

# Oblique effects beyond low-level visual processing

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## Abstract

A number of studies have demonstrated a reduction in neural activity for oblique gratings as compared to horizontal or vertical gratings. This has been associated with the psychophysical oblique effect. Using event-related potentials, we now assessed the neural activity associated with the processing of higher-order stimuli of different orientations. We applied a novel stimulus paradigm that is particularly suited to investigate mid- and high-level vision by obviating low-level responses. It consisted of a line grid that emerged perspicuously from a continuous movement of stimulus elements without any temporal discontinuances in stimulus presentation. This Gestalt could be oriented along the cardinal axes or rotated by 45°. We obtained distinct event-related potentials with a moderate task-dependence. They showed a correlate of Gestalt processing that did not depend on the orientation, followed by a P300-like component that was 50% larger for the 45° Gestalt. Surprisingly, this oblique effect is opposite to previous studies using gratings. We propose that it originated from a bias in neural processing, induced by the long-term environmental experience of the subjects.

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## 1. Introduction

A reduced visual performance for stimuli that are oriented obliquely as opposed to cardinally, has been termed ‘oblique effect’ (e.g., Appelle, 1972).

### 1.1. Psychophysical oblique effect

Several studies have shown that oblique gratings have higher detection thresholds than gratings that are oriented along one of the cardinal axes (i.e. horizontally or vertically) (Appelle, 1972; Meng & Qian, 2005). However, the effect depends on the type of task that the subject has to perform. For instance, when reaction time is measured, the effect is present with identification tasks (“Which orientation?”), but neither with a classification task (“Cardinal or oblique?”) nor with a detection task (Essock, 1980). As

opposed to most studies using different tasks, Zemon, Conte, and Camisa (1993) did not find an oblique effect for contrasts above threshold in a contrast matching task. However, high contrast does not seem to abolish the oblique effect in experiments that are assessing other performance measures such as grating acuity (Berkley, Kitterle, & Watkins, 1975) or orientation discrimination (Caelli, Brettel, Rentschler, & Hilz, 1983).

Based on a contrast matching task with spatial-frequency-filtered stimuli, Essock and coworkers (Essock, DeFord, Hansen, & Sinai, 2003; Hansen & Essock, 2004; Hansen & Essock, 2006) concluded that the polarity of the oblique effect reverses (i.e. better visual performance for oblique orientations) if the visual stimuli have a broad spatial frequency spectrum. Other studies, however, reported a reduced performance for oblique orientations with other broad-band stimuli such lines, square-wave gratings, and vernier targets (Ogilvie & Taylor, 1959; Zemon, Gutowski, & Horton, 1983; Leibowitz, 1955). More specific differences in the spatial frequency distribu-

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tion, beyond being broad-band, might account for performance discrepancies. Unequal stimulus size and differences in spatial attention might also explain part of this seeming disagreement, as the preferred orientation of V1 neurons, at least in monkey, depends on eccentricity. Bauer, Dow, and Vautin (1980) found that vertical orientation preferences dominate within the central 0.5° of eccentricity, while oblique orientation preferences dominate at eccentricities of 0.5–2°, but for humans, these numbers might be different.

### 1.2. Oblique effects in evoked potentials

Using visual evoked potentials, Arakawa et al. (2000) found that the latency of early visual evoked potential (VEP) components depends on an interaction between obliqueness and spatial frequency. Zemon et al. (1983) report that the oblique effect in the VEP is larger for high contrasts than for low contrasts. Freeman and Thibos (1975) found that the oblique effect is larger for fine grating than for coarse gratings.

Steady-state VEP amplitudes are smaller for oblique stimuli (Moskowitz & Sokol, 1985) and functional magnetic resonance responses in V1 are reduced (Furmanski & Engel, 2000). A possible neuroanatomical correlate of the oblique effect is a larger representation of cardinal orientations in the visual cortex. Such a non-uniform representation has been reported for cats (Wang, Ding, & Yunokuchi, 2003) and ferrets (Coppola, White, Fitzpatrick, & Purves, 1998b).

### 1.3. Oblique effects on different processing levels

Essock (1980) has proposed two classes of oblique effects, which he attributed to two different classes of stimulus processing. “Class 1” would be associated with basic visual functions including acuity or contrast threshold. “Class 2”, on the other hand, would involve “memory, learning, perceptual, and cognitive processes”. One might disagree with Essock’s (1980) specific definition of these two classes. Nevertheless, describing vision as a multi-stage process seems adequate and numerous authors frequently proposed a division into low-, mid-, and high-level processing (e.g., Jones, Sinha, Vetter, & Poggio, 1997; Henderson & Hollingworth, 1999; Rensink, 2001; Black, Kahol, Kuchi, Fahmy, & Panchanathan, 2003). It is likely that an oblique effect at a given processing stage occurs within the coordinate system used at that processing stage. This coordinate system might be retinal, body-related, environmental, subjectively distorted, or possibly even imaginary. Some evidence for non-retinal coordinates comes from experiments by Attneave and Olson (1967), who showed that the oblique effect as measured in that study remained stable in gravitational coordinates (or possibly body coordinates) when subjects tilted their head. In a study by Buchanan-Smith and Heeley (1993), acuity estimates were obtained with different head and body orientations. These show strong effects of posture that rule out simple neural anisotropies as the source of the oblique effect

under the given experimental conditions. Meng and Qian (2005) showed that the perceived, rather than physical, tilt of the stimulus determines the orientation of the oblique effect.

### 1.4. The oblique effect in higher-level event-related potentials

While the aforementioned studies help us to understand the oblique effect in low-level vision, investigations of mid- and higher-level influences of obliqueness are rare. Maffei and Campbell (1970) have found a reduced visual evoked potential amplitude for oblique gratings moving orthogonally to their orientation. As they only used one occipital electrode and one basic stimulus type, it is difficult to judge from which processing level the effect originated, since motion processing itself is considered to be a multi-stage process (e.g., Mareschal, Ashida, Bex, Nishida, & Verstraten, 1997; Bex, Metha, & Makous, 1998; Braddick & Quian, 2001). Ito, Sugata, and Kuwabara (1997) report that a cardinal oriented square stimulus evoked a larger response than an oblique square at around 155 ms at occipital locations, which is consistent with the usual oblique effect.

The P300 component (Linden, 2005) is typically regarded as reflecting aspects of high-level processing. Proverbio, Esposito, and Zani (2002) found that it is reduced for oblique gratings, irrespective of the attentional condition. However, there is a possible confounder due to the fact that the stimulus set consisted of only one type of vertical gratings among several types of oblique gratings of different orientation. Thus, the experiment might have represented a traditional oddball-paradigm, where a rare stimulus is presented within a sequence of frequent stimuli.

In the present study, we extended previous findings by using more complex stimuli that involve a higher degree of holistic processing than simple gratings and by using stimulus sets that were balanced between cardinal and oblique stimuli.

As their name indicates, event-related potentials (ERPs) represent responses to stimulus events. Typically, such an event is the sudden appearance or the sudden change of a stimulus. For complex stimuli, this means that the recorded signal is a compound of neural activity elicited by mid- and high-level stimulus features on the one hand and trivial local low-level stimulus changes such as local luminance variations on the other. These two aspects of the stimulus are difficult to separate, as mid- and high-level changes are usually accompanied by low-level changes.

To investigate specifically mid- and high-level processes, several previous studies (none of them investigating the oblique effect) have attempted to eliminate lower-level responses by assessing algebraic combinations of different stimulus conditions. Examples include studies on texture segregation (e.g., Bach & Meigen, 1992; Caputo & Casco, 1999; Lamme, Van Dijk, & Spekreijse, 1992), where homogenous and segregated stimuli were compared, object processing (e.g., Sehatpour, Molholm, Javitt, & Foxe,

2006), where scrambled images served as a reference, ambiguous perception (e.g., Kornmeier & Bach, 2004), where trials with and without perceptual flips were compared, and motion processing, where iso- and antidirectional adaptation were compared to isolate veridical motion responses (e.g., Hoffmann, Unsöld, & Bach, 2001; Heinrich, van der Smagt, Bach, & Hoffmann, 2004). The algebraic combination of different conditions is based on the assumption that the system characteristics are linear (or otherwise simple and well-defined). However, it is not sure that this prerequisite is always fulfilled. For instance, if low-level mechanisms changed their sensitivity (and hence their response strength) due to high-level feedback, they would still perform low-level processing. The associated neural activity, however, would not be distinguishable from veridical high-level activity.

Tallon-Baudry, Bertrand, Delpuech, and Pernier (1997) have attempted to tackle the problem by using a stimulus which was at first undetectable for the subjects, but could be identified after a training period. Under such circumstances, top-down processes play a crucial role. Additionally, unspecific sequential effects may come into play. Moreover, it is not clear whether some subconscious processing might take place, even if the subject fails to see the stimulus.

Keil, Müller, Ray, Gruber, and Elbert (1999) used rotating bistable figures which switched their meaning depending on whether they were upright or rotated by 180°. This type of stimulus does not suffer from the above-mentioned problems. However, the configuration of stimulus elements does not actually change. This stimulus is therefore best suited to study the processing of high-level information such as stimulus meaning, but is less optimal to analyze mid-level processing, such as the binding of stimulus parts into one coherent percept.

In the present study we explored a novel approach to overcome these diverse problems. We used a new paradigm in which a Gestalt emerged from a continuous flow of stimulus elements with each one evolving independently. This avoided most changes in low-level stimulus properties, did not rely on the training of the subject, and is suitable for studying mid-level problems such as the binding of stimulus features. In doing so, we pursued two aims. The first was to validate the new technique by comparing correlates of Gestaltness to previous studies. The second aim was to investigate to what degree the ERP responses depend on the orientation of the Gestalt, i.e. whether they suggest the existence of an oblique effect in mid- or high-level vision.

### 1.5. Gestaltness and ERPs

A number of previous studies have assessed the characteristics of ERPs associated with holistic stimulus processing, such as the detection of contours and texture boundaries. For example, ERPs to subjective contours such as Kanizsa figures are consistently more negative in the time range of 150–200 ms than similar stimuli not pro-

ducing a contour (Sugawara & Morotomi, 1991; Murray et al., 2002). In ERP experiments investigating texture segregation and figure-ground identification, latencies reported for the main specific ERP components are not fully consistent. Most of these studies reported a negativity in the range of 150–200 ms (e.g., Bach & Meigen, 1992; Fahle, Quenzer, Braun, & Spang, 2003; Caputo & Casco, 1999; Lamme et al., 1992), but earlier and later occurrences have also been found for some types of stimuli (e.g., Fahle et al., 2003; Heinrich, Andrés, & Bach, 2007). While segregation-related responses are usually focussed around the occipital pole, the activity evoked by Kanizsa figures extends further to occipito-temporal locations.

Since such holistic processing often appears to be associated with a negative deflection around 150–200 ms, a correlate of Gestaltness within this time interval would provide some validation of the stimulus paradigm applied in the present study.

## 2. Methods

### 2.1. Stimuli and tasks

Stimuli (Fig. 1 and Movie 1 [Supplementary Material]) were generated by a Power Macintosh G4 computer and displayed on a Philips GD 402 monochrome CRT screen at 120 Hz refresh rate. As illustrated in Fig. 1B, in each trial, 24 line elements of 0.9° length continuously moved at 0.4–1.0°/s in seemingly random directions. Speed and direction were constant for each single element. At the same time, the bars rotated around their individual midpoint at 20–60°/s. After 2 s, they had just moved such that together they could form a Gestalt. Following that, due to the continuing movement of the elements, the Gestalt started to disintegrate immediately while the stimulus continued for 1 s.

Within each experimental block, three different versions of this stimulus (Fig. 1A) were presented in random order, each about 70 times: a grid of 9 squares, the same grid rotated by 45°, and a version where the elements never formed a Gestalt ('gestaltless' stimuli).

Before the experiment, the subjects were familiarized with the stimuli. Prior to each block, one of the three stimulus variants ('target') was specified by the experimenter. The subjects were instructed to press a button when a corresponding trial occurred. The button was to be pressed only in the pause (1 s) following the trial, but not during the trial itself, in order to avoid contamination of the EEG due to motor responses. The task was easy to perform and its purpose was to ensure that the subjects would pay attention to the stimuli. The subjects were made aware that the reaction time as such was not important, but that the time window for the button press was limited. We controlled during the experiment that the subjects accomplished the respective tasks with a high accuracy, regarding both the correctness of the response and its timing, which made it unnecessary to sort the trials by the subjects' performance.

The procedure was performed twice for each of the three possible tasks in an ABC–CBA scheme, with the block assignment altered between subjects, such that about 140 trials were obtained for each of the nine possible stimulus/task combinations.

### 2.2. Subjects and EEG recording

The experiment was approved by the local review board and the subjects provided their informed consent. 18 subjects (10 female, 8 male) took part, mostly undergraduate or graduate students. All had normal or corrected-to-normal visual acuity and no known ophthalmological or neurological diseases.

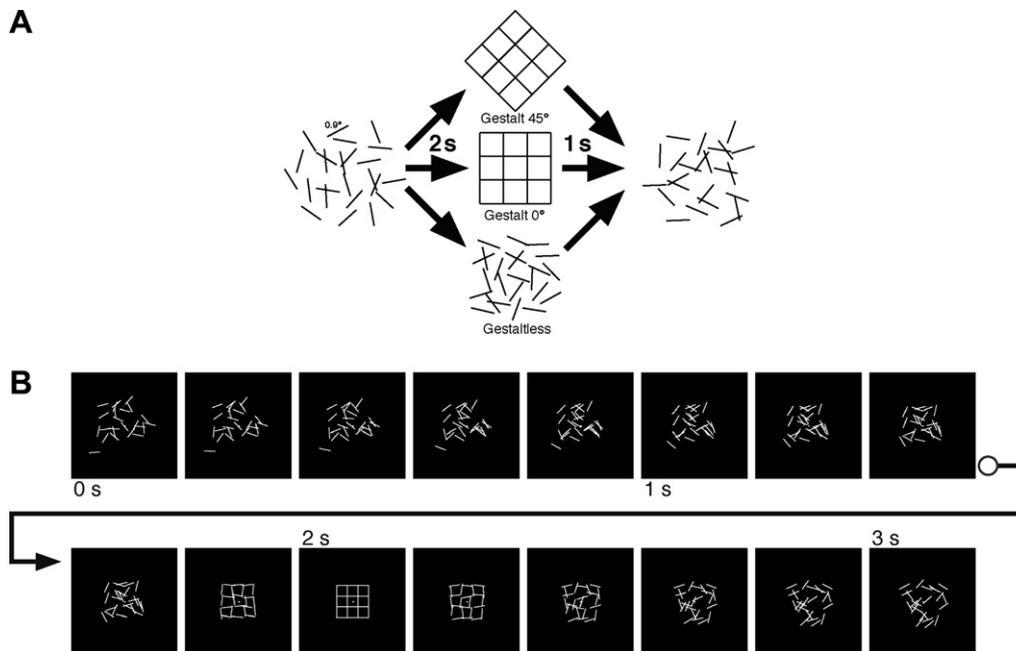


Fig. 1. (A) Stimulus paradigm. Starting from random positions, 24 line elements continuously moved and rotated during a 3-s-epoch. After 2 s, all elements had either moved into a position to form one of two Gestalts ( $0^\circ$  or  $45^\circ$  Gestalt, respectively), or they remained in a gestaltless (random) configuration. (B) Samples of the stimulus sequence taken at 200 ms intervals. For better reproduction, the contrast has been enhanced here as compared to the actual stimulus used in the experiment.

The EEG was recorded with goldcup electrodes from six positions: Fpz, Cz, Pz, and Oz according to standard nomenclature (American Encephalographic Society, 1994) and two occipito-temporal electrodes (OTL and OTR) located 5 cm to the left and right of the occipital pole, respectively. Linked ears served as reference. In addition, the vertical EOG was recorded for detection of blink artifacts. All signals were band-pass-filtered (0.3–110 Hz), amplified (Toennies Physiologic Amplifier), digitized at a rate of 1000 Hz, and written to disk for off-line analysis. Preliminary ERP averages were displayed on-line for control purposes.

### 2.3. Data analysis

All analyses were done with Igor Pro (Wavemetrics Inc.). The moment of physical Gestalt completion (i.e. when the line elements formed a regular grid) was taken as zero time reference for each trial and the time interval from  $-1.0$  to  $+1.0$  s was analyzed. Artifacts were detected based on a  $\pm 100$   $\mu\text{V}$  threshold criterion in EEG and EOG traces. Trials were low-pass filtered at 40 Hz, and sorted by stimulus and task. Baseline correction was based on the first 500 ms of each EEG segment (i.e.  $-1000$  ms to  $-500$  ms). The ERPs were computed by averaging the artifact-free trials for each stimulus/task combination.

The significance of differences between ERP traces was first assessed for the complete time range of  $-1.0$  to  $+1.0$  s by a permutation test (ROTP test, Achim, 1995) with a subsequent sequential Bonferroni adjustment (Holm, 1979). Forgoing temporal information by evaluating the full length of the ERP at once reduces the number of tests and thus alleviates the problem of false negatives due to overcorrection for multiple testing. Since 5000 random permutations were evaluated, the smallest possible  $P$  value was 0.0002. Subsequently, we performed a “running”  $t$  test, where a  $P$  value was computed for each point in time in order to identify those time intervals that account for the differences found with the permutation test.

## 3. Results

The subjects described the emergence of the Gestalt as a striking visual effect and performed the tasks easily and with hardly any errors.

The time values given in this section are relative to the time at which the Gestalt was completed, or would have been completed if it had been there. Fig. 2 provides an overview over all recording sites. For the Gestalt stimuli, occipital and parietal ERPs were dominated by a signal rise that started before Gestalt completion. While this component started at the same time for both orientations, it was approximately 50% larger in the  $45^\circ$  condition, where it reached its maximum only after around 110 ms, as compared to 70 ms in the  $0^\circ$  condition. At occipital and occipito-temporal locations, it declined slowly, possibly affected by the high-pass characteristic of the amplifier ( $\tau \approx 0.5$  s). At Pz and Cz locations, the positive deflection dropped much faster, reaching a negative level at around 400 ms. The Fpz trace showed a broad but weak maximum peaking at 70 ms before completion, followed by a shallow negativity at around 300 ms. At all locations, the  $45^\circ$  Gestalt produced a stronger positive deflection than the  $0^\circ$  Gestalt. OTL (and less pronounced OTR) showed an early negativity, peaking around 180 ms before Gestalt completion. In comparison, the positive ERP peaks for the gestaltless stimuli were clearly smaller and occurred later, with hardly any response at Fpz and no early negativity at occipito-temporal locations.

The permutation tests (Fig. 3) indicate that the differences between the gestaltless condition and either Gestalt condition were significant at all locations ( $P < 0.0002$  at most electrodes). Likewise, the two Gestalt orientations evoked significantly different responses at all locations (between  $P = 0.0098$  and  $P < 0.0002$ , depending on the electrode), except at Fpz ( $P < 0.075$ ). The time-resolved analysis of significance (Fig. 4) showed that the differences

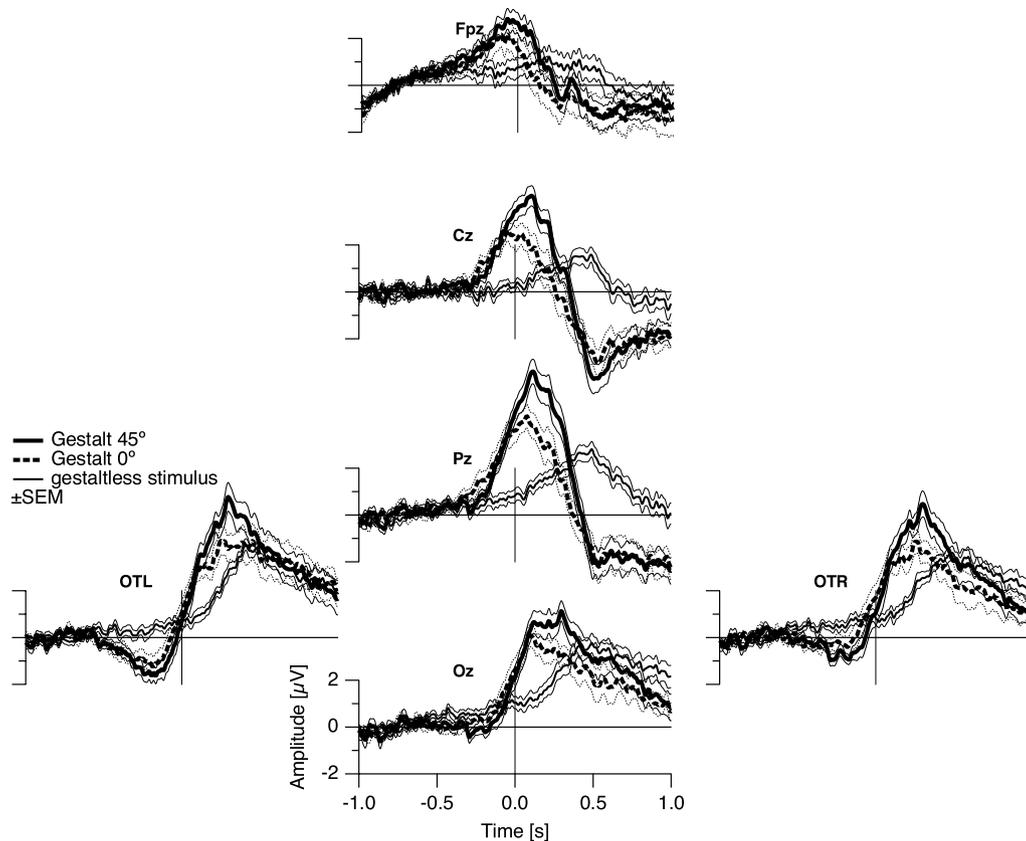


Fig. 2. Grand-mean ERPs ( $\pm$ SEM) of all electrodes topographically arranged, showing the results from all target conditions (i.e. the stimuli corresponded to the task). While the largest difference is between Gestalt and gestaltless stimuli, there is also a clear orientation effect for the two Gestalt stimuli. Fig. 3 provides significance estimates.

between the two orientations primarily originated from the large positivity focussed at the Pz electrode. In the Gestalt vs. gestaltless comparisons, significant differences already occurred around  $-200$  ms at occipito-temporal locations.

The grand-mean event-related potentials for all stimulus conditions as recorded at the Pz location are shown superimposed in Fig. 5. All Gestalt stimuli produced similar results, though the responses in the target conditions were somewhat larger than those in the non-target condition. Likewise, ERPs from the gestaltless stimuli were almost identical for all tasks. The main difference between the target Gestalt and the other two conditions ('gestaltless' task or non-target Gestalt) was an enhanced negativity at Pz, occurring 500 ms after Gestalt completion. The dominant positivity occurred earlier at the frontal than at the occipital and parietal electrodes.

#### 4. Discussion

The novel stimulus paradigm applied in the present study elicited reliable ERPs in all conditions, despite the continuous presentation. The first significant component was an occipito-temporal negativity, followed by a dominating positivity which was strongest in the parietal region, and a subsequent negativity at the central and frontal electrodes.

##### 4.1. General characterization of the ERPs as compared to earlier studies

For comparing the present results to previous studies, we need an estimation of the time at which the subjects start perceiving the Gestalt. This would serve as a reference for time measures analogously to the time of stimulus onset in other experiments. However, to avoid contamination of the ERPs by motor potentials, we had asked the subjects to perform a delayed response task and press the button after the end of the trial and before the beginning of the following trial, rather than immediately after they had identified the stimulus. Therefore, we obtained reaction times from two subjects and compared the stimulus as used for the EEG recordings to a stimulus in which the Gestalt appeared abruptly after 2 s of random movement of line elements. The difference between the reaction times for abrupt and continuous presentation suggests that the subjects are able to identify the stimuli already 430–460 ms before Gestalt completion (cf. Table 1), thereby allowing us to determine "effective" peak times for the ERP components. Since speed was more emphasized in the reaction time experiment than during the ERP recordings, the actual numbers for the ERP experiment might be somewhat lower, but still in a similar range as shown by Kutas, McCarthy, and Donchin (1977) for the P300. Importantly,

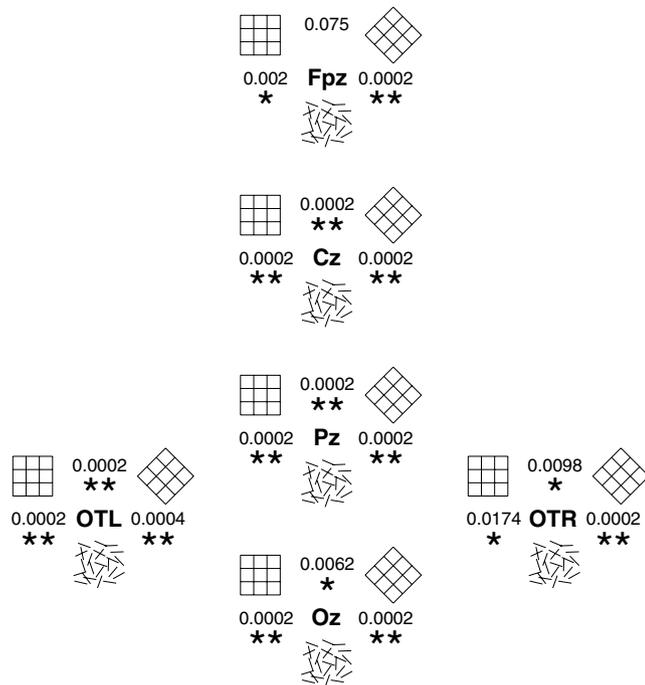


Fig. 3. Significance of ERP differences between all three target stimulus conditions. Each number indicates the  $P$  value for the comparison between the two stimuli depicted next to it. The values were obtained with a permutation test applied to the time interval from  $-1.0$  to  $+1.0$  s. Since 5000 random permutations were evaluated, the smallest possible  $P$  is 0.0002. The asterisks give the significance levels in standard notation (\*, groupwise  $\alpha = 0.05$ ; \*\*, groupwise  $\alpha = 0.01$ ), based on a sequential Bonferroni adjustment. Except for one combination at Fpz, all comparisons were indicating significance, suggesting that ERP differences exist between both Gestalt conditions, and between Gestalt and gestaltless conditions.

the reaction time variability in the continuous conditions was only slightly higher than in the abrupt conditions. Variability hardly differed between Gestalt conditions, but was larger for the gestaltless condition.

The scalp distribution of the positive deflection had its maximum at the parietal electrode, which is characteristic for a P300 component (Picton, 1992). Taking the reaction time estimates into account, the effective peak time was likely to be in the order of 500–600 ms, which is in the upper range of typical P300 values (Comerchero & Polich, 1999). We therefore interpret the positive deflection as a P300. Not unexpectedly, Gestalt stimuli elicited a larger response than non-target Gestalt stimuli. Surprisingly, though, responses to Gestalt stimuli during the ‘gestaltless’ tasks were almost as large as in the target Gestalt trials. However, the ‘gestaltless’ task was essentially a yes/no task without the need to distinguish between Gestalt types, as opposed to the one-out-of-three task if one of the Gestalt stimuli was the target. Thus, during the ‘gestaltless’ task the non-target stimuli might have been almost equivalent to the target stimuli in terms of task relevance.

The negative deflection 190 ms before completion primarily occurs at occipito-temporal electrodes during Gestalt trials. The effective peak time is probably in the

range of 150–250 ms. The strong negativity occurring 500 ms after Gestalt completion might be in part a result of the amplifier filter settings (Duncan-Johnson & Donchin, 1979). However, Soskins, Rosenfeld, and Niendam (2001) found that this does not attenuate the P300 amplitude. Their study instead showed that the amplitude of the negativity appears to correlate inversely with P300 recovery time as measured with different filter settings.

#### 4.2. Absence of low-level responses, but correlates of Gestaltness in mid-level processing

The ERP traces are lacking any early deflection that would represent a low-level response (for instance elicited by local luminance variations, cf. Section 1) and, hence, would equally occur with both Gestalt and gestaltless stimuli. If such an early response had a very short duration and there were a time jitter, it would possibly be difficult to identify in the averaged ERP. However, the absence of even a shallow broad deflection suggests that no such responses were present. If an early response consisted of both positive and negative deflections, extinction due to destructive superposition would be possible, but one would expect the standard error to be elevated. This was neither the case in the grand mean (i.e. no interindividual jitter, cf. Fig. 2), nor in the single-subject SEMs (i.e. no intra-individual jitter, not shown here). We therefore conclude that the stimulus paradigm was successful in avoiding low-level responses.

The first significant deflection in the ERPs was the occipito-temporal negativity around 190 ms before completion. It only occurred with Gestalt stimuli and thus appears to reflect the combination of single line elements into a figure. The timing is compatible with previously reported ERP components that were interpreted as a correlate of holistic processing. For instance, in a similar time range at occipito-temporal locations, Kanizsa shapes yield stronger negativities than their counterparts with rotated inducing discs (Murray et al., 2002). While we found no sizable oblique effect for this early component, Proverbio et al. (2002) report an effect in a comparable time range in a component that they interpreted as selection negativity. In their study, grating stimuli were either vertical or were tilted to various degrees. Responses to attended vertical gratings were larger than those to attended oblique ones, but no such difference was found when unattended stimuli were compared. Ito et al. (1997) used stimuli that were more comparable to those used in the present study, namely cardinally oriented squares and oblique squares. Their stimulus set also included triangles and circles. As opposed to Proverbio et al. (2002), they only used one type of oblique stimuli, i.e. cardinal and oblique stimuli were equiprobable. Nevertheless, they found larger responses for cardinal stimuli than for oblique stimuli. However, similar to the case of the Proverbio et al. (2002) study, one might speculate that stimulus probabilities were not truly balanced. Instead, subjects might have assigned the oblique

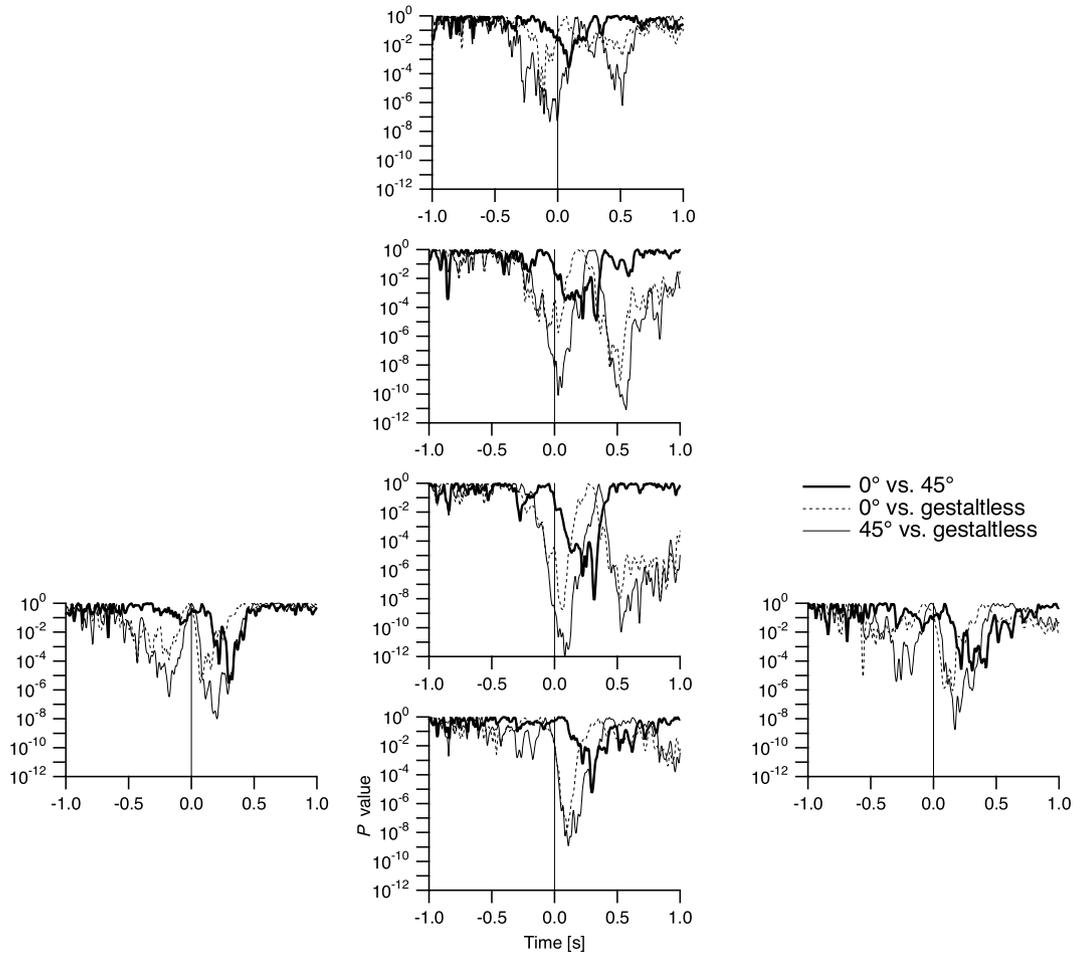


Fig. 4. Time-resolved significance of differences between the three target conditions. Curves show  $P$  values as a function of time and indicate that primarily the differences in the P300-like component account for the small  $P$  value found with the permutation test for the  $0^\circ$  vs.  $45^\circ$  comparison at the Pz electrode (cf. Fig. 3). Gestalt vs. gestaltless comparisons, in particular for the  $45^\circ$  stimulus, revealed robust significant differences already around  $-200$  ms at occipito-temporal locations.

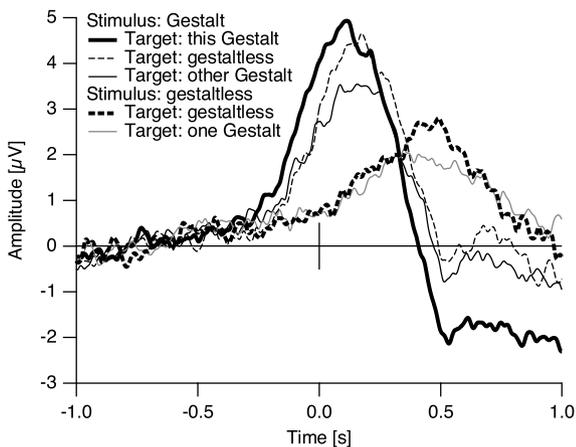


Fig. 5. Grand-mean Pz ERPs for different stimulus/task combinations, overlaid for direct comparison. The most dominant structure is a positive deflection peaking after physical Gestalt completion (time 0), but building up before it. With the Gestalt stimuli it is larger and occurs earlier than with the non-Gestalt stimuli. Compared to these differences, the effect of the task is relatively small.

square and the triangles to the same group (consisting of all shapes that contain oblique lines). If so, this might possibly contribute to the ERP differences.

#### 4.3. A visuo-cognitive oblique effect

The size of the P300-like component differed considerably between  $0^\circ$  and  $45^\circ$  Gestalts. The effect was much stronger than one would have expected from the tiny low-level differences that might have existed due to artifacts caused by the raster-scan display. We furthermore verified that the differences in amplitude are not a consequence of a larger temporal response jitter by assessing standard error of the single-subject ERPs. On average, both,  $0^\circ$  and  $45^\circ$  stimuli resulted in virtually identical standard errors, suggesting a similar variability in both conditions.

Analyzing visual scenes taken from a variety of different environments, including natural scenes, Switkes, Mayer, and Sloan (1978) Coppola, Purves, McCoy, and Purves (1998a) reported that cardinal orientations have a much higher prevalence than other orientations. Our results

Table 1

Median reaction time (RT) and corresponding interquartile range (i.r.) for the three different tasks (0°/45° Gestalt, gestaltless stimuli) and abrupt vs. continuous presentation, as obtained in a supplementary behavioral experiment

Subject	0° Gestalt				45° Gestalt				Gestaltless stimuli			
	Abrupt		Continuous		Abrupt		Continuous		Abrupt <sup>a</sup>		Continuous	
	RT	i.r.	RT	i.r.	RT	i.r.	RT	i.r.	RT	i.r.	RT	i.r.
S1	427	103	-76	127	469	86	43	105	744	375	477	357
S2	440	132	-101	137	432	109	8	143	400	280	219	227

In the trials without Gestalt, the movement of the elements was always continuous. Six blocks (3 tasks × abrupt/continuous presentation), each with 30 trials, were presented. The block order was reversed between subjects. Subjects were instructed to press a button as quickly as possible when they were sure that they had identified the target Gestalt. In the continuous conditions, subjects pressed the button about 400–500 ms earlier than in the abrupt conditions, but the variability as indicated by the interquartile range was only increased by about 20 ms. Responses for the 45° Gestalt occurred more than 100 ms later than those for the 0° Gestalt. RTs are given relative to the time when the Gestalt was presented (abrupt) or completed (continuous). Even though the trials without Gestalt were identical in the two presentation conditions, the reaction times differed by about 200 ms.

<sup>a</sup> Note that the presentation of the gestaltless stimuli was always continuous; the column heading 'abrupt' refers to the block type and indicates that the Gestalt stimuli in this block were presented abruptly.

resemble therefore those of classical P300 paradigms, such as oddball experiments, in the sense that rare stimuli elicit larger responses. The difference is that for oddball experiments rareness is defined in the context of the experiment whereas the P300 modulations in the present study would represent lifetime experience or even phylogenetic development. This is consistent with the finding by Daffner et al. (2000) that the N2–P3 amplitude difference is larger if the stimulus deviates from long-term experience.

A link between the classical oddball paradigms and the present oblique effect might be provided by Duncan-Johnson and Donchin (1977). They found that the amplitude of the P300 depends on the subjective, rather than the factual, stimulus probability. In other words, as the authors put it, P300 amplitude depends on the surprise elicited by the stimulus. The environmental rareness might make oblique stimuli more surprising, even if they occur with exactly the same probability as the other stimuli.

Environmental rareness has also been proposed by Latto (2004) and others as an important factor for the oblique effect. Latto and Russel-Duff (2002) suggested that "the more activity a stimulus generates, the more it is liked", but took this as an explanation why stronger cortical activations for cardinal orientations would be associated with better performance as demonstrated in psychophysical experiments (eg., Appelle, 1972) with gratings. However, it has been shown with other phenomena, such as repetition suppression (Grill-Spector, Henson, & Martin, 2006), that a reduction in activation can coincide with an improved performance.

Based on these considerations, a stronger response to oblique stimuli is not surprising per se. However, the present result is opposite to most studies that found an effect in low-level VEPs. It is also opposite to the one reported by Proverbio et al. (2002), who found a smaller P300 amplitude for oblique gratings. One should keep in mind, though, that in Proverbio et al.'s, 2002 study cardinal and oblique orientations were not presented equally frequently. This imbalance might have disguised an effect similar to the one in the present study. An alternative

explanation would be that obliqueness has different effects on the processing of simple gratings as compared to more complex Gestalt stimuli. Possibly, the surprisingness necessary for a large P300 only occurs with complex stimuli.

The P300 is frequently discussed as a marker of high-level cognitive processes (Linden, 2005). The fact that the oblique effect manifests itself as a modulation of a P300-like component thus hints towards a high-level phenomenon and thus, in Essock's (1980) terminology, towards a Class 2 effect. However, could this simply be inherited from earlier processing stages? In earlier time intervals, including those that we attributed to Gestalt processing (see above), differences between orientations were not statistically significant. Furthermore, characteristic properties of the P300 as known from previous studies make a simple inheritance unlikely. In particular, the size of the P300 does not depend much on the actual stimulus as such, not even on the stimulus modality (Ji, Porjesz, Begleiter, & Chorlian, 1999). In the auditory domain, it has been demonstrated that target environmental sounds embedded into a sequence of tones elicit the same P300 as target tones (Gaeta, Friedman, & Hunt, 2003). If very different stimuli can produce very similar P300 responses, it seems unlikely that a small oblique effect at preceding processing stages would substantially affect the P300.

In the light of the present results, the inverse psychophysical oblique effect that has been reported recently for certain types of broad-band stimuli (Essock et al., 2003; Hansen & Essock, 2004; Hansen & Essock, 2006) is particularly interesting. However, at present it is unclear whether they are directly related. On one hand, these studies, as well as the present study, used stimuli that were to some degree broad-band. On the other hand, these studies used stimuli with a naturalistic frequency distribution while we employed line patterns. In this respect, the present study is closer to studies that found a non-inverted oblique effect using lines or geometric shapes (Ogilvie & Taylor, 1959; Ito et al., 1997).

One might wonder whether the movement of the stimulus elements in the present study contributed to the inver-

sion of the oblique effect, in particular when compared to the study by Ito et al. (1997) who presented cardinal and oblique squares in a simple onset mode. Since the direction of motion was random, object motion and global motion can be excluded as an explanation. Furthermore, previous studies using motion VEPs (which mostly originate from area MT, cf. Heinrich, 2007) suggest that the oblique effect is not inverted in area MT, and the distribution of orientation sensitivity in area MT also appears to favor the non-inverted effect (Xu, Collins, Khaytin, Kaas, & Casagrande, 2006). There is a transient bias in local motion directions during Gestalt completion, though. This is a secondary effect due to the differences between the stimuli in the orientation distribution of line elements. However, as Dakin, Mareschal, and Bex (2005) have demonstrated psychophysically, the oblique effect in local motion processing is not inverted. We therefore feel confident that motion per se is not the reason for the inversion of the oblique effect in the present study. Furthermore, even if local motion had contributed to the P300 effect, this would not substantially affect its interpretation. Nevertheless, of course, the dynamic nature of the stimulus might have had some impact on perceptual and cognitive processing in general.

If the interpretation of the ERP component as a P300 is correct, the actual feature domain as such (e.g., motion or orientation) should be less relevant than some higher-level property, such as the already-discussed environmental rareness. This might provide the link between our results and the above-mentioned findings by Essock et al. (2003) and Hansen and Essock (2004); Hansen and Essock (2006) that showed an inverse oblique effect with using stimuli with a naturalistic spatial frequency distribution. At present, however, this remains speculative.

## 5. Conclusion

The novel stimulus paradigm presented here eliminates low-level responses in the ERP, leaving correlates of mid- and high-level processing. Their characteristics suggest that they reflect holistic Gestalt processing, but also an oblique effect, which affects a response component that likely represents a P300. This oblique effect is opposite to similar effects found in previous studies with abruptly displayed gratings. We propose that it reflects a deviation of the oblique Gestalt from the long-term environmental experience of the subjects.

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## Appendix A. Supplementary data

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.visres.2007.12.012](https://doi.org/10.1016/j.visres.2007.12.012).

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