms post-stimulus onset, suggesting no suppressive competition effects on the early components. The similarity of  $S1_{\text{face}}$  and  $S1_{\text{noise}}$  suggests that, at least at the category-level, there are no differences in the early processing of stimulus pairs. This implies that the competition effects that are observed in the face and object related areas of the human brain during simultaneous stimulus presentations in fMRI experiments are probably due to changes of the representation that take place after 200 ms, presumably at around 250 ms post-stimulus onset (Axelrod & Yovel, 2011; Gentile & Jansma, 2010; Nagy, Greenlee, & Kovács, 2011; Reddy & Kanwisher, 2007; Reddy et al., 2009). Alternatively, it could be that competition takes place early on even in the simultaneous presentation mode, and that the fact that the N170 to two face stimuli with a simultaneous onset is not larger than that of a single stimulus reflects a form of competition between overlapping representations.

Since the major aim of the current study was to compare the two versions of competition paradigms (CONC and SIM) with the widely used adaptation paradigm (SUCC) we did not include in our design a condition where only a single face or noise stimulus is presented (similarly to the sequential conditions of fMRI experiments which test biased competitions (Beck & Kastner, 2007; Kastner et al., 2001)). Hence, we do not have any information about how SIM would relate to the single presentation of a face or noise stimulus. A possible explanation of the enhanced ERP responses is the difference in attentional load during SUCC/CONC vs. SIM condition. Subjects' task was to detect a rarely presented inverted face, a task identical to that of Jacques and Rossion (2006). Since the target could be either S1 or S2 in 50% of the cases (i.e. when the target was presented as S1) during SUCC and CONC conditions subjects did not need to attend to S2 to perform the task while in SIM the target was always one member of the stimulus pair and this could lead to the enhanced processing during SIM. The issue of attentional modulation of sensory competitions was beyond the scope of the current experiments. Thus, additional attentional modulation, similar to the methods of Gentile and Jansma (2010, 2012),

together with a condition with the presentation of single stimuli could test this hypothesis.

#### 4.3. Neural mechanisms of the context effect of SUCC and CONC

On the basis of our results we cannot exclude the possibility that the stimulus specific context effects observed on the N170 are due to neural adaptation processes. This is suggested by the fact that N170 reduction was observed in our study when the onset of S1 preceded the onset of S2, but not when S1 and S2 were presented synchronously. Hence, it is likely that the ongoing activity, elicited by S1 affected the response evoked by S2. Indeed, a number of studies, using different paradigms and stimulation suggest that prolonged exposure to a previous stimulus reduces the amplitude of N170 in a stimulus specific manner (Caharel, Jiang, Blanz, & Rossion, 2009; Ewbank, Smith, Hancock, & Andrews, 2008; Harris & Nakayama, 2007; Heisz, Watter, & Shedden, 2006; Itier & Taylor, 2002; Jacques, d'Arripe, & Rossion, 2007; Kovács et al., 2006; Martens, Schweinberger, Kiefer, & Burton, 2006). While the exact mechanisms of the neural adaptation effects are heavily debated currently (Ewbank, Lawson, Henson, Rowe, Passamonti, & Calder, 2011; Ewbank, Henson, Rowe, Stoyanova, & Calder, 2012; Kovács, Iffland, Vidnyánszky, & Greenlee, 2012; Larsson & Smith, 2012; Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008; Summerfield, Wyart, Johnen, & de Gardelle, 2011) the relatively early time-window where the modulation occurs suggests bottom-up, rather than top-down mechanisms. Bottom-up mechanisms of adaptation suggest neural fatigue, sharpening of the neural tuning or facilitation of the neural responses (for reviews see Grill-Spector et al. (2006) and Krekelberg, Boynton, and van Wezel (2006)).

In conclusion, our results suggest that the stimulus specific reduction of the N170 is due to the asynchronous presentation of S1 and S2 and to common adaptation processes of SUCC and CONC. On the other hand, the absence of such stimulus specific reduction in SIM suggests that competition among simultaneously presented stimuli plays a less important role in determining early response reduction. Overall, it seems that neural adaptation might be the factor behind the previously observed N170 amplitude reductions.

#### Acknowledgments

This work was supported by the Deutsche Forschungsgemeinschaft (KO 3918/1-2 and KO 3918/2-1) and by the Hungarian Scientific Research Fund (OTKA, PD 101499). BR is supported by the Belgian National Fund for Scientific Research (FNRS). We thank the helpful comments of Zoltán Vidnyánszky and Stefan Schweinberger during the preparation of the manuscript.

#### Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.neuropsychologia.2013.04.016>.

#### References

- Axelrod, V., & Yovel, G. (2011). Nonpreferred stimuli modify the representation of faces in the fusiform face area. *Journal of Cognitive Neuroscience*, 23(3), 746–756, <http://dx.doi.org/10.1162/jocn.2010.21481>.
- Beck, D. M., & Kastner, S. (2005). Stimulus context modulates competition in human extrastriate cortex. *Nature Neuroscience*, 8(8), 1110–1116, <http://dx.doi.org/10.1038/nn1501>.

- Beck, D. M., & Kastner, S. (2007). Stimulus similarity modulates competitive interactions in human visual cortex. *Journal of Vision*, 7(2), 1–12, <http://dx.doi.org/10.1167/7.2.19>.
- Beck, D. M., & Kastner, S. (2008). Top-down and bottom-up mechanisms in biasing competition in the human brain. *Vision Research*, 49(10), 1154–1165.
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8(6), 551–565, <http://dx.doi.org/10.1162/jocn.1996.8.6.551>.
- Britten, K. H., & Heuer, H. W. (1999). Spatial summation in the receptive fields of MT neurons. *Journal of Neuroscience*, 19(12), 5074–5084.
- Caharel, S., Jiang, F., Blanz, V., & Rossion, B. (2009). Recognizing an individual face: 3D shape contributes earlier than 2D surface reflectance information. *Neuroimage*, 47(4), 1809–1818.
- Chatrrian, G. E., Lettich, E., & Nelson, P. L. (1985). Ten percent electrode system for topographic studies of spontaneous and evoked EEG activity. *American Journal of EEG Technology*, 25, 83–92.
- Duncan, J. (1996). Cooperating brain systems in selective perception and action. In: T. Inui, & J. L. McClelland (Eds.), *Attention and performance*, Vol. XVI (pp. 549–578). Cambridge: The MIT Press.
- Eimer, M. (2000). Event-related brain potentials distinguish processing stages involved in face perception and recognition. *Clinical Neurophysiology*, 111(4), 694–705.
- Eimer, M., Kiss, M., & Nicholas, S. (2010). Response profile of the face-sensitive N170 component: A rapid adaptation study. *Cerebral Cortex*, 20(10), 2442–2452, <http://dx.doi.org/10.1093/cercor/bhp312>.
- Ewbank, M. P., Smith, W. A., Hancock, E. R., & Andrews, T. J. (2008). The M170 reflects a viewpoint-dependent representation for both familiar and unfamiliar faces. *Cerebral Cortex*, 18(2), 364–370, <http://dx.doi.org/10.1093/cercor/bhm060>.
- Ewbank, M. P., Lawson, R. P., Henson, R. N., Rowe, J. B., Passamonti, L., & Calder, A. J. (2011). Changes in “top-down” connectivity underlie repetition suppression in the ventral visual pathway. *Journal of Neuroscience*, 31(15), 5635–5642, <http://dx.doi.org/10.1523/JNEUROSCI.5013.10.2011>.
- Ewbank, M. P., Henson, R. N., Rowe, J. B., Stoyanova, R. S., & Calder, A. J. (2012). Different neural mechanisms within occipitotemporal cortex underlie repetition suppression across same and different-size faces. *Cerebral Cortex*, 23(5), 1073–1084, <http://dx.doi.org/10.1093/cercor/bhs070>.
- Gentile, F., & Jansma, B. M. (2010). Neural competition through visual similarity in face selection. *Brain Research*, 1351, 172–184.
- Gentile, F., & Jansma, B. M. (2012). Temporal dynamics of face selection mechanism in the context of similar and dissimilar faces: ERP evidences for biased competition within the ventral occipito-temporal cortex using ICA. *Neuroimage*, 59(1), 682–694.
- Gilaie-Dotan, S., & Malach, R. (2006). Sub-exemplar shape tuning in human face-related areas. *Cerebral Cortex*, 17(2), 325–338, <http://dx.doi.org/10.1093/cercor/bhj150>.
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, 10(1), 14–23.
- Harris, A., & Nakayama, K. (2007). Rapid face-selective adaptation of an early extrastriate component in MEG. *Cerebral Cortex*, 17(1), 63–70, <http://dx.doi.org/10.1093/cercor/bhj124>.
- Harris, A., & Nakayama, K. (2008). Rapid adaptation of the m170 response: Importance of face parts. *Cerebral Cortex*, 18(2), 467–476, <http://dx.doi.org/10.1093/cercor/bhm078>.
- Heisz, J. J., Watter, S., & Shedden, J. M. (2006). Progressive N170 habituation to unattended repeated faces. *Vision Research*, 46(1–2), 47–56.
- Henson, R. N., Rylands, A., Ross, E., Vuilleumier, P., & Rugg, M. D. (2004). The effect of repetition lag on electrophysiological and haemodynamic correlates of visual object priming. *Neuroimage*, 21(4), 1674–1689.
- Itier, R. J., & Taylor, M. J. (2002). Inversion and contrast polarity reversal affect both encoding and recognition processes of unfamiliar faces: A repetition study using ERPs. *Neuroimage*, 15(2), 353–372.
- Jacques, C., & Rossion, B. (2004). Concurrent processing reveals competition between visual representations of faces. *Neuroreport*, 15(15), 2417–2421.
- Jacques, C., & Rossion, B. (2006). The time course of visual competition to the presentation of centrally fixated faces. *Journal of Vision*, 6(2), 154–162, <http://dx.doi.org/10.1167/6.2.6>.
- Jacques, C., d’Arripe, O., & Rossion, B. (2007). The time course of the inversion effect during individual face discrimination. *Journal of Vision*, 7(8), 3, <http://dx.doi.org/10.1167/7.8.3>.
- Jacques, C., & Rossion, B. (2007). Electrophysiological evidence for temporal dissociation between spatial attention and sensory competition during human face processing. *Cerebral Cortex*, 17(5), 1055–1065, <http://dx.doi.org/10.1093/cercor/bhl015>.
- Kastner, S., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science*, 282(5386), 108–111, <http://dx.doi.org/10.1126/science.282.5386.108>.
- Kastner, S., De Weerd, P., Pinsk, M. A., Elizondo, M. I., Desimone, R., & Ungerleider, L. G. (2001). Modulation of sensory suppression: Implications for receptive field sizes in the human visual cortex. *Journal of Neurophysiology*, 86(8), 1398–1411.
- Kloth, N., Schweinberger, S. R., & Kovács, G. (2010). Neural correlates of generic versus gender-specific face adaptation. *Journal of Cognitive Neuroscience*, 22(10), 2345–2356, <http://dx.doi.org/10.1162/jocn.2009.21329>.
- Kovács, G., Zimmer, M., Harza, I., Antal, A., & Vidnyánszky, Z. (2005). Position-specificity of facial adaptation. *Neuroreport*, 16(17), 1945–1949.
- Kovács, G., Zimmer, M., Bankó, É., Harza, I., Antal, A., & Vidnyánszky, Z. (2006). Electrophysiological correlates of visual adaptation to faces and body parts in humans. *Cerebral Cortex*, 16(5), 742–753, <http://dx.doi.org/10.1093/cercor/bhj020>.
- Kovács, G., Zimmer, M., Harza, I., & Vidnyánszky, Z. (2007). Adaptation duration affects the spatial selectivity of facial aftereffects. *Vision Research*, 47(25), 3141–3149.
- Kovács, G., Ifland, L., Vidnyánszky, Z., & Greenlee, M. W. (2012). Stimulus repetition probability effects on repetition suppression are position invariant for faces. *Neuroimage*, 60(4), 2128–2135.
- Krekelberg, B., Boynton, G. M., & van Wezel, R. J. (2006). Adaptation: From single cells to BOLD signals. *Trends in Neuroscience*, 29(5), 250–256.
- Lange, J. J., Wijers, A. A., Mulder, L. J., & Mulder, G. (1998). Color selection and location selection in ERPs: Differences, similarities and ‘neural specificity’. *Biological Psychology*, 48(2), 153–182.
- Larsson, J., & Smith, A. T. (2012). fMRI repetition suppression: Neuronal adaptation or stimulus expectation? *Cerebral Cortex*, 22(3), 567–576, <http://dx.doi.org/10.1093/cercor/bhr119>.
- Leopold, D. D., Bondar, I. V., & Giese, M. A. (2006). Norm-based face encoding by single neurons in the monkey inferotemporal cortex. *Nature*, 442(7102), 572–575, <http://dx.doi.org/10.1038/nature04951>.
- Macevoy, S. P., & Epstein, R. A. (2009). Decoding the representation of multiple simultaneous objects in human occipitotemporal cortex. *Current Biology*, 19(11), 943–947.
- Martens, U., Schweinberger, S. R., Kiefer, M., & Burton, M. A. (2006). Masked and unmasked electrophysiological repetition effects of famous faces. *Brain Research*, 1109(1), 146–157.
- McMains, S. A., & Kastner, S. (2010). Defining the units of competition: Influences of perceptual organization on competitive interactions in human visual cortex. *Journal of Cognitive Neuroscience*, 22(11), 2417–2426, <http://dx.doi.org/10.1162/jocn.2009.21391>.
- McMains, S. A., & Kastner, S. (2011). Interactions of top-down and bottom-up mechanisms in human visual cortex. *Journal of Neuroscience*, 31(2), 587–597, <http://dx.doi.org/10.1523/JNEUROSCI.3766-10.2011>.
- Miller, E. K., Gochin, P. M., & Gross, C. G. (1993). Suppression of visual responses of neurons in inferior temporal cortex of the awake macaque by addition of a second stimulus. *Brain Research*, 616(1–2), 25–29.
- Missal, M., Vogels, R., & Orban, G. A. (1997). Responses of macaque inferior temporal neurons to overlapping shapes. *Cerebral Cortex*, 7(8), 758–767, <http://dx.doi.org/10.1093/cercor/7.8.758>.
- Nagy, K., Greenlee, M. W., & Kovács, G. (2011). Sensory competition in the face processing areas of the human brain. *PLoS One*, 6(9), e24450, <http://dx.doi.org/10.1371/journal.pone.0024450>.
- Nasanen, R. (1999). Spatial frequency bandwidth used in the recognition of facial images. *Vision Research*, 39(23), 3824–3833.
- Nemrodov, D., & Itier, R. J. (2012). Is the rapid adaptation paradigm too rapid? Implications for face and object processing. *Neuroimage*, 61(4), 812–822.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.
- Privman, E., Fisch, L., Neufeld, M. Y., Kramer, U., Kipervasser, S., Andelman, F., et al. (2011). Antagonistic relationship between gamma power and visual evoked potentials revealed in human visual cortex. *Cerebral Cortex*, 21(3), 616–624, <http://dx.doi.org/10.1093/cercor/bhq128>.
- Recanzone, G. H., Wurtz, R. H., & Schwartz, U. (1997). Responses of MT and MST neurons to one and two moving objects in the receptive field. *Journal of Neurophysiology*, 78(6), 2904–2915.
- Reddy, L., & Kanwisher, N. (2007). Category selectivity in the ventral visual pathway confers robustness to clutter and diverted attention. *Current Biology*, 17(23), 2067–2072, <http://dx.doi.org/10.1016/j.cub.2007.10.043>.
- Reddy, L., Kanwisher, N. G., & VanRullen, R. (2009). Attention and biased competition in multi-voxel object representations. *Proceeding of the National Academy of Sciences of the United States of America*, 106(50), 21447–21452, <http://dx.doi.org/10.1073/pnas.0907330106>.
- Reynolds, J. H., Chelazzi, L., & Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *Journal of Neuroscience*, 19(5), 1736–1753.
- Rossion, B., Delvenne, J. F., Debatte, D., Goffaux, V., Bruyer, R., Crommelinck, M., et al. (1999). Spatio-temporal localization of the face inversion effect: An event-related potentials study. *Biological Psychology*, 50(3), 173–189.
- Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., et al. (2000). The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: An electrophysiological account of face-specific processes in the human brain. *Neuroreport*, 11(1), 69–74.
- Rossion, B., Kung, C. C., & Tarr, M. J. (2004). Visual expertise with nonface objects leads to competition with the early perceptual processing of faces in the human occipitotemporal cortex. *Proceeding of the National Academy of Sciences of the United States of America*, 101(40), 14521–14526, <http://dx.doi.org/10.1073/pnas.0405613101>.
- Rossion, B., Collins, D., Goffaux, V., & Curran, T. (2007). Long-term expertise with artificial objects increases visual competition with early face categorization processes. *Journal of Cognitive Neuroscience*, 19(3), 543–555, <http://dx.doi.org/10.1162/jocn.2007.19.3.543>.
- Rossion, B., & Jacques, C. (2011). The N170: Understanding the time-course of face perception in the human brain. In: S. Luck, & E. Kappenman (Eds.), *The Oxford handbook of ERP components* (pp. 115–142). Oxford University Press, USA.
- Sadeh, B., & Yovel, G. (2010). Why is the N170 enhanced for inverted faces? An ERP competition experiment. *Neuroimage*, 53(2), 782–789.



- Snowden, R. J., Treue, S., Erickson, R. G., & Andersen, R. A. (1991). The response of area MT and V1 neurons to transparent motion. *Journal of Neuroscience*, 11(9), 2768–2785.
- Summerfield, C., Trittschuh, E. H., Monti, J. M., Mesulam, M. M., & Egner, T. (2008). Neural repetition suppression reflects fulfilled perceptual expectations. *Nature Neuroscience*, 11(9), 1004–1006, <http://dx.doi.org/10.1038/nn.2163>.
- Summerfield, C., Wyart, V., Johnen, V. M., & de Gardelle, V. (2011). Human scalp electroencephalography reveals that repetition suppression varies with expectation. *Frontiers in Human Neuroscience*, 5, 67, <http://dx.doi.org/10.3389/fnhum.2011.00067>.
- Young, M. P., & Yamane, S. (1992). Sparse population coding of faces in the inferotemporal cortex. *Science*, 256(5061), 1327–1331, <http://dx.doi.org/10.1126/science.1598577>.
- Zimmer, M., & Kovács, G. (2011). Electrophysiological correlates of face distortion after-effects. *Quarterly Journal of Experimental Psychology*, 64(3), 533–544, <http://dx.doi.org/10.1080/17470218.2010.501964>.