Electrophysiological correlates of visual adaptation and sensory competition

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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.

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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; Mc mains & 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
The N2b ERP component, occurring at around 280 ms (Lange, Wijers, the effect of attentional task was even more delayed, corresponding to presented the context stimulus (S1) not. On the one hand studies that showed N170 amplitude reductions found competition effects on the face-related N170, and those that did (Kastner et al., 1998; Recanzone et al., 1997; Reynolds et al., 1999), a setup but varying the onset asynchrony of S1 and S2 within 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.

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. Surprisingly, Gentile and Jansma (2012) found similar N170 effects take place at this time-window. The earliest competition effect 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 (mean 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.
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° x 3.7° of visual angle. They were presented on the periphery on a uniform gray background.

We used a 12×12 dB/octave Butterworth zero phase high-pass filter was used to remove IC shifts, and a 50 Hz notch filter was applied to minimize line-noise artifacts. Finally, a 12×12 dB/octave low-pass filter with a cut-off frequency of 25 Hz was applied. Trials that contained voltage fluctuations exceeding ±100 mV, or eye blinks exceeding ±50 mV were rejected. The EEG was segmented offline (Brain VisionAnalyzer, ver.1.05, 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 data 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,PO5/PO7 (left hemisphere, LH) and PO2,PO6/PO8 (right hemisphere, RH) channels. After averaging the individual peak amplitudes were measured for each subject and each condition using a ±20 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 signal (2; S1face, S1noise), visual field (2; LVF, RFV), 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 S1face and S1noise 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, ηp2 = 0.37). P100 was also larger for the intracalvarial vs. the ipsilateral hemifield (main effect of hemifield: F(1,14)=10.3, p=0.006, ηp2 = 0.43), but mostly in the SIM condition (interaction of hemifield and condition: F(2,28)=8.4, p=0.001, ηp2 = 0.38). No
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: $F(1,14)=34.3$, $p=0.00004$, $\eta^2_p = 0.71$) it was also shorter for the S1-face when compared to S1-noise condition (main effect: $F(1,14)=8.5$, $p=0.01$, $\eta^2_p = 0.38$; see also Fig. 3D), but mostly for the ipsilateral visual hemifield (interaction of type of S1 and hemifield: $F(1,14)=8.7$, $p=0.01$, $\eta^2_p = 0.38$).

### N170

We observed a main effect of electrode for the N170 amplitude ($F(2,28)=6.4$, $p=0.008$, $\eta^2_p = 0.31$), 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 S1-noise (main effect of type of S1: $F(1,14)=33.1$, $p=0.00001$, $\eta^2_p = 0.70$; 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 ($F(2,28)=14.1$, $p=0.00014$, $\eta^2_p = 0.50$). In fact the three way condition $\times$ visual hemifield $\times$ type of S1 interaction ($F(2,28)=8.34$, $p=0.0048$, $\eta^2_p = 0.37$) 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: $F(1,14)=48.4$, $p=0.000007$, $\eta^2_p = 0.77$) and for the right when compared to the left hemisphere (main effect of hemisphere: $F(1,14)=27.2$, $p=0.0001$, $\eta^2_p = 0.66$), 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: $F(1,14)=31.2$, $p=0.00007$, $\eta^2_p = 0.69$). It was also shorter for contralateral than ipsilateral hemifields (main effect of hemifield: $F(1,14)=56.1$, $p=0.0000003$, $\eta^2_p = 0.80$) and in the SIM when compared to the other two conditions (main effect of condition: $F(2,28)=4.9$, $p=0.01$, $\eta^2_p = 0.26$).

### 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: $F(2,28)=53.9$, $p=0.00001$, $\eta^2_p = 0.79$). 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: $F(2,28)=4.49$, $p=0.01$, $\eta^2_p = 0.26$).

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**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 S1noise (dark gray) and S1face (light gray). Black lines represent the difference wave of S1noise-S1face. Insets represent the topographical maps (back view of the head) depicting the scalp distribution of the S1noise-S1face differential activity (180–225 ms time-window).
10.7, $p = 0.0003$, $\eta^2_p = 0.43$). The three way interaction of condition $\times$ hemifield $\times$ type of S1 suggests that the difference between the two hemispheres in the SUCC and CONC conditions was smaller for S1$_{\text{noise}}$ than for S1$_{\text{face}}$ conditions ($F(2,28) = 3.5$, $p = 0.048$, $\eta^2_p = 0.19$; Fig. 5B). Furthermore, the main effect of hemisphere ($F(1,14) = 7.3$, $p = 0.044$, $\eta^2_p = 0.34$) 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: $F(2,28) = 3.4$, $p = 0.047$, $\eta^2_p = 0.19$). In addition to that only the condition $\times$ hemisphere $\times$ type of S1 three-way interaction was significant ($F(2,28) = 6.9$, $p = 0.0006$, $\eta^2_p = 0.33$) showing that P2 latencies are longer over the RH than over the LH, specially in the CONC condition with S1$_{\text{noise}}$.

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$_{\text{face}}$ when compared to S1$_{\text{noise}}$. 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. 3. Average (±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$_{\text{noise}}$ (black) and S1$_{\text{face}}$ (gray) separately. B and D represent the average (±95% confidence intervals) for the S1$_{\text{noise}}$ versus S1$_{\text{face}}$ comparisons performed for each condition, hemisphere and hemifield separately. SUCC—black, CONC—light gray, and SIM—dark gray.](image-url)
Fig. 4. Average (± 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 S1noise (black) and S1face (gray) separately. B and D represent the average (± 95% confidence intervals) for the S1noise−S1face comparisons performed for each condition, hemisphere and hemifield separately. SUCC—black, CONC—light gray, and SIM—dark gray.

Fig. 5. Average (± 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 S1noise (black) and S1face (gray) separately. B and D represent the average (± 95% confidence intervals) for the S1noise−S1face 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-face and S1-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-face and S1-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 (SUC), 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, Trüsschutz, Monti, Mesulam, & Egner, 2008; Summerfield, Wyatt, 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.

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