Functional hemispheric asymmetries of global/local processing mirrored by the steady-state visual evoked potential

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While hemispheric differences in global/local processing have been reported by various studies, it is still under dispute at which processing stage they occur. Primarily, it was assumed that these asymmetries originate from an early perceptual stage. Instead, the content-level binding theory (Hübner & Volberg, 2005) suggests that the hemispheres differ at a later stage at which the stimulus information is bound to its respective level. The present study tested this assumption by means of steady-state evoked potentials (SSVEPs). In particular, we presented hierarchical letters flickering at 12 Hz while participants categorised the letters at a pre-cued level (global or local). The information at the two levels could be congruent or incongruent with respect to the required response. Since content-binding is only necessary if there is a response conflict, asymmetric hemispheric processing should be observed only for incongruent stimuli. Indeed, our results show that the cue and congruent stimuli elicited equal SSVEP global/local effects in both hemispheres. In contrast, incongruent stimuli elicited lower SSVEP amplitudes for a local than for a global target level at left posterior electrodes, whereas a reversed pattern was seen at right hemispheric electrodes. These findings provide further evidence for a level-specific hemispheric advantage with respect to content-level binding. Moreover, the fact that the SSVEP is sensitive to these processes offers the possibility to separately track global and local processing by presenting both level contents with different frequencies.

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1. Introduction

Many objects in our environment have a hierarchical structure, i.e. a global form composed of smaller components. A tree, for instance, consists of a trunk, branches, leaves etc., and we can focus on its global shape or on its local details. In other words, our attentional system allows us to select information intentionally from the one or the other level. However it is still under dispute how this selection proceeds. Experiments investigating this issue, usually use hierarchical letters as stimuli (see Fig. 1a; Navon, 1977), and participants are asked to categorise these letters at the global or at the local level. Results indicated that there is a left-hemispheric advantage for processing information at the local level of hierarchical stimuli, whereas the right hemisphere is more specialised for the processing the global shape of stimuli (Boles & Karner, 1996; Evans, Shedd, Hevenor, & Hahn, 2000; Heinze, Hinrichs, Scholz, Burchert, & Mangun, 1998; Heinze & Münte, 1993; Van Kleeck, 1989; Volberg & Hübner, 2004; Yovel, Yovel, & Levy, 2001). Some studies locate these hemispheric asymmetries at an early, sensory stage of processing. It was demonstrated, for instance, that the left hemisphere preferentially processes relatively high spatial frequencies of a visual input, whereas the right hemisphere is more effective at processing relatively low spatial frequencies (Peyrin, Chauvin, Chokron, & Marendaz, 2003; Robertson & Ivry, 2000). Based on these findings, it was assumed that hemispheric differences are purely stimulus driven. In contrast, in various studies hemispheric differences were mainly found when there was a response conflict, i.e. when the information at the two levels activated competing responses (Heinze et al., 1998; Hübner & Malinowski, 2002; Malinowski, Hübner, Keil, & Gruber, 2002; Martens, Trujillo Barreto, & Gruber, 2011; Volberg & Hübner, 2004). This suggests that hemispheric asymmetries originate from processing differences beyond sensory analyses.

Hübner and Volberg (2005) developed their content-level binding (CLB) theory in which they state that information about the hierarchical structure of a stimulus and information about the identity of the content at each level are analysed separately at an early stage of processing, and that the functioning of the hemispheres does not differ at this stage. Rather, hemispheric differences first emerge at a later stage, at which the content has to be bound to its respective level to create a complete object represen-
In particular, the left and right hemisphere are supposed to be superior at binding content information to the local and global level, respectively.

The CLB theory nicely explains why hemispheric differences depend on response congruency of the global and local level (Heinze et al., 1998; Hübner & Malinowski, 2002; Malinowski et al., 2002; Martens et al., 2011; Volberg & Hübner, 2004). If the contents at both levels of a stimulus activate the same response, which is the case for congruent stimuli (for an example see Fig. 1 a), then the level is irrelevant for response selection. Accordingly, no binding of content and level is needed. In contrast, if the content at the non-target level activates a different response than the information at the target level (incongruent stimulus), then the contents need to be bound to their corresponding level in order to select the correct response. For example, if the letters ‘A’ and ‘H’ require a RIGHT and LEFT response, respectively, and participants should respond to a global ‘A’ made of local ‘H’s (Fig. 1a), then it is necessary for a correct response to know which letter was present at which level.

There have been attempts to combine the CLB theory with the spatial-frequency account of hemispheric asymmetries in global/local processing (Flevaris, Bentin, & Robertson, 2010; Hübner & Kruse, 2011). Flevaris et al. (2010) for instance have shown that priming with specific spatial frequencies improves the subsequent binding for the corresponding inferior hemisphere. That is, after attending to low spatial frequencies of a compound Gabor patch, the hemispheric asymmetry for the incongruent global targets was reduced. Likewise, attending to high spatial frequencies reduced the asymmetry for incongruent local targets. This suggests that the CLB mechanism might use spatial-frequency filtering as basis to define the global and local level.

At odds with the CLB theory are studies reporting hemispheric differences during the processing of a level cue in the preparatory phase, i.e. in the cue-stimulus interval (Flevaris, Bentin, & Robertson, 2011; Weissman & Woldorff, 2005; Yamaguchi, Yamagata, & Kobayashi, 2000). Obviously, no binding process is required during cue processing. Therefore, the aim of the present study was to test the assumptions of the CLB theory by investigating both cue and target processing. Moreover, instead of measuring visual field effects or conventional event-related potentials (ERPs), we relied on the so-called steady-state visual evoked potential (SSVEP). The SSVEP is the electrophysiological oscillatory response of the brain to a flickering stimulus in the same frequency as the initiating stimulus (Kaspar, Hassler, Martens, Trujillo-Barreto, & Gruber, 2010). In other words, the neurons that are processing the flickering stimulus respond with the same frequency. Thus, when analysing the evoked brain activity in the frequency range of flicker frequency, one receives a signal (i.e. the SSVEP) that is much less influenced by neuronal activity that is unrelated to the experimental task and stimulus processing (i.e. the so-called noise) than ERPs are. In a previous SSVEP study investigating complex scene perception (Martens et al., 2011), indications for the SSVEP's sensitivity to functional hemispheric asymmetries were observed. In particular, participants were confronted with scenes that contained one local object and a global background. The object was either semantically coherent with the background (e.g. a deer in the woods) or semantically incoherent (e.g. a deer in a swimming pool). Most importantly, a separable brain response to the object from the background was elicited by flickering the object for 3 s at a different frequency (e.g. 12 Hz, i.e. 12 flashes per second) than the background (e.g. 8.6 Hz), which resulted in two distinct SSVEPs.

Fig. 1. (a) Example for congruent and incongruent stimuli. A and S required a response with the same finger/key, while H and E required a response with the other finger/key. (b) Sequence of events within one trial. The yellow or blue cue indicated which level to attend (local vs. global). The target was either congruent or incongruent. All stimuli were continuously presented at 12 Hz. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
Contrasting the SSVEP to coherent and incoherent objects (local level) revealed a left temporal locus of effect, whereas the identical contrast for the background signal (global level) revealed right temporal activations, indicating functional hemispheric asymmetries.

In the present experiment the SSVEP method, as applied in Martens et al. (2011), was utilised to further test the CLB theory. We presented a coloured cue (indicating the target level) and a subsequent Navon letter centrally flickering at 12 Hz for approximately 3.5 s in total, eliciting an SSVEP of the same frequency. According to the CLB theory, the SSVEP effects should be lateralized for incongruent stimuli, because in this case content-to-level binding is necessary for correct task performance. In contrast, no hemispheric differences between SSVEP amplitudes should be observed during the cue-stimulus interval and in response to congruent stimuli, because no binding is necessary in these cases.

We expected that hemispheric specialisation is mirrored by an SSVEP decrease. This assumption is based on two findings: (1) SSVEP amplitude increases with attention (Morgan, Hansen, & Hillyard, 1996; Müller et al., 2006) and working memory load (Silverstein, Nunez, Pipingas, Harris, & Danieli, 2001). Therefore, the hemisphere that binds the less preferred input should elicit higher SSVEP amplitudes than the hemisphere binding the preferred input. (2) Repetition priming studies showed decreased cortical activations (Gruber & Müller, 2005; Henson & Rugg, 2003) and decreased SSVEP amplitudes (Martens & Gruber, 2012) to repeated stimuli. This decrease reflects a sharpening mechanism within the activated neuronal networks, which leads to more effective stimulus processing and better behavioural performance (faster response times, lower error rates). Consequently, hemispheric preferences that are behaviourally mirrored by faster and more accurate target identification (e.g. Christman, 1989; Hellige, 1996; Romei, Driver, Schyns, & Thut, 2011; Yovel et al., 2001) should neuronally be reflected by decreased cortical activity. Specifically, for incongruent conditions we expect left hemispheric SSVEP amplitudes to be smaller in response to local as compared to global targets, whereas right hemispheric SSVEP amplitudes should be smaller in response to global as compared to local targets.

2. Methods

2.1. Participants

We recruited students from the University of Osnabrück by means of advertisement on campus bulletin boards. Twenty participants gave written informed consent and took part in the experiment. Three participants were excluded due to excessive artifacts in the EEG and two due to less than 75% correct responses in the first half of the experiment. Mean age of the remaining fifteen participants contributing data to the experiment was 25.1 years (12 female, all right handed by self-report).

2.2. Stimuli and procedure

Hierarchical stimuli were created by arranging identical local stimuli in a 5 by 5 grid so that they formed a global stimulus (see Fig. 1A). At a viewing distance of 110 cm the local and the global letters subtended a visual angle of 0.5 by 0.8º and 2.4 by 3.9º, respectively. To establish an SSVEP and eliminate overlap with conventional ERPs in the analysis time window, each trial started first with the flickering presentation of a neutral stimulus, which was a white ‘8’ constructed out of ‘8’s at 12 Hz (see Fig. 1B). All subsequent stimuli were continuously presented with the same frequency. After 500–800 ms the colour of the neutral stimulus changed either to blue or to yellow (level cue) for 417 ms, indicating the relevant target level. A jittered interval before its onset was chosen to minimise expectation effects to the upcoming cue. After further 417 ms (resulting in a preparation phase of 834 ms), the neutral letter was replaced by the target letter for 834 ms. This target duration resembled the average response time and prevented a stimulus-offset potential in the analysis time window. The target letter was one of the possible twelve combinations of the letters A, S, H, and E at the global and local level. We refrained from using identical global/local letter combinations in order to make the congruent condition harder, which provides a more conservative test of our hypotheses. The participants’ task was to identify the letter at the target level as quickly as possible. ‘A’ and ‘S’ required a response with the right index finger, whereas ‘H’ and ‘E’ indicated to respond with the right middle finger. Stimulus–response mapping and the assignment of cue-colour to target-level were counterbalanced across participants. Congruent stimuli consisted of a letter at each level that were mapped to the same response (i.e. a global A constructed from local Ss), whereas incongruent stimuli contained a letter at the local level that was mapped to the opposite response than the global letter (i.e. a global H constructed from local Ss). Example stimuli are displayed in Fig. 1A. The target was replaced by the neutral stimulus, which remained on the screen for 1170 ms resulting in a total trial length (i.e. flickering stimuli) of approximately 3500 ms on average. This trial duration allowed for reliable frequency analyses (see below). The trial sequence is displayed in Fig. 1B. The experiment consisted of two practice and 10 experimental blocks. Each experimental block comprised 48 trials with 12 trials for each of the four conditions (two levels × two stimulus-congruency types).

2.3. Electrophysiological recording

The EEG was recorded using 128 electrodes and the BioSemi Active Two amplification system with a sampling rate of 512 Hz. Eye movements and blinks were measured by a vertical and horizontal electrooculogram (EOG). The data were segmented into −500 to 1000 ms epochs relative to the onset of the level cue and relative to the target onset (baseline −200 to 0 ms) and artifact corrected by means of statistical correction of artifacts in dense array studies (Junghöfer, Elbert, Tucker, & Rockstroh, 2000). Single epochs with excessive eye movements and blinks, as well as epochs with more than 20 channels containing artifacts were discarded from further analyses. Finally, the data was re-referenced to the average of all electrodes.

2.4. Data analysis (A): Behavioural data

Response times and error rates were measured and submitted to separate analyses of variance (ANOVA) with the repeated-measures factors target level (global vs. local) and congruency (congruent vs. incongruent). Note that the stimuli were presented centrally. Consequently, the behavioural results could not reveal any hemispheric processing differences with regard to the target level and stimulus congruency.

2.5. Data analysis (B): SSVEPs

To determine the temporally changing magnitude of the SSVEP at 12 Hz, the signal was spectrally decomposed by means of Morlet wavelet analysis as described in previous studies (Kaspar et al., 2010). In short, we used a wavelet family of 12 cycles per second in order to receive an excellent frequency resolution of approximately 12 Hz. This reduced the temporal resolution to a wavelet duration of 320 ms, which did not allow for an analysis of the time-course of hemispheric processing asymmetries.
Experimental factors consisted of SSVEP amplitude values elicited by the cue with the right hemispheric posterior electrodes including O1/O2, PO7/PO8, P7/P8, P9/P10 were chosen at which the SSVEP was largest (see Fig. 3 top). The final data set of the preparation phase consisted of the topographical activation difference between local and global processing (after visual inspection of the topography, an additional t-test was performed at a right temporal electrode cluster indicating no hemispheric asymmetries between local and global processing). The ANOVA on the error rates revealed a main effect of congruency, F(1,14) = 44.2, p < 0.001. Post hoc t-tests revealed that responses to congruent stimuli were less error prone than responses to incongruent stimuli (4.1% [SD = 3.3] vs. 6.6% [SD = 4.9]). There was no overall difference in the error rates when identifying the information at the local target level (3.3% [SD = 3.3]) and the global target level (3.6% [SD = 4.9]).

Fig. 3. Target phase: (Top) Grand average scalp topography (time window 0–700 ms) of the SSVEP amplitude elicited by the target stimulus. Statistical analyses were based on the left and right hemispheric electrode clusters that are indicated. (Left) SSVEP to congruent targets; difference topography of the SSVEPs to local minus global targets (time window 0–700 ms). The line plots display the time course of the SSVEP amplitude to global and local responses, separately for the left and the right hemispheric electrode cluster indicating hemispheric asymmetries between local and global processing. (Right) SSVEP to incongruent targets; difference topography of the SSVEPs to local minus global targets (time window 0–700 ms). The line plots display the time course of the SSVEP amplitude to global and local responses, separately for the left and the right hemispheric electrode cluster indicating hemispheric asymmetries between local and global processing.

3. Results

3.1. Behavioural data

The ANOVA on mean reaction times revealed significant main effects of target level, F(1,14) = 28.6, p < 0.001, and congruency, F(1,14) = 56.6, p < 0.001. Responses to local letters were faster than those to global letters (756 ms [SD = 110] vs. 809 ms [SD = 85]), and responses to congruent stimuli were faster than those to incongruent stimuli (764 ms [SD = 98] vs. 801 ms [SD = 96]). These main effects were further qualified by a significant interaction of both factors, F(1,14) = 44.2, p < 0.001. Post hoc t-tests revealed that the congruency manipulation affected only responses to the global level (464 ms, t(14) = −8.6, p < 0.001, d = 2.2) but not those to the local level (410 ms, t(14) = −2.1, p = 0.029, d = 0.53).

An identical ANOVA on the error rates revealed a main effect of congruency, F(1,14) = 6.8, p < 0.021. Responses to congruent stimuli were less error prone than responses to incongruent stimuli (4.1% [SD = 3.3] vs. 6.6% [SD = 4.9]). There was no overall difference in the error rates when identifying the information at the local target level (3.3% [SD = 3.3]) and the global target level (3.6% [SD = 4.9]) (F < 1). Although the interaction between the factors level and congruency only approached significance, F(1,14) = 4.3, p = 0.056, the difference in error rates between congruent and incongruent stimuli was numerically larger in response to the global target level (44.2%, t(14) = 3.1, p < 0.01, d = 0.81) than those to the local target level (40.9%, t(14) = 0.7, p = 0.47, d = 0.19).
SSVEP amplitude values during the preparation phase were submitted to a repeated-measures ANOVA with the factors hemisphere (left vs. right) and level (global vs. local). Results indicated that none of the factors nor their interaction had a significant effect on the SSVEP amplitude after cue onset (see Fig. 2). A repeated measures ANOVA with the factors hemisphere (left vs. right), target level (global vs. local), and congruency (congruent vs. incongruent) on the SSVEP amplitude values of the stimulus phase revealed a significant three-way interaction of all factors, F(1,14) = 12.4, p < 0.003. For congruent stimuli no effect of hemisphere or level, nor an interaction of these factors was seen, F < 1 (see Fig. 3, left). In contrast and most importantly, for incongruent stimuli, the factors hemisphere and target level interacted significantly, F(1,14) = 11.7, p < 0.004. In particular, processing of local targets tended to elicit smaller SSVEP amplitudes at left hemispheric electrodes compared to the SSVEP elicited by the processing of global targets, t(14) = −1.9, p = 0.042, d = 0.47. The reversed pattern was seen at right hemispheric electrodes. Here, processing of global targets tended to elicit smaller SSVEP amplitudes as opposed to the processing of local targets, t(14) = 1.9, p = 0.037, d = 0.50. The topography of this hemispheric asymmetry as well as their time course are displayed in Fig. 3 on the right side. Note, that we defined the region for statistical analyses a priori and symmetrically on the averaged SSVEP topography. The right hemispheric effect was more temporal and the left hemispheric effect more occipital than the average SSVEP. This deviance was not covered by our regional means, which resulted in only marginal significant post hoc comparisons.

4. Discussion

Using the SSVEP technique, the present study investigated the assumptions of the CLB theory that hemispheric asymmetries for global/local processing occur only when the related task requires binding of stimulus identity and stimulus level. This is the case when the contents at both stimulus levels produce a response conflict (i.e. for incongruent stimuli in our experiment). To resolve this conflict and select a correct response, the stimulus contents (here, letter identities) have to be bound to their respective level (Hübner & Volberg, 2005), and this is the stage at which the functioning of the hemispheres differs. Likewise, no hemispheric differences should occur for stimuli that do not produce a response conflict, such as congruent stimuli and the level cue.

Response times and error rates indicated that the manipulation of response congruency significantly affected behavioural performance. This effect was especially pronounced for the global target level, which resulted from faster accessible local content. Whereas behavioural results could only indicate the effective manipulation of the binding requirements, analysing the SSVEP amplitude to cues and hierarchical stimuli confirmed the predictions of the CLB theory. (1) No hemispheric differences were present during preparation for processing the cued target level. (2) Functional hemispheric differences occurred for the processing of hierarchical stimuli. (3) These differences emerged only for incongruent stimuli, but not for congruent ones. In particular, in corresponding trials reversed SSVEP amplitude patterns were observed for global vs. local target levels at posterior electrodes for the left as opposed to the right hemisphere. These effects were only marginal significant, since we used predefined identical electrodes at both hemispheres. Topographical results though indicated that the right hemispheric effect was located more anterior than the left hemispheric effect. In general our results provide further evidence for the CLB theory and thereby support the idea that binding of stimulus content to the local level proceeds more effective in the left than in the right hemisphere, whereas the binding of information to the global level is superior in the right hemisphere. There are indications that the left hemispheric binding process originates from a different cortical region than the right hemispheric one (Malinowski et al., 2002; Volberg & Hübner, 2004). Addressing this issue in future studies could reveal functional details of the respective binding processes. Furthermore, we can assume that the processing of global and local information per se is not lateralised as is indicated by the results that no hemispheric asymmetries were seen when binding was not behaviourally relevant (in response to the cue and to congruent stimuli). Although null findings can result from lack of statistical power, they are in line with other results (using different methods) for the preparation phase (Volberg & Hübner, 2007) and for incongruent stimuli (Malinowski et al., 2002).

When interpreting the SSVEP results for incongruent stimuli, we assumed that lower amplitudes reflect more effective processing. Studies measuring ERPs reported global/local N2 effects that were inconclusive with regard to the direction of the effect in the hemispheres. While some studies found more negative N2 amplitudes to centrally presented global as opposed to local stimuli over the right hemisphere (Malinowski et al., 2002; Yamaguchi et al., 2000); Volberg and Hübner (2004) found the opposite effect pattern for unilaterally presented stimuli. The SSVEP amplitudes in the present study tended to be smaller for local than for global targets over the left hemispheric and for global as opposed to local targets over the right hemisphere. This replicates the N2 results of Malinowski et al. (2002) who used the identical design with static stimuli. Whereas ERPs are hard to interpret with regard to the direction of effects – a positive component does not necessarily reflect an increase in activity of a brain region while a negative component reflects a decrease – the SSVEP amplitude mirrors the amount of neurons that fire synchronously at the flicker frequency. Thus, here a decrease can be interpreted as reduced activity of a neuronal population or a reduced number of active neurons. As explained in the introduction, repetition–priming studies suggest that reduced cortical activations in response to well-known stimuli reflect more effective processing than enhanced activations (Gruber & Müller, 2005; Henson, Shallice, & Dolan, 2000; Martens & Gruber, 2012). Accordingly, the decreased SSVEP amplitudes are fully compatible and supportive with the hypothesis that binding of stimulus content to the local level proceeds more effective in the left than in the right hemisphere, whereas the binding of information to the global level is superior in the right hemisphere. Furthermore, the processing of global and local information per se seems not to be lateralised as is indicated by the results in our study that no hemispheric asymmetries were seen when binding was not behaviourally relevant.

The extant neuroscientific literature on global/local processing often reported hemispheric asymmetries in which only one hemisphere showed significant differences between task by level conditions and the other did not (Fleviris et al., 2010; Han, Liu, Yun, & Woods, 2000; Heinze et al., 1998; Weissman & Woldorff, 2005). In contrast, our SSVEP studies (the present one, and Martens et al., 2011) demonstrated hemispheric asymmetries with opposite effect patterns in both hemispheres. By flickering the stimulus the neurons processing the visual input respond in the specific flicker frequency. This effect allows for a better detection of the neuronal activity related to stimulus processing. This so-called signal-to-noise ratio of the SSVEP is superior to the one of ERPs. Thus, the SSVEP seems to be a better tool to investigate these processing differences that are of small and differential nature and not an all or nothing phenomenon.

In the present study, local targets were processed faster than global ones, whereas in many other studies there was a global advantage (for a review see Kimchi, 1992). Whether there is a glo-


