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RESEARCH ARTICLE

Dissociation of early evoked cortical activity in perceptual grouping

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Abstract Perceptual grouping is a multi-stage process, irreducible to a single mechanism localized anatomically or chronometrically. To understand how various grouping mechanisms interact, we combined a phenomenological report paradigm with high-density event-related potential (ERP) measurements, using a 256-channel electrode array. We varied the relative salience of competing perceptual organizations in multi-stable dot lattices and asked observers to report perceived groupings. The ability to discriminate groupings (the grouping sensitivity) was positively correlated with the amplitude of the earliest ERP peak C1 (about 60 ms after stimulus onset) over the middle occipital area. This early activity is believed to reflect spontaneous feed-forward processes preceding perceptual awareness. Grouping sensitivity was negatively correlated with the amplitude of the next peak P1 (about 110 ms), which is believed to reflect lateral and feedback interactions associated with perceptual awareness and attention. This dissociation between C1 and P1 activity implies that the recruitment of fast, spontaneous mechanisms for grouping leads to high grouping sensitivity. Observers who fail to recruit these mechanisms are trying to compensate by using later mechanisms, which depend less on stimulus properties such as proximity.

Keywords Perceptual organization · Grouping · Dot lattices · Event-related potentials (ERP)

Introduction

Visual perceptual organization is a process that enables us to experience surfaces and objects as distinct perceptual entities. Gestalt psychologists argued that perceptual organization is a spontaneous process because these experiences emerge without conscious effort (e.g., Wertheimer 1923; Köhler 1947). Others have added that perceptual organization must be a basic process because it is a precondition for our ability to recognize familiar entities, such as trees, animals, or houses (e.g., Neisser 1967; Marr 1982; reviewed by Palmer 1999). On this view, perceptual organization must occur early in the cascade of visual processes.

On the other hand, perceptual organization has certain characteristics that are not typical of early vision. Despite its apparently spontaneous character, we can exert some degree of control over this process. How a figure is perceptually organized often depends on the task (Stins and van Leeuwen 1993), the amount of practice (van Leeuwen et al. 1988) or individual style (Hogeboom and van Leeuwen 1997). To a

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certain degree we can voluntarily control switching between the alternative organizations of ambiguous figures (Attneave 1971; Kubovy 1994; Leopold and Logothetis 1999). These and other (e.g., Rock 1983; Palmer et al. 2003) arguments suggest that perceptual organization is a multistage process, irreducible to a single mechanism that can be pinned down anatomically or chronometrically.

Animal studies suggest that a distinction between stages of perceptual organization should be made according to the distinction between feedforward and recurrent neural mechanisms (reviewed by Watt and Phillips 2000; Roelfsema 2006). The former are responsible for fast, inflexible, mandatory processing of visual information, using “classical” receptive fields tuned to simple features, such as spatial frequency and orientation of contours and edges, and feature conjunctions (Felleman and Van Essen 1991). The latter operate more slowly and flexibly, mediated by horizontal (in the same neuronal layer) and feedback (from the higher levels) cortical connections. The feedforward mechanisms enable the pre-attentive processing that genuinely belongs to the domain of “early vision” and the recurrent mechanisms mediate top–down modulatory influences, associated with endogenous attention and perceptual awareness. Evidence of recurrent processing includes interactions of oriented contour segments through local association fields (Kapadia et al. 1995; Polat et al. 1998; Bauer and Heinze 2002) and sequential activation of, first, V2 neurons and, later, V1 neurons in perception of illusory contours (Lee and Nguyen 2001).

In *human perception*, it is more difficult to distinguish feedforward and recurrent processes since only non-invasive methods are available. The high temporal resolution of the non-invasive EEG and MEG allows one to evaluate chronometry of cortical processes. Chronometric studies of early perceptual processes using event-related potentials (ERP) suggested a temporal “watershed” at about 90–100 ms after stimulus onset between the processes dominated by feedforward and recurrent mechanisms. For example, Murray et al. (2002) studied perception of illusory contours and identified the ERP at about 66 ms after stimulus onset, over the central parietal-occipital area, that was correlated with stimulus configuration but was unrelated to the experience of illusory contours. A later ERP modulation at 88–100 ms after stimulus onset, over the “higher-tier visual areas” (lateral occipital cortex), was associated with the experience of illusory contours. The authors suggested that the early activity triggered a feedback activation of visual areas V1 and V2. For another example, Khoe et al. (2004) used ERP analysis to study interactions between oriented visual stimuli. Such interactions are thought to depend on local associations fields (Kapadia et al. 1995; Polat et al. 1998). Khoe et al. (2004) observed these interactions in ERP at about 100 ms after stimulus onset, a latency similar to the one reported by Murray et al. (2002). Further evidence supporting the distinction between feedforward and recurrent processes comes from studies of decidedly high-level influences on perception, such as the mechanisms of “spatial attention,” which is deployed faster than “non-spatial attention” or “object-oriented attention” (Hillyard et al. 1998). Spatial attention is associated with feedback to area V1 from extrastriate areas (Di Russo et al. 2003). Numerous ERP studies (reviewed by Hillyard et al. 1998) showed that spatial attention affects ERP components not earlier than about 90 ms after stimulus onset. The earliest ERP component C1—which peaks at 60–90 ms after stimulus onset—is not affected by attention (Clark et al. 1995; Martinez et al. 1999; Di Russo et al. 2003), although the later portion of this component may reflect contributions from visual areas other than V1 (Foxe and Simpson 2002).

In the present work we investigated the time course of visual grouping by proximity, which is a classical Gestalt factor of perceptual organization (Wertheimer 1912; Koffka 1935/1963). To our knowledge, the only published works that used ERP analysis to study early processes in perceptual grouping[1] were performed by Han and coworkers (Han et al. 2001, 2005). These authors reported that positive ERP activity about 100 ms after stimulus onset (“Pd100” in terms of Han et al.) reflected grouping by proximity. Since the authors did not vary the strength of grouping within observers, and did not record reports of grouping, their study does not allow one to draw conclusions about the different stages involved in grouping (see “Discussion”).

In the present work we combined the advantages of two methods: ERP analysis and a phenomenological report paradigm with multistable dot lattices. The phenomenological report paradigm is a sensitive tool for measuring the strength of perceptual grouping by proximity (Kubovy et al. 1998; Gepshtein and Kubovy 2005). A systematic manipulation of proximity between the dots and a randomization of stimulus orientation allowed us to separate the effect of grouping strength from other factors that affect grouping. We measured observer sensitivity to changes in proximity and found that the sensitivity was associated with two early peaks of cortical activity: C1 (about 60 ms after stimulus onset) and P1 (about 110 ms after stimulus onset). We also found that neural processes associated with these two peaks play different roles in perceptual grouping. The greater was C1 activity the higher was grouping sensitivity. In contrast, the higher was P1 activity the lower was grouping sensitivity.

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[1] Studies of high-frequency gamma oscillations that are often associated with visual grouping concern later processes, more than 200 ms after stimulus onset (Muller et al. 1996; Tallon-Baudry et al. 1996; Keil et al. 1999; Vidal et al. 2006).

Materials and methods

Observers

Seventeen healthy observers (ages 19–36, median age 22, 9 women) took part in the experiment. All the observers were right-handed and had normal or corrected-to-normal vision. All the observers but one (one of the authors) were unaware of the purpose and design of the experiment. All the observers gave informed consent. RIKEN BSI Institutional Review Board No. 2 (Research Ethics Committee) had approved this study.

Stimuli

We used multistable dot lattices, each of which appears to be grouped into strips of dots (Kubovy 1994). In Fig. 1A the four most likely organizations are labeled **a**, **b**, **c**, and **d**. The inter-dot distances increase from **a** to **d**. (We will refer to the reports of seeing the corresponding organizations as *a*, *b*, *c*, and *d*.) The shorter the distance between the dots in one of the directions, the more likely the dots group along that direction. According to the pure-distance law (Kubovy et al. 1998), the perceived organization of a dot lattice depends on its aspect ratio (AR), which is the ratio of the two shortest inter-dot distances, along **a** and **b**. We used four different values of AR: 1.0, 1.1, 1.2, and 1.3 (Fig. 1B). The lattices were presented at four different orientations, in which the orientation of **a** was rotated counterclockwise from the horizontal for 22.5°, 67.5°, 112.5°, or 157.5°. The 4 aspect ratios and 4 orientations yielded 16 different stimuli.

The diameter of the dots was 0.2° of visual angle. Their luminance was modulated by a bivariate isotropic Gaussian distribution whose maximum was at the center of the lattice (as illustrated in Fig. 1), such that the dots were visible across a circular area with an approximate diameter of 6.9° of visual angle. The distances between dot centers at AR = 1.0 were 0.6° of visual angle. The background luminance was 108 cd/m^2. The largest Weber contrast was 40% for dots at the center of the lattice. The manipulation

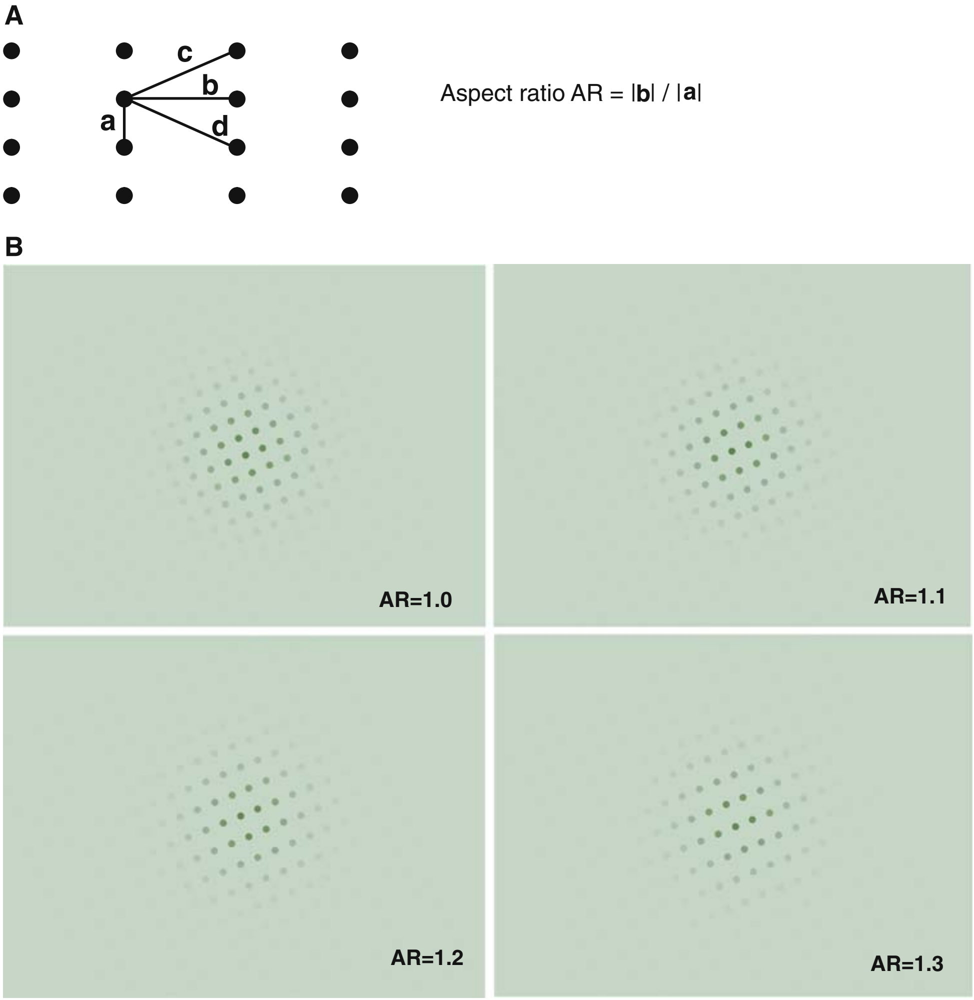

Fig. 1 Dot lattices. The dots appear to group into strips. **A** The four most likely groupings are labeled **a**, **b**, **c**, and **d**, with the inter-dot distance increasing from **a** to **d**. Perception of lattices depends on their aspect ratio (*AR*), which is the ratio of two shortest inter-dot distances: along **a** (the shortest) and **b**. When AR = 1.0, the organizations parallel to *a* and *b* are equally likely. When AR > 1.0, the organization parallel to *a* is more likely than the organization parallel to *b*. These phenomena are manifestations of grouping by proximity. **B** Dot lattices of four aspect ratios. The lattices are shown in the same orientation

of aspect ratio caused small changes in lattice dot density. As a result, the average luminance of lattices at AR = 1.3 was larger than at AR = 1.0 by a factor of 1.25.[2]

Procedure

Observers sat 1.15 m from the screen in a dimly lit room. The stimuli were presented on a 17 in. CRT display (Eizo FlexScan T566) with an 85 Hz (non-interlaced) refresh rate using E-Prime software.

Each trial consisted of four intervals: fixation, stimulus, blank screen, and response screen. During the fixation, observers were instructed to look at a small circle (0.2° in diameter) presented at the center of an otherwise empty screen for a duration that varied randomly according to a uniform distribution on the interval of 1,200–1,500 ms. The duration of the stimulus interval and the blank-screen interval were both fixed at 300 ms. A response screen was presented until a response was received.

The observers' task was to report the orientation of the perceived grouping. They responded by choosing one of four alternatives on a response screen. This screen consisted of four circles ("response icons"), each containing a line tracing a diameter parallel to one of the four likely organizations (*a*, *b*, *c*, or *d*) of the just-presented lattice. The response alternatives were located in the four quadrants of the response screen; their locations were assigned randomly for each trial. Observers responded using a rolling-ball device, by clicking on one of the response icons. (The cursor was visible only during the response interval.) Because sometimes the perceived grouping switched while the stimulus was on, we asked observers to report the first orientation they perceived after stimulus onset. We explained to them that the task had no correct or incorrect answers.

The inter-trial interval varied randomly according to a uniform distribution from 1,000 to 2,000 ms. Each observer practiced the task in a block of 20 trials before the experiment started. Within each experimental block of trials, each of the 16 conditions was presented 10 times in a random order. Four such blocks were presented during an experiment (640 trials in total), which on average took about 1 h including three short (2–5 min) breaks between the blocks.

Electrophysiological recordings

EEG was recorded using a 256-channel Geodesic Sensor Net (Electrical Geodesics Inc., Eugene, OR). The electrode montage included sensors for recording vertical and horizontal electro-oculograms (EOGs). Data were digitized at 250 Hz. All channels were referenced to the vertex electrode (Cz). Impedance was kept below 50 kΩ. All channels were preprocessed on-line using 0.1 Hz high-pass and 100 Hz low-pass filtering.

ERP analysis

We analyzed the ERP data off-line as follows. We filtered the EEG signal using a wide-band 0.3–25 Hz filter. The data were segmented into epochs 500 ms long: 100 ms before and 400 ms after stimulus onset.

We segmented ERP data two ways: by stimulus parameters and observer responses. In the stimulus-based segmentation, we selected parameters independent of observer responses. The parameters were 4 aspect ratios and 4 orientations, yielding 16 conditions. In the response-based segmentation we examined how evoked activity was related to phenomenological reports by observers.[3] Among the four response categories: *a*, *b*, *c*, and *d*, the two less likely ones (*c* and *d*) were reported with frequency insufficient for ERP analysis. We did not include these categories into the response-based analysis. For aspect ratio 1.0, responses *a* and *b* were equally probable, so this aspect ratio was also excluded from analysis. To assure that the amplitudes of average ERP signals were comparable across conditions, we equated the number of trials[4] across conditions as follows. The smallest number of trials was obtained for response *b*. We reduced the number of trials in the response *a* to that number by randomly deleting trials (separately for each observer). Further steps of data analysis were identical in the stimulus-based and response-based segmentations.

We ran an automatic artifact detection procedure using the recording reference Cz. We identified the channels contaminated by artifacts with a threshold for fast transit amplitude changes at 50 μV and a threshold for

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[2] It was shown that increase in stimulus luminance increases the amplitudes of each of the early ERP peaks: C1, P1, and N1 (Johannes et al. 1995). The ERP modulation in Johannes et al. study was found when luminance was changed by a factor of nearly 40. As we show below, we found that the changes in lattice aspect ratio caused changes in the amplitudes of peaks C1 and P1 in different directions on different peaks. This means that the changes in peak amplitudes in response to the manipulation of aspect ratio were not driven by the small changes in lattice luminance.

[3] In both stimulus- and response-based analyses we segmented data relative to stimulus onset.

[4] The relationship between number of single trials and amplitude of the resulted averaged ERP is not linear, so it is impossible to calculate a normalization factor.

differential average amplitude changes at 30 µV. A channel was marked as "bad" in the whole data set if its amplitude exceeded the above thresholds in more than 20% of all segments. A segment was marked as "bad" and excluded from analysis if it contained more than five "bad" channels, in addition to the channels marked "bad" in the whole data set. Data from two observers who had more than 33% artifact segments were excluded from further analysis. In the remaining observers we excluded 9.6% segments, yielding 36.2 ± 1.6 segments per condition in stimulus-based segmentation, and 69.2 ± 26.7 segments per response type in the response-based segmentation.[5] In the remaining segments, the "bad" channels were replaced using spherical spline interpolation across the whole channel set (Perrin et al. 1989). Of the 256 channels, 4.6 ± 2.3 channels were interpolated on average; none of them were in the areas selected for further analysis (see below). Single trials were averaged separately for each observer and each condition. At each moment a spatial average of the signal was calculated and subtracted from each channel to obtain the average-referenced data. The mean of a 100-ms baseline interval prior to stimulus onset was subtracted from every sample in the segment.

Because we were interested in early perceptual processes, we analyzed only the early ERP peaks in posterior areas: C1, P1, and N1, with latencies about 60, 100, and 200 ms, respectively. We measured peak values of amplitudes, since early ERP peaks are typically sharp, and since we had approximately equal number of trials per conditions, as recommended by Picton et al. (2000).

C1 is considered the earliest evoked response of the primary visual cortex; it is usually registered in the central occipital area 45–100 ms after stimulus presentation. An identifying feature of C1 is its polarity: it depends on the hemifield to which the stimulus is presented (Clark et al. 1995; Di Russo et al. 2002). We could not test the polarity of the peak found at 60–90 ms in the middle occipital area because the stimuli were presented at the fixation. Nevertheless, because of its latency and topography we will refer to this peak as C1. This peak was of particular interest to us because of the previous evidence that the evoked activity at this latency can be modulated by perceptual grouping (Nikolaev and van Leeuwen 2004; Wu et al. 2005).

We calculated a grand average across all observers. On the grand-average maps we located areas of voltage maxima (or minima) in the following time windows: 60–90 ms for C1, 100–150 ms for P1, and 170–220 ms for N1. We selected groups of adjacent channels, in which peak values were within 0.3 µV from the maximal or minimal values. These channels are outlined in Fig. 2D. Next, we searched for the peak amplitude values in the individual data, within the above-mentioned time windows. Time windows were initially centered on the grand-average peaks C1, P1, and N1. If a window did not include the peak value, we shifted the window (up to 20–30 ms) to accommodate the individual difference.

For statistical comparison of peak amplitudes between conditions, we used repeated-measures and mixed effects ANOVAs, and adjusted the *P*-values using the Huynh–Feldt correction for repeated-measures factors with more than two levels. We estimated a gradual character of the effects using post-hoc trend analyses with contrast coefficients set across the factors that showed significant effects. For topographical analysis of early evoked activity in the parieto-occipital areas we selected an array of 28 electrodes (marked green in Fig. 2D). The array included four chains (or rows) and seven columns of electrodes. The array overlapped with the areas previously selected on the grand-average maps for the peaks of interest (outlined in Fig. 2 D). The amplitudes of peaks under these electrodes were subjected to a repeated-measures ANOVA with the following factors: the sagittal plane (4 levels = 4 chains in front–back direction) and the frontal plane (7 levels in left–right direction). We used the Tukey HSD test for the post-hoc analyses.

Results

Behavioral results

In Fig. 3A we plot log-odds of responses versus lattice aspect ratios for 13 observers. The definition of log-odds L is

$$L = \log\{[N(\sim a) + 1/6]/[N(a) + 1/6]\},$$

where $N(a)$ is the number of reports of grouping along **a**, and $N(\sim a)$ is the number of other reports (i.e., grouping along **b**, **c**, and **d**) (Kubovy et al. 1998). The thick lines represent linear fits to the data. The slope of the fit for every observer (indicated in the top right corner of each panel) is called *attraction coefficient*. It is a measure of observer's ability in performing the grouping task. We call this ability *grouping sensitivity*. We quantify grouping sensitivity using the absolute value of the attraction coefficient: The higher the magnitude of this measure the more observer responses are controlled by the proximity of dots in the stimulus. The lower the

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[5] In a pilot experiment we determined the number of trials to be used in this study, to achieve a tradeoff between the statistical power needed for measuring changes in peak amplitudes, on the one hand, and the number of stimulus conditions, on the other.

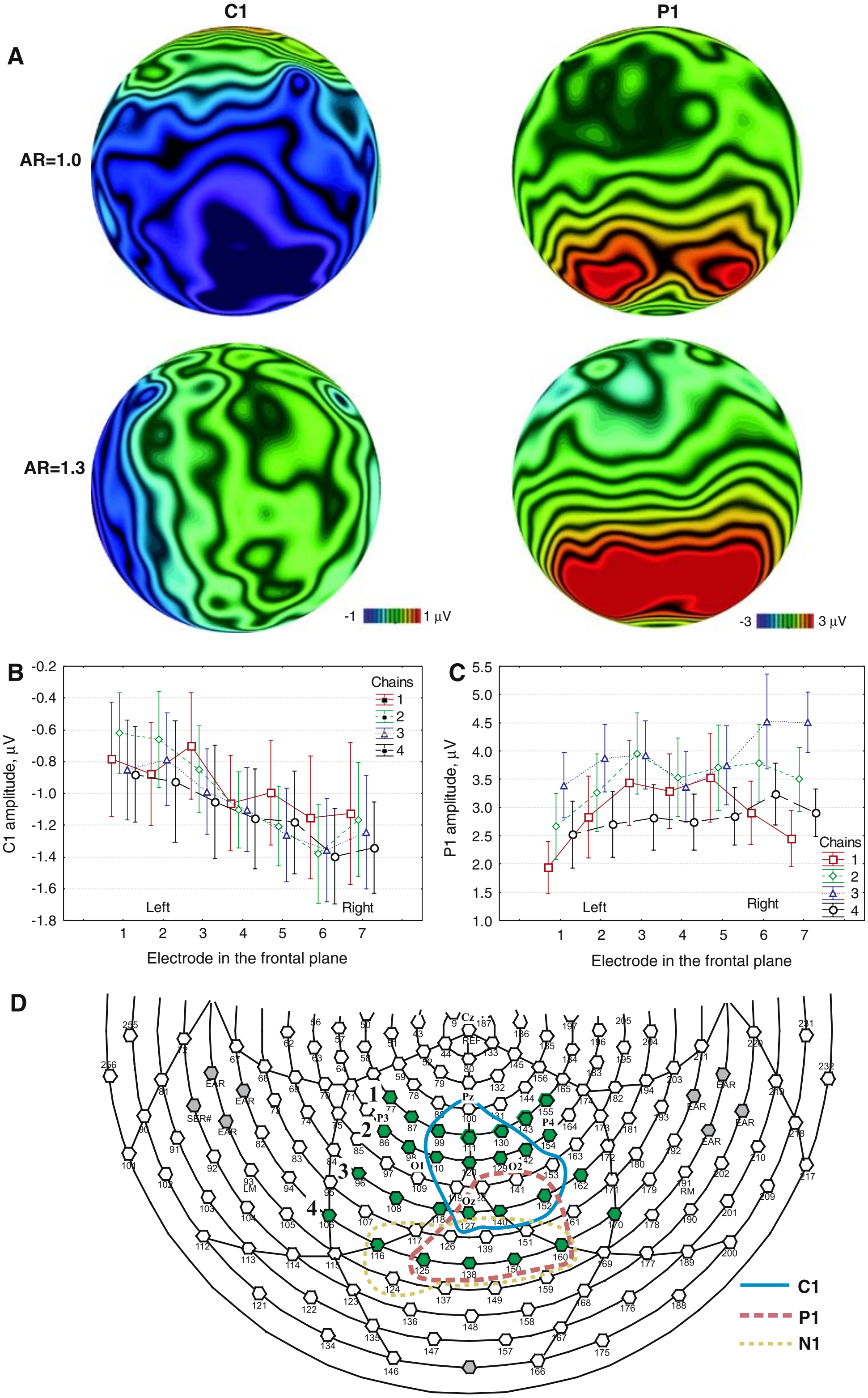

Fig. 2 Topographical distribution of the C1 and P1 activity. **A** Grand-average voltage maps for peaks C1 and P1 at the latency of maximum (or minimum) amplitude for aspect ratios 1.0 and 1.3 (head front is up.) The bottom of the maps corresponds to the electrode chain 4 in **D**. **B** Mean-error plots of C1 amplitude for aspect ratio 1.0, orientation 157.5° in the high-sensitivity group. The amplitudes are shown for 28 channels organized into 4 chains of 7 electrodes, *colored green* in **D**. Numbers on the abscissa correspond to the ordinal numbers of electrodes within each chain, from *left* to *right* in the frontal plane. **C** Mean-error plots of P1 amplitude for aspect ratio 1.3, orientation 112.5° in all observers, for the same 28 channels. **D** Posterior half of the 256 channel Geodesic Sensor Net. Some of the landmark electrodes that correspond to the International 10–20 system of Electrode Placement are labeled in bold (O1, P3, etc.). The electrodes selected for the between-condition statistical analysis of peaks C1, P1, and N1 are outlined. We mark in *green* the four chains of seven electrodes each, used for the topographical analysis of C1 and P1 activity

magnitude the more observer responses depend on other factors, such as individual biases, expectations and attention.

We excluded two observers from the analysis because they were unable to perform the task adequately (as indicated by near-zero grouping sensitivity). We divided the

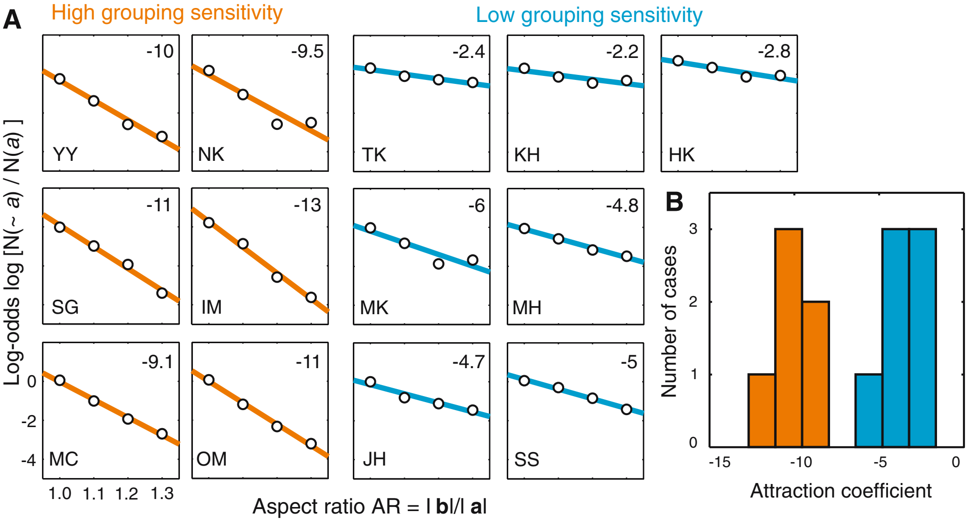

Fig. 3 Grouping sensitivity. **A** The log-odds of responses vs. lattice aspect ratios for each observer. The *thick lines* represent linear fits to the data. The slopes of fits (called attraction coefficients, indicated in the top right corner of each panel) represent observer's grouping sensitivity: the higher the slope the higher the sensitivity. **B** The histogram of attraction coefficients for 13 observers. By the attraction coefficients, observers naturally separate to two groups: a high-sensitivity one and a low-sensitivity one. We use absolute values of attraction coefficients to quantify grouping sensitivity

remaining 13 observers into two groups: the "high sensitivity" group consisted of 6 observers (grouping sensitivity greater than 9) and the "low sensitivity" group of the remaining seven observers (Fig. 3B).[6]

ERP results

Segmentation by stimulus parameters

Our first analysis was based on stimulus parameters. We examined the amplitudes of three earliest ERP peaks (C1, P1, and N1) across aspect ratios and orientations: in the group of all observers, and separately in the groups of low and high grouping sensitivity.

Peak C1

The negative peak C1 (latency 55 ms, SEM 1.2 ms) was prominent in the middle occipital electrodes, slightly shifted to the right. A repeated-measures ANOVA of the amplitude of this peak (factors Aspect Ratio with 4 levels and Orientation with 4 levels) failed to reveal significant effects in the group of all observers [effect of aspect ratio: $F(3, 36) = 0.9$; effect of orientation $F(3, 36) = 0.9$]. In the high-sensitivity group, however, the ANOVA revealed an effect of aspect ratio [$F(3, 15) = 4.3$, $P < 0.05$, $\varepsilon = 0.84$] (Fig. 4A, C)[7]. We also observed a weak effect of orientation [$F(3, 15) = 3.0$, $P = 0.09$, $\varepsilon = 0.71$] (Fig. 5A, C). The interaction was not significant. In the low-sensitivity group, we found neither effects nor an interaction [aspect ratio: $F(3, 18) = 0.7$; orientation: $F(3, 18) = 0.09$] (Figs. 4B, D, 5B, D).

To ascertain that the effect holds in the group of all observers, we did an additional analysis. In a mixed-effects ANOVA (Maxwell and Delaney 2004, Chap. 12), we disregarded the effect of orientation in order to get more power to look at the effect of aspect ratio. We found that across all observers only aspect ratio had a significant effect on amplitude [aspect ratio: $F(1, 12) = 7.9$, $P < 0.05$; orientation: $F(3, 36) = 0.9$; interaction: $F(3, 36) = 0.4$]. The slope of effect of aspect ratio in this restricted model was 0.86. Then we split the data between the high-sensitivity and low-sensitivity observers and found that the slope of this effect was significant for the high-sensitivity observers: 1.29 [$F(1, 5) = 7.0$, $P < 0.05$] and non-significant for the low-sensitivity ones: 0.5 [$F(1, 6) = 1.8$, $P = 0.22$].

To validate our division of observers to groups by their sensitivity, we performed a resampling analysis of dividing

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[6] An alternative method of calculating attraction coefficients, using only responses *a* and *b*, produced similar values of attraction coefficients (Supplementary Table 1) and led to the same division of observers to two groups as the method presented in the text. In the alternative method $L = \log\{[N(b) + 1/6]/[N(a) + 1/6]\}$. We chose the method that took into account responses *c* and *d*, because it allowed us to use a larger number of trials in the analyses of ERP.

[7] The values of mean-error plots do not exactly correspond to the values of the ERP curves, because the plotted values are averaged over groups of channels (used in the statistical analysis), whereas the ERP curves correspond each to a representative channel from the group.

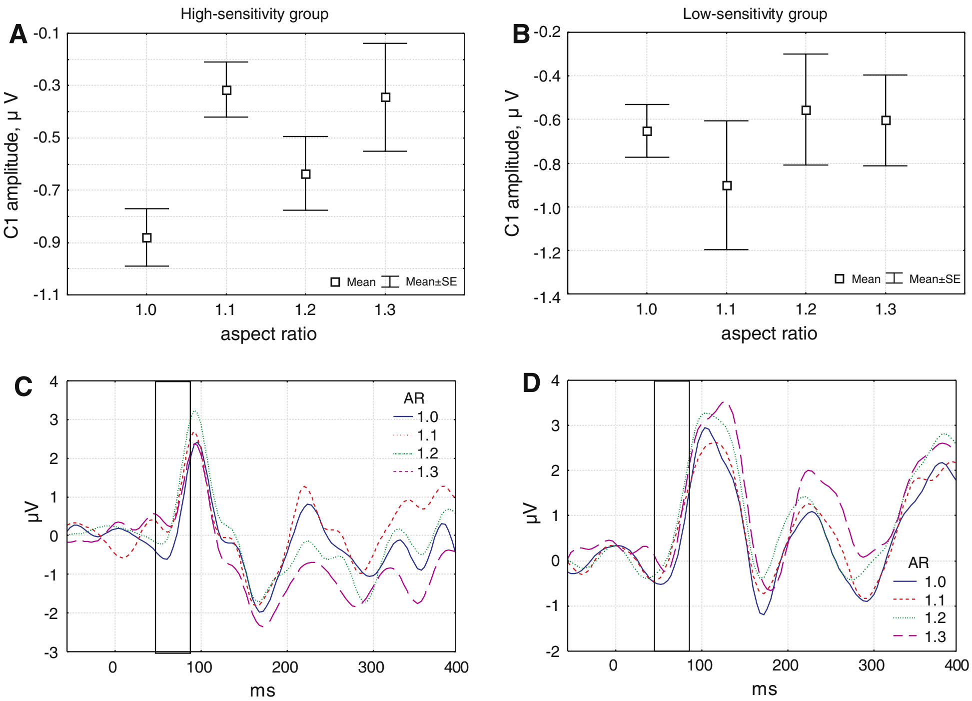

Fig. 4 Effect of aspect ratio on peak C1. **A**, **B** Mean-error plots of C1 amplitude across aspect ratios in the high-sensitivity **A** and low-sensitivity **B** groups of observers, for the group of channels used in the statistical analysis. **C**, **D** Grand-average ERPs in the representative channel 141 from the right occipital areas for the high-sensitivity **C** and low-sensitivity **D** groups, for aspect ratios 1.0–1.3. The *vertical lines* mark the boundaries of the temporal windows we used to extract the peak amplitudes for statistical analyses

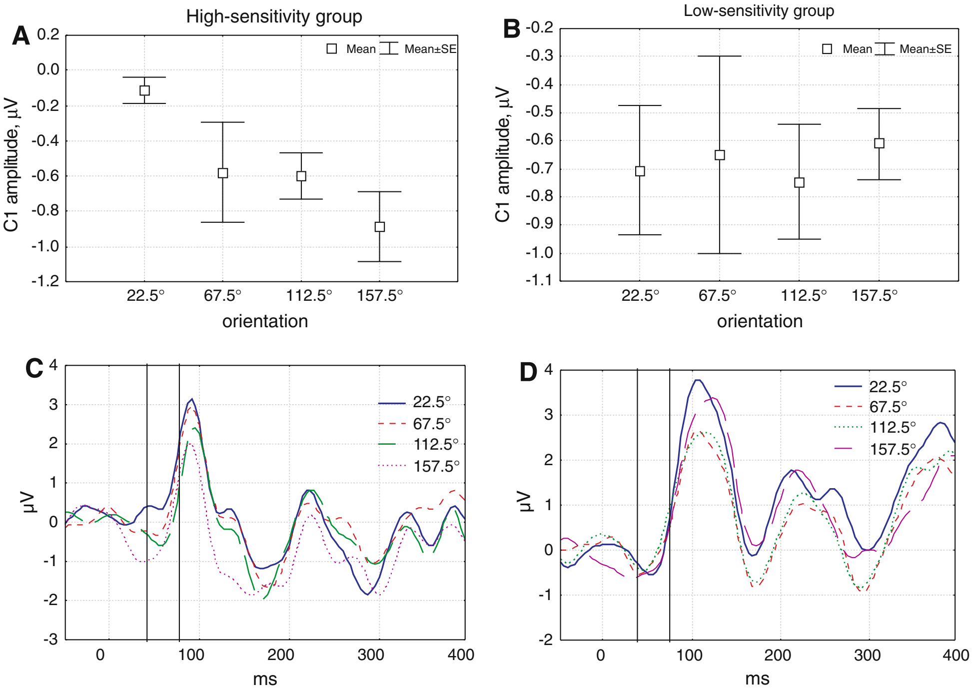

Fig. 5 Effect of orientation on peak C1. **A**, **B** Mean-error plots of C1 amplitude across lattice orientations in the high-sensitivity **A** and low-sensitivity **B** groups, for the group of channels used in the statistical analysis. The gradual changes of peak amplitude with orientation are evident only in the high-sensitivity group. **C**, **D** Grand-average ERPs in the representative channel 141 from the right occipital areas for the high-sensitivity **C** and low-sensitivity **D** groups for the four lattice orientations. The *vertical lines mark* the boundaries of the temporal windows we used to extract the peak amplitudes for statistical analyses

13 observers to the groups of 6 and 7. There are 13!/(6! 7!) = 1,716 combinations of selecting 6 observers out of 13. We repeated the 4 × 4 ANOVA for each combination and obtained the *F*-value for the effect of aspect ratio in every case. The *F*-value we obtained in the high-sensitivity group was the 99th percentile of the resampled *F* distribution. It is, therefore, unlikely that our division of observers to groups was accidental.

Figures 4A and 5A, C suggest that the peak amplitude changes gradually with aspect ratio and orientation. To evaluate this effect we conducted post-hoc trend analysis, using contrast coefficients across the levels of tested factors: aspect ratio and orientation. In the high-sensitivity group we found a significant linear trend across all aspect ratios [$F(1, 5) = 7.0$, $P < 0.05$] and orientations [$F(1, 5) = 9.6$, $P < 0.05$].

To evaluate the scalp distribution of C1 activity, we conducted a topographical analysis in the high-sensitivity group by selecting a condition with maximal C1 amplitude;[8] this condition was at aspect ratio 1.0 and orientation 157.5°. We explored the amplitude of C1 peak in the 4 × 7 array of electrodes placed over the parieto-occipital area (Fig. 2D).[9] A repeated-measures ANOVA (4 × 7) with factors sagittal plane (the 4 levels were the 4 chains of electrodes in front-to-back direction) and frontal plane (7 levels were the 4 chains of electrodes in left-to-right direction) revealed a significant effect of the frontal plane [$F(6, 30) = 3.2$, $P < 0.05$, $\varepsilon = 0.54$], which is evidence of significant left-right hemispheric difference. Over the 28 electrodes, more negative C1 amplitudes were observed over the right hemisphere, gradually changing from right to left hemisphere (Fig. 2B). Neither the effect of sagittal plane nor the interaction was significant. Post-hoc trend analysis with linear contrast showed that the left–right difference was most prominent at the level of chain 2, which crosses electrodes O1–O2 [$F(1, 5) = 9.8$, $P < 0.05$]. In the four chains taken together, the difference was nearly significant [$F(1, 5) = 5.8$, $P = 0.06$].

Peak P1

The positive peak with latency 108 ms (SEM 4.8 ms) was prominent in posterior lateral occipital areas (Fig. 2A). In contrast to the peak C1, we found effects of aspect ratio on this peak in all observers, as well as in both the low- and high-sensitivity groups taken separately. A repeated-measures ANOVA on the amplitude of P1 with factors Aspect Ratio (4 levels) and Orientation (4 levels) revealed a significant effect of aspect ratio in the group of all observers [$F(3, 36) = 3.7$, $P < 0.05$, $\varepsilon = 0.79$], and in the high-sensitivity [$F(3, 15) = 3.5$, $P < 0.05$, $\varepsilon = 1$] and low-sensitivity [$F(3, 18) = 4.9$, $P < 0.05$, $\varepsilon = 1$] groups taken separately. Figure 6A, B shows a gradual effect of aspect ratio, driven by a linear trend [$F(1, 12) = 11.1$, $P < 0.01$]. The direction of this trend was opposite to that of C1. Neither the effect of orientation nor the interaction were significant.

We confirmed these results in a mixed-effects ANOVA. We examined the effects of aspect ratio and angle on P1 amplitude (taking aspect ratio as a continuous variable and angle as a categorical variable). We found that across all observers only aspect ratio had an effect on amplitude [aspect ratio: $F(1, 12) = 11.1$, $P < 0.01$; orientation: $F(3, 36) = 0.2$; interaction: $F(3, 36) = 1.6$]. The average slope of the effect of aspect ratio was 1.75. If we split the data between high-sensitivity and low-sensitivity observers, we find a marginally significant slope of 0.82 [$F(1, 5) = 4.6$, $P = 0.086$] for the high-sensitivity observers, and a significant slope of 2.56 [$F(1, 6) = 9.4$, $P < 0.05$] for the low-sensitivity ones.

An analysis of P1 topography in the condition with maximal P1 amplitude (aspect ratio 1.3, orientation 112.5°) in the group of all observers in the 4 × 7 array showed no main effects but a significant interaction between the sagittal and frontal planes of the array [$F(18, 216) = 3.1$, $P < 0.01$, $\varepsilon = 0.43$]. However, in contrast to C1 activity, which had a prominent right-hemispheric trend, the topographical distribution of P1 activity was mosaic, with no clear inter-hemispheric asymmetry (Fig. 2C). A post-hoc Tukey HSD test revealed several electrodes in which the amplitude was significantly higher (electrodes: 108, 110, 118, 142, 152, 162) or lower (77, 86, 106, 116, 138, 155) than in at least five other electrodes. To summarize, this pattern indicates that P1 activity is higher in the left and right occipital areas, and lower in the lateral (temporo-occipital and posterior) areas, than in the middle occipital areas.

The opposite effect of aspect ratio on peaks C1 and P1 (Fig. 6B) may have resulted from a systematic displacement of the whole ERP curve. The displacement could arise because of a single, condition-relevant, low-frequency component affecting both peaks, rather than two separate processes as we assumed above. To rule out this possibility, we tested whether the effect of aspect ratio was present in peak P1 vicinity rather than across the whole waveform. To do so, we found those electrodes in the electrode map that belonged to both C1 and P1 areas (electrodes 127, 128, 140, 141, and 152 in Fig. 2D). For these electrodes we calculated a series of 4 × 4 repeated-measures ANOVAs of the mean amplitude, using a 8-ms moving window. We did this only in the high-sensitivity group, since in this group the effect of aspect ratio was observed in both C1 and P1. For each observer, we started this calculation by centering the window on the observer-specific peak latency of P1. Then we moved the window in five steps in two directions: toward peaks C1 and N1. The *F*-values and *P*-levels obtained at each step are shown in Fig. 6C. We found that significant effect of aspect ratio was observed only near the peak latency of P1. The fact that the observed difference between ERP curves outside

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[8] See Fig. S1 and accompanying text in Electronic Supplementary Material for the motivation behind this selection.

[9] The contribution of the superficial sources is especially significant for small EEG signals, such as early evoked potentials, which might be generated by a small dipole layer in the primary sensory cortex (Srinivasan 2004). Therefore, we believe that the distribution of scalp potentials in our data roughly reflects the underlying generators (within the known topographical limitations of EEG). Based on this argument, we believe we are in a position to draw conclusions about the topography of ERP components at the scale of large cortical areas.

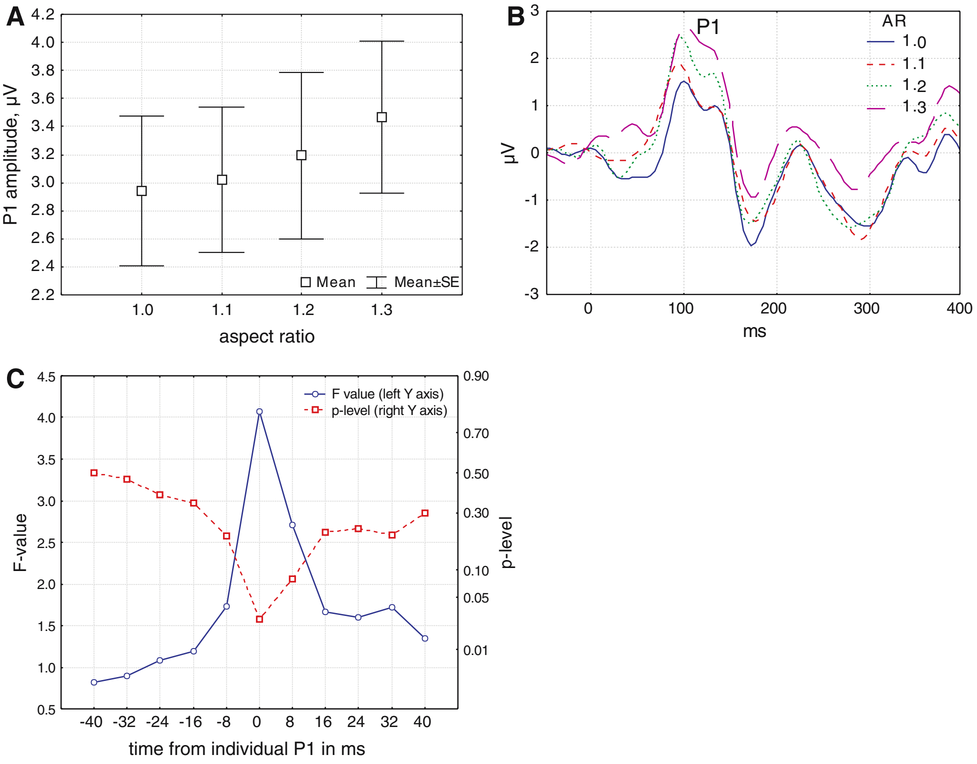

Fig. 6 Effect of aspect ratio on peak P1. **A** Mean-error plot of the amplitude of P1 across aspect ratios for the group of all observers, for the channels used in the statistical analysis. **B** Grand averaged ERPs for all observers in the representative channel 140 for aspect ratios 1.0–1.3. The amplitude of peak P1 changes gradually with lattice aspect ratio. **C** Significance of the effect of aspect ratio as a function of time relative to latency of peak P1. The *F* and *P* values were obtained in a series of analyses of variance of the mean amplitude of activity in a moving window in the vicinity of peak P1. "0 ms" on the abscissa corresponds to the latency of peak P1 of every observer

the peaks was not systematic implies that the difference was not an effect of stimulus aspect ratio. Note that the narrow temporal localization of this effect should not be viewed as evidence of its weakness; the reliability of this effect is supported by our finding of gradual changes of P1 amplitude as a function of AR (Fig. 6A). Thus, the two processes are not only clearly separated in time but they are also well localized in time. Such temporal boundedness indicates once again that distinct early and late mechanisms underlie perceptual grouping.[10]

Peak N1

The negative peak with latency 180 ms (SEM 3.1 ms) was prominent in the lateral occipital areas. A repeated-measures ANOVA of the amplitude of this peak with factors of Aspect Ratio (4 levels) and Orientation (4 levels) across the whole group of observers did not reveal any significant effects. But in the high-sensitivity group, the ANOVA showed a nearly significant effect of orientation [$F(3, 15) = 3.5$, $P = 0.07$, $\varepsilon = 0.65$]. The effect of aspect ratio and the interaction were not significant in this group. In the low-sensitivity group, we found neither significant effects nor interaction [effect of aspect ratio: $F(3, 18) = 0.4$; effect of orientation: $F(3, 18) = 1.0$], which is why we conducted no topographical analysis of N1 activity.

Different roles of C1 and P1 activity in perceptual grouping

The differences between the low- and high-sensitivity groups suggest a systematic relationship between grouping sensitivity and the amplitude of peaks C1 and P1. To further investigate this effect we used differences between peak amplitudes across aspect ratios and orientations. To obtain summary measures of these effects, we calculated the differences ΔC1 and ΔP1 between the extreme values of aspect ratio and orientation:

- For aspect ratio, the largest differences in amplitude were found between conditions AR = 1.0 and 1.3. We obtained ΔC1 and ΔP1 by calculating the differences between the amplitudes of peaks at AR = 1.0 and 1.3 for each orientation. We then averaged the magnitudes of ΔC1 and ΔP1 across orientations within every observer.
- For orientation, the largest differences in amplitude were found between orientations: 22.5° and 157.5°. We obtained ΔC1 and ΔP1 by calculating the differences

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[10] Note that our selection of the peak latency and the areas of activity were independent of the hypotheses tested in the ANOVAs. Therefore the effects within the pre-selected latencies and areas are not false positives that could arise had we selected the latencies and areas using an exhaustive search for differences between conditions across the spatiotemporal matrix of 256 channels and 125 time samples.

between the amplitudes of peaks at 22.5° and 157.5° for each aspect ratio.

Using a general linear regression model we measured the multivariate association between grouping sensitivity (as the predictor) and ΔC1 and ΔP1 for aspect ratio and orientation (as dependent variables). Wilks multivariate test showed that the association was significant [Wilks $\lambda = 0.30$, $F(4, 8) = 4.6$, $P < 0.05$]. Analysis of regression coefficients for each peak and condition of orientation and aspect ratio revealed a significant correlation for aspect ratio with ΔC1: 0.62 ($P < 0.05$) (Fig. 7A). That is, the higher was grouping sensitivity of an observer the greater was the effect of stimulus aspect ratio on the amplitude of C1. For ΔP1, the correlation coefficient was -0.60 ($P < 0.05$) (Fig. 7A). The negative correlation means that a larger ΔP1 corresponds to a lower grouping sensitivity. Thus, we found that the correlations between the effect of AR on peak C1 and grouping sensitivity, and between the effect of AR on peak P1 and grouping sensitivity were of opposite sign. In other words, the larger the effect of AR on C1 amplitude, the smaller was the effect on P1 amplitude. The dissociation between these two earliest ERP events suggests that they correspond to processes that play different roles in perceptual grouping, as we discuss below. Our estimates of slopes using mixed-effects models, summarized in Table 1, show the differences clearly.

Regarding the effect of orientation on the evoked brain activity, the correlation coefficients were: 0.68 ($P < 0.05$) for ΔC1 and 0.57 ($P < 0.05$) for ΔP1 (Fig. 7B). That is, the higher was observers' grouping sensitivity the greater was the effect of stimulus orientation on the amplitude of both peaks. However, that was the case only for the AR = 1.0. We tested whether stimulus orientation for other aspect ratios was related to grouping sensitivity by computing Pearson correlation coefficients between peak amplitudes (ΔC1, ΔP1) and grouping sensitivity for all aspect ratios (Table 2). No significant correlations were found for the aspect ratios other than 1.0.

Table 1 Effect of aspect ratio for the amplitudes of peaks C1 and P1 and sensitivity group, expressed in terms of average slope of this effect in mixed-effect ANOVA

Group	C1	P1
High-sensitivity	1.29	0.82
Low-sensitivity	0.50	2.56

Table 2 Correlation coefficients between (1) grouping sensitivity and (2) the effect of stimulus orientation on peaks C1 and P1, within each aspect ratio

Aspect ratio	C1	P1
1.0	0.68 ($P < 0.05$)	0.56 ($P < 0.05$)
1.1	−0.05 ($P = 0.86$)	0.28 ($P = 0.35$)
1.2	0.31 ($P = 0.31$)	−0.34 ($P = 0.25$)
1.3	0.35 ($P = 0.24$)	0.35 ($P = 0.24$)

To summarize, we found dissociation between the two earliest cortical events evoked by dot lattices in a grouping task. First, we found a reliable effect of aspect ratio on cortical activity as early as 55 ms after stimulus onset (peak C1). This effect predicted observer's ability for perceptual grouping: the greater the effect the greater the grouping ability. Second, we found a reliable relationship between grouping ability and the next cortical event—peak P1, 108 ms after stimulus onset—but this relationship had the opposite trend: the greater the effect of aspect ratio the lower the grouping ability. This dissociation suggests that the two events represent different aspects of perceptual grouping, with the transition between the two taking place on the interval from 55 to 108 ms after stimulus onset. By contrast, the correlations of grouping sensitivity with orientation for both peaks were of the same sign. This implies that the effect of orientation on brain activity does not change during the early stages of perceptual grouping. The finding that stimulus orientation correlated with brain activity only for AR = 1.0, when the stimuli were most ambiguous (i.e., when the stimulus support of organizations **a** and **b** was equal; Gepshtein and Kubovy 2005), suggests that the effect of orientation reflects observer bias in this task.

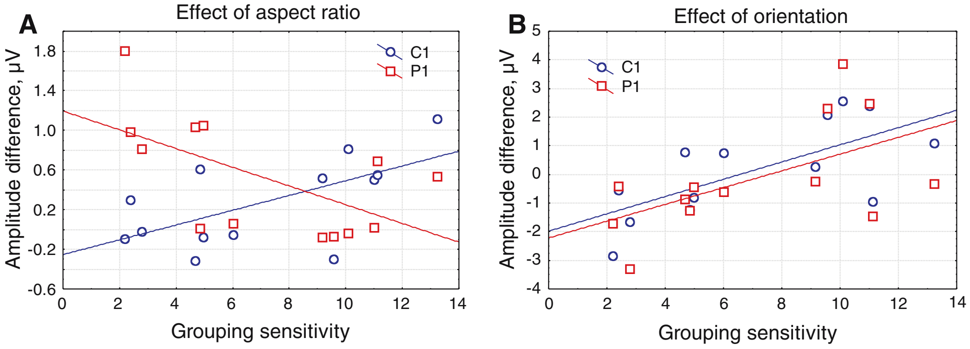

Fig. 7 Correlation between grouping sensitivity (Fig. 3) and the effects of aspect ratio **A** and orientation **B** on cortical activity. ΔC1 and ΔP1 represent the effects of stimulus manipulation of the amplitudes of peaks C1 and P1, respectively, in the group of all observers. Each point represents one observer

Segmentation by response type

To examine brain activity with respect to phenomenal aspects of the grouping task, we analyzed the data by response type: we compared cortical activity in two types of trials: when observers reported seeing the most likely organization (response *a*) and when they reported the second most likely organization (response *b*). For this analysis we pooled together data for all aspect ratios (except for AR = 1.0, where responses *a* and *b* were equally frequent) and orientations. We segmented the data relative to stimulus onset.

A repeated-measures ANOVA with a factor Response Type (2 levels: responses *a* and *b*) was applied separately to amplitudes of peaks C1, P1, and N1, and separately within the low- sensitivity and high-sensitivity groups of observers. We found a significant effect of Response Type on peak P1 only. In the high-sensitivity group, P1 amplitude was higher in response *b* (3.1 µV, SEM = 0.7) than response *a* (2.5 µV, SEM = 0.7), in the right occipital area [$F(1, 5) = 12.6$, $P < 0.05$] (Fig. 8).

This result confirms and extends results of the stimulus-based analysis. As abundant evidence indicates, P1 activity depends on higher-level visual processes (Hillyard et al. 1998; Martinez et al. 1999; Taylor 2002). The higher amplitude of P1 in reporting the less likely perceptual organization (response *b*) suggests a greater contribution of higher visual areas to response *b* than to response *a*. This implies that the opposite signs of correlation between: (1) grouping sensitivity and ΔC1, and (2) grouping sensitivity and ΔP1, which we discovered in the stimulus-based analysis, resulted from an interference of top–down processes. Taken together, these results reveal the rapid dynamics of perceptual grouping: from the stimulus-driven processes (reflected by C1 activity) to the processes that to some degree are independent of the stimulus (reflected by P1 activity).

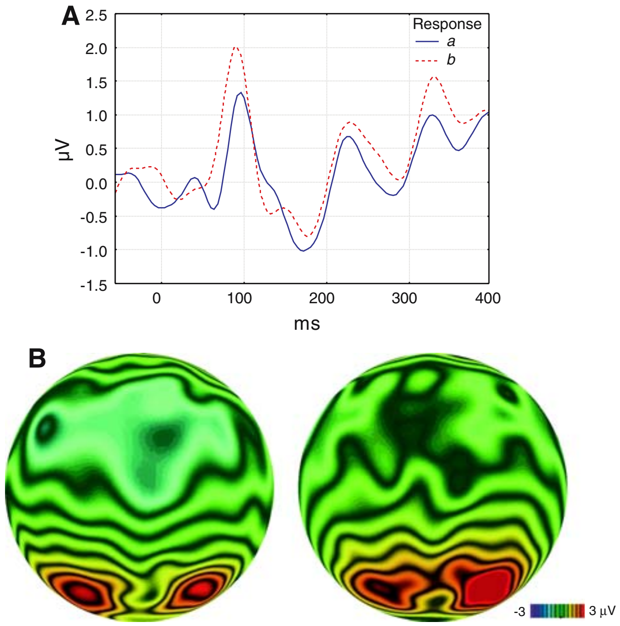

Fig. 8 Effect of response type on peak P1 in the high-sensitivity group of observers. All aspect ratios (except for AR = 1.0) and orientations are pooled together. **A** Grand-average ERPs are shown in the representative channel 154 from the right parieto-occipital area for the most likely (response *a*) and a less likely (response *b*) perceptual groupings. **B** Grand-average voltage maps at the latency of P1 maximum. Amplitude P1 for response *b* (*right map*) was higher than for response *a* in the right occipital area

Discussion

Summary of main results

We studied mechanisms of perceptual grouping by combining a phenomenological report paradigm (Kubovy 1994; Kubovy et al. 1998; Gepshtein and Kubovy 2005) with high-density ERP analysis. Human observers viewed multi-stable dot lattices and reported perceived grouping while we recorded the electrical brain activity evoked by the lattices. We varied lattice orientation and relative distances between the dots (lattice aspect ratio). The latter manipulation gradually biased perception of the lattices: it made grouping of dots along the shorter inter-dot distance increasingly more likely than the other groupings. This effect depended on observer grouping sensitivity: the more sensitive the observer the more they preferred the groupings that corresponded to the shorter inter-dot distance.

We investigated how stimulus parameters (aspect ratio and orientation) and perceptual factors (observer responses) were associated with the evoked brain activity. The two earliest peaks were most informative: the negative peak C1 with latency about 60 ms after stimulus onset, and the subsequent positive peak P1 with latency about 110 ms. The amplitudes of peaks C1 and P1 were affected by aspect ratio and orientation (stimulus parameters) and grouping sensitivity (a perceptual parameter) in a graded fashion.

Effect of aspect ratio

Aspect ratio had opposite effects on C1 and P1 amplitudes: low aspect ratios were associated with greater amplitudes of peak C1, and lower amplitudes of peak P1, than high aspect ratios. This finding suggests that the two earliest events reflect different aspects of perceptual grouping, a conclusion supported by our other results: The amplitudes of peaks C1 and P1 were also correlated with grouping sensitivity. C1 activity was influenced by stimulus aspect ratio more in observers with high than low grouping sensitivity, whereas P1 activity was influenced by the stimulus parameter more in observers with low than high grouping sensitivity (Fig. 7A). In other words, we found that high grouping sensitivity depended on mechanisms activated as early as the earliest ERP peak, whereas low grouping sensitivity depended more on the mechanisms activated at the time of the next peak.

Effect of orientation

The effect of orientation was more pervasive than the effect of aspect ratio: both peaks C1 and P1 correlated positively with grouping sensitivity.

Functional significance of the C1–P1 dissociation

Our finding of dissociation between two earliest cortical events should be interpreted in light of evidence that perceptual grouping depends on multiple mechanisms, as reported in studies in humans (VanRullen and Thorpe 2001; Pins and ffytche 2003; Nikolaev and van Leeuwen 2004) and animals (Super et al. 2001, 2003). It is plausible that the functionally distinct cortical events within the first 100 ms after stimulus onset reflect the different roles played in perceptual organization by the feedforward and recurrent neural connections (e.g., reviewed by Roelfsema 2006), as we mentioned in “Introduction”. On this view, the early peak C1, which is not affected by attention (Clark et al. 1995; Martinez et al. 1999; Di Russo et al. 2003), is associated with stimulus-driven processes mediated by feedforward connections, whereas the later peak P1 is associated with processes that depend on stimulus context (Hillyard et al. 1998; Taylor 2002) mediated by recurrent connections.

Thus, our finding that high grouping sensitivity is associated with C1 activity suggests that high grouping sensitivity depends on the early stimulus-driven processes. Our finding that low grouping sensitivity depends on a later process—our peak P1—suggests that the later mechanism of grouping is less efficient than the early one. Our response-based analysis confirms this idea. We found that high P1 amplitude was associated with perception of less likely groupings (response *b*) in high-sensitive observers. This is evidence that the increase of P1 activity reflected activation of the mechanisms that depend to a lesser extent on stimulus properties, such as proximity. Hence, our finding that P1 activity was high in observers with (1) low C1 activity and (2) low grouping sensitivity implies that the less sensitive observers rely more on later mechanisms.

Mechanisms of perceptual grouping: low-level processes

Since perceptual grouping depends on multiple mechanisms, it cannot be reduced to a single anatomical substrate or chronometric cortical event. But some processes were proposed to play a critical role in perceptual grouping. In particular, it has been suggested that early stages of perceptual grouping depend on spatial-frequency filtering of visual stimuli (Ginsburg 1986; Ben-Av and Sagi 1995).

Previous ERP research showed that spatial-frequency analysis of visual stimuli is associated with C1 activity: The larger was high spatial-frequency power of the stimulus the higher was C1 amplitude (Kenemans et al. 1993, 2000; Boeschoten et al. 2005). Han et al. (2001), too, assumed the relationship between early evoked activity in grouping by proximity and spatial-frequency analysis to interpret their results. In our study, dot lattices with aspect ratio 1.0 (AR = 1.0) contained more high spatial frequency power than other aspect ratios. Hence, our findings that that C1 activity was greatest at AR = 1.0, and that it gradually decreased with aspect ratio, support the view that C1 activity in our task reflects a spatial-frequency analysis of our stimuli. Moreover, we found that C1 activity was higher in the right than left hemisphere (Fig. 2B). Although this hemispheric difference may be explained by variations in cortical geometry and/or in the propagation of electrical fields generated in and around the calcarine sulcus, it may also reflect processing of spatial frequencies. Several studies showed that low spatial frequencies are processed more in the right than left hemisphere (Sergent 1982; Kitterle et al. 1990; Kenemans et al. 2000). Therefore, our results are consistent with the notion that perceptual grouping at this stage depends more on low than high spatial frequency content of visual stimuli (Ginsburg 1971, 1986). Indeed, it is plausible that observer performance in a grouping task benefits more from information at low than high spatial frequencies, because low frequencies generally carry information about large-scale properties of retinal images.[11]

To summarize, our results suggest that C1 activity reflects a stage of perceptual grouping responsible for the spatial-frequency analysis of the stimuli. The shift of C1 activity to the right hemisphere, which has an advantage in processing low spatial frequencies, indicates that

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[11] Although low spatial frequencies deem critical for perceptual grouping, it is incorrect to assume that *only* low frequencies are needed for the task. Janez (1984) showed that grouping is possible with low frequencies filtered out from the stimulus. Consistent with this idea, our results indicate that a broad spectrum of spatial frequencies is used for grouping, manifested by ERP activity in left and right hemispheres, with higher activity in the right hemisphere indicating a greater role of low spatial frequencies.

perceptual grouping depends more on low than high spatial frequencies. This view is inconsistent with the proposal that a later positive wave (with latency 100 ms) is associated with the processing of spatial frequencies in grouping by proximity (Han et al. 2001, 2005).

Along with spatial frequency, stimulus orientation is a basic spatial parameter that was shown to modulate C1 and P1 activity (Proverbio et al. 2002; Romani et al. 2003). In our results, the effect of orientation was more pervasive than the effect of aspect ratio: both peaks C1 and P1 correlated positively with grouping sensitivity. Psychophysical studies of grouping found an intrinsic orientation bias, such that different observers preferred certain orientations of grouping, independent of stimulus properties (Gepshtein and Kubovy 2005). The pervasiveness of the effect of orientation on early cortical activity could be a manifestation of this bias.

Mechanisms of perceptual grouping: lateral interactions

It is often proposed that visual grouping is mediated by lateral interactions, revealed in psychophysical studies of vision at the threshold of visibility (Polat and Sagi 1993, 1994; reviewed by Kovacs 1996) and in physiological studies of intra-cortical connectivity (Schmidt et al. 1997; Polat et al. 1998).

Psychophysical studies of lateral interactions

The psychophysical studies found that observer sensitivity to an oriented stimulus near the threshold of visibility (a "target") is modulated by other oriented stimuli ("flankers") in the vicinity of the target (Polat and Sagi 1993, 1994). The modulation depends on relational properties (e.g., collinearity vs. orthogonality) of target and flankers. Khoe et al. (2004) used these stimuli in an ERP study and found the earliest correlate of the lateral interaction at about 100–120 ms (their Table 2). In our study, this latency corresponds to the second peak, P1, which is subject to top-down influences, such as attention (Martinez et al. 1999), as we discussed above.

Consistent with this evidence, another psychophysical study showed that lateral interactions are modulated by visual attention: Freeman et al. (2001) manipulated attention to flankers and found that "attended flankers produced typical lateral interactions, but ignored flankers did not" (p. 1032). When the flankers were unattended, their effect on the target disappeared, "as if [the flankers were] physically removed from the display" (p. 1035). Khoe et al. (2006) combined this psychophysical paradigm with ERP measurement and found that the aforementioned effect of attentional modulation correlated with cortical activity as late as 180–250 ms after stimulus onset, which is even later than our peak P1.

Physiological studies of lateral interactions

It was proposed that the psychophysical lateral interactions are mediated by horizontal or feedback (recurrent) connections (Kapadia et al. 1995; Bosking et al. 1997; Polat et al. 1998; Li et al. 2004). As we mentioned above, the effects based on recurrent connections (1) require longer time than the effects based on feedforward connections and (2) are subjected to attentional modulations. If grouping mechanism depended on recurrent connections, the associated cortical activity would happen late and would depend on attention, consistent with findings by Freeman et al. (2001) and Khoe et al. (2006).

Thus, both physiological and ERP studies suggest that the psychophysical lateral interactions depend on a relatively late mechanism. By its latency, that mechanism is distinct from the mechanism associated with C1 activity, which we found to control the ability for perceptual grouping. In this sense, our results cast doubt on the notion that neural lateral interactions constitute the mechanism of perceptual grouping.

Mechanisms of perceptual grouping: high-level processes

We used a phenomenological report paradigm to establish the relationship between observer responses and evoked potentials. The paradigm allowed us to discern fine differences in grouping sensitivity across observers. Using these differences we discovered a graded association between grouping sensitivity and evoked potentials. This association elucidates the functional meanings of different components of ERP, which has been impossible in previous studies of grouping, where observer reports were not analyzed. For example, previous application of ERP analysis to perceptual grouping (Han et al. 2005) focused on the positive evoked activity about 100 ms after stimulus onset (Pd100). Han et al. found that *all* the grouping-related evoked activity, starting from Pd100, depended on attention and task relevance. But since the authors did not record observer responses they could not establish the functional meaning of the evoked activity. We, too, found a positive evoked activity about 100 ms (our "P1") which was associated with low grouping sensitivity and with the reports of less likely groupings (response *b*). It is indeed plausible that this activity is influenced by higher-level processes. But in addition to this we found an association of high grouping sensitivity with the early ERP component C1, which does not depend on attention. Thus, in contrast to the conclusion of Han et al. that all grouping-related activity depends on attention, our results support the view of perceptual grouping as a multistage process, which consists of early attention-independent processes and later processes that depend on attention. In this sense our results are consistent with the notion that an early stage of perceptual grouping is preattentive (Kahneman and Henik 1981; Duncan 1984; Julesz 1991).

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