

# Attention and visual texture segregation

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Visual texture segregation is believed to be performed preattentively. Recent evidence, however, suggests that attention does play an important role. Using visual evoked potentials (VEPs), we investigated the effect of different tasks on texture segregation. Stimuli consisted of Gabor-filtered binary noise patterns. In segregated stimuli, local texture orientation contrasts defined global checkerboard patterns. VEP responses specific to texture segregation were obtained by computing the difference between VEPs to homogeneous and segregated stimuli. Four conditions were examined that required attending either the global pattern, the local structure, random numbers displayed on the screen, or a series of tones. Responses specific to texture segregation were dominated by two occipital negativities peaking around 110 and 230 ms. The earlier one was not affected by the task, whereas the later one was completely abolished when the subjects attended to either numbers or tones ( $p = .0005$  and  $p = .006$ , respectively). The results suggest that early stages of texture segregation are not affected by attention, whereas task relevance is crucial for later processes. The timing is compatible with a recurrent processing pattern with initial bottom-up processing of basic stimulus characteristics and a subsequent top-down flow of higher level modulatory information. As attention effects occur across modalities, they cannot be simply explained by competition within the visual cortex.

Keywords: texture segregation, attention, task, top-down, cross-modal interaction, visual evoked potential

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## Introduction

Texture segregation is the effortless division of a visual stimulus into distinct segments based on spatial gradients in local feature properties. Psychophysical studies suggest that texture segregation can be performed preattentively (Julesz, 1981a, 1981b). On the other hand, attention is considered to be essential for controlling perceptual processing, for example, by biasing the competition among stimuli for neural representation (see reviews by Kastner & Pinsk, 2004; Kastner & Ungerleider, 2000; Reynolds & Chelazzi, 2004; Serences & Yantis, 2006).

Visual evoked potentials (VEPs) have been frequently used to investigate texture segregation in the human cortex. In these experiments, VEPs to both homogeneous stimuli (without global pattern) and segregated stimuli (where contrasts in local features form a global pattern) were recorded and the “texture segregation VEP” (tsVEP) was isolated by subtracting the two VEP curves (Bach & Meigen, 1990, 1992; Lamme, Van Dijk, & Spekreijse, 1992). The latencies reported for the main components of tsVEPs considerably differ within and between

studies, from approximately 110 ms to more than 250 ms (e.g., Bach & Meigen, 1999; Caputo & Casco, 1999; Fahle, Quenzer, Braun, & Spang, 2003; Lachapelle, Ouimet, Bach, Ptito, & McKerral, 2004; Schubö, Meinecke, & Schröger, 2001).

It is known from VEPs evoked by simple stimuli, such as luminance-defined checkerboard patterns, that attention may affect early responses including the P100 (e.g., Di Russo & Spinelli, 1999; Hoshiyama & Kakigi, 2001). These early effects were usually found when subjects had to attend to a specific location in the visual field while feature attention was generally associated with later effects (Hillyard & Kutas, 1983). Caputo and Casco (1999) report that an additional component occurs in the VEP when the subjects are performing a discrimination task on a global figure rather than viewing the stimuli passively. In a more recent study investigating the effect of attention on texture segregation, Casco, Grieco, Campana, Corvino, and Caputo (2005) required the subjects either to attend the segregated figure and judge its orientation or to attend to centrally presented numbers. They found that the main tsVEP component spanning the time range of 130–220 ms was reduced by about 40% when the numbers were attended. Demonstrating the

importance of attention in figure-ground processing, the study by Casco et al. prompts new questions:

1. *Symmetric task.* Casco et al. guided the subjects' attention by requiring them to perform a task on the segregated stimulus. This results in an unbalanced situation because the homogenous stimuli are completely irrelevant for the task although the associated VEPs are used for computing the tsVEP.
2. *Underlying mechanisms.* The reduction of segregation-related activity in the number task might be due to competition in visual processing. Such competition might be either a general mechanism to yield the most relevant visual information (cf. Kastner & Ungerleider, 2000) or a result of limited resources. Another possibility, however, is that attentional mechanisms act across sensory modalities. Directing attention to one modality might then result in a deactivation of the other modality, as demonstrated in imaging studies (e.g., Johnson & Zatorre, 2006; Kawashima, O'Sullivan, & Roland, 1995).

In a recent study, Scholte, Witteveen, Spekreijse, and Lamme (2006) used an elaborate rapid sequential visual presentation paradigm. They asked subjects to perform a task on centrally presented letters that appeared together with homogenous textures or occasionally with segregated patterns. In a first run, subjects were unaware of the segregated patterns. In a second run, they were informed and then perceived the segregation. Although the earliest segregation-related components in the magnetoencephalogram occurred already at around 200 ms, differences between runs, that is, between seen and unseen segregation, were only found after 400 ms.

An event-related potentials study by Schubö et al. (2001) specifically aimed at investigating two late segregation-related components. The first, a relative positivity, peaked around 270 ms, that is, substantially later than most segregation-related components in other studies, and did not occur with a distracting task. The second had its maximum parietally around 400 ms and was modulated by task complexity.

In fMRI experiments where subjects had to attend to centrally presented numbers, Kastner, De Weerd, and Ungerleider (2000) and Schira, Fahle, Donner, Kraft, and Brandt (2004) did not find a sizable activation in V1, as opposed to previous studies without a distracting task (Schmitt, Janz, Hennig, & Bach, 1998; Skiera, Petersen, Skalej, & Fahle, 2000). There is no consensus among studies whether conscious perception is necessary for activation of area V3A (Kastner et al., 2000; Schira et al., 2004; Scholte et al., 2006).

The question whether task-related attention affects a perceptual process is closely related to the question to what degree top-down processes are involved. Such attention-related feedback to the visual cortex might originate from frontal and parietal cortex (Kastner &

Ungerleider, 2000; Serences & Yantis, 2006). Specifically for texture segregation, masking experiments in monkeys indicate that feedback at least from extrastriate visual areas to V1 exists (Lamme, Zipser, & Spekreijse, 2002). Task-related response modulations would imply that some feedback streams indeed originate from beyond the visual cortex. The finding that sufficiently deep anesthesia abolishes segregation responses in monkey V1 while leaving the classical receptive field properties unaffected also hints toward higher processing levels being involved in texture segregation (Lamme, Zipser, & Spekreijse, 1998).

We pursued the questions of top-down control and the attention-related modulation of visual processing across sensory modalities through comparison of various visual tasks and an auditory task. In the present study, this auditory task exclusively aimed at distracting the subjects from the visual stimuli. We therefore expected the effect to be of a general modulatory nature. This is different from those experiments that investigated how auditory stimuli alter the perception of visual stimuli in a very specific manner. Such findings have been recently reported by a number of authors. For instance, Shams, Kamitani, Thompson, and Shimojo (2001) and Shams, Iwaki, Chawla, and Bhattacharya (2005) have shown that auditory stimulation is able to trigger additional visual percepts that were not physically present and evoke responses in the visual cortex. Another example is a study by Beer and Röder (2005), which demonstrated that attention to a specific direction of auditory motion altered the detection of that direction in visual motion. This direction-specific psychophysical effect was paralleled by changes in the VEP.

## Methods

### Subjects

Twelve subjects with normal or corrected-to-normal visual acuity participated after providing written informed consent. The study was approved by the institutional review board and followed the tenets of the Declaration of Helsinki.

### Stimuli

The stimulus patterns were presented on a gamma-corrected CRT screen. They consisted of a binary random noise pattern that was convolved with two-dimensional Gabor-like patches (for the formula used, see Appendix A), thereby producing an oriented grayscale texture with a certain spatial frequency characteristic. Details of the pattern are given in Figure 1. The angle of the texture could be either  $+45^\circ$  or  $-45^\circ$ , and the average spatial frequency was 3.0 cpd. To extract responses specific for

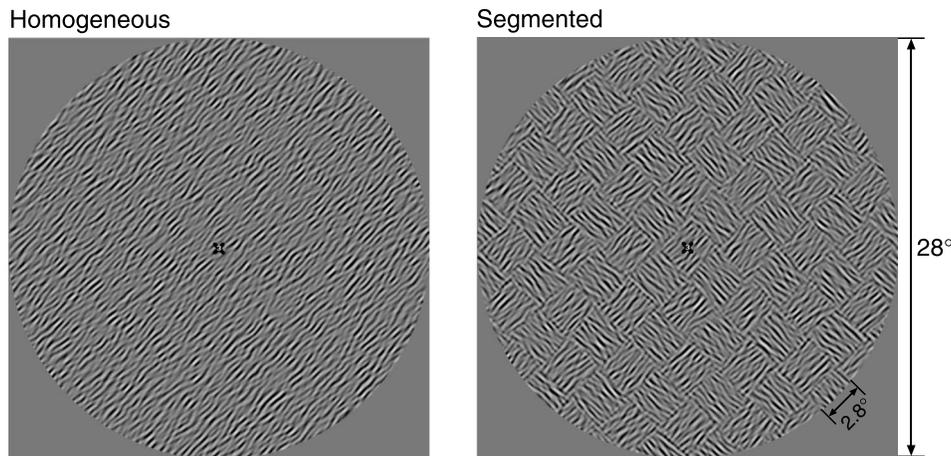


Figure 1. Examples of the stimuli. Left: Homogeneous stimulus without global pattern. Right: Segregated stimulus with a global checkerboard pattern. Subtracting the VEP obtained with homogeneous stimuli from that obtained with segregated stimuli yields the tsVEP.

texture segregation, we used two types of stimuli. “Homogeneous” stimuli consisted of just one texture orientation. In “segregated” stimuli, local orientation varied systematically, such that an orientation-defined checkerboard was formed. Along the segment borders, the two adjacent orientations were blended into each other over a distance equal to the wavelength of the texture’s spatial frequency, such that smooth transitions were achieved. The stimulus set included 10 specimens of each type that were counterbalanced for local texture orientation. Mean luminance was  $77 \text{ cd/m}^2$  with an average Michelson contrast of 52%.

Stimuli were presented on average every 926 ms with a temporal jitter of  $\pm 60$  ms. Stimulus duration was 293 ms. In between the stimuli, the screen was homogeneously gray, except for a fixation cross that was permanently present. Together with each stimulus, a digit was presented in the center of the fixation cross. In addition, a random sequence of high and low pitch sounds (462 and 440 Hz, respectively) was played. Each sound had a duration of 333 ms. The interstimulus interval for the sounds was on average 1000 ms with a temporal jitter of  $\pm 500$  ms, such that the sequence of sounds was completely uncorrelated to the sequence of visual stimuli.

## Tasks

In each experimental run, the subjects were asked to perform one of the following tasks and to respond by pressing buttons.

- *Segregation task.* “Press the left button if a segregated stimulus is presented, and the right button if a homogeneous stimulus is presented.” For this task, we expected to obtain the largest tsVEPs.
- *Local task.* “Press the left button if the local texture in the immediate vicinity of the fixation cross is oriented toward the upper left (which is equal to being oriented

to the lower right), and the right button if the texture is oriented to the upper right (or lower left).” Compared to the segregation task, here we expected the tsVEPs to be smaller but not completely absent.

- *Number task.* “Press the left button if the number that appears in the fixation cross is even, and the right button if it is odd.” This task was similar to the one employed by Casco et al. (2005) to shift attention away from the texture stimuli. It requires visual processing that might potentially compete with texture segregation, thereby reducing the tsVEP responses.
- *Auditory task.* “Press the left button when you hear the high-pitch sound, and the right button if you hear the low-pitch sound.” As this task involves the auditory modality, it disengages attention from the texture stimuli without directly competing with the processing of segregation in the visual system.

Each task was repeated twice in an ABCD-DCBA scheme, with the four tasks randomly assigned to A–D for each subject to avoid sequential effects. The assignment of the responses to the left and right buttons was switched between the two repetitions of the same task. A total of 180–200 artifact-free trials were obtained for each combination of task and stimulus type.

We chose the numbers to simultaneously appear with the texture stimuli to induce competition in the visual cortex. The asynchronous tone sequence, in contrast, was designed to produce a general shift of attention away from the visual modality.

## EEG recording and analysis

The EEG was recorded from Oz, PO7, PO8, TP7, TP8, Pz, Cz, and Fpz according to standard nomenclature (American Encephalographic Society, 1994) with a

linked-ears reference. The horizontal and vertical electro-oculogram (EOG) was also obtained. Signals were amplified and band-pass filtered (0.3–100 Hz), digitized at 500 Hz, and streamed to disk. Concurrently, preliminary VEPs were computed for on-line assessment of the recording.

Subsequent off-line processing included phase-preserving 40 Hz of low-pass filtering, pooling of the trials by stimulus type (segregated or homogeneous), and standard VEP averaging. Trials with artifacts as detected by a  $\pm 100 \mu\text{V}$  EOG threshold criterion were excluded from analysis.

The statistical significance of waveform differences was assessed using an interval-wise ROTp permutation test as described by Achim (1995).

## Results

All visual tasks were easily performed. Most subjects spontaneously reported that they experienced the auditory task as very demanding and that they made more errors than during the visual tasks.

### Original VEPs

The VEPs to stimuli containing global segregation are shown in Figure 2. Overall, early components were similar for all tasks. Permutation tests applied to the 50- to 100-ms and the 100- to 150-ms time intervals of

the responses to segregation stimuli suggest significance only for the difference between local and number task (50–100 ms,  $p = .0039$ ; 100–150 ms,  $p = .0083$ ). Other comparisons missed statistical significance as single comparisons or when the issue of multiple testing is considered ( $p$  values in the range of .044–.82). The largest  $p$  values were obtained for the comparison between segregation task and auditory task.

Starting at around 150 ms, VEPs began to differ markedly, most prominently at Oz with a positive deflection around 200 ms that was much larger for auditory and number tasks than for local and segregation tasks.

Following previous studies, we focused on the analysis of the Oz recordings, although the topography allowed for excluding possible confounding effects (see Discussion). Original VEPs to homogeneous and segregated stimuli as well as the resulting tsVEPs are presented in Figure 3 for the Oz electrode. The original VEPs did not differ in their general shape between tasks, but the positivity around 200–250 ms appeared to be substantially larger for the number task and auditory task than for the segregation and local tasks. This effect was focused at the Oz electrode.

### Segregation-related components

As a first step, we assessed the presence of significant deflections in the tsVEP obtained with the segregation task as we expected to find the largest texture segregation responses here. This was achieved by dividing the time interval from 50 to 300 ms poststimulus into five epochs of 50 ms duration. To each of these, we applied a permutation test, which identified the 100- to 150-ms

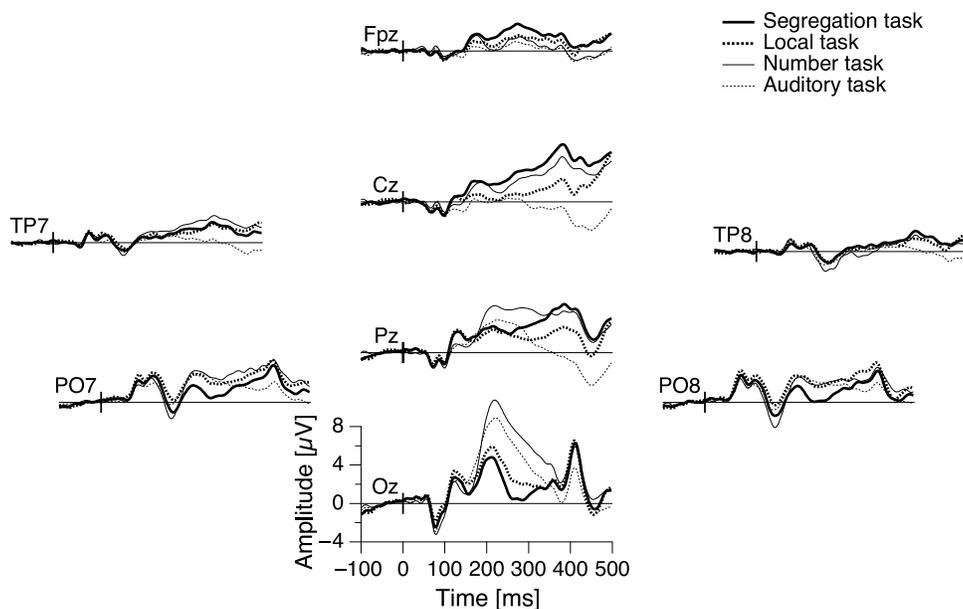


Figure 2. Grand mean VEPs to segregated stimuli. Graphs are arranged in a near-topographical scheme corresponding to the electrode locations on the head. During the first 150 ms, tasks had only little effect. At later times, effects increased, in particular at the Oz electrode where a positive deflection around 200 ms was largest for auditory and number tasks.

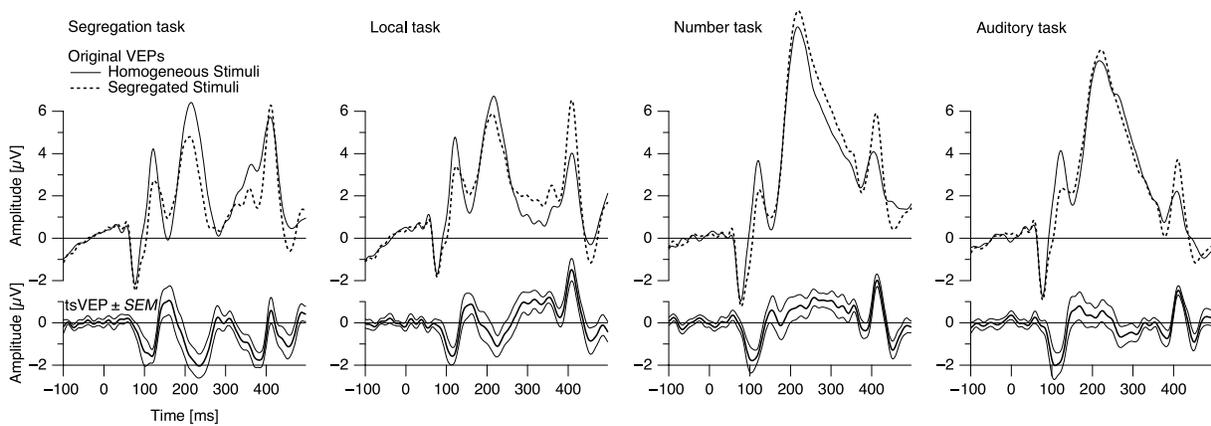


Figure 3. Grand means of original VEPs (top) and tsVEPs (bottom, including *SEM*) for all four conditions as recorded at the Oz electrode. In all tsVEPs there was an early negative deflection around 110 ms. A second negativity was present at around 230 ms for the segregation task, but missing for the number task and the auditory task.

epoch ( $p = .0078$ , including the peak at 110 ms) and the 200- to 250-ms epoch ( $p = .0034$ , including the peak at 230 ms) as significant. The significance remained with a Bonferroni adjustment.

Next, we asked whether differences between the four tasks are present in either of these two epochs. Figure 4 shows the tsVEPs for all electrodes with the traces of the different task conditions plotted together. Visual inspection suggested that there were only small differences in the earlier epoch. The later epoch, however, showed a clear task effect with the negative deflection completely vanishing for the number and auditory tasks. Applying the permutation test to the earlier epoch did not reveal significant differences for any of the six possible pairwise comparisons, with  $p$  values in the range of .29–.97. The same test applied to the later epoch identified several

significant differences as shown in Figure 5. The segregation task versus number task, segregation task versus local task, and local task versus auditory task differences were identified as statistically significant after significance thresholds were Bonferroni adjusted for the number of independent tests. The comparisons of segregation task versus local task and local task versus auditory task were significant as single comparisons, but neither after a regular nor a modified (Keppel, 1991) Bonferroni adjustment. The difference between number task and auditory task was far from being statistically significant.

Both segregation-related components had their maximum at the occipital electrode. However, as visible in Figure 4, the later component seems to extend more toward occipitotemporal locations. This finding is shown in more detail in Figure 6. At PO7 and PO8, the early

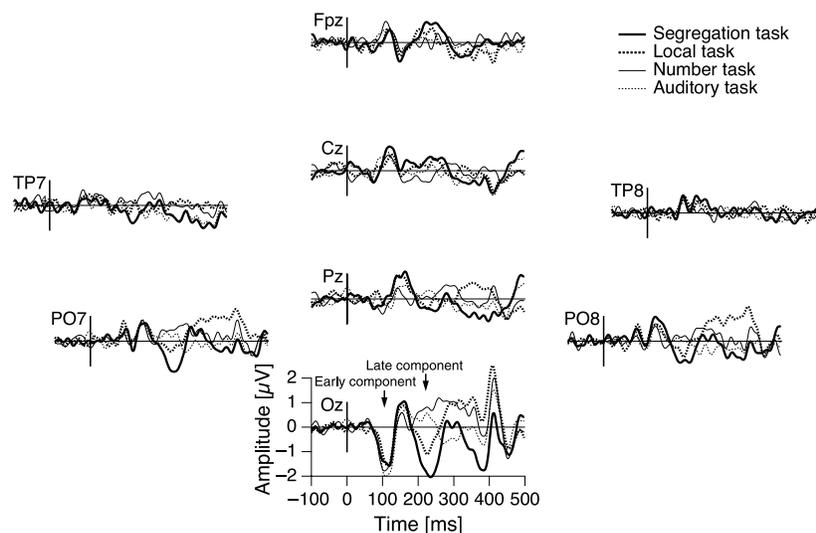


Figure 4. Grand mean tsVEPs. Graphs are arranged in a near-topographical scheme and display the difference between responses to homogenous and segregated stimuli for all four tasks. Components specific for texture segregation were most prominent at the Oz electrode with peaks at around 110 and 230 ms.

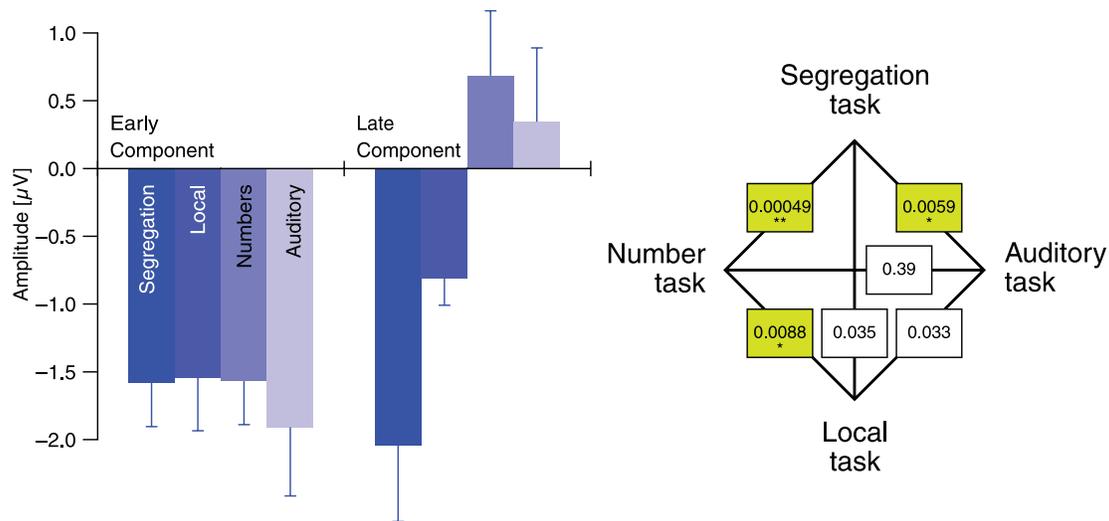


Figure 5. Left: tsVEP amplitudes of both early and late components for all four tasks. The displayed values were taken from the grand mean tsVEP curves at the peak times obtained with the segregation task because number task and auditory task did not produce a clear peak at the time of the later component. Right: Significance of differences between tsVEPs in the later time window. The numbers represent *p* values as obtained with the permutation test. The asterisks indicate the significance levels after Bonferroni correction (family-wise error rates: \* $\alpha = .05$ ; \*\* $\alpha = .01$ ).

component was on average 81% smaller than at Oz. The late component only dropped by 48%. However, this finding could not be statistically confirmed when the ratios between occipital amplitudes and occipitotemporal

amplitudes were assessed. Applying error propagation and Monte Carlo methods to the peak values and standard errors obtained from the grand mean tsVEPs yielded  $p = .25$  and  $p = .12$  for PO7 and PO8, respectively. Performing *t* tests or Wilcoxon signed rank tests on single-subject peak data did not result in smaller *p* values.

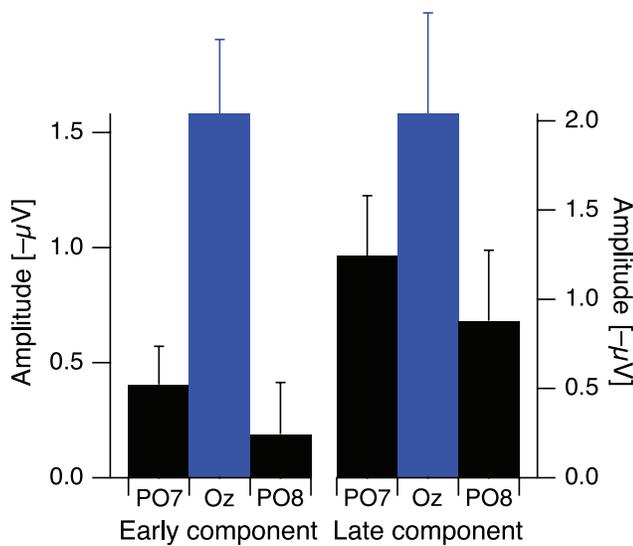


Figure 6. Topographical comparison between the early (left group of bars) and the late component (right group of bars) of the grand mean tsVEPs (cf. Figure 4) as obtained with the segregation task. The occipital amplitude (Oz electrode) is shown in blue and the occipitotemporal amplitudes (PO7 and PO8) are shown in black. For easier comparison, the ordinates are scaled such that both Oz bars have the same height. The early component drops more in amplitude toward occipitotemporal locations than the late component. However, this difference did not prove to be statistically significant.

### Responses after stimulus offset

Responses after stimulus offset were not within the original scope of the study. It is nevertheless interesting to note that these also appeared to be affected by the task. In particular, a sizable negative deflection around 100 ms after offset (approximately 390 ms after onset, cf. Figure 3) occurred only with the segregation task. To

	Local task	Number task	Auditory task
Segregation task	.010	.051	.072
	<b>.0044</b>	<b>.0054</b>	<b>.039</b>
	<i>.0020</i>	<i>.00049</i>	<i>.0024</i>
Local task		.60	.018
		<b>.22</b>	<b>.029</b>
		<i>.0088</i>	<i>.014</i>
Number task			.091
			<b>.16</b>
			<i>.013</i>

Table 1. *P* values as obtained with the permutation test for the 300- to 350-ms (normal typeface), the 350- to 400-ms (bold), and the 400- to 450-ms (italic) time intervals. Due to the post hoc nature of the test, no proper correction for multiple testing could be performed.

further evaluate this, we conducted a supplementary statistical analysis on these late components by performing the permutation test on the 300- to 350-ms and the 350- to 400-ms time intervals. The results are given in [Table 1](#) and provide preliminary evidence that offset responses are also modulated by attention, in particular in the 350- to 400-ms and the 400- to 450-ms time intervals. Due to the post hoc nature of this analysis, proper correction for multiple testing was impossible.

## Discussion

### The early segregation component at around 110 ms

In most previous studies, tsVEP responses had longer latencies than the early component in the present study. However, Meigen, Kastner, and Bach (1997; with similar patterns as in the present study), Lachapelle et al. (2004; with different orientation-defined patterns), and Fahle et al. (2003; with luminance- and color-defined patterns) also found a sizable early deflection. Furthermore, the latency of the present component is compatible to the response timing found in macaques (Lamme et al., 1998, 2002).

The early component is in a latency range that would be affected by low-level differences between the segregated and homogeneous patterns. We therefore double-checked that no luminance artifacts would account for this early effect by performing local luminance measurements around the texture boundaries with a spot meter and by performing statistical analyses on the stimulus patterns. These analyses also confirmed that no differences in local luminance contrast were present.

The lack of attentional modulation suggests that the early component reflects truly preattentive processes. These could be either veridically segregation related or originate from a reduced activation of orientation-selective neurons whose receptive fields coincide with the texture borders. This effect might be particularly strong in studies like the present one where the textures fully extend to the segregation borders. It is interesting to note that the early tsVEPs do not show the significant, albeit small, task effect that was found in the early original VEPs for the local versus number task comparison.

### The late segregation component at around 230 ms

The late component of the tsVEP, which is peaking around 230 ms after stimulus onset, shows a strong task dependence, implying that it does not represent preattentive processes. It is maximal at the occipital electrode, which excludes motor potentials as a possible confound.

The fact that the earlier component was not affected by the task excludes alternative explanations, such as improper fixation during some of the tasks, as the source for the modulations of the late response.

Interestingly, with the segregation task and the local task, not only the late segregation-specific response was present, but at the same time a coinciding positive deflection in the original VEPs was markedly smaller for both segregated and homogeneous stimuli as compared to the number task and the auditory task.

The latency of 230 ms is later than reported by Bach and Meigen (1999) and Lamme et al. (1992), but consistent with Caputo and Casco (1999) and Fahle et al. (2003). A later segregation-related component of opposite polarity with a latency of around 270 ms and some task dependence has been reported by Schubö et al. (2001). At present, it is unclear what causes the differences between the different groups of studies. The timing of one of the segregation-related MEG responses found by Scholte et al. (2006) is similar to the later response in the present study. However, differences between seen and unseen segregation only occurred at around 400 ms.

Because the statistical comparison between occipital and occipitotemporal activations failed to yield a clear result, we cannot conclude from the present data whether the late response originates from different cortical areas than the early response. A task-dependent negativity (“N2pc”) with a timing comparable to the late response has also been found in visual search experiments (Luck, 2005). Because the distribution of activity in such experiments depends on the location of the target with a focus over the contralateral hemisphere, a direct topographical comparison to the present study is difficult.

Being susceptible to attentional modulations, the late component does not qualify as “preattentive”. Rather, its late occurrence provides enough time for the early activity to be assessed by higher processing stages and for feedback signals to be sent down to early visual cortex. This would differ from a basic attentional gain-control mechanism that would not involve the assessment of individual stimuli by higher stages. Rather, it would be equivalent to a change the general state of the affected processing stages. Such a simple modulatory effect could in principle already affect the earliest cortical responses. The lack of early effects, though, does not disprove such a basic gain-control mechanism.

Could the late component in the tsVEP represent a selection negativity, which is an occipital component associated with task-relevant stimuli (Hillyard & Anllo-Vento, 1998)? There are several arguments against such an interpretation. First, the task was not a typical selection negativity task, which would only require a response to one of the two stimuli. Rather, the subjects had to respond to both alternatives of the stimulus, segregated and homogeneous. Second, it does not have the characteristic timing. In particular, a selection negativity extends over a broader time interval of 150–200 ms

duration, whereas the present component is more confined with a width of around 100 ms. Third, the present component appears to primarily result from a reduction of a positive deflection in the original VEPs, as opposed to a selection negativity, which is usually not tied to a specific VEP component (Mangun & Hillyard, 1996). It seems possible, however, that both the selection negativity and the task-dependent tsVEP component reported here are epiphenomena of the same attention-based modulatory mechanism.

Alternatively, the effect reported here might be the result of a general task-dependent feedback process not specific to texture segregation, but possibly also occurring with other visual tasks that involve global stimulus features. For instance, attention-related effects in a similar time range as found in the present study have been reported by Khoe, Freeman, Woldorff, and Mangun (2006) for the grouping of Gabor patches.

Based on the current data, it is difficult to interpret the effect of the local task. It resulted in a significantly larger tsVEP component than the number task. The difference to the segregation task only slightly missed significance when a modified Bonferroni adjustment was performed. Therefore, a difference between local task and segregation task is not unlikely. What processing steps do the two tsVEP components reflect? Possibly, the early component represents segregation in the sense of a detection of texture discontinuities, whereas the later one is related to the grouping of local pattern elements, as suggested by Caputo and Casco (1999) and consistent with some models of grouping that propose attention as an essential ingredient in the grouping process (Roelfsema, 2006).

If no task was given to the subjects, the difference between presence and absence of segregation would be the most salient aspect of the stimulus sequence. Similar to the capture of awareness by salient stimuli, which can be seen as the “inverse” of inattentional blindness (Most, Scholl, Clifford, & Simons, 2005), some attention would be most likely captured by the segregated versus homogenous difference between stimuli even in a no-task condition. The present results might therefore help to explain diverging fMRI findings. The early activation alone might not be enough to induce a statistically significant BOLD response. If so, studies where the subjects were instructed to attend distractors (Kastner et al., 2000; Schira et al., 2004) would not find a significant activation in V1. On the other hand, when no distracting task was performed (Schmitt et al., 1998; Skiera et al., 2000), such an activation would be found due to the double activation as reflected by the two tsVEP components.

## Responses after stimulus offset

The post hoc statistical analysis of very late (>300 ms) time intervals suggested that attention effects also occur later than pattern offset. Not all of these are necessarily

related to the disappearance of the stimulus. Some of these effects seem to reflect ongoing differences that already started before pattern offset. Some might also represent late potentials associated with the processing of the stimulus, irrespective of the pattern offset. This, however, cannot be decided based on the present data because only one stimulus duration was used. Schubö et al. (2001) found task-modulated segregation-related activations peaking around 400 ms. However, that component, a P300-type response, had a markedly different topographical distribution.

## Conclusions

The main conclusions of the present study are threefold:

1. Early tsVEP responses are unaffected by the tasks, consistent with the concept of preattentive processing.
2. Attention affects the later component even with a symmetrical task design.
3. Performing disengaging tasks both within and across modalities abolishes late tsVEP components, suggesting that within-modality competition is not the primary mechanism of attention-related response modulation in texture segregation.

## Appendix A

The formula used in the present study for the Gabor-like filters was slightly different from the one classically applied for Gabor patches, as it employed a two-dimensional Hanning window (raised cosine) rather than a Gaussian function as envelope. Although similar in shape to the Gaussian function, the Hanning window ensures that the filter has a finite spatial extent. For a patch containing a grating with an orientation of  $\varphi$ , this results in

$$G_{\varphi}(x, y) = \begin{cases} \frac{1}{2} \left( \cos \frac{\pi \sqrt{x^2 + y^2}}{d} + 1 \right) \cos(2\pi f(x \sin \varphi + y \cos \varphi)) & : \sqrt{x^2 + y^2} < d \\ 0 & : \text{else} \end{cases} \quad (\text{A1})$$

with the cartesian coordinates  $x$  and  $y$  measured relative to the center of the patch,  $d$  representing the diameter of the patch (FWHM), and  $f$  being the spatial carrier frequency. For the patterns used in the present study, we chose  $f = 3$  cpd and  $d = 0.5^{\circ}$ . The first cosine term defines the Hanning window, whereas the second one determines the oscillations within the patch. The orientation  $\varphi$  was either  $+45^{\circ}$  or  $-45^{\circ}$ .

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