Time-course of perceptual processing of “hole” and “no-hole” figures: An ERP study

Weina Zhu^{1,2,3}, Junjun Zhang⁴, Changle Zhou⁵

¹*School of Information Science, Yunnan University, Kunming 650092, China*

²*Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming 650223, China*

³*Department of Psychology, Giessen University, Giessen 35390, Germany*

⁴*Department of Cognitive Sciences, University of California, Irvine, Irvine, California 92602, USA*

⁵*School of Information Science and Technology, Xiamen University, Xiamen 361005, China*

Corresponding author: Weina Zhu. E-mail: zhuweina.cn@gmail.com

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ABSTRACT

Closure or the presence of a “hole” is an emergent perceptual feature that can be extracted by the visual system early on. This feature has been shown to have perceptual advantages over openness or “no-hole”. In this study, we investigated when and how the human brain differentiates between “hole” and “no-hole” figures. Event-related potentials (ERPs) were recorded during a passive observation paradigm. Two pairs of simple figures (Experiment 1) and two sets of Greek letters (Experiment 2) were used as stimuli. The ERPs of “hole” and “no-hole” figures differed ~90 ms after stimulus onset: “hole” figures elicited smaller P1 and N1 amplitudes than “no-hole” figures. These suggest that both P1 and N1 components are sensitive to the difference between “hole” and “no-hole” figures; perception of “hole” and “no-hole” figures might be differentiated early during visual processing.

Keywords: closure; “hole” stimuli; event-related potentials; P1; N1

INTRODUCTION

Figures containing a “hole” (closed figures) and those without a “hole” (open figures) can be grouped into two

categories based on their topological properties. In psychophysiological studies, it has been proposed that the global topological^[1-4] or configural-wholistic^[5-7] properties of visual patterns, such as hole/no-hole or closure/openness, inherently enjoy some advantage in the early stages of visual perceptual processing. Even infants, at a few days from birth, are able to categorize stimuli into open (without a “hole”, i.e., crosses) and closed forms (with a “hole”, i.e., circles, triangles, and squares)^[8].

In particular, the presence of a “hole” in the figure or closure is considered to be an “emergent feature” that can be extracted by the visual system early on, and processing of “hole” figures is typically faster and easier^[6,9-11], and also more robust against masking effects^[12]. It is important to mention that the concept of a “hole” in the present study is two-dimensional; it does not require any extended surface, or figure-ground structure. Thus, the terminology “hole” used here is fundamentally different from that defined in previous studies on “hole” perception, in which the “hole” is defined as a background region that is surrounded by a foreground figure^[13,14].

In a single-unit recording study on monkeys, neurons in the inferior temporal cortex were found to be selectively activated by “hole” figures, with very short latency (<100 ms)^[15]. The specific nature of “hole” stimuli may be important for the computation of an object representation. However, some questions are still unclear: What is the neural substrate of this perceptual difference? At what time do

“hole” figures begin to deviate from “no-hole” figures? The aim of the present study was to investigate when and how the human brain differentiates between “hole” (closed figures) and “no-hole” (open figures).

Event-related potential (ERP) studies of the human brain have shown that object categories can be distinguished by electrophysiological activity recorded on the surface of the occipito-temporal cortex^[16]. ERPs have been shown to reflect category or identity after roughly 150 ms^[17,18], for faces and other objects^[19,20]. ERPs are suitable for investigating the time-course of object categorization^[17]. The use of ERPs, affording excellent temporal resolution, enables measurements that can help distinguish the processes associated with “hole” and “no-hole” effects.

ERP correlates of object categorization have been reported in multiple latency ranges, including early components beginning at 75–80 ms after stimulus onset^[18], N1^[17,21–22], P2, N2^[23], and later components (450–550 ms)^[21]. In our previous study^[12], we found a tendency towards a larger amplitude associated with “no-hole” stimuli around 140 ms, thus we hypothesize the difference between “hole” and “no-hole” (if there are any differences identifiable in ERPs) should display in early components before 200 ms.

In that study^[12], we used orientation-defined texture figures as stimuli and the texture segregation ERP (tsERP) was measured (the tsERPs is defined as the difference wave resulting from the subtraction of the ERP of a homogeneous figure from that of a segregated figure; it is used to study figure-ground segregation). We found that in a masking condition, “hole” figures appear to be easier to detect than “no hole” figures. In a non-masking condition, though the mean amplitude of the second tsERP component (~140 ms) of a “no-hole” stimulus is larger than that of a “hole” stimulus, the difference is not significant. We concluded that the difference may be caused by perceptual processing after surface segregation^[12]. In order to (i) achieve a more direct comparison between “hole” and “no-hole” figures, (ii) further test whether the difference of “hole” and “no-hole” figures on the tsERP component exists in normal ERP components, and (iii) exclude the effects of surface segregation on the processing of “hole” figures, we used normal figures instead of orientation-defined texture figures as stimuli in this study. Furthermore, all stimuli were displayed to the subjects without masking,

resulting in a more direct response of the visual system to “hole” and “no-hole” figures.

In order to be comparable to previous research, we used the same stimuli: an **O**-like figure and an **S**-like figure (hereafter referred to as **O** and **S**) as in our previous masking experiment^[12] and experiments by Chen on humans^[2,24] and honey bees^[25].

Our previous study^[26], using triangles and arrows with different orientations as stimuli, showed more notable effects of orientation than topological categories. We suggested that “hole” and “no-hole” stimuli that were similarly or less affected by orientation are more suitable for investigating the visual processing of topological categories. Thus a **□**-like figure and a **⊠**-like figure (hereafter referred to as **□** and **⊠**) were used.

In order to record visual-evoked potentials (VEPs), we used an oddball task (Fig. 1). The oddball task consisted of infrequent target stimuli and frequent non-target stimuli. Subjects were asked to respond to the target stimuli only. We concentrated on the difference between the processing of different non-target categories (“hole” and “no-hole”).

In order to remain consistent in our articles and avoid confusion, hereafter, we will use “hole”/“no-hole” but not “closure”/“openness” or “holistic” in the following text.

METHODS

Ethics Statement

Both experiments were approved by the Ethics Committee of the Kunming Institute of Zoology, Chinese Academy of Sciences, and performed according to the principles expressed in the Declaration of Helsinki. All participants were informed about the procedure of the experiment. Written informed consent was obtained from all participants.

Experiment 1

Participants

Fourteen right-handed subjects (seven females and seven males) participated in Experiment 1. Their mean age was 24.5 years (SD = 1.23; range, 21–26). Subjects were undergraduates from Yunnan University with normal or corrected-to-normal vision, and reported no history of neurological disease. All subjects were informed about the procedure of the experiment and were paid for their participation.

Fig. 1. Schematic of the paradigm and procedure of Experiment 1. An oddball paradigm was used: the task consisted of infrequent target stimuli ($P = 0.2$, schematic drawing of a flower) and frequent non-target stimuli ($P = 0.8$). The non-target stimuli consisted of two categories, “hole” and “no-hole” figures, and each contained two figures. Subjects were required to respond only to target stimuli, but analysis was performed on the results of non-target stimuli.

Experimental Procedure

In order to compare the VEPs of “hole” and “no-hole” stimuli, we used a passive paradigm in a visual oddball task: subjects were required to respond only to target stimuli, but we analyzed the results of non-target stimuli (Fig. 1).

The task consisted of infrequent target stimuli ($P = 0.2$, schematic drawing of a flower) and frequent non-target stimuli ($P = 0.8$). The non-target stimuli consisted of two categories, namely “hole” and “no-hole” figures, and each contained two figures spanning $5.18^\circ \times 5.18^\circ$ of visual angle (Fig. 2). Visual stimuli were presented on a CRT screen positioned ~ 100 cm in front of the subject.

The experimental session consisted of four blocks of 100 trials each, presented with an inter-stimulus interval of 400–700 ms. The stimuli were shown at the center of the screen for 500 ms. Target and non-target trials were presented randomly within each session. Subjects were instructed to press a button with their right index finger in response to the target stimulus, and to ignore all other stimuli. The experiment included several practice trials in order to familiarize the subjects with the task.

Stimuli

Two pairs of 2-D figure stimuli (Fig. 2) were used in Experiment 1. All stimuli were black, drawn on a gray background. These stimuli were designed as the non-target stimuli of the oddball paradigm to present both “hole” and “no-hole” figures equally.

All figures were designed to control for the difference of local features between “hole” and “no-hole” stimuli (Fig. 2).

The form of the first pair of stimuli (“hole”) and **S** (“no-hole”) was identical to previous research on “hole”^[2,25-27]. The outer and inner diameters of the were 10.09 and 5.33 cm, respectively. The area of the was 57.7 cm². The **S** was scaled to approximate the area (luminous flux) and perimeter of the , and its shape was purposely made irregular in order to eliminate the possible effects of subjective contours or other organizational factors (such as parallelism, or similarity of length)^[2].

The second pair of stimuli were (“hole”) and **I** (“no-hole”). The outer and inner lengths of each side of the were 10.09 and 5.33 cm, respectively. The height and width of the horizontal arms of **I** were 3.1 and 10.09 cm; and the

Fig. 2. A: Stimuli used in Experiment 1, consisting of two categories (“hole” and “no-hole” stimuli). Each category had two figures, each spanning $5.18^\circ \times 5.18^\circ$; B: Corresponding amplitude spectra (2D Fourier transformation) of the stimuli shown in A. C: Stimuli used in Experiment 2, consisting of two sets of Greek letters (“hole” and “no-hole”). Each set had eight Greek letters with a constant font size.

height and width of the vertical arms of **I** were 3.89 and 2.8 cm. The areas of **□** and **I** were 73.40 cm² and 73.45 cm² respectively. Thus the difference in area (luminous flux) between **□** and **I** was near zero. The **□** and **I** consisted of identical horizontal and vertical line segments, which excluded any orientation cues between “hole” and “no-hole” figures.

The amplitude spectra (2D Fourier transformation) of the stimuli from Experiment 1 revealed that the differences in spatial frequency characteristics within each stimulus set (**○** vs **S**, **□** vs **I**) were much smaller than the differences between stimulus sets (**○** vs **□**, **S** vs **I**; Fig. 2B). Simple cues in the frequency spectra therefore could not be used to determine whether a stimulus was of the “hole” or “no-hole” type.

In summary, the pairs of stimuli were designed to exclude the effects of luminous flux, perimeter length, orienta-

tion cues and spatial frequency components.

Event-Related Potential Recordings

The subjects were seated in a quiet room and fitted with a Quick-Cap (Neuroscan, Charlotte, NC). EEG was recorded from 64 channels, based on the international 10-20 system. The montage included eight midline sites (FPZ, FZ, FCZ, CZ, CPZ, PZ, POZ, OZ), 27 left hemisphere sites (FP1, AF3, F1, F3, F5, F7, FC1, FC3, FC5, FT7, C1, C3, C5, T7, CP1, CP3, CP5, TP7, P1, P3, P5, P7, PO3, PO5, PO7, O1, CB1), and 27 right hemisphere sites (FP2, AF4, F1, F4, F6, F8, FC2, FC4, FC6, FT8, C2, C4, C6, T8, CP2, CP4, CP6, TP8, P2, P4, P6, P8, PO4, PO6, PO8, O2, CB2). All electrode sites were referenced to an electrode placed on the nose tip. Eye movements and blinks were monitored using electrodes placed near the outer canthus of each eye, and above and below the left eye. Inter-electrode impedance

levels were kept below 5 k Ω .

EEG was recorded continuously throughout the experiment, bandpassed from 0.05 to 100 Hz, and sampled at 1 000 Hz. After completing data collection, the EEG recordings were segmented into 800-ms epochs, starting from 200 ms prior to stimulus onset. Epochs contaminated with artifacts (the threshold for artifact rejection was ± 80 μ V in all channels) were rejected before averaging. ERPs were filtered digitally prior to peak detection using a bandwidth from 0.1 to 30 Hz.

Experiment 2

Participants

Ten right-handed subjects (five females and five males) who did not participate in Experiment 1, participated in Experiment 2. The subjects had a mean age of 22 years ($SD = 1.26$; range, 20–24). All were undergraduates from Xiamen University. They were paid for participation and informed about the procedure of the experiment.

Experimental Procedure and Stimuli

The procedure and recording were the same as those in Experiment 1, the only difference being that Greek letters replaced the simple figures as the non-target stimuli. The letters were grouped into two sets, based on the absence or presence of at least one “hole” (Fig. 2). Between sets the average active area (number of black pixels) of the stimuli differed by only 0.038% (“hole” set: 10419 pixels; “no-hole” set: 10415 pixels).

In this experiment, subjects were asked to report their familiarity with each Greek letter on a scale from 1 to 5 (1 for most unfamiliar, 5 for most familiar). The level of familiarity was not significantly different between the two categories ($P = 0.584$; “hole” set: 3.300, “no-hole” set: 3.113).

Event-related Potential Recordings

Recording and analyses were the same as those in Experiment 1.

RESULTS

Experiment 1

The two categories of frequent non-target stimuli (“hole” and “no-hole”) were analyzed separately in order to derive the VEPs recorded during the passive paradigm. We examined the grand average waveforms evoked by the two

categories from three brain areas: left temporal-occipital (LTO: P7, PO5, PO7, CB1), occipital (POZ, O1, O2, OZ) and right temporal-occipital (RTO: P8, PO6, PO8, CB2) (Fig. 3). Here, we focus on the analysis of the P1 (50–150 ms) and N1 (80–180 ms) components. P1 and N1 were quantified as peak amplitude and peak latency, with amplitude measured relative to baseline and latency measured from stimulus onset.

The amplitudes and latencies of P1 and N1 were analyzed using an ANOVA design for repeated measures with three factors: categories (“hole”, “no-hole”), figure sets (set 1, and ; set 2, and) and brain areas (LTO, occipital, and RTO). Greenhouse–Geisser adjustments to the degrees of freedom were applied when appropriate.

“Hole” induced a smaller P1 amplitude (3.52 μ V) than “no-hole” (4.53 μ V) [$F(1, 13) = 9.78$, $P = 0.008$]. The interaction between categories and groups showed: the P1 amplitude of (3.51 μ V) was almost identical to (3.53 μ V), while the P1 amplitudes of (5.00 μ V) and (4.06 μ V) were significantly different [$F(1, 13) = 7.64$, $P = 0.016$] (Fig. 3). There was no main effect or interaction on P1 peak latency (“hole”, 97.39 ms; “no-hole”, 98.5 ms).

From the grand average ERP waveforms (Fig. 3A, B), the N1 had a significantly lower amplitude for “hole” (–5.07 μ V) than “no-hole” figures (–9.04 μ V) [$F(1, 13) = 28.99$, $P < 0.001$]. There was no significant difference between the two sets [set 1: –6.66 μ V; set 2: –7.45 μ V; $F(1, 13) = 3.01$, $P = 0.11$]. The N1 amplitude on the RTO (–7.49 μ V) was significantly higher ($P = 0.02$) than that on the occipital area (–6.66 μ V). There was no significant interaction of N1 amplitude between the factors. Analysis of N1 peak latencies showed no main effect or interaction (“hole”, 150.57 ms; “no-hole”, 152.67 ms).

We plotted topographic maps for the ERP difference waves (Fig. 3C). The ERPs were integrated across 10-ms time windows, from 80 ms to 180 ms. There were two components in the topographic maps: (i) P1 was located mainly in the occipital area, and this difference began at ~90–99 ms (Fig. 3C, left), and (ii) N1 was located mainly in the occipital area and bilateral temporal-occipital areas, and this difference began at ~130–139 ms (Fig. 3C, right). In order to test at which time points the N1 of the “hole” stimuli differed significantly from that of the “no-hole” stimuli, we calculated a paired t -test at each time point of the difference ERPs between 0 and 250 ms (Fig. 3E; the calculation of

Fig. 3. Experiment 1. Grand average ERP waveforms from three brain areas: left temporal-occipital (LTO), occipital and right temporal-occipital (RTO). A: ERP waveforms elicited by four stimuli. B: ERPs of the two stimulus categories and their difference wave ("hole" stimuli subtracted from "no-hole" stimuli). C: Topographic mapping of the difference waves. The ERPs were integrated across 10-ms time windows from 80 ms to 110 ms for P1 (left) and 120 ms to 189 ms for N1 (right). Maps are viewed from above, with the nose pointing upwards. D: Statistics of P1 (left) and N1 amplitudes (right). E: Paired t -test at each time point of difference ERPs between 0 and 250 ms ($n = 10$, $t(14) = 2.145$, $P < 0.05$) at LTO (left), occipital (middle) and RTO (right) areas.

difference ERPs was performed on signals from the same three brain areas as in Fig. 3A: LTO, occipital and RTO). Since 14 subjects participated in this test, the point of time when the t -value was >2.145 [$t(14) = 2.145$, $P < 0.05$] was the point of significance. Therefore, we chose the point after at least 10 consecutive points whose t -values were >2.145 , as the beginning of the difference. This difference was statistically significant from 90 ms for P1 and 127 ms for N1 ($P < 0.05$).

Experiment 2

Amplitude and peak latency of P1 and N1 were analyzed by a repeated-measure ANOVA with two factors: categories (“hole”, “no-hole”) and brain areas (LTO, occipital, RTO). Greenhouse–Geisser adjustments to the degrees of freedom were applied when appropriate.

The results were similar to those of Experiment 1. The P1 amplitude of “hole” Greek letters (4.55 μ V) was lower than that of “no-hole” (4.95 μ V) (Fig. 4). Although the main effect of categories was not significant, the interaction between categories and brain areas showed that the difference of the P1 amplitude between “hole” and “no-hole” Greek letters was greater in the right brain (4.88 μ V vs 5.45 μ V) than in the left brain (4.23 μ V vs 4.44 μ V), $F(2, 18) = 5.59$, $P = 0.042$ (Fig. 4C). From the topographic difference map for P1, a difference occurred first in the right parietal-occipital (Fig. 4). There were no main effects or interactions on P1 peak latency (“hole”, 92.7 ms; “no-hole”, 93.9 ms).

The N1 latency of “hole” Greek letters (146.00 ms) was similar to that of “no-hole” (145.63 ms), and there was no significant main effect or interaction effect on the N1 latency. For the N1 amplitude, there was neither a main effect of brain area, nor an interaction effect between categories and brain areas (Fig. 4B). While the main effect of stimulus category on the N1 amplitude was significant [$F(1, 9) = 9.516$, $P = 0.013$], “hole” Greek letters (−3.994 μ V) elicited a smaller N1 than “no-hole” (−6.239 μ V). Paired t -tests on the group averages showed the difference to be statistically significant from 121 ms ($t = 2.262$, $P < 0.05$) (Fig. 4D). For comparison with Experiment 1, we calculated the ERP difference on the same three brain areas: LTO, occipital area and RTO (Fig. 4D).

DISCUSSION

In Experiment 1, we used simple geometric forms as stim-

uli, whose local features were controlled between “hole” and “no-hole” within each stimulus set. However, since the shapes of all four stimuli are similar to meaningful symbols in either Chinese (◻ and 田 are meaningful Chinese characters) or Latin script (O and S), it might be argued that the effect we observed stems from semantic (meaning of script) differences. In order to test this hypothesis, we designed Experiment 2 to use Greek letters, which were all equally familiar to the participants, instead of the simple forms used in Experiment 1. Similarly, we sorted these Greek letters into “hole” and “no-hole” categories.

In Experiment 2, we replaced the simple geometric figures by two sets of Greek letters. Both experiments showed “non-hole” stimuli to induce higher P1 (significant only in Experiment 1) and N1 amplitudes (significant in both experiments) than “hole” stimuli. We thus excluded the possibility that the effect was due to semantic difference.

The main results from our experiments were that (1) ERPs of “hole” and “no-hole” stimuli differed as early as 90 ms after stimulus onset; (2) both P1 and N1 components showed sensitivity to the difference between “hole” and “no-hole” stimuli; (3) “no-hole” stimuli induced higher P1 and N1 amplitudes than “hole” stimuli; and (4) the effect found with the N1 component appeared to be more robust and also more sensitive than that found with the P1 component.

It has been shown that faces and other stimulus categories vary in a number of visual properties such as luminance, contrast, spatial frequency, orientation, and size, some of which may modulate N1 amplitude^[27]. The P1 component is also sensitive to some of the same visual stimulus properties as the N1, and can be similarly influenced by the same variations^[28]. On the other hand, a major challenge to interpretation of our experiments is that there seem to be, in principle, no two geometric figures that differ only in the “hole” without any differences in local features^[25]. In other words, the presence or absence of closure is never the only difference between “hole” and “no-hole” stimuli. Thus, one cannot test the differences between “hole” and “no-hole” in complete isolation^[2,29]. To minimize this problem and rule out an obvious explanation based on local features, we designed the stimuli carefully and performed an additional control experiment.

First, the pairs of stimuli were designed to exclude the use of luminous flux (O, S), perimeter length (O, S), orientation cues (◻, 田), and spatial frequency components (O,

Fig. 4. Experiment 2. Grand average ERP waveforms from three brain areas: left temporal-occipital (LTO), occipital and right temporal-occipital (RTO). A: ERPs of the two groups of Greek letters and their difference wave ("hole" subtracted from "no-hole"). B: Topographic mapping for the difference waves. The ERPs were integrated across 10-ms time windows, from 80 ms to 119 ms for P1 (left) and 120 ms to 179 ms for N1 (right). Maps are viewed from above, with the nose pointing upwards. C: Statistical results of P1 (left) and N1 amplitudes (right). D: Paired t -test at each time-point of the difference ERPs between 0 and 250 ms ($n = 10$, $t(10) = 2.262$, $P < 0.05$) at LTO (left), occipital (middle) and RTO (right) areas.

S, **□**, **I**). With the possible exception of semantic meaning, the difference between “hole” and “no-hole” was the only one that explained all of our results in a unified manner. If we assumed the luminous flux to be the explanation of the result, then the P1 and N1 amplitudes of **○** should be similar to that of **S**. If we consider orientation as the explanation, the P1 and N1 amplitudes of **□** should be similar to those of **I**. If we consider spatial frequency components as an explanation, the P1 and N1 amplitudes should be grouped into (**○**, **S**) and (**□**, **I**), but not (**○**, **□**) and (**S**, **I**). Thus, the local features commonly considered in the study of vision cannot explain our results in a consistent manner.

Furthermore, in Experiment 2, by using Greek letters as stimuli, we ruled out the possible effects of the semantic meaning of the symbols, which come from the shape similarity of the stimuli with Chinese (**□**, **I**) or Latin script (**○** and **S**). In Experiment 2, the two sets of stimuli had identical familiarity to our subjects, which excluded an effect of familiarity as an explanation for our results. In Experiment 1, only four figure stimuli were used. If any one of these figures had any special effect on the ERPs, then this might have changed the characteristics of the whole group. Thus using more stimuli in Experiment 2 avoided possible unintentional biases through the effects of single stimuli. In particular, in Experiment 1, it might be argued that the difference between “hole” and “no-hole” stimuli was due to easier recognition of (**○**, **□**) than (**S**, **I**); the increased number and diversity of the stimuli used in Experiment 2 ruled out this possibility.

Although the amplitudes of P1 and N1 in Experiment 1 were different from those in Experiment 2, the main tendency of difference between “hole” and “no-hole” was consistent in both experiments. In Tarkiainen’s study, the response magnitude at 100 ms was found to increase linearly with the visual complexity of the images^[30]. Since the stimuli in Experiment 2 were more complicated than those in Experiment 1, the P1 amplitudes were bigger in Experiment 2 than in Experiment 1. Through this, in Experiment 2, the significant difference between stimulus categories found with the P1 amplitudes of Experiment 1 may have been masked by the effect of complexity, resulting also in a reduced difference between “hole” and “no-hole” stimuli in general.

Our experiments showed larger P1 and N1 amplitudes for the “no-hole” stimuli, with the difference being more

significant on the RTO than on the LTO. On the one hand, it has been suggested that early differences in EEG signals (prior to 150 ms) may reflect systematic differences in low-level stimulus properties common to objects in a given category such as spatial frequency content, simple spatial patterns and textures^[18,31]. At times after 150 ms, higher-level cognitive processes related to the recognition and categorization of a particular object are more likely to be found^[31-33]. On the other hand, both P1 and N1 are regarded as sensitive to object category^[27,28]. However, in our experiments, both early (P1, ~90 ms) and (relatively) late components (N1, ~140 ms) exhibited a difference between “hole” and “no-hole” stimuli. Therefore, we concluded that both P1 and N1 are sensitive to discriminate “hole” from “no-hole” stimuli. However, the effect found with the N1 component between these stimuli was more robust and also more sensitive than that found with the P1 component.

Both experiments showed enhanced P1 and N1 amplitudes for “no-hole” stimuli, which reflected their perceptual differences from “hole” stimuli. However, what contributes to the smaller P1 and N1 of “hole”? In our previous study using a backward masking paradigm, we showed that under the same masking effect, “hole” can be detected more easily than “no-hole”. Texture segregation ERPs also suggested that the feedback connection in the visual ventral pathway is disturbed by backward masking only for the perception of “no-hole”, but not for the perception of “hole” stimuli^[12]. Furthermore, both newborn babies with functionally immature visual cortex^[8] and elderly people with degeneration of the visual cortex^[34] can detect “hole” information. These findings suggest that the processing of “hole” may be mediated by a very different neural mechanism or pathway, not within the typical processing model with a hierarchy of visual areas. This, as well as evidence from single-unit recordings^[15], leads us to suggest that the temporal visual area might be selectively activated by “hole”, thus facilitating figure-ground-segregation in an automatic fashion. On the other hand, it is probable that segregating “no-hole” from its background is not as ‘automatic’ as the segregation of “hole”, and therefore more effort is required for the perception of “no-hole” stimuli.

There might be other possible explanations for the change of P1 and N1. Increased amplitudes of P1 and N1 are observed for inverted faces when compared to upright faces^[35-41]. Face inversion is known to disrupt the

holistic processing of recognition, which elicits increased amplitudes of P1 and N1 (N170)^[35–37,42]. This inversion effect has also been observed for other object classes such as houses and words^[16,36,43]. The amplitudes of P1 and N1 can be used to measure the competition between global and local processing^[35]. Since “hole” stimuli elicited smaller amplitudes of P1 and N1 than “no-hole” stimuli, we suggest that “hole” stimuli may be processed predominantly globally, while “no-hole” stimuli are processed predominantly by local mechanisms. These differences in P1 and N1 components appear to be consistent with the effects of upright and inverted faces or objects.

In summary, we showed that ERPs of “hole” and “no-hole” stimuli differ as early as 90 ms after stimulus onset, with increased P1 and N1 amplitudes for “no-hole” stimuli. However, the possible reasons that we give here for enhanced “no-hole” P1 and N1 components will certainly require further scrutiny.

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REFERENCES

- [1] Chen L. Topological structure in visual perception. *Science* 1982, 218: 699–700.
- [2] Chen L. Holes and wholes: a reply to Rubin and Kanwisher. *Percept Psychophys* 1990, 47: 47–53.
- [3] Chen L. The topological approach to perceptual organization. *Vis Cogn* 2005, 12: 553–701.
- [4] Zhuo Y, Zhou TG, Rao HY, Wang JJ, Meng M, Chen M, *et al*. Contributions of the visual ventral pathway to long-range apparent motion. *Science* 2003, 299: 417–420.
- [5] Kimchi R. Primacy of wholistic processing and global/local paradigm: a critical review. *Psychol Bull* 1992, 112: 24–38.
- [6] Kimchi R. The role of wholistic/configural properties versus global properties in visual form perception. *Perception* 1994, 23: 489–504.
- [7] Kimchi R, Bloch B. Dominance of configural properties in visual form perception. *Psychon Bull Rev* 1998, 5: 135–139.
- [8] Turati C, Simion F, Zanon L. Newborns' perceptual categorization for closed and open geometric forms. *Infancy* 2003, 4: 309–325.
- [9] Donnelly N, Humphreys GW, Riddoch MJ. Parallel computation of primitive shape descriptions. *J Exp Psychol Hum Percept Perform* 1991, 17: 561–570.
- [10] Pomerantz JR, Sager LC, Stoever RJ. Perception of wholes and of their component parts: some configural superiority effects. *J Exp Psychol Hum Percept Perform* 1977, 3: 422–435.
- [11] Treisman A, Paterson R. Emergent features, attention, and object perception. *J Exp Psychol Hum Percept Perform* 1984, 10: 12–31.
- [12] Zhang J, Zhu W, Ding X, Zhou C, Hu X, Ma Y. Different masking effects on “hole” and “no-hole” figures. *J Vis* 2009, 9: 6.1–14.
- [13] Bertamini M, Lawson R. Visual search for a circular region perceived as a figure *versus* as a hole: evidence of the importance of part structure. *Percept Psychophys* 2006, 68: 776–791.
- [14] Bertamini M. Who owns the contour of a visual hole? *Perception* 2006, 35: 883–894.
- [15] Komatsu H, Ideura Y. Relationships between color, shape, and pattern selectivities of neurons in the inferior temporal cortex of the monkey. *J Neurophysiol* 1993, 70: 677–694.
- [16] Rossion B, Joyce CA, Cottrell GW, Tarr MJ. Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. *Neuroimage* 2003, 20: 1609–1624.
- [17] Thorpe S, Fize D, Marlot C. Speed of processing in the human visual system. *Nature* 1996, 381: 520–522.
- [18] VanRullen R, Thorpe SJ. The time course of visual processing: from early perception to decision-making. *J Cogn Neurosci* 2001, 13: 454–461.
- [19] Jeffreys DA. Evoked studies of face and object processing. *Vis Cogn* 1996, 3: 1–38.
- [20] Rossion B, Gauthier I, Tarr MJ, Despland P, Bruyer R, Linotte S, *et al*. The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain. *Neuroreport* 2000, 11: 69–74.
- [21] Large ME, Kiss I, McMullen PA. Electrophysiological correlates of object categorization: back to basics. *Brain Res Cogn Brain Res* 2004, 20: 415–426.
- [22] Tanaka J, Luu P, Weisbrod M, Kiefer M. Tracking the time course of object categorization using event-related potentials. *Neuroreport* 1999, 10: 829–835.

- [23] Pernet C, Basan S, Doyon B, Cardebat D, Demonet JF, Celsis P. Neural timing of visual implicit categorization. *Brain Res Cogn Brain Res* 2003, 17: 327–338.
- [24] Zhou K, Luo H, Zhou T, Zhuo Y, Chen L. Topological change disturbs object continuity in attentive tracking. *Proc Natl Acad Sci U S A* 2010, 107: 21920–21924.
- [25] Chen L, Zhang S, Srinivasan MV. Global perception in small brains: topological pattern recognition in honey bees. *Proc Natl Acad Sci U S A* 2003, 100: 6884–6889.
- [26] Zhang J, Zhu W, Ding X, Zhou C, Hu X, Ma Y. Configural processing of different topologically structured figures: an ERP study. *Sci China C Life Sci* 2009, 52: 1198–1204.
- [27] Thierry G, Martin CD, Downing P, Pegna AJ. Controlling for interstimulus perceptual variance abolishes N170 face selectivity. *Nat Neurosci* 2007, 10: 505–511.
- [28] Dering B, Martin CD, Thierry G. Is the N170 peak of visual event-related brain potentials car-selective? *Neuroreport* 2009, 20: 902–906.
- [29] Elder J, Zucker S. The effect of contour closure on the rapid discrimination of two-dimensional shapes. *Vision Res* 1993, 33: 981–991.
- [30] Tarkiainen A, Cornelissen PL, Salmelin R. Dynamics of visual feature analysis and object-level processing in face versus letter-string perception. *Brain* 2002, 125: 1125–1136.
- [31] Johnson JS, Olshausen BA. Timecourse of neural signatures of object recognition. *J Vis* 2003, 3: 499–512.
- [32] Curran T, Tanaka JW, Weiskopf DM. An electrophysiological comparison of visual categorization and recognition memory. *Cogn Affect Behav Neurosci* 2002, 2: 1–18.
- [33] Low A, Bentin S, Rockstroh B, Silberman Y, Gomolla A, Cohen R, *et al.* Semantic categorization in the human brain: spatiotemporal dynamics revealed by magnetoencephalography. *Psychol Sci* 2003, 14: 367–372.
- [34] Meng QL, Wang B, Liu N, Ma YY. Topological perception of different age people. *Acta Biophys Sin* 2006, 22: 87.
- [35] Bentin S, Allison T, Puce A, Perez E, McCarthy G. Electrophysiological studies of face perception in humans. *J Cogn Neurosci* 1996, 8: 551–565.
- [36] Eimer M. Effects of face inversion on the structural encoding and recognition of faces. Evidence from event-related brain potentials. *Brain Res Cogn Brain Res* 2000, 10: 145–158.
- [37] Itier RJ, Taylor MJ. N170 or N1? Spatiotemporal differences between object and face processing using ERPs. *Cereb Cortex* 2004, 14: 132–142.
- [38] Itier RJ, Taylor MJ. Effects of repetition and configural changes on the development of face recognition processes. *Dev Sci* 2004, 7: 469–487.
- [39] Itier RJ, Taylor MJ. Face recognition memory and configural processing: a developmental ERP study using upright, inverted, and contrast-reversed faces. *J Cogn Neurosci* 2004, 16: 487–502.
- [40] Linkenkaer-Hansen K, Palva JM, Sams M, Hietanen JK, Aronen HJ, Ilmoniemi RJ. Face-selective processing in human extrastriate cortex around 120 ms after stimulus onset revealed by magneto- and electroencephalography. *Neurosci Lett* 1998, 253: 147–150.
- [41] Taylor MJ, Batty M, Itier RJ. The faces of development: a review of early face processing over childhood. *J Cogn Neurosci* 2004, 16: 1426–1442.
- [42] Boehm SG, Dering B, Thierry G. Category-sensitivity in the N170 range: a question of topography and inversion, not one of amplitude. *Neuropsychologia* 2011, 49: 2082–2089.
- [43] Itier RJ, Latinus M, Taylor MJ. Face, eye and object early processing: what is the face specificity? *Neuroimage* 2006, 29: 667–676.