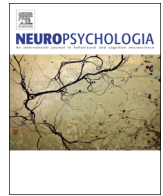




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The Poggendorff illusion driven by real and illusory contour: Behavioral and neural mechanisms

Lu Shen^a, Ming Zhang^d, Qi Chen^{a,b,c,*}

^a Center for Studies of Psychological Application and School of Psychology, South China Normal University, Guangzhou 510631, China

^b Epilepsy Center, Guangdong 999 Brain Hospital, Guangzhou 510631, China

^c Guangdong Key Laboratory of Mental Health and Cognitive Science, South China Normal University, Guangzhou 510631, China

^d School of Education, Soochow University, Suzhou 215123, China

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ABSTRACT

The Poggendorff illusion refers to the phenomenon that the human brain misperceives a diagonal line as being apparently misaligned once the diagonal line is interrupted by two parallel edges, and the size of illusion is negatively correlated with the angle of interception of the oblique, i.e. the sharper the oblique angle, the larger the illusion. This optical illusion can be produced by both real and illusory contour. In this fMRI study, by parametrically varying the oblique angle, we investigated the shared and specific neural mechanisms underlying the Poggendorff illusion induced by real and illusory contour. At the behavioral level, not only the real but also the illusory contours were capable of inducing significant Poggendorff illusion. The size of illusion induced by the real contour, however, was larger than that induced by the illusory contour. At the neural level, real and illusory contours commonly activated more dorsal visual areas, and the real contours specifically activated more ventral visual areas. More importantly, examinations on the parametric modulation effects of the size of illusion revealed the specific neural mechanisms underlying the Poggendorff illusion induced by the real and the illusory contours, respectively. Left precentral gyrus and right middle occipital cortex were specifically involved in the Poggendorff illusion induced by the real contour. On the other hand, bilateral intraparietal sulcus (IPS) and right lateral occipital complex (LOC) were specifically involved in the Poggendorff illusion induced by the illusory contour. Functional implications of the above findings were further discussed.

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1. Introduction

The Poggendorff illusion refers to a distorted perception of two collinear segments separated by a pair of parallels (Fig. 1A). The difference between the physical collinear and the perceived non-collinear is defined as the strength of the illusion. It has been well documented that the magnitude of the Poggendorff illusion varies as a function of the intersection angle between the oblique and the parallel lines: the size of illusion is negatively correlated with the tangent of the angle, the sharper the angle, the larger the illusion, and the size of illusion approached zero when the angle is 90° (Weintraub and Krantz, 1971; Pressey and Sweeney, 1972; Day et al., 1977; Predebon, 1986; Sereno and Maunsell, 1998; Avenanti et al., 2012). However, strikingly little is known with regard to the neural correlates underlying the Poggendorff illusion.

The Poggendorff illusion is classically induced by real geometric contours. In contrast to the real contour, the illusory contour is another

kind of visual illusion which refers to the perception of contours, lines, edges, or surfaces that are not physically present in the stimuli array (Purghé and Coren, 1992). For example, the Kanizsa figures create striking illusory contours by apparent occlusion (Kanizsa, 1979). It has been proposed that the cortical processing of illusory contours involves both early visual areas in V1/V2 and higher-order visual cortex in lateral occipital cortex, which partially overlap with neural regions processing real contours (Larsson et al., 1999; Ramsden et al., 2001; Lee, 2002; Wu et al., 2012). Here, an interesting question to ask is that in addition to the real interrupting lines, whether the Poggendorff illusion can be induced by illusory outlines (Fig. 1C). Previous behavioral evidence suggested that the illusory contours were indeed capable of driving the Poggendorff effect, but the size of the Poggendorff illusion induced by illusory contours was smaller than that induced by real contours (Day et al., 1977; Meyer et al., 1979; Beckett, 1989, 1990; Tibber et al., 2008).

It remains unknown, however, what are the shared and specific neural correlates underlying the Poggendorff illusion induced by the real and illusory contours. In the present fMRI study, by parametrically varying the size of the Poggendorff illusion via manipulating the angle of interception of the oblique, we aimed to

* Correspondence to: Department of Psychology, South China Normal University, 510631 Guangzhou, China.

E-mail address: qi.chen27@gmail.com (Q. Chen).

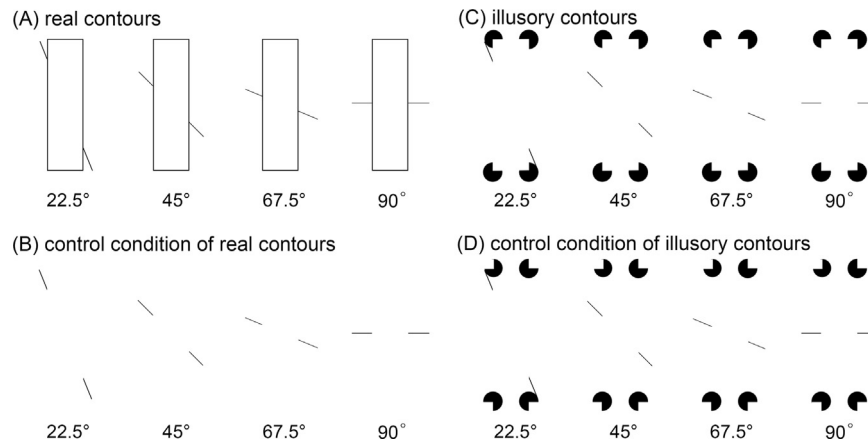


Fig. 1. Examples of the four experimental conditions in the present study. (A) the Poggendorff illusion under the real contours; (B) the control condition of the real contour condition; (C) the Poggendorff illusion under the illusory contours; (D) the control condition of the illusory contour condition. For each condition, the angles between the oblique line and the vertical edges varied across four levels, that is, 22.5°, 45°, 67.5°, and 90°. The oblique could intersect the vertical edges either leftward or rightward.

answer the above question. Four experimental conditions were adopted: (1) the real contour condition in which the Poggendorff illusion was induced by a rectangle (Fig. 1A); (2) the control condition of the real contour condition in which only the two separated segments were displayed (Fig. 1B). Since no intersecting rectangle was presented, no illusion should be induced; (3) the illusory contour condition in which the two segments were separated by an illusory Kanisza rectangle (Fig. 1C); and (4) the control condition of the illusory contour condition in which the four inducing disks were rotated 180° such that no illusory contour was generated (Fig. 1D). Since neurons in the striate and extrastriate visual areas respond best to lines and edges (Houck and Mefferd, 1973; Gregory, 1997), we expected both the real and the illusory contours to activate these visual areas. Contour processing involves the process of completing the local discrete contour edges (contour completion) and the subsequent process of representing the global completed contour information (contour representation). It has been accordingly suggested that the two processes implicate distinct neural correlates, with low-level visual areas (V1 and V2) being involved in contour completion, and higher-order visual areas in lateral occipital complex (LOC) being involved in contour presentation (Wu et al., 2012). The major difference between the real and the illusory contour focuses on the process of contour completion: real contours defined by geometric lines were more salient than illusory contours. We thus predicted that the relatively more salient real contour might more significantly evoke the contour completion process in the early visual cortex. Although there was no previous evidence with regard to the neural correlates underlying the Poggendorff illusion, bilateral LOC and right parietal cortex have been reported to be consistently involved in optical illusions, such as the Müller-Lyer illusion (Weidner and Fink, 2007). We thus aimed to investigate whether neural activity in LOC and the parietal cortex was differentially modulated by the Poggendorff illusion induced by the real and illusory contour.

2. Materials and methods

2.1. Participants

Fifteen participants (4 males) took part in a single fMRI session. All the participants were right handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). Participants' age ranged from 19 to 24 years with a mean age of 21.5. All the participants had normal or corrected to normal vision, gave informed written consent prior to the experiments in accordance with the Helsinki declaration, and were paid for their participations after the experiment. This study

was approved by the Ethics Committee of School of Psychology, South China Normal University.

2.2. Stimuli

Stimuli were displayed by an LCD projector on a back-projection screen mounted on the bore of the magnet in front of the subject's head. The screen was seen via a mirror system, which was mounted on top of the head coil. The distance between the eyes and the mirror was 16 cm.

Four sets of visual stimuli were adopted: (1) the real contour stimuli; (2) the control stimuli of the real contour stimuli; (3) the illusory contour stimuli; and (4) the control stimuli of the illusory contour stimuli (Fig. 1). The length of traversal segment was 0.9° of visual angle. The height of the rectangle was 5.8° of visual angle and the width was 1.7° of visual angle. The radius of the disks inducing the illusory contour was 0.6° of visual angle. Stimuli were randomly presented at 1 of 4 quadrants of the screen on a white background. Across trials, the visual stimuli in different conditions were independently varied in 2 aspects: (1) the intersection angles between the oblique and the rectangle; and (2) the position of the intersection between the traversal segments and the rectangle.

First, the strength of the Poggendorff illusion was parametrically manipulated by varying the angle between the oblique and the rectangle. Four different angles were selected (i.e., 22.5°, 45°, 67.5°, and 90°) so that the size of illusion kept decreasing with the increasing angle. In order to quantify the size of illusion induced by the real and illusory contours at each of the four angles for each participant individually, a psychophysical pretest was introduced prior to the scanning. In the psychophysical pretest, there were 512 trials in total: for each of the four types of stimuli, there were 32 trials at each of the four levels of angle. Participants were randomly presented with the stimuli described above, with one of the two segments being shifted up or down to an obviously non-collinear position. To rule out the possibility that the participants could use the central fixation or the midline of the screen as a spatial reference to judge the collinearity of the two segments, stimuli in the present study were randomly presented at one of the four quadrants of the screen (i.e., upper/left, upper/right, lower/left, or lower/right, relative to the center of the screen) (see also Weidner and Fink, 2007). The position of the stimulus in each trial was randomly assigned, with the constraint that no stimuli on two consecutive trials were presented in the same quadrant, resulting in 8 trials per quadrant for each of the 16 conditions. Since trials with stimuli in different quadrants were combined for each experimental condition during data analysis, the potential contribution of the various stimulus positions to the illusion was canceled out. The participants were instructed to adjust the vertical position of one of the two segments until they subjectively perceived the two segments as collinear via pressing buttons on the mouse. For example, the target segment shifted up if the left button was pressed and down if the right button was pressed, and the up-down button assignment was counter-balanced across participants. The final average vertical position of the target segment at each of the four angles was taken as an index of the apparent collinearity at each of the four levels for each participant. The difference between this subjectively judged vertical position and the objectively collinear vertical position reflected the size of illusion. Subsequently, the size of illusion on each of the four angles of the four types of stimuli was utilized in the formal fMRI experiment for calculating the vertical positions of the two segments.

In the fMRI experiment, participants were instructed to judge whether they subjectively perceived the two segments as collinear or not via pressing one of the two buttons on a response pad. The correspondence between collinearity and response button was counter-balanced across participants.

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