



## Psychophysical and electrophysiological evidence of independent facilitation by collinearity and similarity in texture grouping and segmentation

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### ARTICLE INFO

#### Article history:

Received 6 March 2008

Received in revised form 30 January 2009

#### Keywords:

Textures  
Collinearity  
Grouping  
Segmentation  
ERPs

### ABSTRACT

Gestalt factors of collinearity and similarity facilitate two fundamental perceptual tasks: grouping elements into figures and segmentation of figures from the ground.

We have used a global–local paradigm to examine the psychophysical and neural correlates of these processes in humans: observers discriminated between orientations of either a three-Gabor group (grouping), or of a central Gabor within the group (segmentation). Groups were centered on a background of differently oriented Gabors. In both tasks, accuracy was increased by the collinearity (Experiment 1) and similarity (Experiment 2) of elements within the three-Gabor group. ERP correlates of facilitation differed across tasks. For segmentation, they were indexed by increased amplitude of negative ERP components, specific for processing textures, peaking at 75–250 and 150–250 ms, respectively. For grouping, collinearity and similarity had different effects. Collinearity produced a positive polarity deflection between 40 and 179 ms (i.e. the opposite to segmentation). This task-dependent switch in sign of polarity change, without corresponding changes in the stimulus or perception, reflects distinct neural mechanisms for collinear facilitation in grouping and segmentation. In contrast, similarity reduced positivity at 275 ms. Results show similar modulation of segmentation components via the distinct mechanism underlying collinearity and similarity, but distinct modulation of grouping components via collinearity and similarity.

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### 1. Introduction

Two visual tasks are important for survival: deciding which fragmented contours forming the retinal image belong to one same object, and segmenting the contour of a given object from the surround. For these visual operations, grouping and segmentation of contour elements the geometrical relationships between contour segments are extremely important. Gestalt psychologists (Wertheimer, 1923) provided phenomenological demonstrations of the laws of perceptual grouping and figure-ground segmentation and their work has been an important source of inspiration for later psychological and neurophysiological experiments that unveiled the mechanisms underlying grouping and segmentation. Using multistable dot patterns that can be perceptually organized into alternative collections of parallel strips of dots, the law of grouping by proximity has been extensively studied both in isolation (Kubovy, Holcombe, & Wagemans, 1998; Kubovy & Wagemans, 1995) and in its interactions with other grouping factors: similarity and alignment (Claessens & Wagemans, 2005; Kubovy & van den Berg, 2008).

In the present study we focused on similarity and alignment. With stimuli made up of line segments or oriented Gabors, similarity and alignment can be respectively manipulated by varying orientation and collinearity (alignment of elements along the orientation axes). Psychophysical studies showed that collinearity and similarity determine contrast detection enhancement (Polat, 1999; Polat & Sagi, 1994) and modulate both grouping of elements into contour (Field, Hayes, & Hess, 1993) and texture segmentation (Giora & Casco, 2007; Nothdurft, 1992; Polat & Bonneh, 2000).

These configurational effects based on orientation similarity and collinearity may result from modulation of the response in V1 to stimuli presented within the receptive field (RF) by stimuli outside the RF (Kapadia, Ito, Gilbert, & Westheimer, 1995; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998). This modulation can be facilitatory, based on short- and long-range horizontal connections, or suppressive, based on short-range interactions (Adini, Sagi, & Tsodyks, 1997; Lamme, 2003; Mizobe, Polat, Pettet, & Kasamatsu, 2001; Polat & Bonneh, 2000).

With a high contrast target and extended background, these “contextual influences” are facilitatory when the elements outside the RF are collinear to and iso-oriented with those inside (Kapadia et al., 1995), and this could account for facilitation by collinearity and similarity in perceptual grouping with consequent increased

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saliency of the group (Field et al., 1993; Hess & Field, 1999; Li, Piech, & Gilbert, 2006). With iso-oriented but non-collinear flanks, an inhibition of the target is observed (Kastner, Nothdurft, & Pigarev, 1997; Knierim & van Essen, 1992), and reduction of this background-to-target surround suppression due to orientation contrast may be the neural correlate of local texture segmentation.

In the present study we asked whether collinearity and similarity between target elements modulate not only the efficiency with which they group together but also the efficiency with which they segment from a background of differently oriented elements (45° orientation contrast). In order to answer this question, performance in grouping and segmentation was compared within each experiment to find out whether these two tasks were differently affected (facilitated or interfered) by the congruency of either global and local orientation (Experiment 1) or of local orientations of target elements (Experiment 2). The prediction was that collinearity and similarity may improve the efficiency of these two tasks through involvement of different mechanisms: they may facilitate grouping operations (Field & Hayes, 2003; Field et al., 1993; Hess & Field, 1999), and this can increase group saliency per se, but they can also increase the efficiency of a second operation, the reduction of surround suppression leading to segmentation (see Polat & Bonneh, 2000 for a similar question in contrast detection), and this also results in increased saliency. In other words, we predicted that not only grouping based on facilitatory interactions but also segmentation of target elements from the background – which is based on surround suppression reduction – may be facilitated by target element collinearity and similarity. Although the facilitation may be similar the neural correlates in humans may be different. To test this hypothesis we combined the psychophysical and ERP measurements while observers viewed a texture of Gabors all iso-oriented except for a three-Gabor group and were asked to perform a segmentation either of the central Gabor in the group (local segmentation task) or of the whole group (grouping task), this second task involving both segmentation from background and grouping within the target.

Facilitatory and inhibitory contextual influences may occur in the target and, to a lesser extent, in the uniform texture background. Use of a uniform texture allowed us to determine how target grouping and segmentation resulted from a modulation of facilitatory and inhibitory contextual influences in the target with respect to the background region.

## 2. Materials and methods

### 2.1. Stimuli

Stimuli were generated using a Pentium IV computer and displayed on a 17-in. Sonic P70 monitor driven by a NVIDIA GeForce4 MX graphics card, with a resolution of 1024 × 768 pixels, refreshed at 100 Hz. Stimuli were presented in a darkened room at 57 cm viewing distance.

The texture stimuli consisted of 9 × 9 matrices of circular cosine-phase Gabor-elements (the product of a sinusoidal grating and a Gaussian blob all oriented at 45° (in half of the trials) or 135° (in the other half) except for the three-Gabors displayed foveally at the center of the matrix to form a three-Gabor group (either horizontal or vertical). They had an orientation of either 90° or 180°, to form the configuration most suitable to investigate facilitatory and inhibitory lateral interactions (Khoe, Freeman, Woldorff, & Mangun, 2004; Polat & Sagi, 1993; Polat & Sagi, 1994). The three-Gabor target was iso-oriented, either collinear (iso/collinear) or non-collinear (iso/non-collinear) in Experiment 1 – as well as non-collinear, either iso-oriented (iso/non-collinear) or ortho-oriented (ortho/non-collinear) in Experiment 2 (see

Fig. 1). The uniform stimulus was always oblique, made up of either 45° (half the trials) or 135° (half the trials) oriented Gabors.

Each Gabor had spatial frequency equal to 3.2 cycles/deg, corresponding to a wavelength ( $\lambda$ ) of .31°, multiplied by a Gaussian envelope, with standard deviation ( $\sigma$ ) of .19°. Center-to-center element separation was 3.66  $\lambda$ . Mean luminance of a Gabor element was equal to the luminance of background (50 cd/m<sup>2</sup>). Orientation of the Gabor matrices of the texture mask was varied randomly from trial to trial.

### 2.2. Procedure

We used an experimental design in which the task was varied within-experiment but in independent blocks: in both experiments observers had to discriminate the orientation of either the three-Gabor group or the central Gabor. Each block consisted of 234 trials, comprising 78 repetitions of three conditions randomly intermixed: uniform, iso/collinear and iso/non-collinear textures, in Experiment 1, and uniform, iso/non-collinear and ortho/non-collinear textures, in Experiment 2. The two experimental blocks were preceded by 12 practice trials.

Each trial (see Fig. 2) started with a central fixation point, presented for 1000 ms on a gray background. The stimulus texture was then presented for 160 ms and replaced immediately (no interval) by the mask texture made up of randomly oriented Gabors, presented for 200 ms. Finally, the screen was turned black and the subject's response (horizontal or vertical) recorded. Following the standard psychophysical method of forced-choice, observers were asked to respond horizontal or vertical to the uniform texture without targets that produced chance response. Time limit for each response was set to 2500 ms.

### 2.3. Subjects

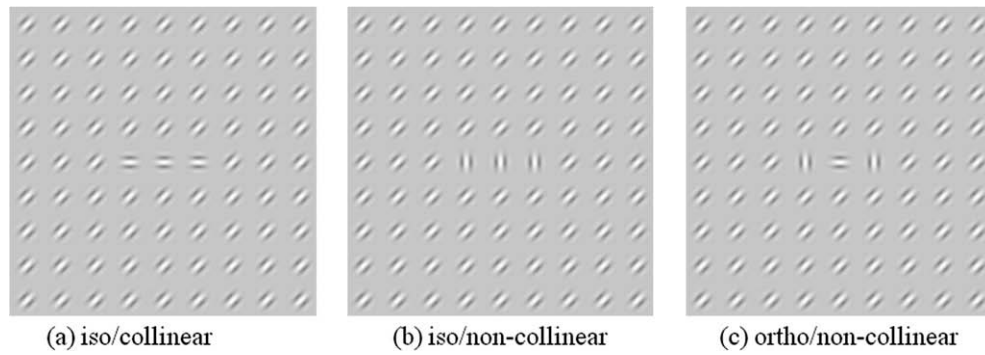
Fifteen (six males) and eight right-handed subjects (three males), aged 20–35 years, with normal or corrected-to-normal visual acuity participated in Experiments 1 and 2, respectively. All subjects were volunteers and naïve to the purposes of the experiments. Half of the subjects executed the segmentation task first; the other half performed the grouping task first.

### 2.4. ERP recordings

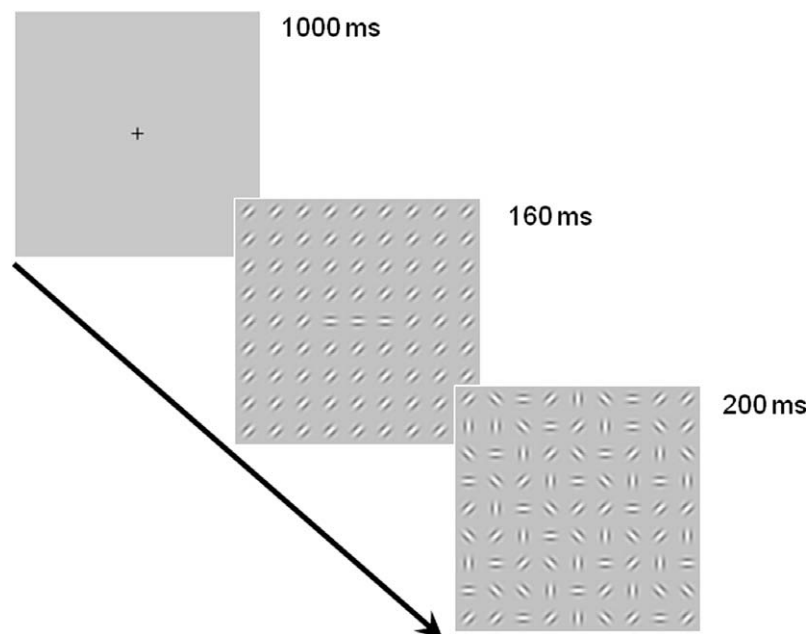
Electroencephalographic activity (EEG) was recorded continuously from 12 scalp electrodes (O1, O2, Oz, P3, P4, Pz, C3, C4, Cz, F3, F4, Fz) using sintered Ag/AgCl ring scalp electrodes and Brain-Cap, labeled according to the 10–20 international system. All scalp channels were referenced to the average reference. Recording was carried out at 12 electrodes because with the QuickAmp72 the unipolar electrophysiological inputs are configured as a reference amplifier. The ground electrode was positioned in front of Fz. The EEG was amplified, band-passed (0.1–40 Hz), and digitized at a sampling rate of 1000 Hz (Recorder software, QuickAmp amplifier). Scalp electrode impedance was maintained below 5 k $\Omega$ . Scalp electrooculogram (EOG) was also recorded bipolarly through four additional electrodes placed left and right of external canthi for horizontal eye movements, and above and below the right eye for blinks and vertical eye movements. All trials in which the subject made an eye movement larger than 1° were rejected.

### 2.5. Data analysis

Accuracy data were analyzed with repeated-measures ANOVAs both separately for each experiment, with Task and Configuration as factors, and in a general analysis, with Experiment, Task and Configurations as factors.



**Fig. 1.** Texture segmented by horizontal three-Gabor group. Gabors in the group were iso-oriented and collinear (a) or non-collinear (b); in (c) they were oriented orthogonally and non-collinear. Experiment 1 compared targets (a) and (b) and Experiment 2 targets (b) and (c).



**Fig. 2.** Trial sequence that began with the fixation point presented for 1000 ms, the texture stimulus lasting 160 ms and, with no interval, the mask disappearing after 200 ms.

ERPs were constructed offline, according to stimulus type. The epochs, starting 100 ms before stimulus onset and continuing for 400 ms, were constructed. Separate averages were computed for each stimulus type (uniform, iso/collinear, iso/non-collinear, ortho/non-collinear) in both segmentation and grouping tasks. All amplitude values were referred to the 100 ms pre-stimulus baseline. Trials associated to response errors (only for segmented textures) and/or contaminated by artifacts (eye blinks, eye movements, or muscle potentials) at any electrode were excluded from the average. On average 2.5% of the trials in Experiment 1 (2.7% in the grouping task and 2.3% in the segmentation task) and 0.75% in Experiment 2 (0.5% in the grouping task and 1% in segmentation task) were excluded owing to presence of artifacts. Artifacts were considered according to the following criteria: gradients (1 ms interval) exceeding  $50 \mu\text{V}$ , potentials exceeding  $200 \mu\text{V}$  (peak-to-peak amplitude) within 200 ms, potentials exceeding  $\pm 250 \mu\text{V}$  (absolute amplitude) or low activity (below  $0.5 \mu\text{V}$ ) for more than 100 ms.

The visual ERPs were characterized by a series of components with latency ranging from 40 ms to 300 ms.

“Difference-waves” (D-waves) were calculated by subtracting point-by-point the ERPs to uniform texture from ERPs to segmented textures. Amplitude and latency for each component was

determined from the grand average of the D-waves. The amplitude of D-wave components was quantified in terms of peak amplitude (maximum or minimum deflection within a specified time window). Five windows were considered for the analysis: two (40–70 and 262–300 ms) referring to a positive D-wave peaking at about 60 ms and 275 ms, and three (71–120, 121–179 and 180–261) referring to negative deflections peaking around 75, 150 and 200 ms, respectively. It is worth considering whether the presence of the mask at 160 ms after the onset affects these waveforms. Since the same kind of mask was used, any effect should not depend on the configuration. It is possible however that the effect of mask covaried with that of the configuration, but with an SOA of 160 ms, this could not manifest before 220 ms, considering the latency of cortical D-waves components. Instead, we found much earlier configurational effects.

Three-way repeated-measures ANOVAs with Electrode (Oz, O1, O2), Task (Grouping and Segmentation) and Configuration (iso/collinear, iso/non-collinear and ortho/non-collinear) as factors were conducted on both the amplitude and latency of the D-wave components peaking at 60, 75, 150, 200 and 275 ms in each experiment, and a general ANOVA with Experiment, Electrode, Task and Configuration as factors was also executed. Only occipital electrodes were entered into the ANOVA since parietal, frontal and

central electrodes showed no ERPs with negative peak at the latency reflecting texture segmentation. Post hoc *t*-test with Bonferroni correction was used for pair-wise comparisons. The Greenhouse–Geisser epsilon correction factor was applied where appropriate, to compensate for possible effects of non-sphericity in the measurements compared.

None of the main effects or the interactions proved significant when latency data were analyzed. Consequently, only the amplitude data were described and discussed.

### 3. Results

#### 3.1. The effects of collinearity

##### 3.1.1. Psychophysical results

The percentage of correct responses for segmentation and grouping are shown in Fig. 3. ANOVA revealed a significant effect of Configuration [ $F_{1,13} = 18.2, p < .001$ ], indicating that performance decreases in both tasks from 93.5% with the collinear configuration to 85% with the iso/non-collinear configuration. The effect of Task [ $F_{1,13} = .964; p = .35$ ] and the interaction Configuration \* Task [ $F_{1,13} = .81; p = .38$ ] were not significant, indicating that collinearity increased the ease of segmentation and grouping in a similar way despite, as the ERP data indeed show, the electrophysiological correlates of these facilitations being qualitatively different.

##### 3.1.2. ERP results

ERPs to uniform, iso/collinear and iso/non-collinear, recorded at medial occipito-parietal (Oz, Pz and Fz) and occipito-lateral (O1 and O2) sites, are illustrated in Fig. 4a and b, separately for both tasks.

In both tasks, ERPs were characterized with a first (C1), second (N1), third (N2) and fourth (N3) negative peak respectively at about 60, 140, 250 and 300 ms and with a first (P1), second (P2) and third (P3) positive peak at 90, 190 and 270 ms, respectively (Table 1). A configurational modulation was present at the occipital electrodes as early as in C1, more clearly in grouping. There appears to be an opposite effect of collinearity in the two tasks, this occurring in a temporal window that is earlier in grouping than in segmentation.

To confirm these indicative ERP results, ANOVAs were applied to D-waves from occipital electrodes (Fig. 5). If a similar collinear facilitation in the two tasks was associated to a modulation of ERP amplitude by different mechanisms in grouping and segmentation, this should be reflected in D-waves, as indeed confirmed below.

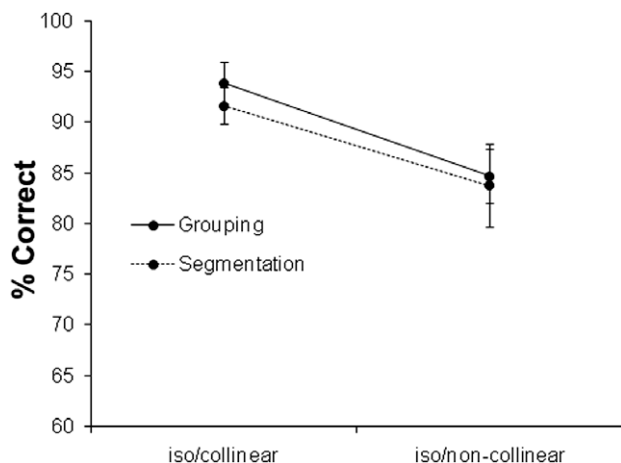


Fig. 3. Results of Experiment 1. Percentage of correct responses obtained in iso/collinear and iso/non-collinear conditions for grouping (continuous line) and local segmentation tasks (dotted line).

ANOVA revealed an effect of Configuration, significant for components peaking at 60 [ $F_{1,13} = 17.1, p < .001$ ], 150 [ $F_{1,13} = 4.8, p < .05$ ] and 275 ms [ $F_{1,13} = 7.4, p < .02$ ] and approaching significance at 200 ms [ $F_{1,13} = 4.2, p < .06$ ]. The effect of task was significant at 275 ms, only in Oz and O1 [ $F_{2,26} = 8.3, p < .005$ ]. The interaction Configuration \* Task was significant for D-waves peaking at 75 [ $F_{1,13} = 16.9, p < .001$ ], 150 [ $F_{1,13} = 15.7, p < .001$ ], 200 [ $F_{1,13} = 10.01, p < .009$ ] and 275 ms (only for Oz and O1) [ $F_{2,26} = 3.6, p < .05$ ] but not for those peaking at 60 ms [ $F_{1,13} = 3.9, p > .05$ ].

Pairwise comparisons showed that, after 60 ms latency, the effect of collinearity diverged in the two tasks. In the grouping task, collinearity shifted polarity towards positive values at 75 and 150 ms whereas in the local segmentation task collinearity increased negativity at 75 and 200 ms. A shift of collinear with respect to non-collinear and of non-collinear with respect to uniform towards positive values, between 40 and 179 ms, resulted therefore in a shift, larger for collinear, of D-waves towards positive values in the grouping task. In the segmentation task, the shift was towards negative values, resulting in a larger D-wave negativity between 71 and 261 ms in the collinear condition. Collinearity increased positivity at 275 ms also, but only in grouping, suggesting a higher saliency of the collinear Gabor group in this task that may have biased the attended receptive field towards group size.

#### 3.2. The effect of similarity

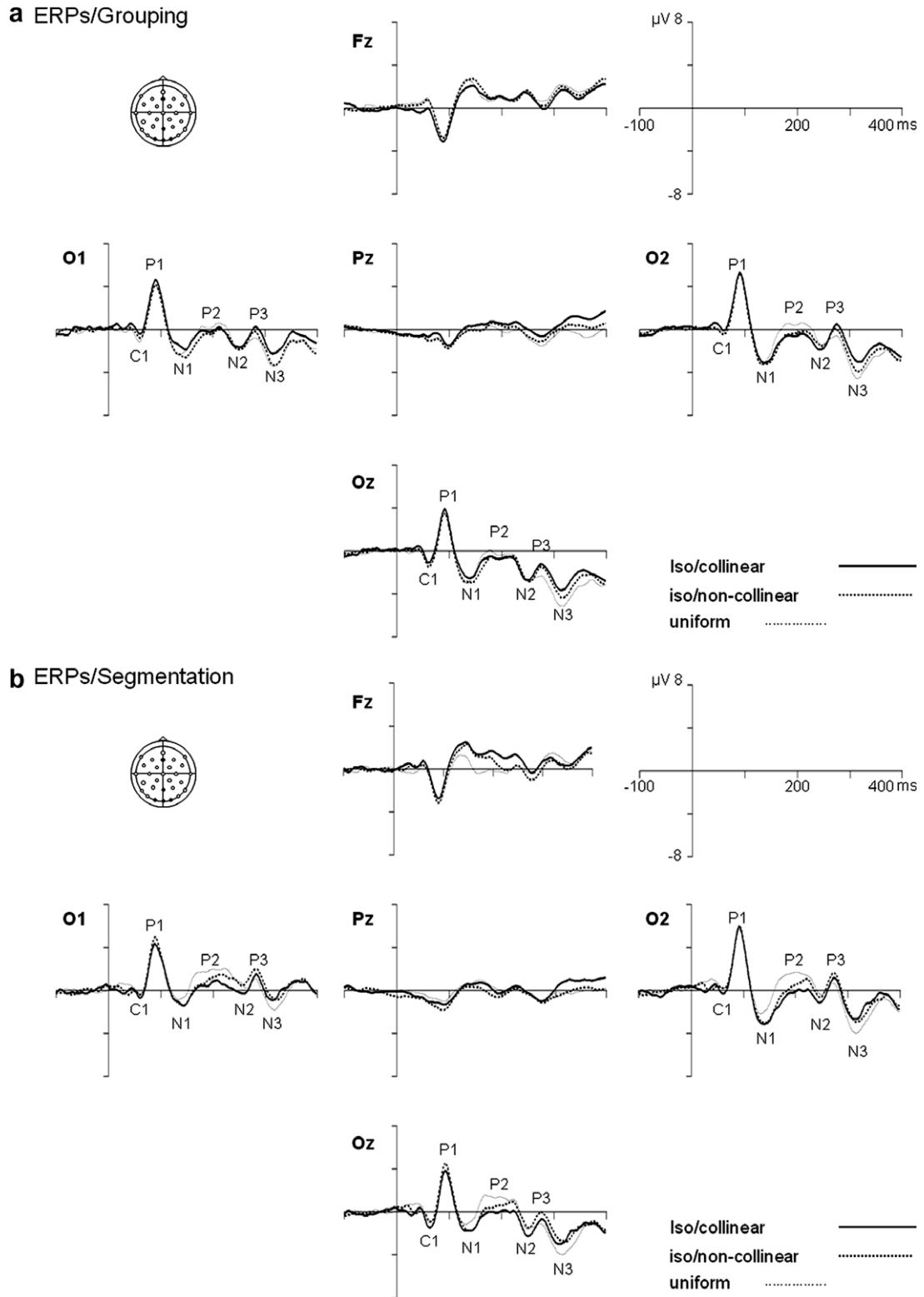
The seminal work of Gestalt psychology established that both similarity and collinearity affect figural organization by modulating the ease with which elements group into figures (Wertheimer, 1923). However, the electrophysiological correlates of these two grouping effects may be different. Han, Ding, and Song (2002) showed that whereas grouping by collinearity is associated to a short-latency effect on D-waves, grouping by similarity is indexed by a long latency occipito-temporal negativity.

In the non-collinear stimulus of Experiment 1 the elements were non-collinear but had the same orientation so we were actually comparing the effect of similar and collinear elements with that of similar but non-collinear elements. To analyze the effect of similarity, the grouping and segmentation tasks were repeated to compare both accuracy and D-waves obtained in the non-collinear condition with iso-oriented elements of the previous experiment (iso/non-collinear) with a different non-collinear condition, in which both collinearity and similarity of elements was disrupted in the three-Gabor group (ortho/non-collinear).

In this way, we aimed at isolating, when elements were non-collinear, the psychophysical and electrophysiological correlates of contextual modulation by orientation similarity, in contrast with Han (2004) who used color similarity. In so doing, we aimed at establishing whether these correlates of similarity, if present, depended on the task and were different from those resulting from collinearity. The question of interest is how the perturbation of similarity that makes the flanks orthogonal to the central Gabor affects segmentation and grouping. A straightforward prediction, however not confirmed by the data, is that perturbing flank orientation may reduce inhibitory interactions within the target group with consequent reduction of surround suppression (Kastner et al., 1997; Knierim & van Essen, 1992) and the effect could be task-dependent. Indeed, surround suppression disappears when the relative orientation between target and lateral mask exceeds 45° (Petrov, Carandini, & McKee, 2005).

##### 3.2.1. Psychophysical results

ANOVA (Fig. 6) revealed a significant effect of Configuration [ $F_{1,7} = 19.4, p < .003$ ] and Configuration \* Task interactions [ $F_{1,7} = 6.6, p < .04$ ]. Pairwise comparisons revealed a significant reduction



**Fig. 4.** Results of Experiment 1. Grand average event-related potentials (ERPs), in grouping (a) and segmentation tasks (b), recorded from iso/collinear (black line), iso/non-collinear (dotted line) and uniform (fine dotted line) configurations.

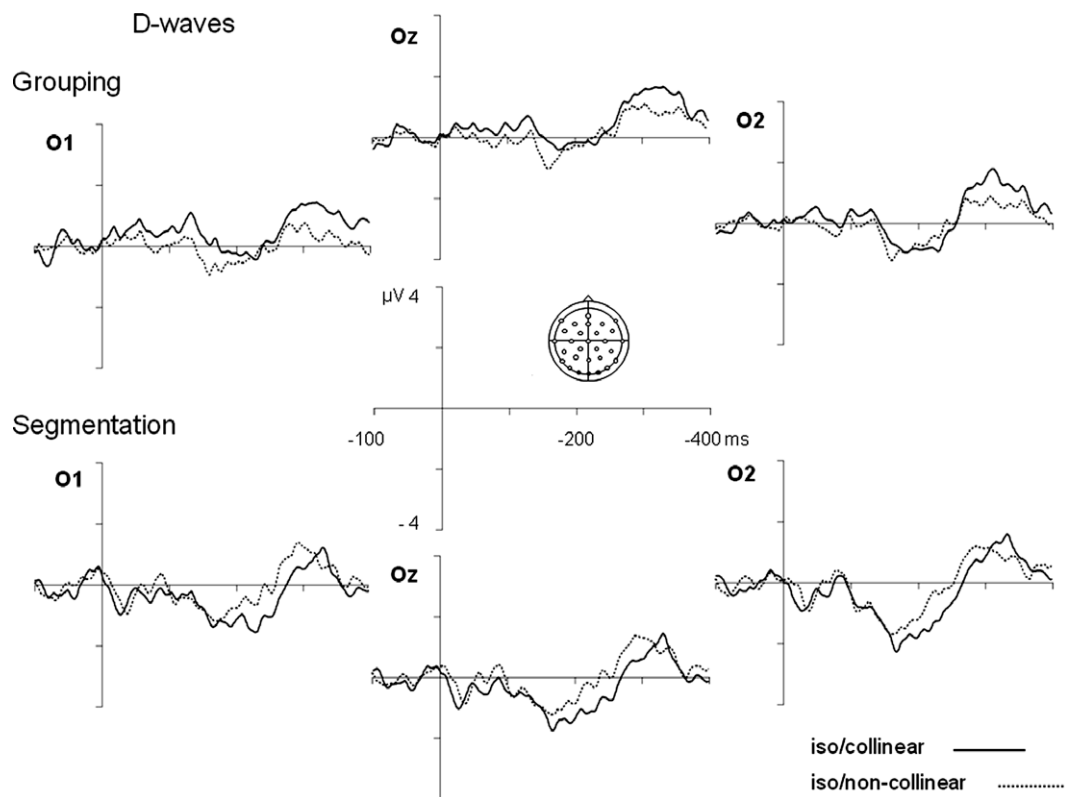
of accuracy in the ortho/non-collinear condition (73.2%) compared to iso/non-collinear condition (83.4%), only for grouping ( $p < .01$ ).

In segmentation, accuracy was reduced, not significantly ( $p = .16$ ), when the flanks were orthogonal (84.1%) compared to when they were iso-oriented (86.9%) for most subjects.

We would have expected opposite results if ortho-oriented flanks reduced surround suppression. The results obtained are also hardly explained by cross-orientation inhibition because this occurs with overlay simultaneous mask rather than lateral flanks (Petrov et al., 2005). The result that perturbation of sim-

**Table 1**  
ERPs amplitude in the two tasks for iso/collinear (i/c), iso/non-collinear (i/n-c) and uniform (u) configurations (Experiment 1).

		Grouping			Segmentation			
		i/c	i/n-c	u	i/c	i/n-c	u	
C1	Oz	-1.2	-1.8	-1.8	-1.5	-1.0	-0.9	
	O1	-0.8	-1.0	-1.3	-0.9	-0.4	-0.3	
	O2	-0.2	-0.5	-0.2	-0.3	0.2	0.3	
P1	Oz	4.1	3.6	3.8	4	4.8	4	
	O1	4.9	4.3	4	4.5	5.0	4.5	
	O2	5.3	5.4	5.3	6.1	5.9	6.0	
N1	Oz	-2.5	-3.0	-2.9	-2.0	-1.9	-1.1	
	O1	-2.0	-2.9	-2.3	-1.5	-1.5	-1.0	
	O2	-3.2	-3.3	-3	-3.2	-3.0	-2.0	
P2	Oz	-0.4	-0.3	0.2	0.3	1.0	1.9	
	O1	-0.2	-0.5	0.4	0.5	1.3	2.0	
	O2	-0.5	-0.3	0.5	-0.1	0.5	1.9	
N2	Oz	-2.9	-2.9	-2.7	-2.3	-1.3	-1.3	
	O1	-1.8	-1.9	-1.7	-0.4	0.5	0.3	
	O2	-1.9	-1.8	-1.4	-1.0	-0.8	-0.6	
P3	Oz	-1.0	-1.3	-2.4	-0.6	0.2	-1.0	
	O1	0.5	-0.1	-1	2.0	2.1	1.0	
	O2	0.5	0.2	-0.7	1.4	1.9	1.0	
N3	Oz	-3.3	-4.0	-5	-3.0	-2.9	-3.9	
	O1	-2.0	-2.9	-3	-1.0	-1.0	-2.0	
	O2	-2.9	-3.9	-4.5	-2.7	-3.0	-4.0	

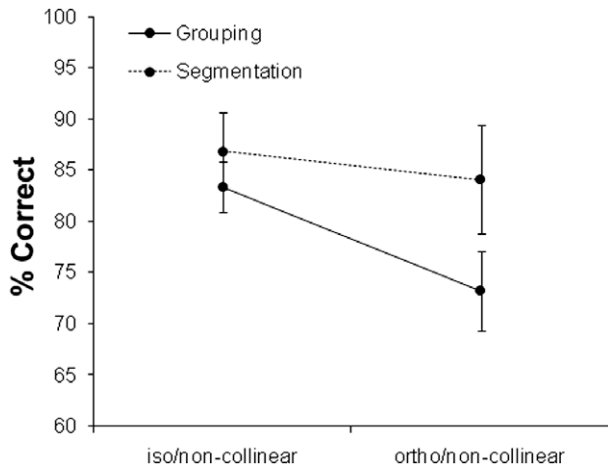


**Fig. 5.** Results of Experiment 1. D-waves obtained from electrodes in Oz, O1 and O2, in grouping and segmentation task with iso/collinear (continuous line) and iso/non-collinear stimuli (dotted line). Zero marks stimulus onset.

ilarity hampers grouping more than segmentation suggests that bottom-up attention was directed versus individual target Gabors having very salient conflicting orientation, which were therefore not easily integrable into a group, in the grouping task, and not easily distinguishable one from the others to discriminate the orientation of the central Gabor, in the segmentation task.

### 3.2.2. ERP results: peak amplitude

In both tasks, ERPs (Fig. 7a and b) were characterized with a first (C1), second (N1), third (N2) and fourth (N3) negative peak at about 60, 140, 230 and 300 ms, respectively, and with a first (P1), second (P2) and third (P3) positive peak at 90, 190 and 270 ms, respectively (Table 2). An effect of similarity is present around 200 and 300 ms in both tasks.



**Fig. 6.** Results of Experiment 2. Percentage of correct responses in iso/non-collinear and ortho/non-collinear conditions for grouping (continuous line) and local segmentation tasks (dotted line).

To confirm these indicative ERP results, ANOVAs were applied to D-waves. If similarity facilitation in the two tasks resulted in late effects, this should be reflected in D-waves, as indeed confirmed below.

The interaction Configuration \* Task was found to be significant at 150 [ $F_{1,7} = 11.6, p < .01$ ] and 200 ms [ $F_{1,7} = 10.3, p < .02$ ], indicating a reduced negativity of the segmentation component in the ortho/non-collinear condition but only in the segmentation task. The D-wave component peaking at 275 ms was significantly larger in the segmentation task [ $F_{1,7} = 6.4, p < .05$ ], and, in both tasks, significantly larger in the ortho/non-collinear than in the iso/non-collinear configuration [ $F_{1,7} = 25.2, p < .002$ ].

When compared with those of Experiment 1, the effects at 275 ms are unexpected. Indeed, in Experiment 1, the amplitude of this component was larger in the iso-collinear than in the iso/non-collinear condition only for grouping. Taking into account both results, one explanation is that at 275 ms the D-waves elicited by the iso/non-collinear target were strongly modulated by the other stimulus in the block. The relative modulation of the amplitude of this component in a block may indicate a bias in the attended receptive field: the size of the attended receptive field may correspond to that of the three-Gabor group when they are iso-oriented in both stimuli in a block (Experiment 1) and may correspond instead to that of individual Gabors when one of the stimuli in a block has ortho-oriented flanks (Experiment 2). In Experiment 2, this bottom-up attentional bias may have produced a local-to-global conflict (in performing the grouping task) and a local-to-local conflict, in judging segmentation. This task-dependent orientation conflict may have accounted for the impairment with ortho-oriented targets, rather than early inhibitory lateral interactions, either surround suppression or cross-orientation inhibition (Petrov et al., 2005).

Note that a local-to-global orientation conflict, similar to that in Navon-like configurations (Casco, Campana, Grieco, & Fuggetta, 2004; Casco, Grieco, Campana, Corvino, & Caputo, 2005; Navon, 1977), cannot account for reduced grouping performance in the iso/non-collinear with respect to iso/collinear condition of Experiment 1. Indeed, in this case we would have obtained a late effect, not the early one at the level of C1 that we found and, in the grouping task of Experiment 2, lower accuracy in the iso/non-collinear than ortho/non-collinear configuration, since in this latter only some of the elements conflict with the orientation discrimination task (See Fig. 8).

#### 4. General discussion

This study has made a first-ever direct comparison between the ERP correlates of facilitation by similarity and collinearity in grouping and segmentation task: a clear dissociation is shown.

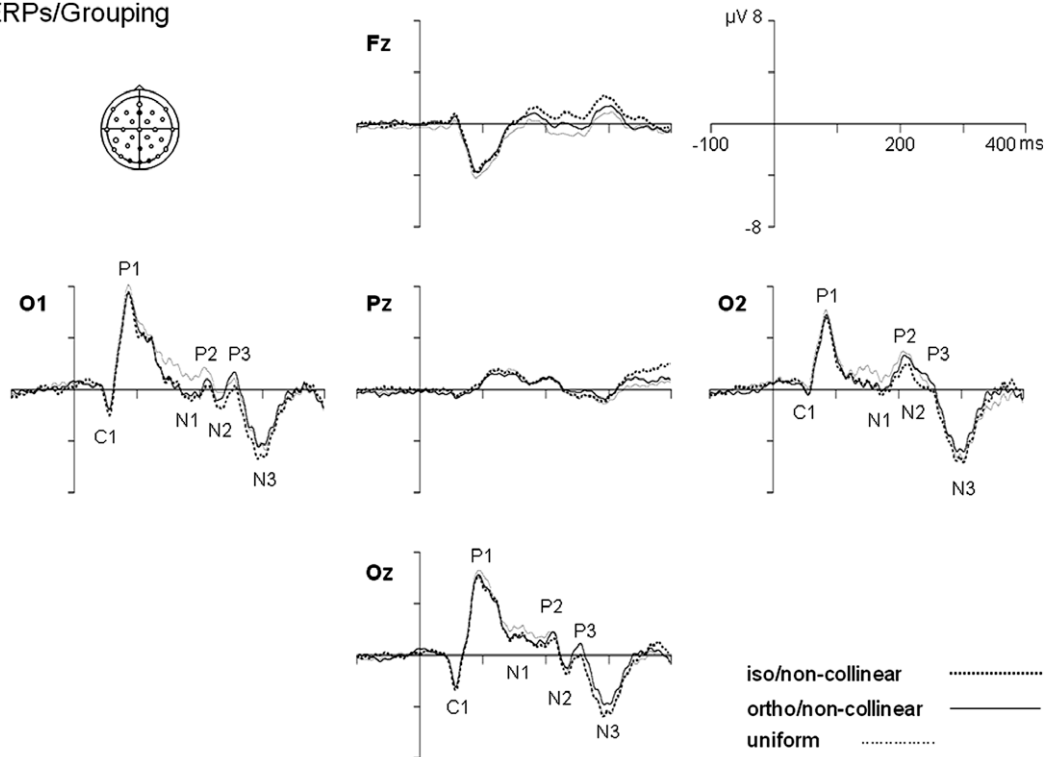
Let first discuss the effect of collinearity, that consists in a similar increased accuracy in the two tasks. Although collinear facilitation is usually found with low contrast stimuli, Polat and Bonneh (2000) also found it at high contrast levels, using a contrast detection threshold paradigm. The collinearity effect on ERPs consists in opposite polarity deflection with respect to uniform in the two tasks. In grouping, a shift of polarity towards positive values for D-waves between 40 and 179 ms is observed, an effect associated to facilitation of grouping by collinearity. This result agrees with the results of Khoe et al. (2004) showing an ERP correlate of the configurational effect by the flanks in a contrast discrimination task with relatively high contrast target without background; a positive polarity response in collinear condition at occipital electrodes with latencies longer than ours was observed, which had a scalp topology consistent with V1 source. In segmentation, the collinearity effect resulted in an later increased amplitude of negative D-waves peaking between 75 and 261 ms and this agrees with our previous findings (Casco et al., 2004; Casco et al., 2005). These components – reflecting segmentation (Bach & Meigen, 1992; Caputo & Casco, 1999; Casco et al., 2004, 2005) – are larger in the non-collinear than in the uniform condition and larger in the collinear than in the non-collinear, resulting in the largest negative D-waves in the collinear condition.

These data can be explained on the basis of neurophysiological and psychophysical findings. Neurophysiological studies suggest that these task-dependent configurational effects of collinearity may result from the modulation of the response in V1 to stimuli presented within the RF by stimuli outside the RF (Kapadia et al., 1995; Polat et al., 1998). Probably subserved by facilitatory short- and long-range lateral interactions, these “contextual influences” by collinear iso-oriented stimuli outside the RF facilitate the response inside (Kapadia et al., 1995; Polat, 1999; Polat et al., 1998); this has been put forward as the explanation underlying contour integration (grouping) and perceptual saliency (Gilbert, Ito, Kapadia, & Westheimer, 2000; Li et al., 2006). Data from Polat et al. (1998) support the suggestion that facilitatory interactions – although more common at low contrast – are also present at relatively high contrast for 1/5 of the cells with relatively high contrast threshold.

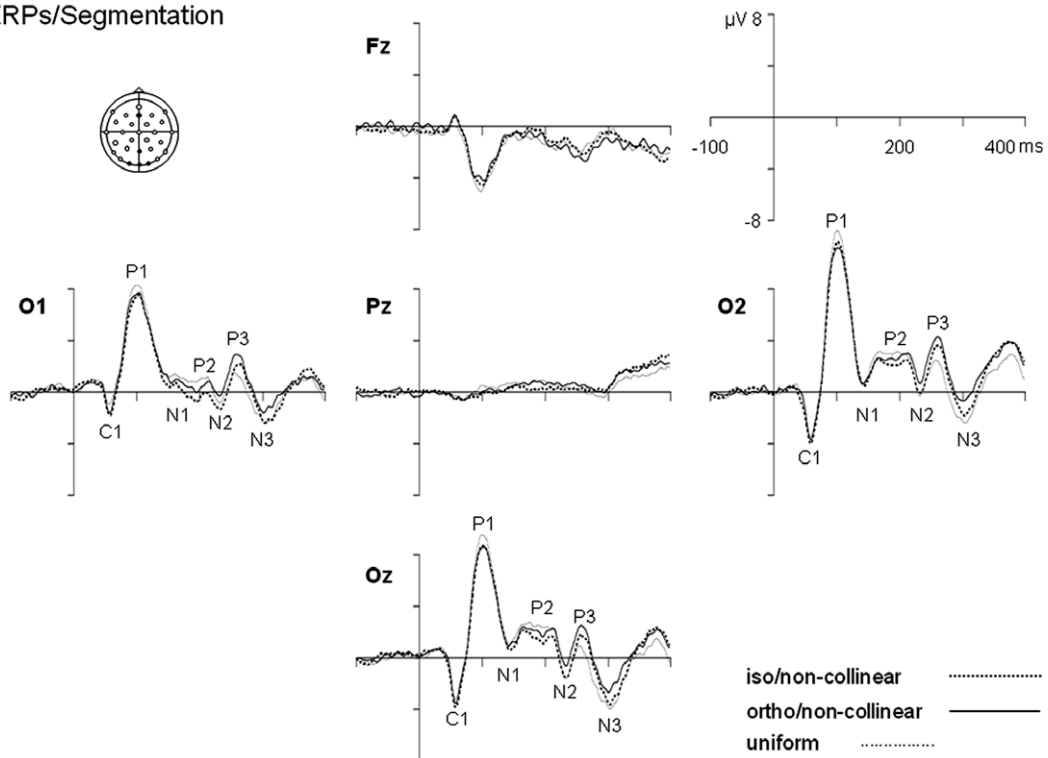
Likely mediated by short-range inhibitory connections (Das & Gilbert, 1999), contextual iso-oriented elements produce suppression. Orientation contrast reduced this surround suppression, and several authors (Akasaki, Sato, Yoshimura, Ozeki, & Shimegi, 2002; Kastner et al., 1997; Knierim & van Essen, 1992; Lamme, 1995) have suggested that the differential expression of the suppressive surround due to the presence of orientation contrast between elements in the classical and non-classical receptive field might be the neuronal correlate of pop-out in the primary visual cortex. Collinearity may further reduce background-to-target surround suppression in Experiment 1. The effect of collinearity can be interpreted as reflecting a further disinhibitory mechanism (Walker, Ohzawa, & Freeman, 2002) that, together with feature contrast, contribute negatively to surround suppression by reducing it.

In sum, the specific layout of the surrounding features, orientation similarity, proximity and collinearity (Kapadia et al., 1995; Li & Gilbert, 2002; Polat et al., 1998) is important in determining the relative strength of these so-called “contextual influences”. Collinearity and iso-orientation in the uniform texture engage these excitatory and suppressive mechanisms, and the balance between these facilitatory and suppressive effects changes in the

## a ERPs/Grouping



## b ERPs/Segmentation



**Fig. 7.** Results of Experiment 2. Grand average event-related potentials (ERPs), in grouping (a) and segmentation tasks (b), associated to iso/non-collinear (dotted line), ortho/non-collinear (fine black line) and uniform (fine dotted line) configurations.

target region where elements have a different orientation. Indeed, although the distance between Gabors does not vary with orientation since it is determined by the center-to-center separation between them, collinear Gabors are perceived as “closer” than orthogonal Gabors and this phenomenon is due to the interaction between their “association field” projections (Field et al., 1993).

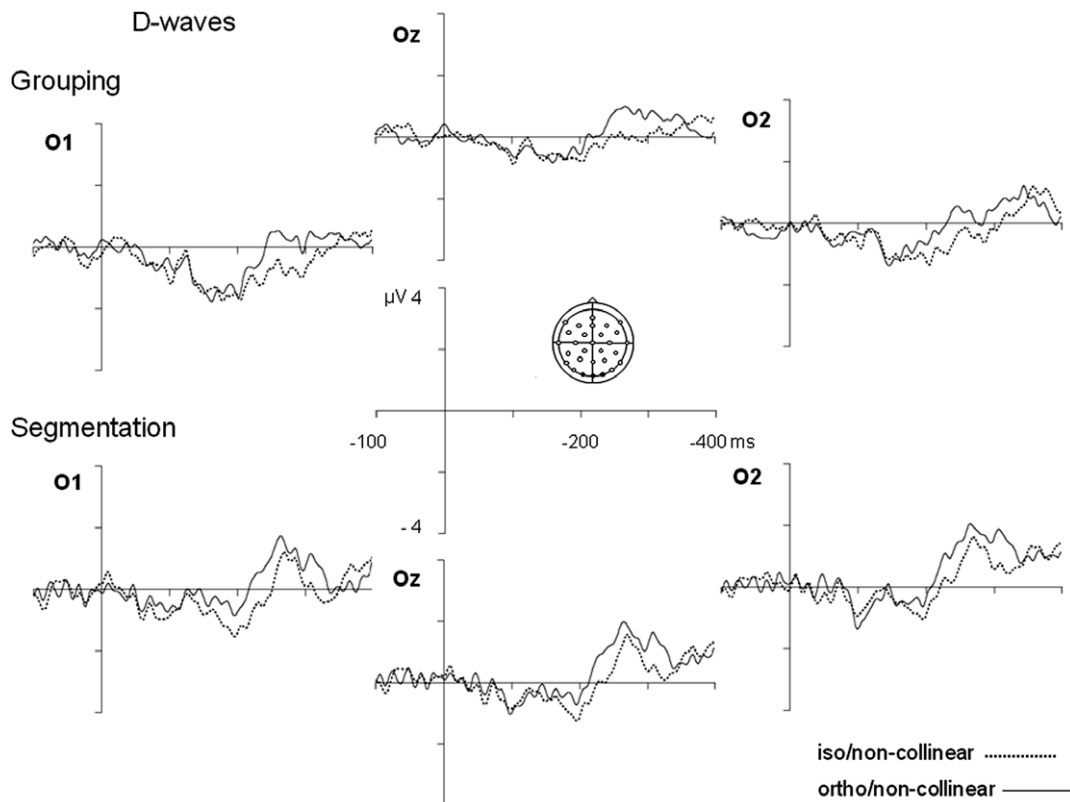
Our data suggest that this change of balance leads to increased saliency (Li et al., 2006) via different, task-dependent, mechanisms: a larger facilitation by collinearity in grouping, having as correlate a shift of ERP towards positive values in the iso/collinear with respect to non-collinear and to uniform; and a reduced background-to-target surround suppression by collinearity in segmen-



**Table 2**

ERPs amplitude in the two tasks for iso/non-collinear (i/n-c), ortho/non-collinear (o/n-c) and uniform (u) configurations (Experiment 2).

		Grouping			Segmentation		
		i/n-c	o/n-c	u	i/n-c	o/n-c	u
C1	Oz	-2.7	-2.3	-2.2	-4.3	-3.9	-3.2
	O1	-2.3	-1.9	-2	-2.0	-1.8	-1.0
	O2	-0.3	-0.6	0.2	-4.5	-4.0	-3.9
P1	Oz	5.7	6.1	6.5	9.0	8.8	9.2
	O1	7.4	7.5	7.9	7.8	8.0	8.2
	O2	5.4	5.8	6	12.6	11.8	13.4
N1	Oz	0.6	0.4	1.1	0.6	1.1	1.0
	O1	-1.9	-1.3	1	-1.0	-0.2	1.5
	O2	0.3	0.0	1.1	0.6	0.8	0.5
P2	Oz	1.0	1.5	1.6	1.8	2.3	2.3
	O1	0.1	0.3	1.3	-0.2	0.9	1.1
	O2	2.6	2.7	3	2.3	2.5	2.9
N2	Oz	-1.9	-1.2	-1.3	-1.9	-0.9	-1.5
	O1	-2.0	-1.2	-0.6	-1.6	-0.5	-0.9
	O2	-0.6	0.0	0.8	-0.2	0.5	-0.1
P3	Oz	0.0	1.0	0.1	2.0	3.0	1.0
	O1	0.1	1.1	0.5	2.5	3.5	1.8
	O2	0.3	0.8	0.5	3.9	4.4	2.4
N3	Oz	-4.6	-4.0	-5	-3.4	-2.4	-4.1
	O1	-6.0	-4.9	-5	-2.3	-1.3	-2.9
	O2	-5.3	-4.8	-5.0	-1.2	-0.8	-2.4

**Fig. 8.** Results of Experiment 2. D-waves obtained with stimuli iso/non-collinear (dotted line) and ortho/non-collinear (fine black line), in Oz, O1 and O2 for grouping and segmentation tasks. Zero marks stimulus onset.

tation, with ERP correlate a larger ERP negativity with respect to uniform. Angelucci and Bressloff (2006) suggested that the balance between excitation and inhibition around the RF may be modulated by task-driven backward propagations.

We are aware that D-wave modulation alone is not sufficient to support the notion that stimulus configuration effects in ERPs

are due to facilitatory and inhibitory lateral interactions, depending on task. Indeed, there is no basis for associating the sign of a surface potential with the sign of modulation of a specific process, since it is not possible to unambiguously determine whether a given polarity at the scalp reflects EPSP or IPSP. However, the opposite ERP modulation by collinearity in the two

tasks, with no change in stimulus or perception, as we found in Experiment 1, strongly suggests that this difference in the sign of a difference reflects different effect of collinearity: either increased excitatory influences or larger reduction of surround suppression by lateral interactions. In support of the two-mechanisms interpretation is our finding that the ERP correlates of collinear facilitation have shorter latency in grouping than in segmentation.

The effects of similarity are also task-dependent, but differ from those of collinearity. Perturbing similarity, by having flanks orthogonal to the central Gabor in the three-Gabor group, reduced accuracy, and to a greater extent in the global task. This perturbation of similarity affects D-waves at long latencies, producing an increased positivity at 275 ms in both tasks. We interpret these results by suggesting that the presence, in half of trials, of an orthogonal Gabor in the target group biases the attended receptive field towards the size of individual Gabors. This suggestion is supported by the result that the larger positivity at 275 ms for the orthogonal stimulus is not significantly different from that produced by the collinear stimulus in Experiment 1. Indeed, the general ANOVA did not show a significant interaction between Configuration \* Experiment [ $F_{1,20} = .603$ ;  $p = .45$ ]. The bias has different consequences in the two tasks. In segmentation, orientation of central target and flanks conflict and this reduces both accuracy and negativity at 200 ms. In grouping task, that engages larger receptive fields, the reduced size of the attended receptive field hampers even more performance. Comparison between experiments casts revealing light on the question of whether similarity and collinearity between target elements modulate in a similar or different way the efficiency with which texture elements group together, as well as the efficiency with which they segment from background elements presenting orientation contrast with the targets. Our interpretation, supported by the results of the general ANOVA, is that collinearity and similarity produce different effects in grouping and similar effects, having different origin, in segmentation tasks. Indeed, we found a nearly significant Experiment \* Task \* Configuration at 150 ms [ $F_{1,20} = 3.9$ ,  $p = .06$ ], indicating a configurational effect due to collinearity ( $p < .0001$ ) but not to similarity ( $p = .91$ ) in the grouping task. Moreover, the interaction Task \* Configuration for D-waves peaking at 200 ms was significant [ $F_{1,20} = 9.186$ ,  $p < .007$ ] but not the interaction Experiment \* Task \* Configuration [ $F_{1,20} = 1.62$ ,  $p > .05$ ], indicating a configurational effect for segmentation ( $p < .0001$ ) but not for grouping ( $p > .05$ ) in both experiments. This suggests that collinearity and similarity both increase negativity of the segmentation component. Despite this common effect, the associated modulations of other ERPs components is distinct, suggesting different temporal dynamics: early, when due to collinearity, as suggested by the increased positivity at 60 ms, and late (at 275 ms, possibly reflecting reduced interference by ortho-oriented flanks in the discrimination of orientation of the central Gabor top-down) when due to similarity.

## 5. Conclusions

The role of contextual influences in human perception cannot be understood without integrating phenomenological, psychophysical and neurophysiological data into a common interpretative framework. By combining psychophysical and electrophysiological data we have done a step further in understanding the way in which contextual influences may provide the neural bases of figure-ground segmentation in humans.

## Acknowledgments

This work was supported by grants from MIUR to Clara Casco and from a co-operation grant for scientific-technical China–Italy

collaboration (2002–2006). We would like to acknowledge Chiara Sambo for her help in running the experiments.

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