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Biases and Sensitivities in the Poggendorff Effect when Driven by Subjective Contours

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Abstract

Purpose—A consensus in the existing literature suggests that the Poggendorff effect (a perceptual misalignment of two collinear transversal segments when separated by a pair of parallel contours) persists when the parallels are defined by Kanizsa-like subjective contours. However, previous studies have often been complicated by a lack of quantitative measures of effect size, statistical tests of significance, appropriate measures of baseline and control biases, or stringent definition of subjective contours. The aim of this study was thus to determine whether subjective contours are capable of driving the Poggendorff effect once other factors are accounted for.

Methods—Twenty participants were tested on a number of test and control figures incorporating first-order (luminance-defined) and subjective parallels using the method of adjustment. All figures were tested at two different orientations, and observer sensitivities and observer biases were assessed.

Results—A systematic response bias (in the direction of the classical effect) was found for Poggendorff figures that incorporated subjective parallels. The effect was highly significant and greater than for control figures. There was no concomitant change in judgment sensitivity (positional certainty). Finally, there was a positive correlation between the effect size for figures incorporating first-order and subjective parallels.

Conclusions—The findings reported demonstrate conclusively that true Kanizsa-like subjective contours are capable of driving the Poggendorff effect. Further, the data are consistent with a growing body of evidence that suggests both first-order and subjective contours are processed at early loci in the visual pathways when position is encoded.

The Poggendorff effect (1860) is a well-documented geometric illusion in which there is a perceptual misalignment of two collinear oblique lines when separated by a pair of parallel contours (henceforth referred to as the transversals and parallels respectively; see Fig. 1A). Several explanations have been put forward to account for the effect, including a misestimation of the orientation of the transversals through lateral inhibition, obtuse angle contraction, or angular induction,¹⁻⁵ a bowing of the transversals at points of intersection with the parallels,⁶ a misestimation of the orientation of a projected line connecting the transversals as a result of neural blurring,^{7,8} a perceptual contraction or expansion of the space between the parallels,⁹⁻¹¹ a misinterpretation of the transversals as receding in depth,

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12-14 or an inherent calibration bias in the visual system reflecting the statistics of natural scene geometry.¹⁵ Deconstruction of the Poggendorff figure into its component parts, however, suggests that the illusion is a combination of several composite effects,^{9,16-19} the influence of which may be either additive or subtractive on the perceived degree of misalignment, depending on the precise configuration used.

If the parallel lines in a Poggendorff figure are replaced with subjective contours, the effect would seem to persist.²⁰ This may be true of subjective contours defined by Kanizsa-like Pac-Man tokens,²⁰ luminance steps, texture borders,²¹ and complex composite images that define the parallels through “good continuation” or “closure.”²² However, in many of these studies, interpretation of the results is complicated by the absence of quantitative measures of effect size, a lack of statistical tests of significance, or a failure to include the appropriate controls and measures of baseline biases.^{20,21,23-25} To demonstrate that subjective contours are truly driving the Poggendorff effect, the baseline bias (the degree of misalignment perceived between two transversal lines in the absence of further context) must first be subtracted from the overall bias. This is because reports of colinearity between spatially separated lines (even in the absence of parallel contours) may be distorted^{26,27} as a result of tilt assimilation toward the nearest cardinal axis,^{16,28} a perceptual expansion of the vertical axis,⁹ the Zehender effect,²⁹ or personal response biases. In addition, the magnitude of the bias must be significantly larger than the effect induced by a suitable control image in which the perception of subjective contours is abolished without changing the overall image structure.

Meyer and Garges³⁰ and Day et al.³¹ addressed the issue of control figures and baseline biases in their examination of subjective contours and the Poggendorff effect. Taken together, these papers demonstrate that significant differences from baseline were not significant when the basic Kanizsa-like Pac-Man tokens were used to generate the parallels. Significant effects were only observed when high contrast hemisegments were added along the length of the subjective contours to increase their saliency (Figs. 1B,³⁰ 1D,³¹). This introduces a genuine luminance step across sections of the subjective contours, raising the question whether they are true subjective contours or simply luminance-defined contours with periodic discontinuities. This is of particular relevance to the study by Day et al.³¹ in which sections of luminance-defined contour separated by $<1^\circ$ of visual angle constituted over half of the subjective contours length.

Finally, it is unclear whether the presence of subjective contours in the Poggendorff figure causes a reduction in judgment precision (i.e., increased positional uncertainty) and a systematic bias. In the study of geometric illusions this issue is rarely addressed, despite the fact that differences in bias and sensitivity may be informative as to the underlying mechanisms of a visual phenomenon.³² Thus, in a study by Morgan et al.,⁷ a misestimation of length associated with the Müller-Lyer illusion did not entail a parallel decrease in sensitivity to length differences, a finding which the authors took as evidence for an early site of action, i.e., when length is first encoded. The purpose of this study was thus to consolidate previous reports of the Poggendorff effect using true subjective contours and appropriate control conditions, addressing the issues of judgment sensitivity and judgment bias.

Methods

Observers

Twenty observers (13 men, 7 women) between the ages of 19 and 41 years took part in the experiment. Informed written consent was obtained in accordance with the Declaration of Helsinki.

Procedure

The method of adjustment was used to measure the strength of the Poggendorff effect for a number of test and control figures using first-order (luminance-defined) and subjective contours (Figs. 1C–1F). In all figures, a single transversal line was used in conjunction with a target dot as opposed to two transversals. Using this design, the effect has been found to persist and may even be augmented.¹⁹ On each trial the observers were asked to position a target dot so that it fell on a theoretical line projecting from the upper transversal. The transversal was always oriented at 45° to the parallels because this configuration has been shown to induce the greatest effect.¹⁹ The position of the target could be shifted in a single plane (horizontal or vertical, depending on the overall orientation of the test configuration) in 10, 5, or single pixel steps. On each trial, the position of the transversal was randomized so that the number of steps needed to put the figure in true alignment could not be learned. For 4 of the 5 Poggendorff figures tested (Figs. 1C–1F), 20 trials were completed (10 with the target point starting above the position of true alignment and 10 starting below). For the baseline condition (the fifth figure type tested: Fig. 1B) 40 trials were completed. All figures were tested at two orientations (horizontal [Figs. 1B–1F] and vertical [Figs. 1G–1K]) so that each participant completed 240 trials in total (approximately 2 hours' duration). Different figure types were presented in a pseudorandomized order. Horizontal and vertical figures were tested in separate blocks undertaken in a counterbalanced order.

Each observer was tested to determine the degree of misalignment associated with the 10 test figure configurations shown in Figure 1 (B–K). These conditions are referred to here as baseline, classical, and subjective. Each person's baseline bias was determined using a single transversal line and a target point (no parallels; Figs. 1B, 1G). Each observer's average bias for Figure 1 was subsequently subtracted from the bias on the other test figures so that any residual bias could be attributed to additional components of the stimulus. Luminance-defined parallel contours were used to assess the relative strength of the classical Poggendorff effect (Figs. 1C, 1H). Subjective parallel contours were created using Kanizsa-like Pac-Man tokens to test the ability of subjective contours to drive the Poggendorff effect (Figs. 1D, 1I).

In addition, four control figures were generated (Figs. 1E, 1F, 1J, 1K) in which one or both of the subjective contours were abolished without changing the overall stimulus structure. These were included in the study to ensure that any bias induced by the subjective contours was truly a result of their inclusion rather than a consequence of the presence of the Pac-Man tokens. Previous studies have achieved this by occluding the open sectors of the Pac-Man tokens²¹ or by filling them in.^{30,31} Here, the subjective contours were removed by rotating the Pac-Man tokens 180°. In Figures 1E and 1J (control 1), only the inducing contour is absent, whereas in Figures 1F and 1K, both parallel contours have been abolished (control 2).

Stimulus

Stimuli were generated (MATLAB; MathWorks, Natick, MA) with the Cambridge Research Systems toolbox (CRS Ltd.) and were presented on a Protouch monitor (Aspen Touch Solutions, Evergreen, CO) in conjunction with the Cambridge VSG graphics card. Images were presented at a spatial and temporal resolution of 928 × 799 pixels and 60 Hz, respectively, and were viewed under ambient light conditions at a distance of approximately 50 cm. All image components were generated in black (5 cd/m²) and were presented on a white background (80 cd/m²), giving a Michelson contrast of 88%. Image dimensions are given in Figure 1A.

Results

Positive misalignments in the data represent a bias in the typical Poggendorff direction. Thus, in the horizontal orientation (Fig. 1C), a positive bias would indicate that the observer had positioned the target too far to the left of true alignment. Similarly, in the vertical orientation (Fig. 1H), a positive bias represents a target placed above the point of true alignment.

All data were analyzed using SPSS (Chicago, IL). All data were shown to be normally distributed using the one-sample Kolmogorov-Smirnov (KS) test. Consequently, parametric statistical methods were used.

Observer Bias

The extent of misalignment (observer bias) is presented for the four main Poggendorff figures (classical, subjective, control 1, and control 2) for both horizontal and vertical presentations (Figs. 1C–1F, 1H–1K). All data were calculated by subtracting each observer's baseline bias (the degree of misalignment induced by the transversal and target alone: Figs. 1B, 1G) from each measurement. These values of the residual bias should thus reflect the direct effects of adding other components to the image structure (parallel contours, Pac-Man tokens, or both).

Data are shown for each of the four Poggendorff figures (Fig. 2A; classical Poggendorff [Class], Poggendorff with subjective contours [Sub], control 1 [Con1], control 2 [Con2]). For the main statistical analyses, data from the two control figures (Con1 and Con2) were combined by calculating an average control value for each observer (Con). This was performed because the degree of misalignment induced by the control figures did not differ significantly for either the horizontal ($t_{38} = 0.078$; $P = 0.94$) or the vertical ($t_{38} = 0.078$; $P = 0.89$) presentation, and it simplifies interpretation of the results.

Next, a repeated-measures analysis of variance (ANOVA) was performed on all the data with one within-factor (figure type classical, subjective, or control) and one between-factor (figure orientation horizontal or vertical). The degree of misalignment was not found to vary as a function of figure orientation ($F_{(1,38)} = 0.09$; $P = 0.77$). In other words, the strength of the illusion was not affected by the orientation at which the figure was presented. However, there was a main effect of figure type ($F_{(2,76)} = 238.94$; $P < 0.001$), indicating that the degree of misalignment differed among the three Poggendorff figures (Class, Sub, Con).

To explore this finding further, data were reanalyzed separately for horizontal and vertical presentations using the oneway ANOVA test with Tukey HSD post hoc analysis. For both the horizontal and the vertical presentations, the degree of misalignment differed significantly between the various Poggendorff figures (horizontal, $F_{(2,59)} = 68.19$, $P < 0.001$; vertical, $F_{(2,59)} = 64.38$, $P < 0.001$). As was expected, the classical Poggendorff figure induced a greater misalignment than either the control figure (horizontal, $P < 0.001$; vertical, $P < 0.001$) or the Poggendorff figure with subjective contours (horizontal, $P < 0.001$; vertical, $P < 0.001$). However, the critical comparisons indicate that the Poggendorff figure with subjective contours induced a greater misalignment than the control figures (horizontal, $P < 0.01$; vertical, $P < 0.05$). Taken together these findings clearly demonstrate that, though less marked than first-order contours, subjective contours can drive the Poggendorff effect. Further, the effect is significantly attenuated by rotating the Pac-Man tokens.

Observer Precision

In addition to analyzing the bias inherent in observer judgment, the precision of observer judgment was examined. These two measurements relate to the P(50) point and slope,

respectively, of the underlying psychometric functions.⁷ A measure of each observer's precision (the dispersion of settings) was thus calculated for each Poggendorff figure by taking the SD of judgment ($n = 20$ judgments [trials] for all figures except baseline conditions, for which $n = 40$; Fig. 2B).

Repeated-measures ANOVA was performed on all the data, with one within-factor (figure type: baseline, classical, subjective, control 1, and control 2) and one between-factor (figure orientation: horizontal or vertical). The degree of precision did not vary as a function of figure orientation ($F_{(1,38)} = 0.44$; $P = 0.51$) or as a function of Poggendorff figure type ($F_{(4,152)} = 0.33$, $P = 0.86$). Thus, despite the fact that the Poggendorff figure (with first-order or subjective parallel contours) induced alignment errors (bias), there was no accompanying loss in judgment precision.

Correlations

In Figure 3, individual biases for the Poggendorff figures with subjective contours are plotted against biases induced using luminance-defined parallels. These data are shown for horizontal (Fig. 3A) and vertical (Fig. 3B) figure orientations. Positive correlations between the two measures were found to be highly significant at both orientations (horizontal, $r = 0.73$, $P < 0.001$; vertical, $r = 0.54$, $P < 0.01$), indicating that observers who were highly susceptible to the classical Poggendorff effect were also likely to experience large biases when the parallels were defined by subjective contours.

Discussion

The results reported here provide clear evidence that true Kanizsa-like subjective contours are able to drive the Poggendorff effect. By defining observer performance as the residual bias in judgment that remains after subtracting the baseline bias (in response to the transversal and target alone), it was clear that the results were not confounded by other factors such as the Zehender effect, tilt assimilation, or individual response bias. Further, the inclusion of appropriate control images (in which the Pac-Man tokens are rotated 180°) suggests that the effect is driven, to a significant extent, by the presence of the subjective contours rather than as a result of the Pac-Man tokens. Although the consensus in the existing literature is that subjective contours are capable of driving the Poggendorff effect, to our knowledge this is the first study to demonstrate a statistically significant effect using the basic Kanizsa-like Pac-Man tokens and appropriate control images.

In the present study, subjective contours were defined using only four Pac-Man tokens positioned in the four corners of the occluding space separating the transversals. In contrast, previous reports of the Poggendorff effect using subjective contours have found significant effects only when the salience of the contours was reinforced by the addition of luminance-defined hemicircles along their lengths. In a critical study by Day et al.,³¹ luminance edges separated by less than 1° of visual angle constituted more than 50% of the “subjective” parallel contours. Thus, sections of adjacent luminance edges would have been detected by individual V1 cell receptive fields, which on average covered 1.6° of the visual field.³³ Even in the study by Meyer and Garges,³⁰ the distance between adjacent hemicircles was only in the region of 2.5° to 3.2°. As this separation is reduced, the distinction between a subjective contour and a luminance contour with periodic discontinuities becomes ambiguous. By using a much larger image in which the Pac-Man tokens were separated by some 19.6° of visual angle, it was clear that the effects reported here cannot be driven by simple low-level filters and that they involve the perception of true subjective contours.

Despite the fact that the Poggendorff effect was shown to be driven by first-order and subjective contours, the precision of observer judgment did not differ between the different

tests and the control figure configurations. In support of Morgan et al.,³⁴ these data suggest that some geometric illusions induce a perceptual bias in position, size, or distance without affecting the precision of that representation. Thus, the classical Poggendorff effect (driven by first-order parallel contours) induces a systematic bias in the judgment of colinearity but adds no extra uncertainty to the judgment. In much the same way, the Müller-Lyer illusion drives a misestimation of length without a concomitant reduction in positional certainty, as does a variation of the Judd illusion.³⁴ Perceptual bias in the absence of a change in sensitivity suggests that the effect of interest either acts at a level in the processing stream at which the stimulus parameter is encoded or involves some further factor that has much lower decision uncertainty.³⁴ The most parsimonious interpretation of the data is thus that, at least with respect to these three well-documented geometric illusions (Poggendorff, Müller-Lyer, Judd), biases arise relatively early in the visual pathway when length, orientation, or position are encoded.

By a similar pattern of logic, the fact that the precision of observers' performance did not differ between judgments made on the classical Poggendorff figure and the Poggendorff figure with subjective contours suggests that luminance-defined and subjective contours are encoded at a similar level in the visual system. This was reinforced by the high correlation in alignment biases for the Poggendorff figure using first-order and subjective parallels. The findings reported here thus support a growing body of evidence from psychophysical,³⁵ electrophysiological,³⁶⁻³⁸ optical imaging,³⁹ positron emission tomography,^{40,41} and functional magnetic resonance imaging⁴²⁻⁴⁴ studies that suggest subjective contours are processed early in the visual pathways, most probably in V2 or even V1. In the Poggendorff effect interactions between first-order contours such as lateral inhibition, tilt assimilation, obtuse angle contraction, and angular induction, which are usually invoked to explain the classical effect, may thus be equally relevant to interactions between luminance-defined and subjective contours. Hence, tilt aftereffects (related to the process of lateral inhibition in the primary visual cortex¹) have been demonstrated using probes defined by first-order contours after adaptation to subjective contours, and vice versa.⁴⁵ Further, reduced orientation discrimination thresholds resulting from practice effects using subjective contour stimuli are transferable to performance with first-order stimuli.⁴⁶

A study by Westheimer and Wehrhahn²¹ examined the effect of subjective contours and first-order contours of differing contrasts on the Poggendorff illusion and concluded that a subjective contour was perceptually equivalent to a luminance border of approximately 1% (Michelson contrast) with respect to its ability to drive the effect. Although the data presented here are not directly comparable with those of Westheimer and Wehrhahn²¹ because contrast was not manipulated, the findings reported are consistent with a low-level locus for subjective contour processing and suggest that, in common with low-contrast first-order contours,⁴⁷ subjective contours are capable of driving a reliable, though attenuated, version of the Poggendorff effect. This attenuation of the effect when subjective contours are used to define the parallels may thus reflect that subjective contours are relatively low-salience stimuli detected by a small subset of cortical cells in the early visual areas.³⁶⁻³⁸ Consequently, any lateral interactions between cell populations tuned to the parallels and those tuned to other components of the stimulus will be weaker than if the entire stimulus was defined by first-order contours.

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References

1. Blakemore C, Carpenter RH, Georgeson MA. Lateral inhibition between orientation detectors in the human visual system. *Nature*. 1970; 228:37–39. [PubMed: 5456209]
2. Greene E. The corner Poggendorff. *Perception*. 1988; 17:65–70. [PubMed: 3205671]
3. Greene E. The relative contribution of contact and target lines in the magnitude of the Poggendorff effect. *Perception*. 1987; 16:385–388. [PubMed: 3432033]
4. Greene E, Pavlov G. Angular induction as a function of contact and target orientation. *Perception*. 1989; 18:143–154. [PubMed: 2771600]
5. Yu, Y.; Choe, Y. Angular disinhibition effect in a modified Poggendorff illusion. In: Forbus, KD.; Gentner, D.; Regier, T., editors. *Proceedings of the 26th Annual Conference of the Cognitive Science Society*; Chicago, IL. 2004. p. 1500-1505.
6. Wenderoth P. Alignment errors in Poggendorff-like displays when the variable segment is a dot, a dot series, or a line. *Percept Psychophys*. 1980; 27:505–518. [PubMed: 7393697]
7. Morgan MJ. The Poggendorff illusion: a bias in the estimation of the orientation of virtual lines by second-stage filters. *Vision Res*. 1999; 39:2361–2380. [PubMed: 10367057]
8. Glass L. Effect of blurring on perception of a simple geometric pattern. *Nature*. 1970; 228:1341–1342. [PubMed: 5488118]
9. Day RH, Dickinson RG. The components of the Poggendorff illusion. *Br J Psychol*. 1976; 67:537–552. [PubMed: 1009285]
10. Greist-Bousquet S, Schiffman HR. The Poggendorff illusion: an illusion of linear extent? *Perception*. 1981; 10:155–164. [PubMed: 7279544]
11. Masini R, Costa T, Ferraro M, De Marco A. Modifications of the Poggendorff effect as a function of random dot textures between the verticals. *Percept Psychophys*. 1994; 55:505–512. [PubMed: 8008552]
12. Gillam B. A depth processing theory of the Poggendorff illusion. *Percept Psychophys*. 1971; 10:211–216.
13. Koning A, van Lier R. 3-D processing in the Poggendorff illusion. *Acta Psychol (Amst)*. 2007; 126:46–58. [PubMed: 17098205]
14. Spehar B, Gillam B. Modal completion in the Poggendorff illusion: support for the depth-processing theory. *Psychol Sci*. 2002; 13:306–312. [PubMed: 12137132]
15. Howe CQ, Yang Z, Purves D. The Poggendorff illusion explained by natural scene geometry. *Proc Natl Acad Sci USA*. 2005; 102:7707–7712. [PubMed: 15888555]
16. Hotopf WH, Hibberd MC. The role of angles in inducing misalignment in the Poggendorff figure. *Q J Exp Psychol A*. 1989; 41:355–383. [PubMed: 2748935]
17. Hotopf WH, Ollerearnshaw C, Brown S. The regression to right angles tendency and the Poggendorff illusion, 3. *Br J Psychol*. 1974; 65:213–231. [PubMed: 4841318]
18. Ninio J, O'Regan JK. Characterisation of the misalignment and misangulation components in the Poggendorff and corner-Poggendorff illusions. *Perception*. 1999; 28:949–964. [PubMed: 10664747]
19. Weintraub DJ, Krantz DH. The Poggendorff illusion: amputations, rotations, and other perturbations. *Percept Psychophys*. 1971; 10:257–264.
20. Gregory RL. Cognitive contours. *Nature*. 1972; 238:51–52. [PubMed: 12635278]
21. Westheimer G, Wehrhahn C. Real and virtual borders in the Poggendorff illusion. *Perception*. 1997; 26:1495–1501. [PubMed: 9616477]
22. Goldstein MB, Weintraub DJ. The parallel-less Poggendorff: virtual contours put the illusion down but not out. *Percept Psychophys*. 1972; 11:353–355.
23. Beckett PA. Illusion decrement and transfer of illusion decrement in real- and subjective-contour Poggendorff figures. *Percept Psychophys*. 1989; 45:550–556. [PubMed: 2740195]
24. Beckett PA. Similar processing of real- and subjective-contour Poggendorff figures by men and women. *Percept Mot Skills*. 1990; 70:51–56. [PubMed: 2326138]
25. Beckett PA, Hurajt S. Real and subjective contour Poggendorff illusions: no differences based on eye color. *Perception*. 1988; 17:311–313. [PubMed: 3226872]

26. Day RH. The oblique line illusion: the Poggendorff effect without parallels. *Q J Exp Psychol.* 1973; 25:535–541. [PubMed: 4767535]
27. Wenderoth P. The role of the second oblique in the Poggendorff illusion. *Perception.* 1981; 10:605–614. [PubMed: 7346772]
28. Weintraub DJ, Virsu V. The misperception of angles: estimating the vertex of converging line segments. *Percept Psychophys.* 1971; 9:5–8.
29. Hotopf WH. Mistracking in alignment illusions. *J Exp Psychol Hum Percept Perform.* 1981; 7:1211–1246. [PubMed: 6458648]
30. Meyer GE, Garges C. Subjective contours and the Poggendorff illusion. *Percept Psychophys.* 1979; 26:302–304.
31. Day RH, Dickinson RG, Jory MK. The Poggendorff illusion with subjective contours. *Q J Exp Psychol.* 1977; 29:219–226. [PubMed: 877216]
32. Solomon JA, Felisberti FM, Morgan MJ. Crowding and the tilt illusion: toward a unified account. *J Vision.* 2004; 4:500–508.
33. Hubel DH, Wiesel TN. Receptive fields and functional architecture of monkey striate cortex. *J Physiol.* 1968; 195:215–243. [PubMed: 4966457]
34. Morgan MJ, Hole GJ, Glennerster A. Biases and sensitivities in geometrical illusions. *Vision Res.* 1990; 30:1793–1810. [PubMed: 2288091]
35. Dresch B, Bonnet C. Psychophysical evidence for low-level processing of illusory contours and surfaces in the Kanizsa square. *Vision Res.* 1991; 31:1813–1817. [PubMed: 1767499]
36. Grosz DH, Shapley RM, Hawken MJ. Macaque V1 neurons can signal 'illusory' contours. *Nature.* 1993; 365:550–552. [PubMed: 8413610]
37. Peterhans E, von der Heydt R. Mechanisms of contour perception in monkey visual cortex, II: contours bridging gaps. *J Neurosci.* 1989; 9:1749–1763. [PubMed: 2723748]
38. von der Heydt R, Peterhans E. Mechanisms of contour perception in monkey visual cortex, I: lines of pattern discontinuity. *J Neurosci.* 1989; 9:1731–1748. [PubMed: 2723747]
39. Ramsden BM, Hung CP, Roe AW. Real and illusory contour processing in area V1 of the primate: a cortical balancing act. *Cereb Cortex.* 2001; 11:648–665. [PubMed: 11415967]
40. Ffytche DH, Zeki S. Brain activity related to the perception of illusory contours. *Neuroimage.* 1996; 3:104–108. [PubMed: 9345481]
41. Larsson J, Amunts K, Gulyas B, Malikovic A, Zilles K, Roland PE. Neuronal correlates of real and illusory contour perception: functional anatomy with PET. *Eur J Neurosci.* 1999; 11:4024–4036. [PubMed: 10583491]
42. Hirsch J, DeLaPaz RL, Relkin NR, et al. Illusory contours activate specific regions in human visual cortex: evidence from functional magnetic resonance imaging. *Proc Natl Acad Sci USA.* 1995; 92:6469–6473. [PubMed: 7604015]
43. Montaser-Kouhsari L, Landy MS, Heeger DJ, Larsson J. Orientation-selective adaptation to illusory contours in human visual cortex. *J Neurosci.* 2007; 27:2186–2195. [PubMed: 17329415]
44. Seghier M, Dojat M, Delon-Martin C, et al. Moving illusory contours activate primary visual cortex: an fMRI study. *Cereb Cortex.* 2000; 10:663–670. [PubMed: 10906313]
45. Berkley MA, DeBruyn B, Orban G. Illusory, motion, and luminance-defined contours interact in the human visual system. *Vision Res.* 1994; 34:209–216. [PubMed: 8116280]
46. Vogels R, Orban GA. Illusory contour orientation discrimination. *Vision Res.* 1987; 27:453–467. [PubMed: 3660605]
47. Westheimer G, Brincat S, Wehrhahn C. Contrast dependency of foveal spatial functions: orientation, vernier, separation, blur and displacement discrimination and the tilt and Poggendorff illusions. *Vision Res.* 1999; 39:1631–1639. [PubMed: 10343856]

Figure 1.

The range of Poggendorff and control figures used throughout the study. The classical Poggendorff figure (**A**) is shown in its less common horizontal orientation. Dimensions of the figure are indicated in degrees of visual angle when viewed from a distance of 50 cm. Figures were tested for horizontal (**B–F**) and vertical (**G–K**) orientations. Baseline biases were measured using a single transversal line and target dot (**B**, **G**) and were subtracted from the biases recorded on the other test figures. As well as the classical Poggendorff figure (**C**, **H**), figures were generated in which the parallels were defined by subjective contours (**D**, **I**). In addition, data were collected on performance using control figures in which perception of one (**E**, **J**) or both (**F**, **K**) subjective contours were abolished.

Figure 2.

The bias (**A**) and precision (**B**) of observer judgment for the test and control figures. (**A**) Mean bias, relating to P(50) on the underlying psychometric function or the point of subjective alignment, is plotted for each figure. Error bars represent the SEM. Note: for the statistical analyses, data from the two control figures (Con1 and Con2) were combined for each observer to produce a single control measure. (**B**) The precision of observer judgment (relating to the threshold or slope of the underlying psychometric function) were calculated as the SD of observer performance across the 20 trials undertaken per figure (40 in the case of the baseline figures). Mean data are plotted. Error bars represent SEM. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Figure 3.

Correlations between biases for the Poggendorff figures using luminance-defined and subjective parallels. Individual biases for the Poggendorff figures with subjective parallels are plotted on the abscissa against biases induced using luminance-defined parallels on the ordinate. Data are shown for horizontal (**A**) and vertical (**B**) figure orientations. Correlations were highly significant at both orientations (horizontal, $P < 0.001$; vertical, $P < 0.01$).