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A visual evoked potential correlate of global figure-ground segmentation

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Abstract

Human observers discriminated the global orientation of a texture-defined figure which segregated from a texture surround. Global figure discriminability was manipulated through within-figure collinearity, figure-surround interaction, and figure connectedness, while the local orientation contrast at edges between figure and surround was kept constant throughout all the experiments. Visual evoked potentials (VEPs) were recorded during onset–offset stimulation in which the figure cyclically appeared and disappeared from a uniform texture background. A difference component was obtained by subtraction of offset- from onset-VEP. Two negative peaks of the difference component are found with latencies around 140–160 and 200–260 ms, respectively. Enhanced discriminability of the global figure reduced (11–25 ms) the latency of the second peak, hence indicating that the 200–260 ms component was produced by global figure-ground segmentation. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Figure-ground segmentation describes a number of perceptual phenomena which allow the subdivision of the visual image into coherent objects, or figures. In the case of a single figure which is segmented from the background, its border is perceived as not belonging to the background, its surface appears more compact than the background surface, and the figure perceptually lays in a front plane while the background amodally completes behind (Kanizsa, 1979).

Classical demonstrations of figure-ground segmentation employed stimuli defined by luminance differences. Recent psychophysical research on human subjects as well as neurophysiological studies on cat and monkey, have employed texture stimuli. Electrophysiological studies on the humans (Bach & Meigen, 1990, 1992; Lamme, Van Dijk & Spekreijse, 1992; Lamme, Van Dijk & Spekreijse, 1993; Bach & Meigen, 1997) utilized a stimulus in which line element orientation was modulated in such a way that a texture checkerboard appeared and disappeared from a uniform texture background. In the range of about 100–250 ms, the VEP in response to the texture checkerboard was more negative than the VEP in response to the texture background. Since the VEP in response to the checkerboard presumably summons activity produced both by the texture pattern and by segregation per se, it is possible to isolate a difference component produced by segregation per se through the algebraic subtraction of the background-VEP from the checkerboard-VEP.

However, the previously employed texture checkerboard cannot be used to investigate figure-ground segmentation because it does not allows a single strong segmentation of a figure against a background (i.e. it is a multi-stable stimulus). In the present paper, the texture checkerboard was modified in order to manipulate variables that influence figure-ground segmentation.

Neurophysiological studies have investigated the neuronal bases of figure-ground segmentation. Lamme (1995) found that cells in area V1 of macaque monkey had stronger discharges when their 'classical' receptive fields (RFs) were placed on a texture-defined figure compared to a condition in which their RFs were

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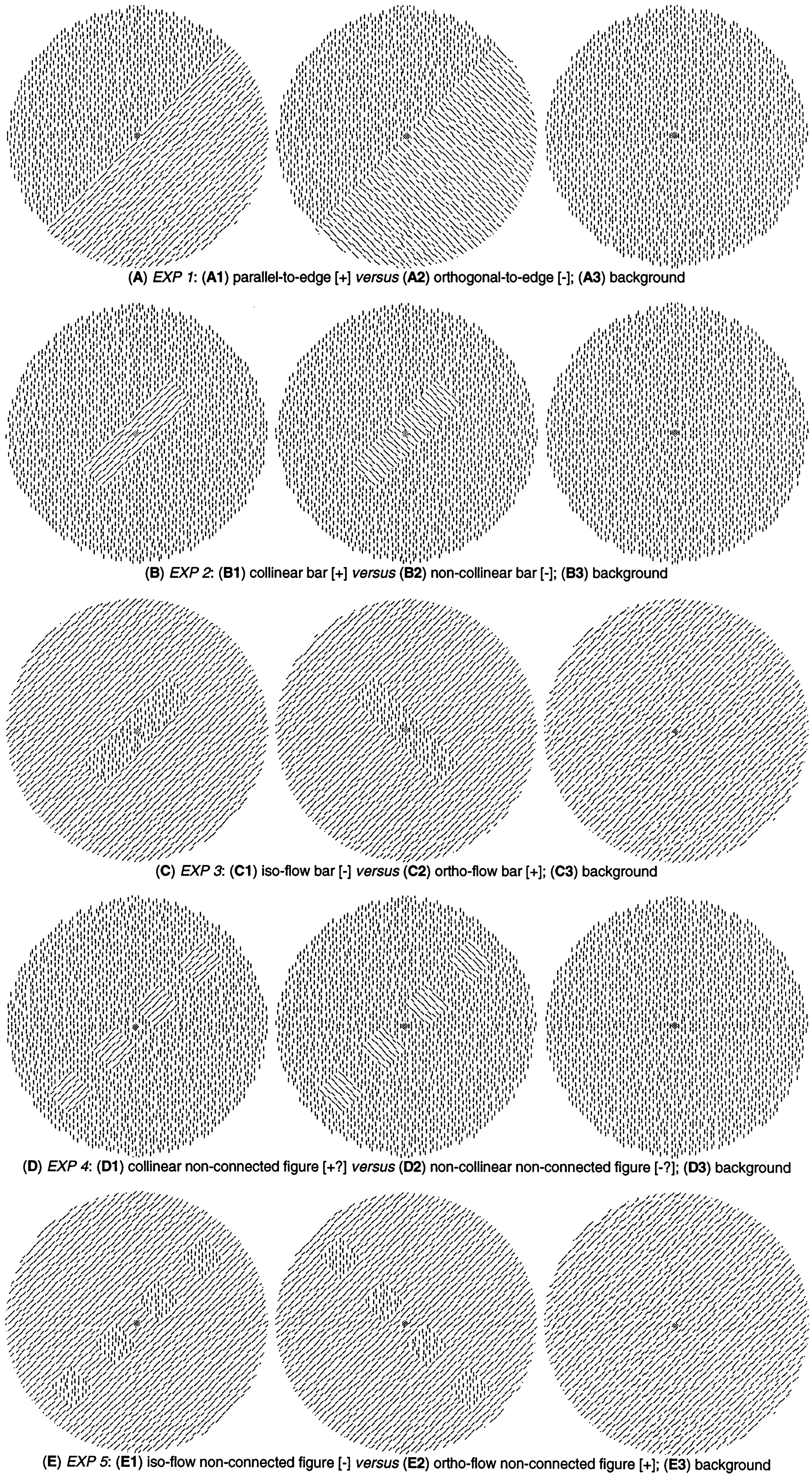

Fig. 1. (*Caption opposite*)

placed on the texture surround outside the figure. This increase of the interior responses was not dependent on the orientation selectivity of the cells. Zipser, Lamme and Schiller (1996) demonstrated that the increase of the interior responses is based on a neuronal process which is distinct from the RF functioning. Lee, Mumford, Romero and Lamme (1998) further investigated the spatial and temporal characteristics of figure-ground interior response increase. They found that the initial responses (40–60 ms) of the neurons were determined by filter responses to local features within the RFs, while the later responses (80–350 ms) depended on contextual information. These later responses comprised, in addition to the increase of responses of the interior of the figure (from 80 ms), the increase of responses in correspondence of the figure boundary (from 80 ms) and the emergence of a central peak in correspondence of the medial-axis of the figure (from 110 ms).

On the basis of these neurophysiological findings, we expected that figure-ground manipulations could influence the latency and/or the amplitude of specific VEP components. In the following introduction we describe the design of our texture stimuli in relation to previous psychophysical and neurophysiological findings about figure-ground segmentation.

1.1. Texture edge

The simpler stimulus for a figure-ground segmentation with texture stimuli is a segregation edge. In the examples of Fig. 1A1 and A2 a segregation edge separates two hemi-disks filled with line elements of different orientation despite no contour is explicitly present. Edge segregation was psychophysically analyzed by Wolfson and Landy (1995) using stimuli similar to those shown in Fig. 1A. Their results indicate that three factors are involved: (1) the difference in orientation, which enhances segregation depending on the local orientation contrast at the texture edge (Nothdurft, 1992); (2) the oblique effect, in which segregation edges and line elements with horizontal and vertical orientations are better perceived with respect to tilted orientations (Appelle, 1972); and (3) the configural effect, in which edge perception is enhanced when line elements are parallel to the orientation of the segregation edge (cf. Olson & Attneave, 1970).

It should be noted that in Fig. 1A1 the orientation contrast (i.e. a 45° difference) between the two hemi-disks is the same that in Fig. 1A2. It should be noted that the oblique effect is the same in the two figures (i.e. both the edge and the manipulated line elements are always oriented at 45° either clockwise or counterclockwise). Altogether, the edge in Fig. 1A1 is perceptually

Fig. 1. Illustrations of the stimuli used in the experiments. Figure-ground discriminability is manipulated (left and middle columns) while the orientation contrast, which is used to segregate texture regions, is kept constant at 45°. Previous psychophysical results are labeled with '[+]' to indicate enhanced discriminability of the figure with respect to '[−]' to indicate reduced discriminability. The '?' symbol for stimuli of Experiment 4 is only to indicate that discriminability differences are hypothesized in absence of psychophysical data. In the actual stimuli, line elements were white on a dark monitor, the fixation dot in the center of the circular aperture was red, and the stimulus diameter was 16°. Stimulation consisted in onset–offset displays in which a segregation-stimulus (shown in the left and middle column) cyclically appeared and disappeared when a uniform texture background (shown in the right column) was displayed. The duration of each stimulus was 840 ms. (A) Examples of the stimuli used in Experiment 1. The parallel-to-edge stimulus and the orthogonal-to-edge stimulus contained a segregation edge oriented 45° either clockwise or counterclockwise at random. One hemi-disk contained vertical line elements, randomly on the upper or the lower hemi-disk. The other hemi-disk contained 45° line elements. (A1) In the parallel-to-edge stimulus, 45° line elements were tilted in the direction of the segregation edge. (A2) In the orthogonal-to-edge stimulus, 45° line elements were tilted orthogonally with respect to the segregation edge. (A3) The background-stimulus (displayed at the offset of the segregation-stimulus) was a uniform texture made of vertical line elements. (B) Examples of the stimuli used in Experiment 2 in which the collinearity of the line elements within a segregating texture bar were manipulated. In these examples the texture bar is oriented 45° clockwise, while in the actual experiments it could be clockwise or counterclockwise at random. (B1) In the collinear stimulus, the orientation of the line elements within the segregating bar and whole bar orientation were the same. (B2) In the non-collinear stimulus, 45° line elements were tilted orthogonally with respect to the whole bar orientation. (B3) The background-stimulus (displayed at the offset of the segregation-stimulus) was a uniform texture made of vertical line elements. (C) Examples of the segregation-stimuli used in the Experiment 3 in which the interaction between the global bar and the surrounding texture was manipulated. (C1) In the *iso*-flow stimulus, the global bar had the same orientation of the surround line elements (clockwise in this example). (C2) In the *ortho*-flow stimulus, the global bar (counterclockwise in this example) and the surround line elements (clockwise in this example) were orthogonal. (C3) The background-stimulus (displayed at the offset of the segregation-stimulus) was a uniform texture made of line elements oriented 45° either clockwise or counterclockwise. (D) Examples of the segregation-stimuli used in the Experiment 4: the four segregating patches can be grouped, thus giving rise to the perception of a global non-connected figure which slants 45° clockwise (in the experiment the global figure could be either clockwise or counterclockwise at random). (D1) In the collinear stimulus, line elements within the segregating patches were tilted in the direction of the global figure. (D2) In the non-collinear stimulus, 45° line elements were tilted orthogonally with respect to the global figure. (D3) The background-stimulus (displayed at the offset of the segregation-stimulus) was a uniform texture made of vertical line elements. (E) Examples of the segregation-stimuli used in the Experiment 5. The segregating patches were made of vertical line elements. The surround was made of line elements oriented 45° either clockwise or counterclockwise at random. (E1) In the *iso*-flow stimulus, the global figure made by grouping the four patches had the same orientation of the surround line elements (clockwise in this example). (E2) In the *ortho*-flow stimulus, the global figure (counterclockwise in this example) and the surround line elements (clockwise in this example) were orthogonal. (E3) The background-stimulus (displayed at the offset of the segregation-stimulus) was a uniform texture made of line elements oriented 45° either clockwise or counterclockwise.

stronger than in Fig. 1A2 because of the configural effect. On the basis of the plots in Wolfson and Landy (1995), when the discriminability of the edge in Fig. 1A1 is about 80%, the discriminability of the edge in Fig. 1A2 decreases to about 72%. From a phenomenological viewpoint, in Fig. 1A1 the configural effect corresponds to an unambiguous figure-ground segmentation of the disk, while in Fig. 1A2 it corresponds to the perception of a mere edge.

1.2. Texture bar

A set of line elements can be integrated (or grouped) into a global object which is segmented from the surround[1] texture. For example, in Fig. 1B1 and B2 the oblique line elements which segregate from the vertical texture can be integrated into a whole texture bar. The texture bar is perceived as a connected object which slants 45° clockwise.

Integration is in part independent of the elements employed (Bravo & Blake, 1992), hence indicating the involvement of a global process. For example, in Fig. 1C1 and C2 the orientations of the line elements are changed in both the segregating region and the surround with respect to Fig. 1B1 and B2, nevertheless the perceived texture bars are similar in the different stimuli (apart that in Fig. 1C2 the texture bar slants counterclockwise).

Notice in these examples (as well as in the following examples) that, at segregation edges, the local orientation contrast between the line elements of the figure and surround line elements was kept constant (i.e. the orientation difference was always 45°). Similarly, the oblique effect was controlled by slanting the figure 45° clockwise or counterclockwise. Since these two factors were controlled, any perceptual difference between the stimuli can only be produced by global processes involved in figure-ground segmentation.

In the examples in Fig. 1B we manipulate collinearity: in one condition the line elements within the texture bar are collinear to the orientation of the global object (collinear condition, Fig. 1B1); in the second condition they are orthogonal (non-collinear condition, Fig. 1B2). Nothdurft (1992) found that discriminability of whole bar orientation improves with collinear configurations. Field, Hayes and Hess (1993) studied the detection of a jagged chain of oriented Gabor-elements embedded in a surround of randomly oriented Gabor-elements. Detection of the chain was highest when the Gabor-elements were aligned (collinear) to the chain. Kapadia, Ito, Gilbert and Westheimer (1995) measured the V1 cells response to a target line element placed within the RF and surrounded outside the RF by a texture of randomly oriented line elements. When some surround line elements adjacent to the target were made collinear to it, the response of the cell increased and this increase was stronger the larger was the number of collinear elements. On the basis of these psychophysical and neurophysiological results, we expected the texture bar with collinear line elements (Fig. 1B1) to produce an increased neuronal activity and a higher discriminability than the non-collinear texture bar (Fig. 1B2).

Another psychophysical finding concerning grouping involves the interaction between the global object and the surround texture surface. A texture made of uniformly oriented line elements can be represented by the visual system as a surface flow (Caputo, 1998) having the direction of the orientation of texture line elements. Caputo (1997) found that the discriminability of a texture bar depended on the difference between the orientation of the whole bar and the orientation of the line elements of the surround texture. In other words, the discriminability of the global object depended on the extent to which the global object interrupted the surround texture flow.

In the examples of Fig. 1C, we manipulate figure-ground interaction: in one condition the orientation of the texture bar is the same as the surround flow (*iso*-flow condition, Fig. 1C1); in the second condition they are orthogonal (*ortho*-flow condition, Fig. 1C2). Previous psychophysical findings (Caputo, 1997) show that the *ortho*-flow global object (which interrupts the surround flow) is discriminated with a shorter latency than the *iso*-flow object. Therefore, we expected an increased neuronal activity in the *ortho*-flow configuration with respect to the *iso*-flow configuration.

1.3. Non-connected figure

We can try a further stimulus manipulation. A non-connected figure can be perceived by grouping spatially separated texture regions. In Fig. 1D1 and D2, the four patches which segregate from the background can be grouped into a whole non-connected figure that slants 45° clockwise. The two stimuli differ with respect to collinearity which is present in D1 but not in D2.

In the stimuli shown in Fig. 1E1 and E2 another manipulation involving figure-ground interaction is used. The global figure interrupts the surround texture flow in Fig. 1E2 but not in Fig. 1E1. On the basis of previous psychophysical findings (Caputo, 1997), we expected an increased neuronal activity in the *ortho*-flow configuration with respect to the *iso*-flow configuration.

[1] To avoid confusion, we will hereafter use the term ‘surround’ to indicate the texture within the segregation-stimulus. Instead, we reserve the term ‘backround’ to the backround stimulus (i.e. the uniform textur stimulus displayed at the offset of the segregation-stimulus; see Procedure below.

2. Methods

2.1. Subjects

In total 11 subjects (six males and five females) aged 25–35 years voluntarily participated in the experiments. Six or seven subjects took part in each experiment. The subjects were selected on the basis of the absence of astigmatism. Five subjects were psychophysically experienced observers; six subjects were naive observers. Four subjects had normal vision; seven subjects had corrected-to-normal slight myopia. The subjects had their recording session after training in steady fixation during preliminary sessions with similar stimuli.

2.2. Procedure

Two kinds of stimuli were interleaved: segregation-stimuli (i.e. the examples above) and background-stimuli (i.e. a uniform texture). Onset–offset stimulation consisted of the cyclical alternation of segregation-stimuli (containing either an edge (Experiment 1), a texture bar (Experiment 2 and 3), or four texture patches (Experiment 4 and 5)) and of background-stimuli. In such a way, the observer's perception was that either a segregation edge (in Experiment 1), a texture bar (Experiment 2 and 3), or four segregating patches (in Experiment 4 and 5) cyclically appeared and disappeared from a uniform texture background. Both segregation- and background-stimulus were presented for 840 ms and were instantly replaced by the next display. At each display a new texture stimulus was generated.

A two-alternative forced-choice (2AFC) task was used in which the subject had to judge the orientation (either clockwise or counterclockwise) of the global figure. This discrimination task was employed solely to engaging the observer because it is well known (and confirmed by our preliminary VEP recordings) that 'focused' attention (e.g. to the fixation point or to the line elements around it) can destroy many Gestalt-grouping percepts (cf. Ben-Av, Sagi & Braun, 1992). In order to avoid a situation where a manual response by the observer (in the discrimination task) could introduce artifacts into the EEG, we used the following technique. The discrimination task was not performed on every trial but only at randomly chosen moments under computer control: after presentation of three segregation-stimuli on average, the next background-stimulus was followed by the darkening of the monitor and the onset–offset stimulation was momentarily suspended waiting for the response by the subject. In Experiment 1, the subject had to report the orientation of the last presented segregation edge before the stop of the stimulation. In Experiment 2 and 3, the subject had to report the orientation of the last displayed texture bar. In Experiment 4 and 5, the subject had to report the orientation of the last displayed figure made by grouping the four patches. The subject used two keys to respond; an acoustic feedback was given to errors. The response of the subject re-started the onset–offset stimulation which began with a 2000 ms display of a background-stimulus to prepare fixation. In such a way, no finger movement was made during the recording period. No time pressure was imposed on the observer; instead, she/he was invited to employ the waiting period for resting.

In each experiment a two-level factor was manipulated in the segregation-stimuli (see Stimulus section below). Each background-stimulus (i.e. the uniform texture displayed after the offset of the segregation-stimulus) was classified with respect to the segregation-stimulus that preceded it. For example, in Experiment 1 the background-stimulus was classified depending on whether it followed the parallel-to-edge stimulus, or if it followed the orthogonal-to-edge stimulus. Therefore, in each experiment there were two experimental conditions per segregation-/background-stimulus condition. The two experimental conditions were randomly intermixed within the session. A session comprised 200 presentations per condition. Overall, a session involved 800 presentations.

2.3. Stimulus

Stimuli were generated by a PC, displayed on a 15″ color monitor (70 Hz vertical refresh) and viewed from a distance of 57 cm in a dark room. The resolution of the monitor was 640×350 with square pixel 2.7×2.7 min arc. The monitor was seen through a circular aperture 16° diameter. A red dot was displayed in the middle of the monitor to help fixation.

Line elements were arranged on a diamond raster, with raster step of 30.5 min arc. Each line element measured 19×2.7 min arc and its position was jittered around its raster center by 0–2.7 min arc. Line elements had a vertical or 45° orientation.

Textures were made of white line elements on a dark monitor (0.6 cd m^{-2}). The look-up table was set in such a way that the space average luminance of the texture was matched for both vertical (11.45 cd m^{-2}), 45 and 135° (11.51 cd m^{-2}) orientations of the texture line elements.

2.3.1. Experiment 1

Two kinds of segregation-stimuli appeared (Fig. 1A1 and A2, parallel- vs. orthogonal-to-edge conditions). The parallel-to-edge stimulus and the orthogonal-to-edge stimulus contained a segregation edge oriented 45° either clockwise or counterclockwise at random. One hemi-disk contained vertical line elements, randomly placed in the upper or the lower hemi-disk. The other hemi-disk contained 45° line elements. In the parallel-to-edge stimulus (Fig. 1A1), 45° line elements were tilted in the direction of the segregation edge. In the orthogonal-to-edge stimulus (Fig. 1A2), 45° line elements were tilted orthogonally with respect to the segregation edge.

The background-stimulus (which was displayed at the offset of the segregation-stimulus) was a uniform texture made of vertical line elements (Fig. 1A3).

2.3.2. Experiment 2

Two kinds of segregation-stimuli appeared (Fig. 1B1 and B2, collinear vs. non-collinear conditions) which contained a texture bar that segregated from a uniform vertical texture. The texture bar was made of 6×24 line elements tilted 45° either clockwise or counterclockwise at random. The bar was centered on the fixation dot. In the collinear configuration (Fig. 1B1), the bar had the same orientation of its line elements, while in the non-collinear configuration (Fig. 1B2) they were orthogonal.

The background-stimulus (which was displayed at the offset of the segregation-stimulus) was a uniform texture made of vertical line elements (Fig. 1B3).

2.3.3. Experiment 3

Two kinds of segregation-stimuli appeared (Fig. 1C1 and C2, *iso*-flow vs. *ortho*-flow conditions). In this experiment, the line elements of the bar were always vertically oriented, while the line elements of the texture surround had a 45° orientation either clockwise or counterclockwise at random. In the *iso*-flow condition (Fig. 1C1), the global bar had an overall orientation which was the same as the surround line elements, while in the *ortho*-flow condition (Fig. 1C2) they were reciprocally orthogonal.

In Experiment 3 (and Experiment 5), the background-stimulus (which was displayed at the offset of the segregation-stimulus) was made of line elements equally oriented, 45° either clockwise or counterclockwise at random (Fig. 1C3). Since the orientation of background line elements changed randomly between onset–offset displays, we made the constraint that a segregation-stimulus always had the surround texture with the same orientation of the preceding background-stimulus. Instead, the background-stimulus that followed a segregation-stimulus had a texture orientation which was randomly chosen. The background-VEPs were calculated only over the background-stimuli which had the same orientation as the texture surround of the preceding segregation-stimuli; otherwise they were discarded. In such a way, both segregation- and background-VEP were only due to the appearance and disappearance of the segregating texture bar (or patches in Experiment 5), while they were not due to changes of the orientation of the surround or background line elements. This procedure approximately halved the number of background-stimulus trials useful for calculating background-VEP.

2.3.4. Experiment 4

Two kinds of segregation-stimuli appeared (Fig. 1D1 and D2, collinear vs. non-collinear conditions). They were made of four segregating square patches of 6×6 line elements ($3 \times 3°$) at a distance of 3°. The four patches produced a non-connected global object that slanted 45° either clockwise or counterclockwise at random. The object was centered on the fixation dot. It should be noted that the texture bar employed in Experiment 2 and Experiment 3, and the four non-connected patches contained the same number of line elements.

The collinear stimulus (Fig. 1D1) had segregating patches containing line elements which had the same orientation as the global object (45° randomly clockwise or counterclockwise). The non-collinear stimulus (Fig. 1D2) had segregating patches containing line elements which were orthogonal to the orientation of the global object.

The background-stimulus (which was displayed at the offset of the segregation-stimulus) was a uniform vertical texture without segregating patches (Fig. 1D3).

2.3.5. Experiment 5

Two kinds of segregation-stimuli appeared (Fig. 1E1 and E2, *iso*-flow vs. *ortho*-flow conditions). The line elements within the segregating texture patches were always vertical. The orientation of the surround line elements was 45° randomly clockwise or counterclockwise. In the *iso*-flow stimulus (Fig. 1E1) the global object had the same orientation of surround line elements. In the *ortho*-flow stimulus (Fig. 1E2) the global object had the orthogonal orientation of surround line elements.

The background-stimulus (which was displayed at the offset of the segregation-stimulus) was a uniform texture made of line elements oriented 45° either clockwise or counterclockwise at random (Fig. 1E3; see Experiment 3 above for details).

2.4. Recording and analysis

The electroencephalogram (EEG) was recorded from Ag/AgCl-coated cup electrodes placed at O_z and left and right earlobes for reference and ground, respectively. Electrode placement followed the international 10/20 system. Electrode impedance was kept below 5 k Ω. The EEG was amplified (BM 623, Biomedica Mangoni, Pisa, Italy) and digitally converted (CED 1401, Cambridge Electronic Design, Cambridge, UK) under control of a second PC. Stimulation and recording onsets were synchronized on the basis of the vertical retrace signal of the monitor that displayed the stimu-

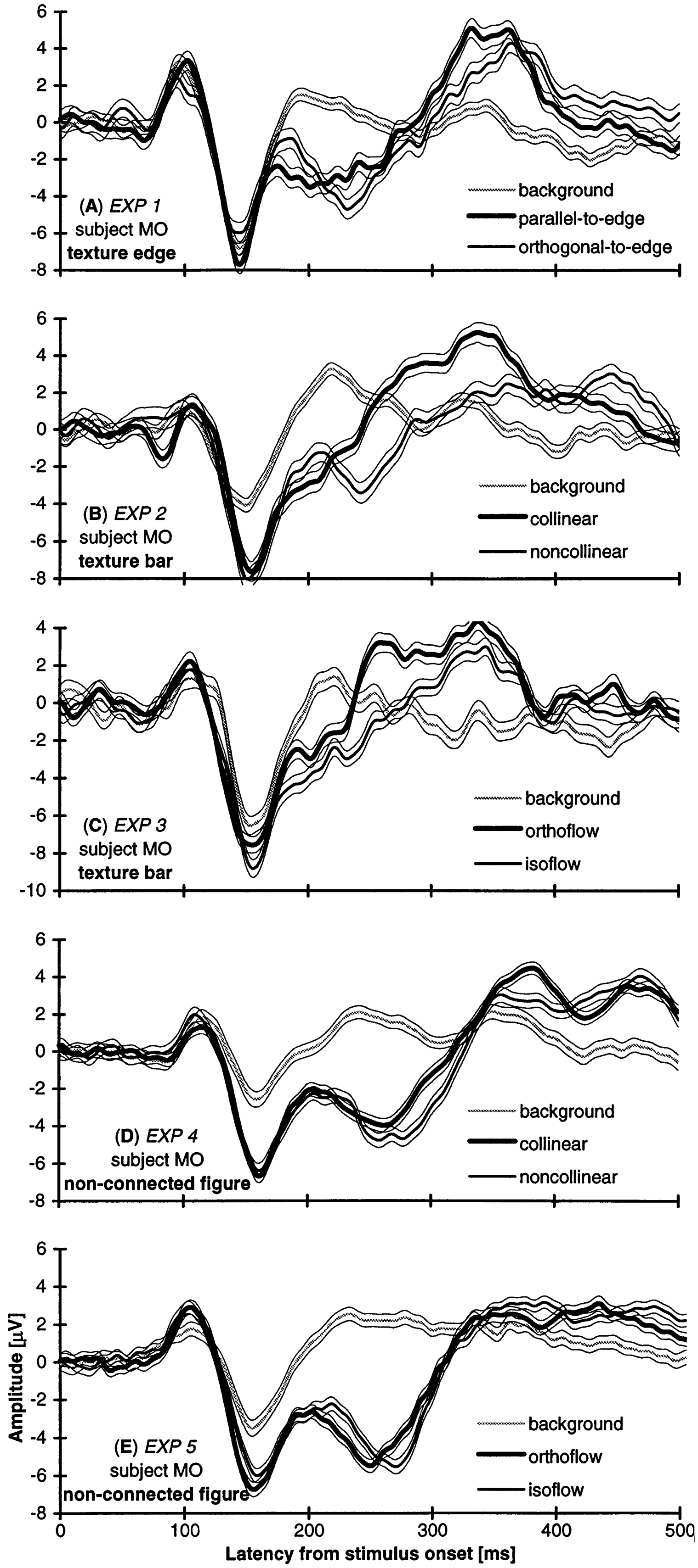

Fig. 2. VEPs by observer MO in the five experiments. The EEG was obtained from an O_z derivation referenced to the left earlobe. Each VEP trace is surrounded by two thin traces placed at ± 1 S.E.M. across EEG trials. The noise level is fairly limited and lower than VEP differences.

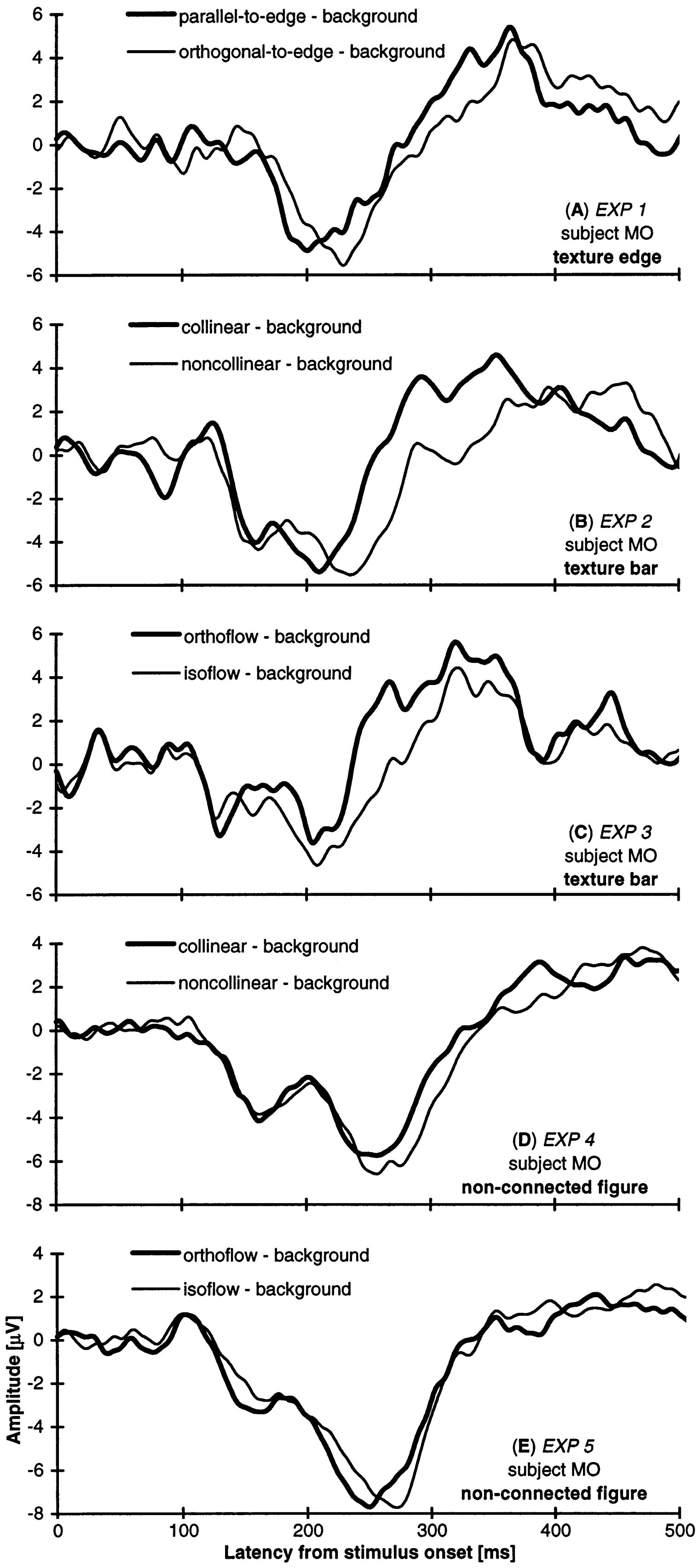

Fig. 3. (*Caption opposite*)

lus. The EEG was amplified 50000 times, bandpass filtered at 1–50 Hz, sampled at 1 kHz with a resolution of 12 bits, and stored on hard disk. Artifact rejection was done off-line when the signal amplitude exceeded ± 100 μV.

The VEPs were obtained by averaging the signal separately for the two experimental conditions and for the segregation-/background-stimulus conditions. For each condition, the VEP was then vertically aligned by taking as baseline its mean amplitude in the 0–50 ms range after stimulus onset. Examination of the VEPs of the two background-stimulus conditions showed that they were overlapping; therefore, they were averaged into a single trace.

The difference components were determined by algebraically subtracting the background-stimulus VEP from either segregation-stimulus VEP. For each subject, the negative peaks of the difference component were identified with latency in the 130–280 ms range, and their amplitude and latency stored for statistical analysis. To help localization of the peaks, the difference components were low-pass filtered through discrete Fourier transform (Press et al., 1992). The analysis of variance (ANOVA) with repeated measures was used to test statistical significance. The difference components were then averaged across the subjects.

3. Results

Before reporting the results of each experiment in turn, we show in Fig. 2 an example of the VEPs by a subject which participated in all the experiments. In these plots each VEP trace is surrounded by two thin lines which indicate ± 1 S.E.M. across EEG trials. As can be noticed, the overall level of noise was lower than the differences between VEP conditions which we discuss in the following sections. In Fig. 3 the difference component are obtained for the same observer.

3.1. Experiment 1: texture edge

In Fig. 4A the average difference components are shown together with ± 1 S.E.M. across the difference components of six subjects. The amplitude of the difference component is significant ($|z| > 2.81$, $P < 0.005$) at 157–226 ms (163–223 ms) in the parallel-to-edge (orthogonal-to-edge) condition. Notice moreover the very small variability between subjects from about 170 to about 200 ms in the parallel-to-edge and, to a lesser degree, in the orthogonal-to-edge condition.

The negative peak of the difference component has a latency of 219 ± 13 ms (245 ± 13 ms) in the parallel-to-edge (orthogonal-to-edge) condition. The average latency difference between the peaks of the two conditions is 25 ± 8 ms. The ANOVA showed that this latency difference was significant ($F_{1,5} = 10.0$, $P < 0.025$).

The ANOVA carried out on the amplitude of the negative peak showed a non-significant effect of edge configuration. (Similar non-significant effects on the peak amplitude were found in all the experiments and will not be thereby reported.)

3.2. Experiment 2: collinearity within the texture bar

In Fig. 4B the average difference components are shown together with ± 1 S.E.M. across the difference components of six subjects. The amplitude of the difference component is significant ($P < 0.005$) at 137–213 ms (139–210 ms) in the collinear (non-collinear) condition.

The overall difference component has two negative peaks around 160 and 200 ms, respectively. The first negative peak was clearly present in two out of six observers, with a latency of 162 ± 4 ms (161 ± 2 ms) in the collinear (non-collinear) condition. The second negative peak of the difference component (present in six out of six observers) has a latency of 199 ± 7 ms (219 ± 8 ms) in the collinear (non-collinear) condition. The average latency difference between the peaks of the two conditions is 20 ± 5 ms ($F_{1,5} = 16.6$, $P < 0.01$).

3.3. Experiment 3: interaction between texture surround and texture bar

In Fig. 4C the average difference components are shown together with ± 1 S.E.M. across the difference components of seven subjects. In the *ortho*-flow condition, the amplitude of the difference component is significant ($P < 0.005$) at 126–155 and 171–217 ms. In the *iso*-flow condition, the amplitude of the difference component is significant ($P < 0.005$) at 129–158 and 176–215 ms.

The overall difference component has two negative peaks around 140 and 210 ms, respectively. The first

Fig. 3. Difference components by observer MO in the five experiments. For each experiment, each difference component is obtained by algebraic subtraction of the background-stimulus VEP from either segregation-stimulus VEP. Four results are present in the case of a figure (Experiments 2–5 (B–E)): (1) the difference component has an early negative peak (140–160 ms) and a late negative peak (200–260 ms); (2) the early peak is not affected by figure-ground manipulations; (3) the late peak has a latency reduction when figure-ground segmentation is enhanced (this is also found for a texture edge, Experiment 1 (A)); (4) the latency of the late peak increases (about 40 ms) when the figure is made by non-connected patches while the latency differences produced by global figure segmentation remain relegated to the second peak. These results suggest that the late negative peak of the difference component is produced by global figure-ground segmentation.

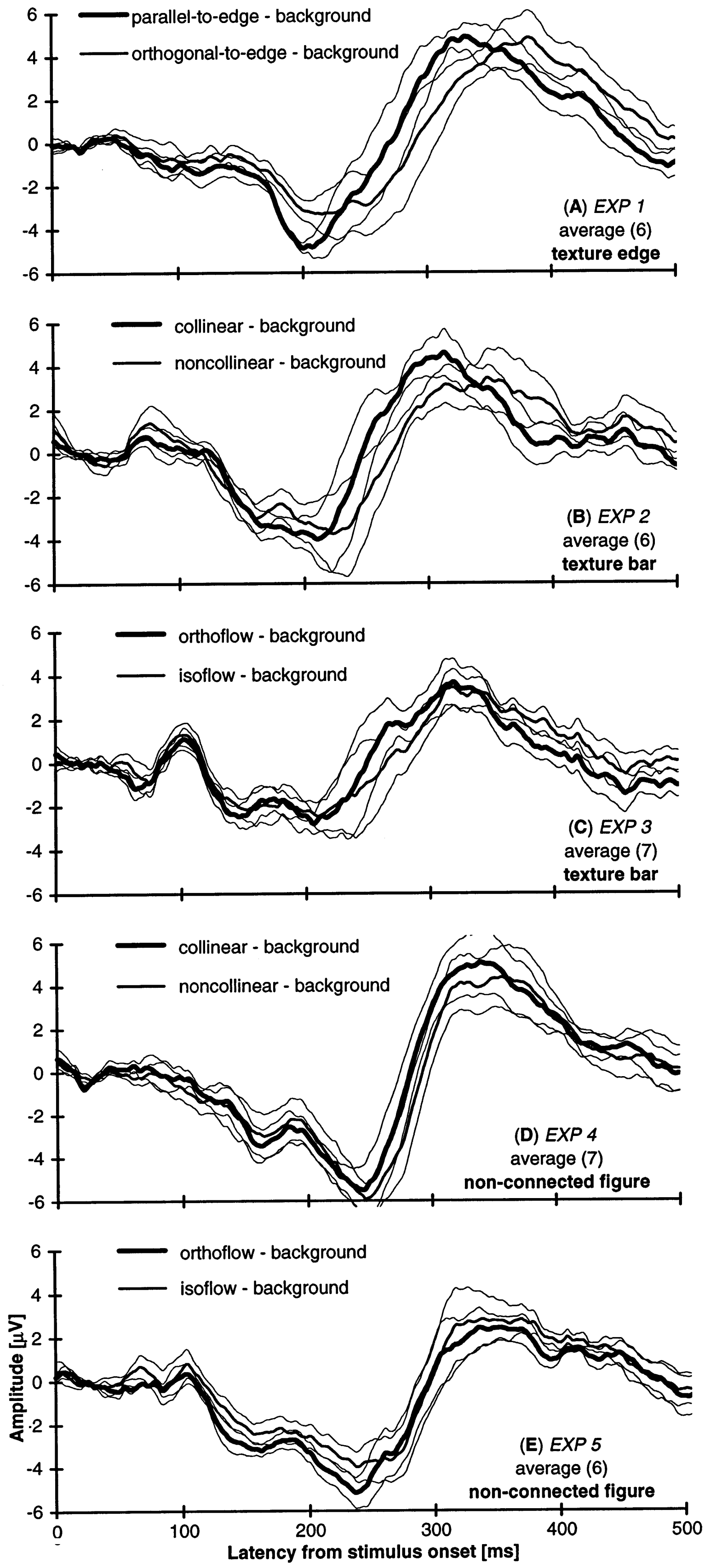

Fig. 4. (*Caption opposite*)

negative peak of the difference component (present in six out of seven observers) has a latency of 145 ± 4 ms (146 ± 6 ms) in the *ortho*-flow (*iso*-flow) condition, and a 2 ± 3 ms peak difference between the two conditions (non-significant). The second negative peak of the difference component (present in seven out of seven observers) has a latency of 206 ± 7 ms (217 ± 7 ms) in the *ortho*-flow (*iso*-flow) condition, and a 11 ± 1 ms peak difference between the two conditions ($F_{1,6} = 55.2$, $P < 0.001$).

3.4. Experiment 4: collinearity within the non-connected figure

In Fig. 4D the average difference components are shown together with ± 1 S.E.M. across the difference components of seven subjects. The amplitude of the difference component is significant ($P < 0.005$) at 148–257 ms (199–270 ms) in the collinear (non-collinear) condition.

The overall difference component has two negative peaks. The first negative peak of the difference component (present in four out of seven observers) has a latency of 158 ± 1 ms (160 ± 4 ms) in the collinear (non-collinear) condition, and a 2 ± 3 ms peak difference between the two conditions (non-significant). The second negative peak of the difference component (present in seven out of seven observers) has a latency of 238 ± 6 ms (254 ± 7 ms) in the collinear (non-collinear) condition, and a 16 ± 3 ms peak difference between the two conditions ($F_{1,6} = 20.4$, $P < 0.004$).

An ANOVA was carried out to compare the effects of connectedness (as a factor between subjects) and collinearity (as a factor within subject) on the latencies of the second peak of the difference component in Experiment 2 versus Experiment 4. The effect of connectedness ($F_{1,11} = 14.6$, $P < 0.003$) and of collinearity ($F_{1,11} = 36.7$, $P < 0.001$) were significant. Their interaction was non-significant ($F_{1,11} = 0.6$, $P > 0.4$).

3.5. Experiment 5: interaction between texture surround and non-connected figure

In Fig. 4E the average difference components are shown together with ± 1 S.E.M. across the difference components of six subjects. The amplitude of the difference component is significant ($P < 0.005$) at 119–271 ms (137–273 ms) in the *ortho*-flow (*iso*-flow) condition.

The overall difference component has two negative peaks which were both present in six out of six observers. The first negative peak of the difference component has a latency of 156 ± 5 ms (160 ± 6 ms) in the *ortho*-flow (*iso*-flow) condition, and a 4 ± 3 ms peak difference between the two conditions (non-significant). The second negative peak of the difference component has a latency of 238 ± 7 ms (258 ± 8 ms) in the *ortho*-flow (*iso*-flow) condition, and a 20 ± 4 ms peak difference between the two conditions ($F_{1,5} = 18.2$, $P < 0.008$).

An ANOVA was carried out to compare the effects of connectedness (as a factor between subjects) and *iso*/*ortho* (as a factor within subject) on the latencies of the first peak of the difference component in Experiment 3 vs. Experiment 5. The effect of connectedness ($F_{1,10} = 2.8$, $P > 0.1$), of *iso*/*ortho* ($F_{1,10} = 1.9$, $P > 0.1$), and their interaction ($F_{1,10} = 0.3$, $P > 0.5$) were non-significant.

A second ANOVA was carried out to compare the same factors on the latencies of the second peak of the difference component in Experiment 3 versus Experiment 5. The effect of connectedness ($F_{1,11} = 11.9$, $P < 0.005$) and of *iso*/*ortho* ($F_{1,11} = 45.1$, $P < 0.001$) were significant. Their interaction ($F_{1,11} = 4.0$, $P > 0.07$) was non-significant.

Fig. 4. Results of the experiments. The average difference components are shown in which the background-VEP was algebraically subtracted from either segregation-VEP. Each average difference component is surrounded by two thin lines which indicate ± 1 S.E.M. across the difference components of the observers (the number of observers is indicated into parentheses). (A) Results of Experiment 1: the difference components show a negative amplitude of the difference component at 157–226 ms (163–223 ms) in parallel-to-edge (orthogonal-to-edge) condition. The latency of the peak of the difference component is 219 ± 13 ms (245 ± 13 ms) in the parallel-to-edge (orthogonal-to-edge) condition. The parallel-to-edge configuration reduces (25 ± 8 ms) the latency of the negative peak of the difference component. (B) Results of Experiment 2: the difference components show a negative amplitude at 137–213 ms (139–210 ms) in the collinear (non-collinear) condition. Two peaks are present with latencies 162 ± 4 (161 ± 2 ms) and 199 ± 7 ms (219 ± 8 ms) in the collinear (non-collinear) condition. The collinear stimulus configuration reduces (20 ± 5 ms) the latency of the negative peak of the difference component. The first peak was present in two of the six subjects, the second peak in six of the six subjects. (C) Results of Experiment 3: the difference components show a negative amplitude at about 130–210 ms. Two peaks are present with latencies 145 ± 4 (146 ± 6 ms) and 206 ± 7 ms (217 ± 7 ms) in the *ortho*-flow (*iso*-flow) condition. The *ortho*-flow configuration reduces (11 ± 1 ms) the latency of the second negative peak of the difference component. The first peak was present in six of the seven subjects, the second peak in seven of the seven subjects. (D) Results of Experiment 4: the difference components show a negative amplitude at 148–257 ms (199–270 ms) in the collinear (non-collinear) condition. Two peaks are present with latencies 158 ± 1 (160 ± 4 ms) and 238 ± 6 ms (254 ± 7 ms) in the collinear (non-collinear) condition. The collinear stimulus configuration reduces (16 ± 3 ms) the latency of the second negative peak of the difference component. The first peak was present in four of the seven subjects, the second peak in seven of the seven subjects. (E) Results of Experiment 5: the difference components show a negative amplitude at 119–271 ms (137–273 ms) in the *ortho*-flow (*iso*-flow) condition. Two peaks are present with latencies 156 ± 5 (160 ± 6 ms) and 238 ± 7 ms (258 ± 8 ms) in the *ortho*-flow (*iso*-flow) condition. The *ortho*-flow configuration reduces (20 ± 4 ms) the latency of the second negative peak of the difference component. Both peaks were present in all subjects.

4. Discussion

In the present study, we measured VEPs in response to stimuli which produced a figure-ground segmentation. We extended over previous texture-VEP studies (Bach & Meigen, 1990, 1992; Lamme et al., 1992, 1993; Bach & Meigen, 1997) in two respects: firstly, the stimulus was perceptually manipulated in a larger number of ways; secondly, the observer was actively engaged in figure perception by means of a discrimination task.

As found in previous texture-VEP studies, texture segregation produces a VEP that is more negative than the VEP in response to a uniform texture background. This increased negativity can be characterized by a difference component. The main result of the present paper is that the difference component has two negative peaks. The early negative peak (latency 140–160 ms) is not affected by global figure-ground manipulations. This early peak was found in four of the five experiments, and in the majority of observers. The latest negative peak (latency 200–260 ms) was found in all the experiments and in all the observers. This second peak was influenced by global figure-ground segmentation.

The latency of the early peak (140–160 ms) is similar to the latency of the peak of the difference component as found in some previous texture-VEP studies (about 160 ms, Lamme et al., 1992; Caputo, Romani, Callieco, Gaspari & Cosi, 1999). This early peak can be produced by texture segregation at local orientation contrasts. (The orientation contrast was kept constant at 45° throughout all our experiments.) This early peak was absent only in Experiment 1, presumably because the entity of the segregation edges was reduced in those stimuli.

The emergence of the latest peak (200–260 ms) of the difference component is a new finding which has not been documented in previous VEP studies. The latency of this second peak was influenced by figure-ground segmentation. In Experiment 1, enhanced figure-ground segmentation due to edge global configuration produces a reduction of peak latency (25 ms) of the difference component in the parallel-to-edge with respect to the orthogonal-to-edge configuration. This finding can be related to enhanced discriminability (Wolfson & Landy, 1995) and shorter reaction times (Olson & Attneave, 1970) in the behavioral response to parallel-to-edge with respect to orthogonal-to-edge stimuli. In Experiment 2, enhanced figure-ground segmentation due to within-object configuration produces a peak latency reduction (20 ms) of the difference component in the collinear with respect to non-collinear configuration. This finding can be related to detection enhancement with collinear with respect to non-collinear (orthogonally aligned) stimuli (Nothdurft, 1992; Field et al., 1993). In Experiment 3, enhanced figure-ground segmentation due to the interaction between the figure and the flow of the texture surround, produces a peak latency reduction (11 ms) of the difference component in the *ortho*-flow with respect to *iso*-flow configuration. This finding can be related to enhanced discriminability and lower temporal thresholds in the behavioral response to *ortho*-flow with respect to *iso*-flow objects (Caputo, 1997). In Experiment 4, enhanced segmentation due to the configuration within a non-connected figure produces a peak latency reduction (16 ms) of the difference component in the collinear with respect to non-collinear configuration. (In the case of Experiment 4 no psychophysical data are available. It is commonly found that collinearity is effective only over a connected texture region (Kapadia et al., 1995) like a spread of the neuronal activity or of the textural pattern (Saarinen, Levi & Shen, 1997; Caputo, 1998). Instead, the results of Experiment 4 indicate that collinearity can allow spreading over non-connected parts of the same figure). In Experiment 5, enhanced figure-ground segmentation due to the interaction between the non-connected figure and the flow of the texture surround, produces a peak latency reduction (20 ms) of the difference component in the *ortho*-flow with respect to *iso*-flow configuration. This finding can be related to enhanced discriminability and lower temporal thresholds in the behavioral response to *ortho*-flow with respect to *iso*-flow non-connected stimuli (Caputo, 1997). Thus, the common feature that may be inferred from the findings of the present experiments is that enhancement of global figure perception correlates with the latency reduction of the 200–260 ms peak of the difference component.

Another result of the present experiments is that a non-connected figure (Experiment 4 and 5) produces a latency increase of about 40 ms of the second peak with respect to a connected figure (Experiment 2 and 3). This increase might be produced by the difference in eccentricity between the two stimuli. However, this interpretation would likely predict that a latency increase should be also present in the latency of the first peak of the difference component, contrarily to our results (see the Results section of Experiment 5). Our results suggest that the 40 ms increase of the second peak can be produced by the involvement (or stronger involvement) of an extra-striate area having cells with RFs large enough to collecting signals from the non-connected texture patches.

The experiments of the present study are methodologically different from the neurophysiological studies of figure-ground segmentation reviewed in the Introduction (Lamme, 1995; Zipser et al., 1996; Lee et al., 1998). In fact, we investigated figure discriminability (through a 2AFC task about the global orientation of the figure), while in the neurophysiological studies on macaque monkey the researchers focused their interest on figure detection (through a task of saccadic eye movement to the figure). It is plausible (and confirmed by our preliminary experiments) that our discrimination task has greatly amplified some neuronal processes involved in the high-level representation of the global shape of the figure. Akin to current views (Kovacs, Feher, & Julesz, 1998), a candidate for such a high-level representation is the processing of the medial-axis of the figure.

Given these cautions, recent findings by Lee et al. (1998) are most relevant. The authors found that a collinear configuration of a texture stripe (similar to our Fig. 1B1 stimulus) produces strong medial-axis responses in some V1 cells which are selective for the orientation of the boundary of the stripe (see their Fig.10C). The onset of this medial-axis representation was later (110 ms) than the boundary representation (80 ms). In addition, the medial-axis response seems to be the true signature of figure-ground segmentation because, at least in some cells, its emergence was influenced by the perceptual organization of the image (see their Fig.13C). From the plot by Lee et al. the peak latency of the boundary response can be estimated to be about 140 ms, while the peak of the medial-axis response seems to extend from 110 to 200 ms (see their Fig.10C). In relation to our findings, the boundary and medial-axis responses might respectively be related to the first and second negative VEP peaks. In the collinear configuration of our Experiment 2, the latency reduction of the second VEP peak can be due to the increased response of cells signaling the medial-axis of the texture bar. At least in the case of our texture bars, the latencies of the two VEP peaks seem to roughly correspond with the neurophysiological data by Lee et al. while we stress that our discrimination task can have greatly increased the strength of the second peak in our experiments.

Closely related to our behavioral task, the study by Merigan, Nealey and Maunsell (1993) on macaque monkey demonstrated that area V2 is involved in the discrimination of the global orientation of a texture bar. The authors found that the ability to detect a texture line element which segregates from a uniform texture surround was unchanged by a V2 lesion, while the same lesion completely disrupted (to chance level) the ability to discriminate the global orientation of a texture bar (similar to our Fig. 1C2 stimulus).

Lee et al. (1998) hypothesized that the medial-axis response of V1 cells can correspond to a high-resolution processing of the visual image carried out by V1 cells, after that high-level information, coming from extra-striate areas V2 and V4, is made available to V1 cells through feed-back connections. We suggest that extra-striate cortex can produce a high-level (like the medial-axis) representation of the figure which is essential per se to visual processing some of our stimuli. Such a representation should be in part independent of the high-resolution representation of the texture surface. In fact, let us consider the case of the non-connected figure (Experiment 4 and 5): the center-of-mass (i.e. the most salient point of the medial-axis representation) of the figure is in a spatial position occupied by texture elements which belong to the background surface. If the high-level representation of the figure (in V2) would be tightly bound to the high-resolution representation of the texture (in V1), this would lead to the erroneous binding of figure and ground at the center position of the non-connected figure, and segmentation would fail. Hence, a dynamic binding of the different scales of figure representation should be hypothesized.

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