



Summation of texture segregation across orientation and spatial frequency: electrophysiological and psychophysical findings

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Abstract

Objects are usually segregated from ground by several visual dimensions. We studied texture segregation in checkerboards defined by gradients in spatial frequency, orientation or both frequency and orientation, using Gabor-filtered noise patterns. Saliency was measured electrophysiologically using the visual evoked potential (VEP) associated with texture segregation ('tsVEP') (an associated component in the visual evoked potential), and psychophysically by a 2AFC task. Spatial frequency and orientation stimuli evoked percepts of texture segregation and tsVEPs in all 11 subjects. The tsVEPs to combined stimuli were larger than those to each dimension alone, but smaller (74%) than the algebraic sum of tsVEPs to both individual dimensions. Psychophysical detection rates differed significantly between all conditions ($P < 0.001$), with highest rates for the combined stimuli. The findings suggest that segregation based on a combination of 'orientation' and 'spatial frequency' is more salient than that based on either of these alone. The significant deviation from full additivity in the tsVEPs suggests that simultaneous contrasts in spatial frequency and orientation have a common processing stage. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Our visual system continuously analyses the visual surrounding using parallel cortical processing. As an early step to segregate a figure from its background, neural mechanisms process the visual input across the entire visual field without focal attention. These mechanisms rely on certain local features ('stimulus dimensions') which include luminance, color, orientation, spatial frequency, motion, stereo disparity and temporal features. If there is a sufficiently strong spatial gradient in one of these stimulus dimensions, global structures 'pop out', 'group', or 'segregate' preattentively (Neisser, 1967; Beck, 1972, 1983; Treisman, 1985; Julesz, 1986; Julesz & Bergen, 1983; Nothdurft, 1990, 1993; Fahle, 1993).

Evoked potentials provide a tool to study neuronal processing in humans. Components of the visual evoked potential (VEP) associated with texture segregation (tsVEPs) offer an opportunity to quantify supra-threshold processing and to follow its time course with high temporal resolution (Bach & Meigen, 1990, 1992, 1997; Lamme, van Dijk, & Spekreijse, 1992, 1993a,b; Meigen & Bach, 1993; Meigen, Kastner, & Bach, 1997; Regan & He, 1996; Caputo & Casco, 1999; Caputo, Romani, Callieco, Gaspari, & Cosi, 1999).

If texture segregation can be based on various stimulus dimensions, to what degree does it differ between dimensions and how do dimensions interact? In a related psychophysical paradigm, Rivest and Cavanagh (1996) found that the activity of contour-defining attributes (they tested luminance, color, and texture) is summed in a common site (see also Bach & Meigen, 1997, 1998). Nothdurft (2000) recently addressed psychophysically the properties of additivity across the

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dimensions orientation, motion, luminance and color contrast. He found ‘overlap’ between all subserving saliency mechanisms, with the strongest overlap (50%) for color and orientation, 50% between motion and orientation, and $< 30\%$ between luminance and all other stimulus dimensions, suggesting a common processing stage.

We here analyze the summation properties of texture segregation across spatial frequency and orientation and asked to what degree do combinations of visual dimensions summate perceptually and in the tsVEP?

In Gabor-filtered noise textures (Landy & Bergen, 1991), ‘orientation’ and ‘spatial frequency’ can be separately manipulated with little luminance and aliasing artifacts (Fig. 1) (Bach, Meigen, & Strasburger, 1997; Pelli, 1997). We used these kinds of patterns to generate stimuli that contained a ‘preattentive checkerboard’ based on gradients in either of orientation, spatial frequency, or both.

2. Methods

2.1. Subjects

Eleven visually normal observers served as subjects in the electrophysiological, nine in the psychophysical experiments, one of the subjects participated in both experiments. They wore appropriate correction if necessary, decimal acuity was ≥ 1.2 . The subjects gave their informed consent to participate in the experiment. Eight of the 11 subjects were naive as to the specific aim of the experiment.

2.2. Stimuli

The basic paradigm to isolate tsVEPs was the one used by Bach and Meigen (1990, 1992); Lamme et al. (1992, 1993b); Lamme, van Dijk, and Spekreijse (1994), Meigen and Bach (1993). The stimuli (Fig. 1) were presented using a Macintosh 8500 computer with a resolution of 640×480 pixels at a frame rate of 120 Hz (mainboard graphics). Viewed at a distance of 114 cm, the screen covered $16^\circ \times 12^\circ$.

For independent control of spatial frequency and orientation, we used Gabor-filtered noise textures (Landy & Bergen, 1991; Meigen et al., 1997; Fig. 1). Textures were generated as follows: each pixel served as the center of a Gabor patch, whose orientation and/or spatial frequency depended on the location in a checkerboard arrangement. Each Gabor patch was assigned a random amplitude; the algebraic sum of all these Gabor patches defined the gray level of the pixel. Due to the ensuing high correlation between neighboring pixels, aliasing and luminance artifacts are greatly reduced compared with line-type stimuli (Bach et al., 1997).

The ‘global checkerboard’ was eight checks wide and six checks high, each check covering $2 \times 2^\circ$. We chose two spatial frequencies (SF) with a frequency ratio of 12/7, corresponding to about 2.5 and 1.5 cyc deg^{-1} (SF_h and SF_l). For orientation (OR), we chose vertical (OR_v) and horizontal (OR_h). Following Landy & Bergen (1991), we chose the bandwidth σ of the Gabor patch to be a function of the spatial frequency f via the following equation: $\sigma = 1/2f\sqrt{\log 2}$. Thus Gabor patches for different spatial frequencies contained the same number of cycles. The following stimulus-pattern

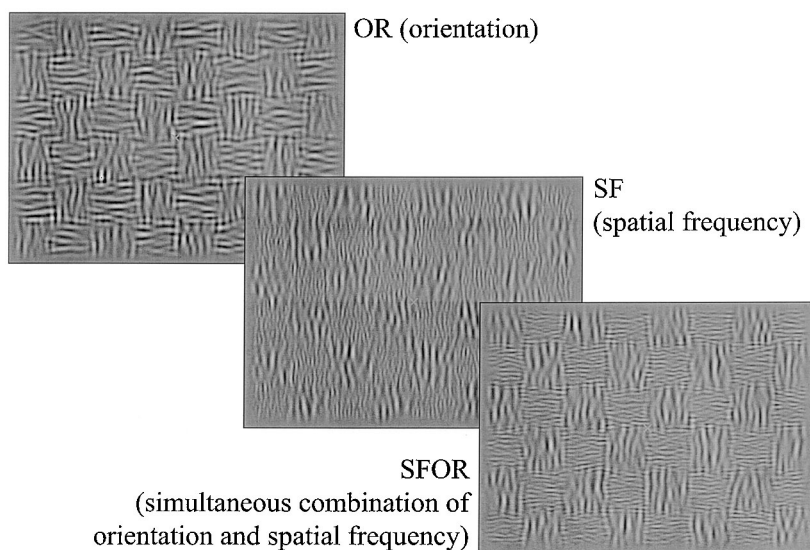


Fig. 1. Examples of actual stimuli for the two single visual dimensions (top, middle), and the combination stimulus that segregates simultaneously by gradients in orientation and spatial frequency (SFOR, bottom). Depending on reproduction quality, the reader may be able to verify that the SFOR stimulus has a higher saliency than SF or OR alone.

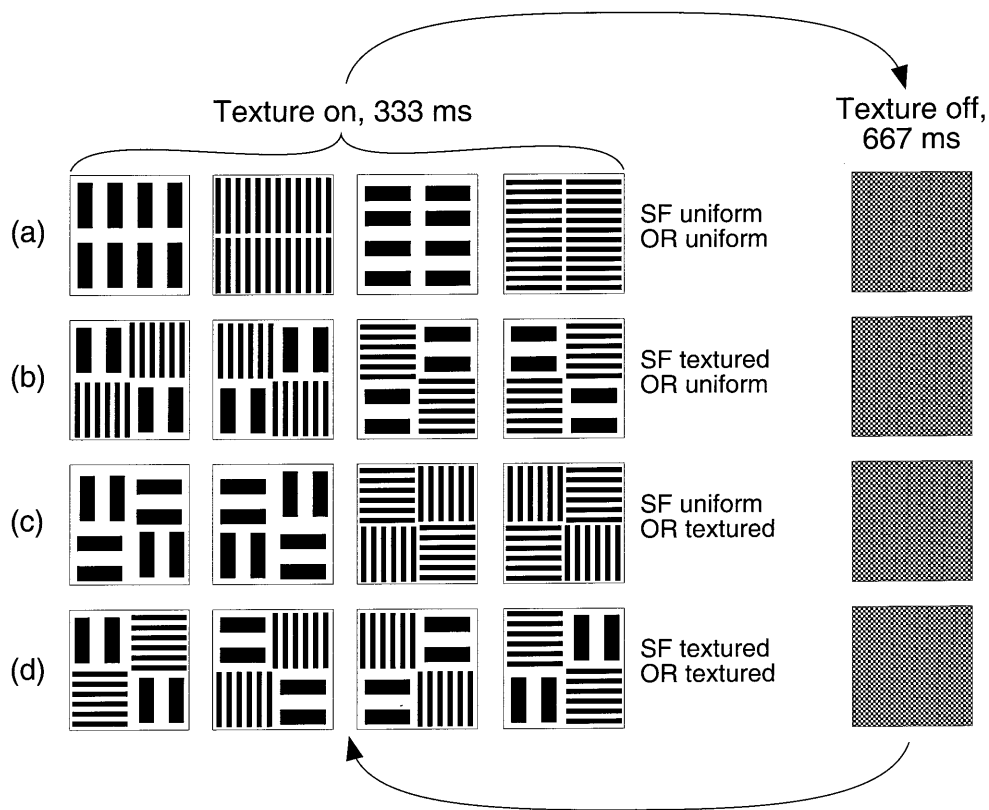


Fig. 2. Schematic combinations of all stimuli. Appropriate linear combinations of responses of the stimuli are calculated to extract the VEP component associated with texture segregation (tsVEP).

types were calculated (see Figs. 1 and 2): (a) four 'uniform' patterns which did not contain a gradient in SF or OR — $SF_v|OR_v$, $SF_v|OR_h$, $SF_h|OR_v$, $SF_h|OR_h$ (not depicted in Fig. 1, but in Fig. 2a); (b, c) uni-dimensional 'global checkerboards' were based on a single dimension: (b) gradient in SF, (Fig. 1 center, Fig. 2b) — $SF_v/SF_h|OR_v$ and $SF_v/SF_h|OR_h$; (c) gradient in OR, Fig. 1 top left, Fig. 2c — $SF_v|OR_v/OR_h$, and $SF_h|OR_v/OR_h$. For each dimension, four variations were calculated, with either SF_v/SF_h or OR_v/OR_h in the top left, and with both variants of the other dimension; (d) two-dimensional global checkerboards (gradient 'SFOR'), see Fig. 1, bottom right, and Fig. 2d.

Four different sets of each of these 16 pattern types (Fig. 2) were calculated with different randomization to average over possible structures created by chance. For the psychophysical experiments, we also calculated neutral patterns by choosing a random Gabor function from one of (SF_v , SF_h , OR_v , OR_h) for each pixel. This resulted in 'neutral' noise patterns without global structure.

2.3. Electrophysiological procedures

The VEP was recorded from an Oz-FPz derivation using gold-cup electrodes. Signals were amplified and filtered (first-order bandpass, 0.3–70 Hz, Toennies

'physiologic amplifier') and digitized to a resolution of 12 bits at a sampling interval of 1 ms with a Macintosh 7200 computer. Signals were streamed to disk and also averaged on-line (across all stimuli) using LabView (National Instruments). Off-line analysis was done in Igor (WaveMetrics) and included artifact rejection if the amplitude exceeded $\pm 100 \mu V$, stimulus-specific averaging, and filtering with a phase-free Fourier filter with a pass band of 0–45 Hz.

The stimulus screen was blank for 667 ms (80 frames). Then one of the above pattern types appeared for 333 ms (40 frames), followed again by a blank screen. The appropriate combinations of responses to different stimuli to extract the tsVEP are detailed below. In the center there was always a small cross which the subjects were instructed to fixate.

We presented the various texture stimuli in a random blocked design — in any block, each of the 16 patterns appeared once. After a block the sequence of the patterns was reshuffled, the next of the four sets of 16 patterns was selected and similar blocks repeated until 240 sweeps for each condition were accumulated. The entire recording session lasted for about 2 h.

Onset of a stimulus as depicted in Fig. 1 evokes activity on most levels of the visual system. At a low level, responses are dominated by processes tuned to local expressions of stimulus dimensions, e.g. local spa-

tial frequency and/or local orientation; at a conceptually higher level, gradients within visual dimensions are detected leading to texture segregation (Bach & Meigen, 1997). To selectively extract the associated tsVEPs, it is assumed that the latter mechanisms additively superimpose with those evoking the 'low-level VEP'. Thus tsVEPs can be isolated by calculating linear combinations of appropriate responses with and without global segmentation (= global checkerboard). In the current experiments, the tsVEP is calculated as the difference between the response to the onset of a global checkerboard and the mean of the responses to the onset of a uniform expression of the participating visual dimensions. Results were averaged over both variants of the respective non-segregating dimension for stimuli where segregation was based on one dimension (SF or OR). Thus three responses per subjects remained: a tsVEP to gradients in SF, one to gradients in OR, and one to the combination stimuli (SFOR). Finally, we calculated the algebraic sum of the tsVEPs to orientation and to spatial frequency (SF + OR).

2.4. Psychophysical procedures

To estimate the psychophysical saliency of the various stimuli, we chose the following procedure: at an observation distance of 60 cm, two test patterns, separated by 1.4° , appeared for 100 ms on the screen left and right of the fixation point. This was followed by a mask of random black and white elements of 2×2 pixel size. One of the test patterns was a neutral pattern as defined above, the other contained a 'global checkerboard' (as in Fig. 1, each type OR/SF/SFOR in two versions differing by the 'polarity' of the top left check to balance all conditions, resulting in six types of patterns). Stimuli were spatially scaled relative to the electrophysiological experiment by a factor of 0.8. The subjects indicated the position (left or right) of the 'global checkerboard pattern' in a two alternative forced choice task. Training runs preceded the sessions proper. Altogether about 6000 trials were collected (about 130 trials per subject for each of the six pattern types). All stimulus types as defined above were presented, and the results sorted into the three categories SF, OR, and SFOR as in the electrophysiological experiment. Interpretation was based on the percentage of correct responses.

3. Results

3.1. Electrophysiology

Significant tsVEP responses could be isolated in most subjects, though varying widely between subjects with respect to amplitude and latency. Fig. 3 depicts the

tsVEPs from all subjects. For each subject there are four traces: the top pair of traces results from a stimulus with segregation in a single dimension (SF, top; OR, middle). The bottom trace (black line) results from segregation due to simultaneous gradients in SF and OR (SFOR); superimposed (gray) is the algebraic summation of the SF and OR traces ('SF + OR'). The tsVEP appears as a negative peak after 140 ms. The individual latencies vary widely, including the appearance of double peaks or shoulders. Since there is evidence suggesting that the 'later' troughs (above 210 ms) are more strongly modulated by attention than earlier troughs (Meigen & Bach, 1999), we choose 210 ms as the upper limit for tsVEP troughs. In 9 of 11 subjects there are clear early troughs, in two subjects (# 1 and # 6) there are local troughs before 210 ms (Fig. 3). The amplitudes of the SF- and OR-responses also vary widely between subjects. Finally, the relative weight of the SF- and OR-responses varies between subjects, sometimes the tsVEP to SF- (# 3, # 5), sometimes the tsVEP to OR-segregation (# 2, # 9) is larger. Due to the high variability in latency, we did not calculate grand mean traces across all subjects, especially as this would have hidden an unexpected finding — the close similarity of the SFOR and SF + OR traces for all subjects in the time window below 210 ms. The algebraic sum of SF and OR reproduces even details of the SFOR-waveshape, and its major negative excursion slightly exceeds the trace from the SFOR combination stimulus in all subjects but one.

Fig. 4 quantitatively presents the degree of additivity of the stimulus combination for all subjects (only negative excursions before 210 ms were evaluated). The ordinate displays the amplitude of the SFOR-combination stimulus, the abscissa the amplitude of the algebraic sum (SF + OR). If complete linearity held, all data points would be arranged on the dotted 45° -line with a slope of 1.0. SFOR and SF + OR are significantly correlated with $r^2 = 0.94$ ($P < 0.0001$, oblique regression line in Fig. 4). Thus 94% of the SFOR amplitude variability is explained by the SF + OR amplitude. The slope of SFOR-amplitude versus (SF + OR)-amplitude is 0.74, the 95%-confidence interval ranging from 0.60 to 0.87. In other words, the combination stimulus (SFOR) produces a response that is 74% of the algebraic sum of the response to the single dimension stimuli (SF + OR).

3.2. Psychophysics

The psychophysical detection rate, averaged across subjects, was as follows: 78.3% correct detection for texture segregation defined by spatial frequency, 88.0% for orientation, and 91.1% for the combination SFOR. Details on a per-subject basis are given in Table 1. There was a large between-subject variance. As extreme

examples we found a range of 56–87% for one subject, and 97–100% for another subject. This suggests that the psychophysical design could have been improved by adjusting the stimuli for the individual threshold, resulting in better discrimination between conditions.

Since detection rates cannot be normally distributed, we performed the non-parametric Friedman test. A highly significant effect of stimulus was found ($P < 0.001$); post-hoc analysis revealed significant differences between all conditions (SF–OR, SF–SFOR, $P < 0.01$; and OR–SFOR, $P < 0.05$).

4. Discussion

As an electrophysiological correlate of the ‘preattentive’ percept, we found significant tsVEPs in most subjects for both stimulus dimensions tested. This extends previous work based on the stimulus dimension ‘orien-

tation’ (Bach & Meigen, 1990, 1992; Lamme et al., 1992, 1993b) to ‘spatial frequency’, and was an expected finding. Texture segregation based on a combination of spatial frequency and orientation always evoked larger amplitudes compared with any single dimension. This result is in qualitative accordance with the psychophysical findings, where a highly significant effect ($P < 0.001$) of stimulus was found; detection rates were 78% for SF, 88% for OR and 91% for SFOR. With a 50% guessing rate, the SF detection rate is near the steepest point of the psychometric function, while for SFOR it is within the saturation region. The combination stimulus (SFOR) was most salient.

There was a marked degree of additivity in the VEP data. The amplitude of the tsVEPs to a presentation of an SFOR-combined stimulus was 74% that of the sum of the tsVEPs to separate presentation of the visual dimensions SF and OR. The 95%-confidence interval ranges from 60 to 87%, rejecting both the hypothesis of

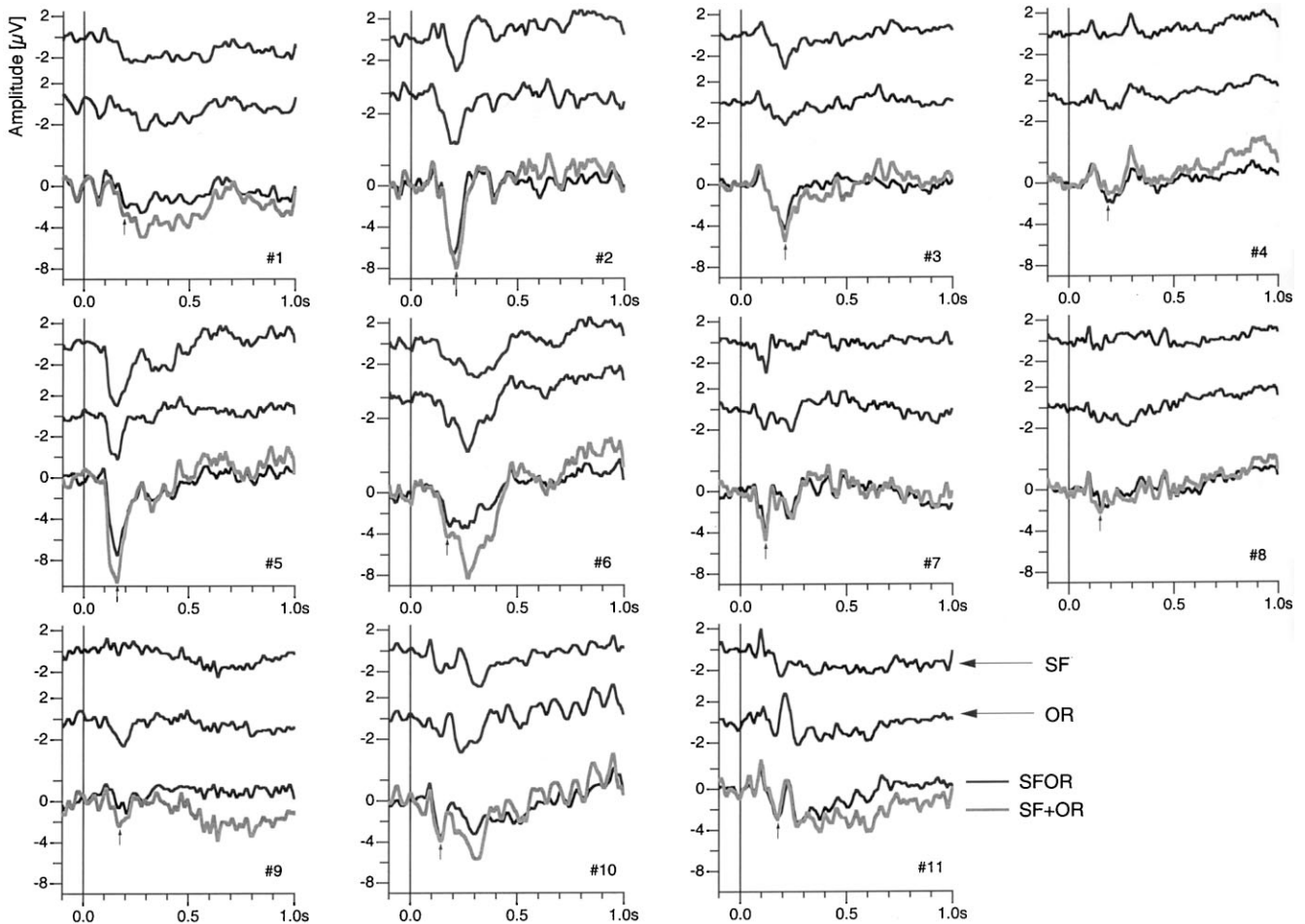


Fig. 3. Original tsVEP traces for all 11 subjects. Each set of traces per subjects displays the tsVEP to segregation based on spatial frequency (SF, top), orientation (OR, middle), and the combination stimulus (SFOR, bottom, full line). Superimposed on the SFOR trace is the algebraic sum of the respective SF and OR traces (SF + OR, gray). The small vertical arrows indicate the main tsVEP structure in the SF + OR trace, the numbers at bottom right of each subplot identify the subject. The SF + OR-trace closely approximates the tsVEP to the combination stimulus SFOR, but only during the time interval from about 130 to 210 ms.

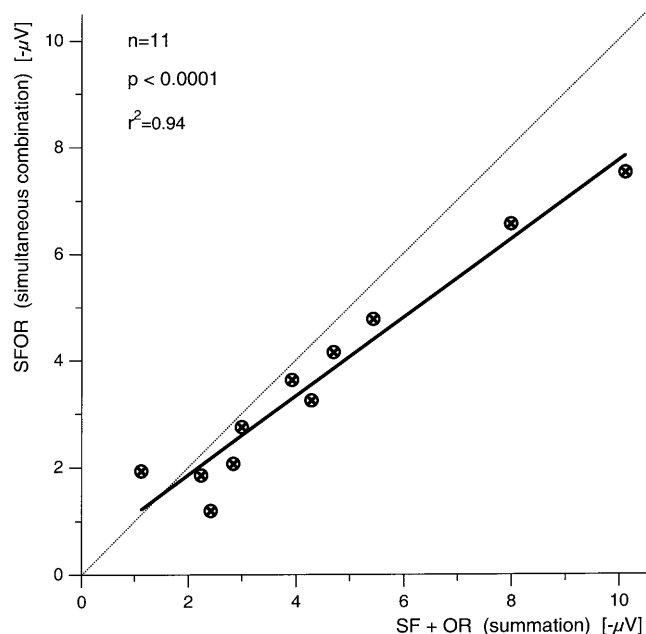


Fig. 4. Scatterplot of the tsVEP amplitudes (troughs before 210 ms) to the SFOR combination stimulus (ordinate) vs. the algebraic sum SF + OR to the single visual dimension stimuli. The negative tsVEP peaks are depicted as positive values to aid visual interpretation. The two amplitude values differ widely across subjects, but have 94% variance in common.

Table 1
Psychophysical results^a

Subject	Correct (%)		
	SF	OR	SFOR
1	69.3	88.4	93.6
2	92.6	97.6	100
3	87.9	94.0	98.1
4	55.6	81.9	86.7
5	96.7	100	100
6	68.6	73.8	81.1
7	72.6	83.1	87.8
8	70.8	76.0	75.1
9	91.0	97.7	98.1
Means	78.3	88.0	91.2

^a Detection rates are given for all subjects and conditions.

no summation (which would yield 50%) and the hypothesis of full linearity (100%). The similarity between the sum of the tsVEPs to SF and OR alone and the tsVEPs to the SFOR-combination obtained also in details of shape (Fig. 3), but generally only in the time range below 210 ms. The loss of additivity above 210 ms in some subjects might be explained by intrusion of cognitive potentials, as our subjects did not have a well-defined stimulus-related task during recording.

The present finding may be specific for the combination of the visual dimensions 'spatial frequency' and

'orientation' (see below). We had selected this combination on the assumption that the latencies of the tsVEPs would be highly similar, as other visual dimensions like motion and stereo depth evoke tsVEPs with markedly higher latencies (Bach & Meigen, 1997). It is known that many neurons are selective to both SF/OR-dimensions simultaneously (begging the question how to unconfound them). The lack of full additivity suggests that the tsVEPs to the SFOR-combination stimulus are not simply the electrotonic sum of tsVEPs from separate sites. This agrees with previous tsVEP findings (Bach & Meigen) which suggested that a common site generates the tsVEPs across stimulus dimensions. Although the segregation was 'weak' in our noise-derived stimuli, some saturation may have occurred in early processing. The question of saturation needs to be addressed with a range of stimuli starting at much lower contrast values in future work.

Leonards and Singer (1998) explored the related, if opposite problem, 'cues from different dimensions ... need not always be congruent'. They report a considerable flexibility when targets, defined by the visual dimensions 'orientation' and 'temporal asynchrony' were presented in a rivalrous situation, one dimension defined a horizontal, the other a vertical bar. For low luminance contrasts, the dimension 'temporal asynchrony' dominated, while for equiluminant colors the dimension 'orientation' dominated. Rivest and Cavanagh (1996) analyzed precision (in terms of 'just noticeable difference') of contours defined by luminance, color, motion and texture, either one of these stimulus dimensions ('attributes') alone or by combinations. They found that combination increased contour definition and that their findings could be quantitatively predicted by a model that assumed RMS-summation of attributes at a 'common site'. They found this for all combinations of luminance, color, texture and motion. This finding is in qualitative agreement with our present one.

Zipser, Lamme, and Schiller (1996) analyzed the effect of texture defined figures on single cell responses in V1 of behaving monkeys. They found an enhancement of the latter part of the response (> 80 ms) when the classic receptive field was inside a figure defined by a gradient in one of the stimulus dimensions luminance, orientation, disparity or color. They also analyzed the situation when their texture-defined figure was defined by a combination of all four visual dimensions simultaneously. The combination response averaged the same enhancement as the single dimension response in the 64 cells studied; response saturation was considered to be unlikely. This finding disagrees with Rivest and Cavanagh (1996), Nothdurft (2000) (who found 'overlap' between orientation, motion, luminance and color contrast) and our present results of strong additivity in the tsVEP. How can this difference

be explained? Since most of Zipser et al.'s cells were driven when the figure was defined by any of the four stimulus dimensions, the disagreement cannot be explained by the assumption that the tsVEP as mass response sums over different cell types when using combination stimuli. Possibly the conflicting findings might be traced to the visual dimensions used. We combined the two dimensions 'spatial frequency' and 'orientation', which are confounded in Gabor-type receptive fields. Thus this combination of visual dimensions might be special and not be fully generalizable to other dimensional combinations. This assumption does, however, not resolve the conflict between the findings of Zipser et al. and Nothdurft.

It is of interest whether texture segregation mechanisms are located in a specific cortical area, possibly depending on visual dimension. Currently, there are a number of findings suggesting that segregation occurs as early as in V1, irrespective of visual dimension: Lamme et al. (1994) found in a current source density analysis of field potentials in monkeys tsVEP-like components in V1 in the layers above and below IVc for motion- and orientation-defined textures. Using dipole-analysis of tsVEP surface potentials, Lamme et al. (1992) found medial occipital locations. Similar tsVEP locations were found by Meigen et al. (1997) Fahle, Braun and Quenzer (2000). Reppas, Niyogi, Dale, Sereno and Tootell (1997) defined textures by motion gradients in fMRI experiments. While the motion stimuli themselves activated most visual areas, including a lateral possible MT homologue, processing specific for motion gradients did not activate MT, but V1–V2. Schmitt, Janz, Hennig and Bach (1998) compared motion and orientation-defined textures in an fMRI experiment. They replicated Reppas et al.'s finding and also found V1–V3 activation for orientation-defined textures.

We conclude, when texture segregation is based on congruent gradients in the two visual dimensions 'spatial frequency' and 'orientation', there is partial summation both regarding the psychophysical salience and the amplitude of segregation-related visual evoked potentials (tsVEPs). The significant amount of deviation from full additivity suggests that simultaneous contrasts in spatial frequency and orientation have a processing stage in common. Further experiments, combining other visual dimensions are necessary to test whether these results are specific for the combination of 'spatial frequency' and 'orientation', and to what degree saturation may have played a role.

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