

# Circles are different: The perception of Glass patterns modulates early event-related potentials

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## Abstract

Glass patterns are randomized dot arrays that generate the perception of a global structure. They consist of correlated dot pairs which are generated by geometric transformations. The present study employed behavioral and event-related brain potential (ERP) measures to characterize the underlying neuronal processing when such patterns are perceived. Stimuli were circular, parallel, and randomized Glass patterns presented in two isoluminant colors using a choice reaction paradigm. Sixteen subjects were instructed to differentiate between colors with a button-press response. The N170 component increased in amplitude for circular patterns, and this effect was most pronounced bilaterally over occipito-temporal areas. The results suggest that the global percept of form generated by Glass patterns occurs at a stage of visual processing past area V1.

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**Keywords:** Glass pattern; N170; Event-related potential (ERP); Visual evoked potential (VEP); Random dots

## 1. Introduction

The visual system is able to detect global correlations within a noisy pattern. However, it is still unclear how a distributed system of neurons represents global Gestalts that can influence the perception of the distributed elements of which they are formed.

Glass patterns (Glass, 1969) are very simple stimuli composed of randomly positioned dot pairs. They have been used numerous times in the past to investigate how the visual system combines correlated elements into a global percept. The original Glass patterns were at first described as resulting from superimposing a transparency of one pattern on itself and rotating it slightly such that a global pattern of concentric circles was perceived

(Glass, 1969). Several shapes of global Gestalts act as the basis of today's Glass patterns which are often hyperbolic, radial, spiral, or parallel patterns.

Previous studies have found lower detection thresholds for concentric and radial than for parallel Glass patterns (Seu & Ferrera, 2001; Wilson & Wilkinson, 1998; Wilson, Wilkinson, & Asaad, 1997). When circular, radial, and spiral Gabor patterns were evaluated, a perceptual advantage (lower detection thresholds) was found for circular patterns (Achtman, Hess, & Wang, 2003). Moreover, it was found that a global circular structure appears more stable when noise is added (Kurki & Saarinen, 2004; Seu & Ferrera, 2001; Wilson et al., 1997). These findings suggest an increase in neural activity in response to or more neurons specialized for circular patterns (Seu & Ferrera, 2001). It was suggested that circular patterns are more easily discriminated because Glass patterns are typically presented in circular windows providing a cue for detecting circular patterns

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but not for parallel ones (Dakin & Bex, 2002, 2003). However, other authors criticized that Dakin and Bex (2002) failed to provide data supporting their hypothesis convincingly since they reported lower detection thresholds for circular patterns when presented in a circularly shaped window but no consistent increase in thresholds for the same patterns when presented in square windows.

Since the cue of a circularly shaped window is not absolutely comparable to the cue which is provided by a square window further experiments are needed which exclusively deal with this problem of window cueing. So far the edge artifact of round windowed patterns could not be replicated by others (Wilson & Wilkinson, 2003). Moreover, threshold differences favoring circular Gabor patterns were found in spite of using rectangular windows (Achtman et al., 2003). Recently, McGraw, Badcock, and Khuu (2004) demonstrated that the global percept of circular and radial Glass patterns is vulnerable to steady-viewing. In contrast, parallel Glass patterns appeared to be relatively robust under this condition. The authors replicated this effect for both circularly and rectangularly shaped windows and argued for different mechanisms underlying the perception of global form in each pattern. Thus, the argument raised by Dakin and Bex (2002) is still under debate. Taken together, these findings suggest that the visual system detects circular patterns more easily and with increased stability (as indicated by lower detection thresholds and higher tolerance of lower signal-to-noise ratios, respectively) than other pattern types. It is reasonable that different mechanisms underly the perception of circular (as well as radial and spiral) patterns compared to parallel Glass patterns.

Several models have been proposed that attempt to integrate behavioral data on Glass pattern perception with functional neuroanatomy of the visual system. Two competing models should be discussed here. An initial, influential model was proposed by Glass (1969) post-hoc to his discovery of Glass patterns. He proposed that orientation sensitive units in V1 detect the entire Glass pattern by combining responses across orientation columns. This detection mechanism requires the following assumptions: line detectors in visual cortex are activated by two corresponding dots only if both dots of one dot pair fall into the excitatory field of the same detector. Additionally, the number of dots falling into the detector's inhibitory field has to be small enough to produce overall excitation. If such an activation was produced for other dot pairs along the circumference of a circle but not for randomly oriented dots, perception of a circular pattern would occur. For that purpose the proportion of activated detectors along the circumference of the circle grows inversely proportional to the angle of rotation (Glass, 1969). According to this model the visual system must detect the line segments

falling along the circumference of the circles centered at the point of rotation, and “disregard” the line segments lying in random directions (Glass, 1969, p. 579). This appears to reflect the selective sensitivity of V1 neurons to lines and edges (Hubel & Wiesel, 1968). According to these proposals, Glass pattern perception is directly related to the functional properties of primary visual cortex (Glass, 1969). Although this model appeared to conform with knowledge about the physiology of the primate visual system at the time it was proposed more recent evidence argues against the generation of perception of circular patterns entirely in V1. Receptive fields of line detector cells in V1 have been shown to be too small to detect orientation structure over a larger region (Smith, Bair, & Movshon, 2002; Wilson & Wilkinson, 1998). Therefore, long-range circuitry which connect neurons with different orientation preferences or detector cells for curvature would be required to detect a circular pattern entirely within V1.

A more recent model has been proposed which attempts to be consistent with data from behavior, physiology, and anatomy. This multi-stage filtering detection theory of circular Glass patterns assumes multiple parallel pathways each representing a certain orientation (Wilson & Wilkinson, 1998; Wilson et al., 1997). The first stage is proposed to be localized in V1, wherein stimuli are filtered for orientation. The second stage is thought to be located in V2 and performs rectification and further pairwise filtering by center-surround filters. The third and final stage is hypothesized to occur in V4 and is thought to pool and sum the output from the previous stages and to pass the information through a threshold function. This neural model is in good agreement with experimental data and physiology of primate area V4, an intermediate level of the form vision pathway. Electrophysiological findings in primates revealed feature selective neurons and enhanced activity to concentric and hyperbolic patterns (Gallant, Braun, & Van Essen, 1993). Additionally, most V4 neurons respond to sinusoidal as well as to polar patterns, so that V4 neurons seem to act as efficient encoding mechanisms of complex features rather than as simple edge detectors (Gallant, Connor, Rakshit, Lewis, & Van Essen, 1996). This interpretation has also been applied to neurons in posterior inferior temporal cortex (IT), which respond maximally to complex object features such as faces. The neurons in posterior IT have smaller receptive fields (compared to those in anterior IT) which facilitates integration of components and position detection in a visual scene (Kobatake & Tanaka, 1994). In addition, a study of memory influence on V4 revealed that neurons in V4 can detect natural scenes in degraded images after monkeys have been trained on a detection task (Rainer, Lee, & Logothetis, 2004). These neurons appear to be especially recruited for difficult discriminations and represent a learning dependent mode of attention in a

fashion that reflects an interaction between top–down and bottom–up input resulting in response enhancement (Rainer et al., 2004). In summary, there is good evidence that the involvement of extrastriate visual areas like V4 and IT is necessary for the perception of complex visual patterns.

The present study was designed to assess human neuroelectric correlates of Glass pattern perception by using event-related potential (ERP) methods to obtain high temporal precision. ERPs are an ideal tool to investigate the time point at which Glass patterns elicit measurably different responses than random patterns. While neuroimaging methods (e. g. fMRI) offer better spatial resolution it is often hard to determine whether observed activation in visual areas was already present during the initial response of that area or whether it resulted from later feedback signals sent from higher visual areas. Moreover, since EEG reflects synchronous activity of larger patches of cortex it might be more effective than single-unit recordings in detecting perceptual phenomena that rely on integration of neurons (Fries, Schroder, Roelfsema, Singer, & Engel, 2002; Tallon-Baudry, Mandon, Freiwald, & Kreiter, 2004). Despite EEG's lower spatial resolution the approximate location of generators of EEG potentials can be estimated by source localization techniques. The neural generators of early ERPs have been studied extensively (see below). Thus, the latency of pattern effects in EEG can be used to infer which region of the visual system processes specific aspects of Glass patterns.

The earliest visual evoked ERP components are the C1, P1, and N1. The C1 is the first component of cortical origin. Due to the location of its generators it is greatly diminished under full field stimulation (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2001) and was, therefore, not considered in this study. The P1 and N1 components are the first prominent positive and negative deflections of the ERP, respectively. These ERP components are sometimes alternatively labeled P100 and N170 according to their average latencies (approximately 100 ms and 170 ms, respectively; Picton et al., 2000). In the present report, we will adhere to this second notation of ERPs.

As the P100 and N170 components are known to be sensitive to simple visual features such as spatial frequency or contrast (cf. Celesia, 1993), one can expect to find general effects of Glass pattern perception on these components. Furthermore, N170 has been linked to the processing of edge detection in Kanizsa figures, with enhancement of N170 to illusory contours (Herrmann & Bosch, 2001). N170 is also considered a neurophysiological correlate of face perception (Itier & Taylor, 2004). Some studies found evidence for N170 generators in extrastriate areas, especially in V2, which suggests that the N170 component and the integration of contours occur at a temporally and anatomically

early stage of visual processing (Proverbio & Zani, 2002). Another study located N170 generators mainly in lateral extrastriate areas such as V4. The activity of these generators was found to increase in response to spatially attended stimuli (Gomez Gonzalez, Clark, Fan, Luck, & Hillyard, 1994). Other findings point to multiple generators in different visual areas including V3, V3a, and V4 (Di Russo et al., 2001). As ERPs are not influenced exclusively by sensory processes but also processes involved in target detection, attention, motor responses etc. we decided to employ a task that is unrelated to pattern structure. Thus, we attempted not to confound effects of pattern perception with effects of target detection, response preparation, etc. In conclusion, we hypothesized that the existence of circular feature detection mechanisms or summation units should manifest in modulations of the N170 component with circular patterns eliciting the largest ERP amplitudes.

## 2. Materials and methods

### 2.1. Subjects

A total of 16 students at Magdeburg University (mean 23.6, 20–29 years; 8 female; 15 right handed) participated in the study and were paid for participation. All subjects had normal or corrected to normal vision. None reported neurological or psychiatric disorders, and all provided informed written consent.

### 2.2. Stimuli and procedure

Glass patterns were constructed using the following algorithm. The overall pattern density was 4800 dots of 2.2' diameter. Dots were arranged pairwise with 7.2' separation (2400 pairs or dipoles) in a circular window of 3.4° radius. Using a constant distance within a dipole makes these stimulus patterns different from the original Glass pattern (Glass, 1969), such that the gap between dots in the original study increased with increasing distance from center to periphery of the pattern. A constant distance, as applied here, permits comparison of rotation (circular patterns) and translation (parallel patterns). Hence, a circular pattern was constructed by shifting all dots (no matter at which eccentricity) with a certain angle of rotation, such that the arc length was the same between two dots of a pair (see also Wilson & Wilkinson, 1998; Wilson et al., 1997).

Dot pairs were 100% signal dots and either arranged in randomized fashion, by vertical translation, or along an arc length (rotation) resulting in three stimulus conditions. In this respect our stimuli differed from those used in previous studies which included noise dots also in circular and parallel patterns. The stimuli were presented in isoluminant colors of red (rgb 120, 10, 60)

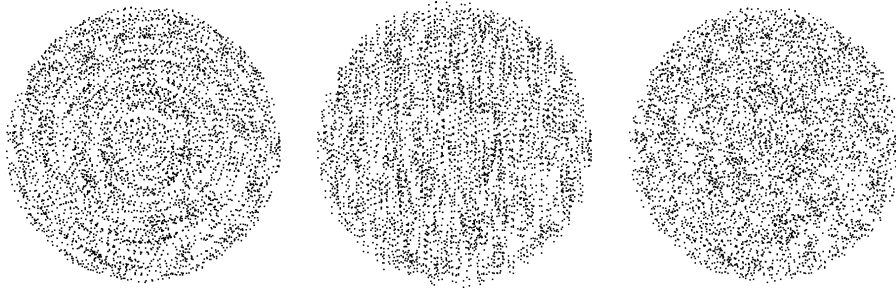


Fig. 1. A circular (left), parallel (middle), and randomized (right) Glass pattern as used in this study. All pattern conditions underly the same construction mechanism including the same number of dot pairs. In the experiment, patterns were presented in two isoluminant colors (red, violet) on a white background. Therefore, the patterns were identical with respect to most physical parameters.

and violet (rgb 90, 20, 100) on a white background. Isoluminance (mean  $3.5 \text{ cd/m}^2$ ) was not equated perceptually for each subject but tested by a chromameter (Minolta). Fig. 1 illustrates the stimuli and indicates that all patterns were identical with respect to most physical parameters such as number of dots, dot size, distance between dots, and luminance. Patterns and colors were presented in pseudo-randomized order resulting in a pattern probability of 0.33 and a color probability of 0.50, with 70 stimuli presented for each combination of pattern (randomized, parallel, circular) and color (red, violet) condition resulting in a total of 420 stimulus presentations. A forced-choice response task required subjects to press a button with the index finger of one hand if the pattern was red and to press another button with the other hand if it was violet. Response hand was counterbalanced across subjects and gender. Subjects were instructed to respond as quickly as possible and were not informed about the three different pattern conditions before the start of the experiment.

Stimuli were presented on a computer monitor placed at a distance of 1 m in front of the subjects. Monitor refresh rate was 100 Hz. Stimuli subtended a visual angle of  $6.8^\circ$  and were presented centrally for 1000 ms, with a randomized variable inter-stimulus interval of 1500, 1600, or 1700 ms. During the ISI a fixation cross ( $0.6^\circ \times 0.6^\circ$ ) was presented to have subjects maintain fixation. Because onset and offset responses produce a similar signal, and offset responses overlap with other ERP components stimulus duration should last at least as long as the latency of the latest component analyzed (Busch, Debener, Kranczioch, Engel, & Herrmann, 2004). Subjects were provided rest periods and were interviewed after the experiment about strategies to discriminate colors and noticed pattern differences.

### 2.3. Data acquisition

EEG was recorded with a BrainAmp amplifier (Brain Products, Munich) using 32 sintered Ag/AgCl electrodes mounted in an elastic cap (EasyCap, FalkMinow Services, Munich) and placed according to the 10–10 sys-

tem, with a nose-tip reference and ground electrode at AFz. Eye movement activity was monitored with an electrode placed supraorbitally to the right eye and also referenced to the nose. Electrode impedances were below  $10 \text{ k}\Omega$ . Data were sampled at 500 Hz, analog filtered between 0.01–200 Hz and stored on hard disk for off-line analysis. Recordings were made while subjects sat in an electrically shielded, sound-attenuated room.

Averaging epochs lasted from 200 ms before to 900 ms after stimulus onset. Baselines were computed in the interval from 200 to 0 ms prior stimulus onset and subtracted before averaging. An automatic artifact rejection was computed which excluded trials from averaging if the standard deviation within a moving 200 ms time interval exceeded  $40 \mu\text{V}$ . All epochs were also visually inspected for artifacts and rejected in case of eye movement or electrode drifts. Trials containing rejected sampling points were excluded from further analysis, as were error trials or trials in which response time exceeded the grand mean by more than two standard deviations.

In a semi-standardized post experimental interview subjects were interrogated whether they noticed any pattern differences or followed any strategies referring to the color discrimination task. Seven of 16 subjects reported in the interview having noticed neither circular patterns nor any pattern differences at all. Nine subjects reported having seen circular structures during the experiment. Subjects were, therefore, divided into two groups (perception “yes” and “no”) for a first analysis but pooled together later.

### 2.4. Data analysis

After first computing ERPs for single electrodes selected electrodes were merged into three regions of interest (ROIs) to avoid a loss of statistical power (Oken & Chiappa, 1986). ROIs and corresponding electrodes were named anterior (Fp1, Fp2, F3, F4, F7, F8, Ft9, Ft10, Fz), central (FC1, FC2, T7, T8, C3, C4, Cz, TP9, TP10, CP5, CP6), and posterior (CP1, Cp2, P3, P4, P7, P8, O1, O2). ERP components were defined as peak amplitudes in the time intervals 80–100 ms (P100)

and 140–170 ms (N170). Time windows were based on the grand mean average. In order to visualize the topographical distribution of pattern effects on the N170 component a difference topography was computed. Mean voltage in the time window from 140 to 170 ms in the circular condition was subtracted from the mean voltage in the randomized condition thereby revealing the locations at which N170 amplitude was modulated by Glass pattern perception.

Repeated measures ANOVAs of ERP effects were at first computed for the within subjects factors pattern (circular, parallel, randomized), color (red, violet), ROI (anterior, central, and posterior), and the between-subjects factor perception (yes, no). Since there was no effect of the between-subjects factor (perception) it was excluded from further analyses and all reported analyses were computed for the entire sample. Response time (RT) was analyzed for valid responses in the time interval 200–1200 ms after stimulus onset. Excluded data (RT exceeding time window, or 2 standard deviations from mean) represented 3.78% of all trials. Repeated measures ANOVAs of behavioral effects were at first computed for the within subjects factors pattern (circular, parallel, randomized), color (red, violet), ROI (anterior, central, posterior), and the between subjects factor perception (yes, no). Post-hoc contrasts were computed for ERP as well as for behavioral data by repeated measures ANOVAs with a single factor comprising two levels. The alpha level was a priori set to 0.05. Greenhouse-Geisser correction was used where appropriate. Uncorrected degrees of freedom and corrected  $p$ -values are reported. The eta square statistic was adopted to describe the estimated proportion of variance explained by the factors.

### 3. Results

#### 3.1. Behavioral performance

A two-factor (3 pattern [circular, parallel, randomized]  $\times$  2 color [red, violet]) analysis of variance was applied to the error data of all subjects. Analysis of error rates (ER) yielded an increase for randomized violet (27.94%) patterns, compared to parallel violet (18.66%) and circular violet (16.97%) ones. This outcome contributed to the significant differences between colors,  $F(1,15) = 4.986$ ;  $p = 0.041$ ;  $\eta^2 = 0.249$ , an interaction between pattern and color conditions,  $F(2,28) = 6.363$ ;  $p < 0.008$ ;  $\eta^2 = 0.312$ , as well as significant differences between patterns across colors,  $F(2,28) = 35.995$ ;  $p < 0.001$ ;  $\eta^2 = 0.720$ . The same analysis was applied to the RT data. No significant effects of pattern or color were revealed for RT.

The ER was comparatively high and RTs were long. The mean ER was 15.57% which corresponds to 10.9 er-

Table 1

Mean response times (left) and mean error rates (right) with standard deviations (SD) of 16 subjects in response to circular, parallel, and randomized Glass patterns of red or violet color

Condition	Response times [ms]		Error rates [%]	
	Mean	SD	Mean	SD
Randomized red	586.78	118.10	18.04	9.59
Randomized violet	576.69	97.11	27.94	12.41
Parallel red	575.30	107.59	16.34	11.07
Parallel violet	586.04	91.43	18.65	10.53
Circular red	587.53	105.14	16.61	8.81
Circular violet	584.83	96.77	16.97	8.73

rors. The mean RT was 582.86 ms (SD = 102.9 ms). This outcome reflects the high task difficulty (Table 1).

#### 3.2. ERP analyses

Fig. 2 shows the grand averaged ERPs at nine representative electrodes (three from each ROI). A three-factor (3 patterns [circular, parallel, randomized]  $\times$  2 colors [red, violet]  $\times$  3 ROIs [anterior, central, posterior]) repeated measures ANOVA was applied to ERP data. All significant results are reported in Table 2.

Analyses of P100 amplitudes yielded increasing amplitudes from anterior ( $-0.530 \mu\text{V}$ ) over central ( $1.195 \mu\text{V}$ ) to posterior ( $4.460 \mu\text{V}$ ) regions across patterns and colors resulting in a significant main effect of ROIs,  $F(2,28) = 26.334$ ;  $p < 0.001$ ;  $\eta^2 = 0.653$ . No further main effects or interactions were found for this component.

Circular patterns produced a significantly larger N170 in the posterior region compared to randomized patterns,  $F(1,15) = 13.034$ ;  $p = 0.003$ ;  $\eta^2 = 0.465$ , and showed a marginally significant increase to parallel ones,  $F(1,15) = 4.244$ ;  $p = 0.056$ ;  $\eta^2 = 0.221$ . Moreover, N170 peak amplitude increased as hypothesized from randomized ( $0.984 \mu\text{V}$ ) to parallel ( $0.695 \mu\text{V}$ ) to circular ( $-0.078 \mu\text{V}$ ) patterns within this region. This outcome contributed to the significant interaction between pattern conditions and ROIs,  $F(4,56) = 14.755$ ;  $p < 0.001$ ;  $\eta^2 = 0.513$ , resulting from significant pattern differences in the posterior region,  $F(2,30) = 4.973$ ;  $p = 0.016$ ;  $\eta^2 = 0.249$ . This effect was most pronounced at O1 and O2 (Fig. 3), but still significant over the whole posterior region. Accordingly, the difference topography of the N170 effect (randomized–circular) shows a widespread posterior effect (Fig. 4).

### 4. Discussion

The aim of the present study was to find electrophysiological correlates of Glass pattern processing and perception. Behavioral data showed no effects of stimulus

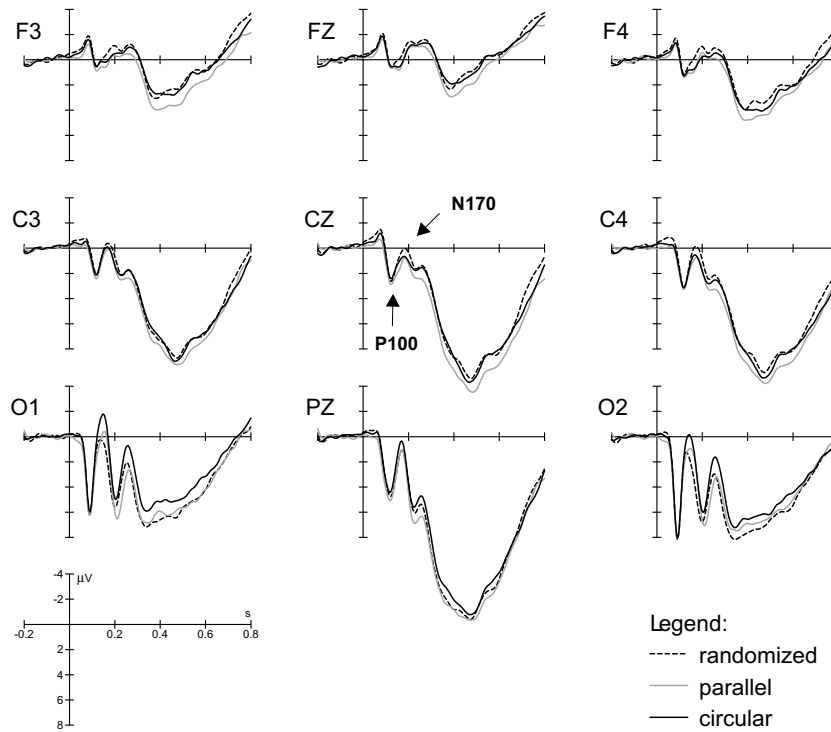


Fig. 2. Grand-averaged ERPs at 9 electrodes in response to circular (black), parallel (grey), and randomized (dotted) Glass patterns ( $n = 16$ ). At frontal sites (F3, Fz, and F4) neither P100 nor N170 show pattern effects. At central (C3, Cz, and C4) as well as at occipital sites (O1, O2, and Pz) circular patterns show an increased N170 amplitude, although this effect was significant only for the posterior region.

Table 2

Summary of  $F$ -values and probabilities from the three-factor (3 patterns [circular, parallel, randomized]  $\times$  2 colors [red, violet]  $\times$  3 ROIs [anterior, central, posterior]) ANOVA performed on the P100 and N170 amplitude ( $n = 16$ )

Source	df	P100		N170	
		$F$	$P$	$F$	$P$
<i>Repeated measures comparisons</i>					
Pattern (P)	–	–	–	–	–
Color (C)	–	–	–	–	–
ROI (R)	2,30	27.51	<b>&lt;0.001</b>	–	–
$P \times C$	–	–	–	–	–
$R \times C$	–	–	–	–	–
$P \times R$	–	–	–	14.76	<b>&lt;0.001</b>
$P \times C \times R$	–	–	–	–	–
<i>Post-hoc comparison ROI</i>					
Anterior vs. posterior	1,15	28.78	<b>&lt;0.001</b>	–	–
Anterior vs. central	1,15	39.99	<b>&lt;0.001</b>	–	–
Central vs. posterior	1,15	23.11	<b>&lt;0.001</b>	–	–
<i>Post-hoc comparison <math>P \times R</math></i>					
$P \times$ anterior	2,30	–	–	–	–
$P \times$ central	2,30	–	–	–	–
$P \times$ posterior	2,30	–	–	4.97	<b>0.016</b>
<i>Post-hoc comparison <math>P \times R</math> (posterior)</i>					
Parallel vs. randomized	1,15	–	–	–	–
Circular vs. parallel	1,15	–	–	4.24	0.056
Circular vs. randomized	1,15	–	–	13.03	<b>0.003</b>

The reported  $F$ - and  $p$ -values were Greenhouse-Geisser corrected. Only significant results are listed.

features except for the increased ER to randomized violet patterns. However, neither response times nor ERPs showed this interaction effect. Therefore, one can not

conclude that color discrimination of circular and parallel (but not randomized) patterns is facilitated for specific colors. The lack of significant RT and ERP

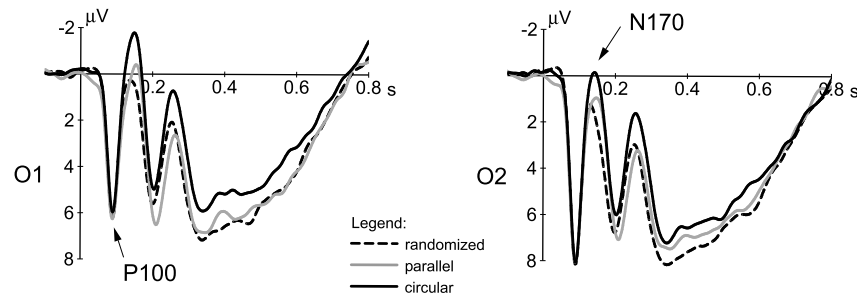


Fig. 3. Grand-averaged ERPs at two representative occipital electrodes (O1 and O2) in response to circular (black), parallel (grey), and randomized (dotted) Glass patterns ( $n = 16$ ). The N170 amplitudes show a clear enhancement in response to circular patterns. No such differences were found for P100 amplitude.

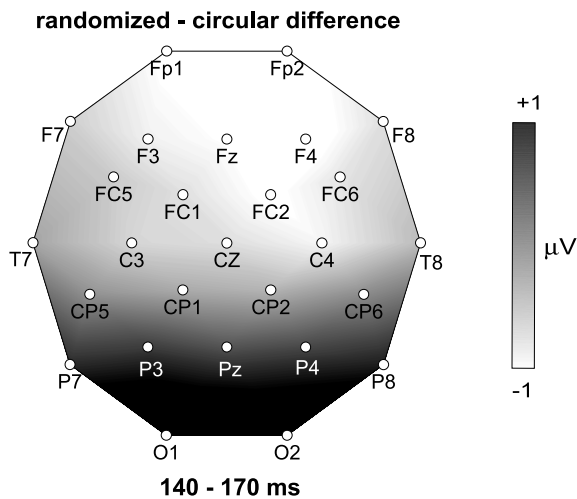


Fig. 4. For the difference topography the circular condition was subtracted from the mean voltage of the randomized condition in the time window from 140 to 170 ms. The topography shows a widespread posterior effect which corresponds to the N170 amplitude modulation by circular Glass pattern perception.

effects for this contrast supports this argument. Since other studies (Cardinal & Kiper, 2003) found an interaction between pattern detection thresholds and dot color it might be valuable to conduct future studies to clarify this issue.

ERPs revealed the predicted modulation of N170 with stimulus properties, i.e. larger responses for circular patterns. No effects of stimulus patterns were found for the earlier P100 component. Our results show that circular Glass patterns evoke stronger N170 amplitudes than randomized patterns. We failed to find such a strong effect for parallel patterns. However, this might be due to the fact that the circular global shape of all our patterns might have supported the perception of circular Glass patterns (Dakin & Bex, 2002). It is conceivable that a rectangular global shape might yield similar results also for parallel Glass patterns. Further experiments should therefore vary the global shape of the patterns.

Glass (1969) explained his phenomenon by properties of primary visual cortex. In contrast, Wilson et al. (1997) assumed V4 as the final stage in Glass pattern perception, which is strongly supported by the present outcomes. The first significant effect of stimulus type was found on the N170 component the generators of which have been located in extrastriate areas such as V2, V3, V3a and V4 (Di Russo et al., 2001; Gomez Gonzalez et al., 1994; Proverbio & Zani, 2002). In line with these electrophysiological data an fMRI experiment using Glass patterns revealed increased activity in V4 for circular Glass patterns (Tse et al., 2002). Hence, the present data are consistent with models proposing that the critical processes of Glass pattern perception are located in the same areas that have been shown to be the generators of the N170 component.

In addition, the larger amplitudes in response to circular as compared to parallel patterns argue for a specialization of the human visual system for global circular forms. This approach opens the question for the functional role of this specialization. Wilkinson et al. (2000) demonstrated that face selective portions of the fusiform gyrus were also activated by concentric patterns. In line with this, Allison, Puce, Spencer, and McCarthy (1999) used intracranial recordings in humans to show that recording sites that were especially selective for complex patterns (e.g. circular or spiral gratings) were located more posterior and were activated slightly earlier than sites selective for faces. The authors interpreted the pattern selective regions as the human equivalent of monkey V4 and argued that processing of complex patterns occurs at a pre-stage to face perception. For primates it is important to be sensitive to circular shapes for this is a fundamental of face perception which is on its part crucial for social interaction. This outcome might explain the lower detection thresholds for circular patterns revealed by behavioural data from detection tasks (Seu & Ferrera, 2001; Wilson & Wilkinson, 1998; Wilson et al., 1997) as well as increased negativity of N170 for circular patterns in the present study. Findings of N170 modulation by face perception

resulting in enhanced amplitudes to faces compared to non-face stimuli are also consistent with the present findings (Horowitz, Rossion, Skudlarski, & Gore, 2004). Moreover, N170 has been shown to be associated with structural encoding processes prior to face identification (Eimer & McCarthy, 1999). The results suggest that processes responsible for circular Glass pattern perception are also involved in (and may be primarily designed for) identification of faces. Furthermore, N170 increases during the perception of illusory contours of Kanizsa figures (Proverbio & Zani, 2002; Herrmann & Bosch, 2001). N170 modulation by Gestalt and contour perception can be applied assumedly to Glass pattern perception, particularly to circular Glass patterns. One might even call the circular Glass patterns illusory circles with respect to the similar N170 findings for illusory contours. It is conceivable, however, that a specialization exists not for circular patterns per se but for complex patterns in general (Wilson & Wilkinson, 1998; Allison et al., 1999). Further electrophysiological experiments using different complex patterns should be conducted to clarify this issue.

A second non-contradictory interpretation takes into account that V4 activity is also modulated by learning and memory (Rainer et al., 2004). Circular shapes are common in our environment and everyday life. It can be assumed that humans develop strong memory representations of familiar stimuli as compared to stimuli which have never been presented before (Herrmann, Lenz, Junge, Busch, & Maess, 2004). Hence, V4 activity and ERPs generated in or near V4 such as the N170 might be enhanced in response to circular patterns because circular patterns provide a better match with memory representations than noise patterns. Tanaka and Curran (2001) found the visual system able to learn to tune itself to respond selectively to specific visual information. However, mechanisms of this selection are still unknown but it seems that relevance of the information (ecologically as well as personal) plays an important role. Moreover, the authors revealed enhanced N170 amplitudes when categorizing objects of expertise compared to objects outside this expertise. Taken together, N170 is not only a good neurophysiological index of face perception and its underlying encoding mechanisms but also of expert object recognition which both are based on a strong memory representation of specific visual information.

## 5. Conclusions

In summary, the present study demonstrates that the perception of circular Glass patterns evokes an increase in N170 amplitude in almost the same manner as the perception of faces, objects of expertise, and illusory contours in Kanizsa figures do. Our findings support

assumptions that the visual system is specialized for circular shapes as it has been already shown in numerous behavioral investigations. Moreover, the increase in N170 amplitude for circular Glass pattern perception supports the multi-stage filtering model of circular Glass pattern perception (Wilson et al., 1997). Thus, a large body of evidence indicates that different neuronal mechanisms underly the perception of circular vs. parallel and randomized Glass patterns. Moreover, our results are consistent with the idea that circular Glass patterns share a common neural substrate with face perception.

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