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Illusory edges comingle with real edges in the neural representation of objects

Sarah L. Elliott^{1,3} and Steven K. Shevell^{2,3,4}

¹Department of Psychology, Roosevelt University, 430 S. Michigan Ave, Chicago, IL, 60605

²Department of Psychology, The University of Chicago, 940 E. 57th St., Chicago, IL, 60637

³Institute for Mind & Biology, University of Chicago

⁴Department of Ophthalmology & Visual Science, University of Chicago

Abstract

The visual system must transform a point-by-point biological representation from the photoreceptors into neural representations of separate objects. Even a uniform circular patch of light that slowly modulates in luminance can be segmented into separate central and surrounding areas merely by introducing black lines to outline a central square. The black lines cause brightness induction in the center even though the light inside and outside the square is always identical, as predicted by spatial antagonism between the square central area and its surround. Importantly, illusory Kanizsa lines forming the square are as effective for this brightness induction as real black lines, suggesting a ‘form-cue invariant’ cortical neural representation that does not distinguish between a central region set off by real or illusory edges. An open question is whether separate subsystems generate objects defined by real versus illusory edges, each providing the same form-cue invariant neural representation of an object, or whether form-cue invariance extends to integrating component pieces that together define an object. Experiments here show object segmentation when subparts of a square are defined by a mixture of real and illusory edges. Subjects adjusted the Michelson contrast of a separate patch to match the perceived modulation depth within the central region of a circular field that slowly oscillated in luminance. A closed, four-sided figure, no matter how constructed, reduced the perceived modulation depth within the central region. This shows that both real and illusory subparts can be integrated to segment center from surround. It supports a strong version of form-cue invariance in which neural mechanisms responsible for object segmentation are impartial to the piecemeal cues that are integrated to define an object.

Corresponding Author: Sarah L. Elliott, slelliott99@gmail.com.

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INTRODUCTION

Edges defining objects in natural scenes can be formed by several different aspects of a stimulus, including luminance contrast, motion, texture, color, or illusory inference. The neural representation of a form, therefore, may not depend on the low-level features defining a form's edge. This is the hypothesis of form-cue invariance: an object's representation does not depend on the information that defines object shape. Previous studies support form-cue invariance for the neural representation of objects, comparing both physiological (e.g., von der Heydt, Peterhans, & Baumgartner, 1984) and behavioral (e.g., Paradiso, Shimojo, & Nakayama, 1989) responses between real luminance-defined edges and illusory edges. No study, however, has considered whether only the neural representation of *whole objects* is form-cue invariant, as opposed to the sub-parts that together define the object. In the strong version of form-cue invariance, the neural representation of an object should be insensitive to the physical cues defining each individual edge of a complete form. The current study tested this strong version of form-cue invariance using combinations of real and illusory edges.

Neural mechanisms involved in the perception of illusory edges are known to overlap with mechanisms sensitive to real edges defined by luminance-contrast. Single-cell responses in monkey show that neurons as early as V1 (Grosz, Shapley, & Hawken, 1993) and V2 (Peterhans & von der Heydt, 1989; von der Heydt et al., 1984; von der Heydt & Peterhans, 1989) carry signals related to illusory contours. In V2, orientation selectivity is form-cue invariant in that cells can be activated by any appropriately orientated contour, whether the contour is defined by a luminance edge or illusory edge (von der Heydt et al., 1984).

Form-cue invariant neural representations of contours are supported also by behavioral studies focused on the interaction between illusory and real edges. Many visual illusions are seen whether contours are defined by real or illusory edges. Examples include the Bourdon illusion (Walker & Shank, 1987; 1988a), in which collinear sides of two triangles positioned apex to apex appear to bend inward (Bourdon, 1902), the Zöllner illusion (Pastore, 1971), the Poggendorff illusion (Gregory, 1972), and the Ponzo illusion (Farne, 1968). Color filling-in is corralled by contours defined by either illusory edges or real luminance edges (Feitosa-Santana, D'Antona, & Shevell, 2011). Interactions between real and illusory edges are seen also in Vernier acuity tasks (Greene & Brown, 1997) as well as in measures of the tilt-aftereffect, which reveal a form-cue invariant neural mechanism of orientation selectivity. In these latter studies, a form-cue invariant perceived tilt in the orientation of a test stimulus is found when participants adapt to a contour defined by one type of edge (e.g., luminance contrast) but test with a different type (e.g., illusory edge; Berkley, Debruyn, & Orban, 1994; Paradiso et al., 1989; Smith & Over, 1975). Illusory edges may also contribute to object-construction processes that precede figure-ground segregation in the same manner as luminance defined edges (Peterson & Gibson, 1994; Shank & Walker, 1989). In sum, behavioral evidence supports form-cue invariance for edges, but whether all edge types are equal as *components* of a complete representation of a whole object remains an open question.

The current study tests if the visual representation of an object can integrate sub-parts created by some real edges and some illusory edges. Shifts in luminance contrast were measured within a central part of a field that slowly oscillated in luminance. A combination of real and illusory edges was used to create the percept of a square defining the central area within a larger surround. Segmentation of a center from its surround by edges defined by either all real or all illusory edges was previously shown to attenuate perceived chromatic fluctuation within a temporally oscillating center (Elliott & Shevell, 2013). Form-cue invariance was supported in that the influence of the segmenting edges essentially was equivalent whether due to real luminance edges or to illusory edges. This result raises two possible explanations: (1) a form-cue invariant visual representation of each individual edge forming the segmenting object, or (2) form-cue invariance for each complete integrated object, but not for each sub-part forming the complete object. These two alternatives are distinguished here using a combination of real and illusory edges to form a complete object.

METHODS

Stimuli & Procedure

Stimuli were displayed on a 21-inch calibrated color CRT (NEC Accusync 120) controlled by an Apple iMac computer and viewed at 1 meter. The software was set to display a resolution of 1280×1024 with a 75 Hz non-interlaced refresh rate. Using a photometer (International Light 1700), the light level of each phosphor was measured throughout its range to find 990 equal steps (0.1% increments) between 1% and 100% of the phosphor's maximal output.

Stimuli were presented on a 6×13 deg steady field maintained at a chromaticity metameric to equal energy white (EEW) and a luminance of 5 cd/m². The test stimulus was an EEW uniform circular disc 6-deg in diameter, presented in the upper 6 degs of the steady field. The disc modulated sinusoidally in luminance over time at 2 Hz. The depth of modulation was set to one of four different levels of Michelson contrast (10, 20, 30, or 40%), with an average luminance of 5 cd/m². Participants adjusted the Michelson contrast of a separate 2 deg-wide square matching stimulus to match the perceived modulation depth within the central 2-deg square area of the test disc (fig. 1). The matching stimulus oscillated at 2 Hz in-phase with the test stimulus, and was presented in the center of the lower 6 degs of the steady field. Participants were free to look back and forth between the test and matching stimuli while they adjusted contrast using a hand-held game pad.

There were 10 conditions in all (fig. 2). The first condition used the uniform 6-deg disc alone so served as a baseline condition, for which the matched contrasts should be very close to the physical test contrasts. Five primary conditions (cond. 2-6) were similar but also included a 2-deg wide square presented in the center of the 6-deg disc. The five conditions varied in how many sides of the central square were defined by illusory contours, with 0, 1, 2, 3, or 4 sides of the square having illusory contours formed by "pac-men" (Kanizsa, 1979). Each pac-man was a 1-deg diameter disc with a pie-shaped region removed. The remaining sides of the square were defined by a dark, luminance edge (0.2 deg in width). With 0 illusory sides, therefore, the full square was defined by all real edges (cond. 2), and with 4 illusory sides the square was defined by all illusory edges (cond. 3). Two additional

conditions were similar to the two-illusory-edges condition, except *only* two edges of the square were presented (see cond. 7 & 8 in fig. 2).

A potential ambiguity in condition 7 is that the pac-men created partial illusory edges where none was intended. That is, this stimulus might be interpreted as having two full illusory edges and two partial edges from the pac-men. Two remaining conditions (9 & 10) addressed this issue by replacing two of the pac-men in the two-illusory-edges-alone and the all-illusory-edges conditions with half circles (see fig. 2).

The order of testing the four contrast levels was randomized within a session for a single condition; each contrast was repeated 5 times within a session. The order of the 10 conditions was randomized within a two-hour block of testing, and the full experiment was repeated three times on separate days. Measurements from each of the 5 replications at one contrast level were averaged within each session. A final average was taken across the three daily mean values. Standard errors of the mean were calculated using the three days' values as well.

Participants

Five participants (3 male), ranging in age from 22-35, participated in the study. All participants wore their usual lens correction, if needed. Two participants had previous experience completing psychophysical tasks, but were naïve to the purpose of the experiment. Two additional participants were paid volunteers with no previous experience in psychophysical testing. The final participant was author SE (labeled "participant #2" in the results). Participants performed the experiment binocularly with the exception of author SE, who has strabismic amblyopia and therefore wore an eye patch over the affected eye. All procedures were performed in compliance with institutional guidelines, and were approved by the Institutional Review Board at the University of Chicago following the Declaration of Helsinki. Written informed consent was obtained from each participant.

Before starting the experiment, participants completed three practice sessions using the uniform disc (cond. 1), the all-real edges (cond. 2), and the all-illusory edges (cond. 3) to familiarize themselves with the task. The practice sessions also served as a screening procedure to check that participants perceived the reduction in perceived contrast within the central square, as found previously by Elliott and Shevell (2013). Two participants, both paid volunteers, did not show significant attenuation in perceived modulation depth with the complete objects compared to the uniform disc, and therefore did not complete the main experiment. Individual differences in the strength of induction from a temporally varying surround have been found in previous studies (e.g., D'Antona & Shevell, 2009; D'Antona, Kremers, & Shevell, 2011; Elliott & Shevell, 2013). Although the temporal modulation and organization of the central test region varied in these previous studies, each one illustrated at least one participant who showed little to no attenuation into the central test when the luminance modulation of the surround was near 2 Hz. As the design of the current study requires comparing the magnitude of attenuation in various conditions to attenuation from these three conditions, dropping participants who showed no attenuation does not affect inferences relating to the aims of the study. Results are presented for the remaining participants.

Statistical analysis

To identify potential outliers, for each participant the median absolute deviation (MAD; Leys, Ley, Klein, et al. 2013) was calculated using 12 values for each condition (the session average from 3 separate sessions $\times$ 4 contrast levels). If any session average had an absolute deviation from the median greater than twice the MAD then the participant repeated 5 within-session measurements for that condition at all four contrast levels, and the four new session averages replaced the original ones. Outliers were very rare: only three among the 90 possible cases (10 conditions $\times$ 3 sessions $\times$ 3 participants), two for participant #2 and one for participant #3.

The measurements from each participant were arranged as if to perform a two-way analysis of variance with two fixed factors (condition $\times$ contrast level); thus a participant's results had 120 values (10 conditions $\times$ 4 contrast levels $\times$ 3 sessions). The mean square error as normally calculated in analysis of variance was then used to test seven protected Dunn-Sidak *a priori* non-orthogonal contrasts. The contrasts were chosen to focus on specific substantive questions requiring different comparisons, described below, among the 10 conditions in fig. 1. The planned Dunn-Sidak contrasts were performed *in place of* a standard ANOVA to control the experiment-wise Type I error (Kirk, 2013, p.163) while testing seven different null hypotheses.

A failure of form-cue invariance is supported if the complete objects defined by a single type of edge (all real or all illusory, cond. 2 & 3) show significantly stronger perceived contrast attenuation than complete objects defined by a combination of real and illusory sub-parts (cond. 4-6). Therefore, the first three *a priori* comparisons compared the uniform disc (#1) to the complete objects defined by a single edge type (cond. 1 vs. 2 & 3); (#2) the complete objects defined by sub-parts (cond. 1 vs. 4-6); and (#3) the complete single edge-type objects vs. complete objects defined by sub-parts (cond. 2 & 3 vs. 4-6). The next two comparisons (#4 & #5) were between the two-illusory-edges condition (cond. 5) to each condition containing the unique edge sub-parts alone (cond. 7 or 8). This was to determine whether a partial edge of a specific type can attenuate perceived contrast, or if the perceived attenuation depends instead on a complete object with all 4 edges fully defined. The final two contrasts determined whether eliminating cues to unintended illusory edges, which might contribute to the *percept* of a complete square, altered the perceived modulation depth. Specifically, one contrast (#6) compared condition 7 to condition 9, and another (#7) compared condition 3 to condition 10.

RESULTS

Figure 3 shows the perceived modulation depth within the central square as a function of stimulus contrast, with the uniform disc alone, a central square defined by all-real edges, and a square defined by all-illusory edges for naïve participant #1. When the center was perceptually segmented from the surround with all-real (squares) or all-illusory (diamonds) edges, perceived modulation in the center was significantly less ($t_{DS}(7, 80) = -9.76$, $p < 0.01$, *a priori* contrast #1) compared to the uniform disc (circles). This is consistent with previous findings using chromatic modulation (Elliott & Shevell, 2013), and was

corroborated by participant #2 ($tDS(7, 80) = -4.09$, $p < 0.01$) and #3 ($tDS(7, 80) = -4.04$, $p < 0.01$).

Differences between the uniform disc and conditions that contained a complete object are more clearly shown in figure 4. Each panel shows results for one of three participants, and plots the mean matched Michelson contrast for each condition, averaged across the four test contrast levels. The perceived modulation depth was significantly less for the complete squares defined by sub-parts (cond. 4-6) compared to the uniform disc of cond. 1 ($tDS(7, 80) = -10.36$, $p < 0.01$ for participant #1, $tDS(7, 80) = -3.14$, $p < 0.05$ for participant #2, and, $tDS(7, 80) = -3.03$, $p < 0.05$ for participant #3).

Form-cue invariance requires that all conditions attenuate the perceived modulation depth to a similar degree. If, however, form-cue invariance holds for only complete objects, but not for the sub-parts of an object (that is, not for individual sides of the square), then greater attenuation of modulation depth should occur for objects defined by a singular edge type (i.e., all-real or all-illusory edge conditions) compared to conditions that contain objects created by a mixture of edge types. The strength of attenuation for complete objects defined by a singular edge type (cond. 2 & 3) was *not* significantly different from complete objects defined by sub-parts for any participant (cond. 4-6; $tDS(7, 80) < 1.58$, NS for all participants). While being mindful not to accept the null hypothesis, this result is expected with form-cue invariance for a complete, integrated object, regardless of how the object is defined.

Figure 5 shows the attenuation in perceived contrast for the two-illusory-edges condition (cond. 5), compared to the corresponding individual pieces (cond. 7 & 8). The separate panels show results for individual participants. Overall, the attenuation measured with the two illusory pieces alone is *not* significantly different from the complete object defined by sub-parts ($tDS(7, 80) < |2.44|$, NS for all participants), though the attenuation measured with the two-*real*-edges alone is significantly weaker for participant #1 ($tDS(7, 80) = 5.55$, $p < 0.01$) and nearly so for participant #3 ($tDS(7, 80) = 2.62$, $p < 0.10$; $tDS(7, 80) = 2.18$ NS for participant 2). In general, adding two real edges to two illusory edges did not significantly reduce further the perceived modulation depth compared to two-illusory-edges alone.

A possible explanation for the strength of attenuation with only two illusory edges is that they create the percept of additional partial illusory sides. There is some evidence that illusory edges can be generated from a single inducer (Halko, Mingolla, & Somers, 2008). An illusory surface can be seen with as few as two inducing elements presented in depth (Anderson, 1994) or in motion (Anderson & Sinha, 1997; Halko et al., 2008). A related explanation may be found in the support ratio, which is defined as the ratio of the inducer length (e.g., diameter of the pacman) to the length of the illusory edge (Shipley & Kellman, 1992). A higher support ratio predicts better visibility of the edges defining the illusory figure (Shipley & Kellman, 1992). The support ratio here was 0.5. Perhaps when 3 corners of the square are presented (as in cond. 7), the “pac-men” may provide some “support” to create the percept of a complete 4-sided illusory square.

The perceived contrast was always less (i.e., more attenuation) for the two-illusory-edges-alone (cond. 7) compared to the two-partial-illusory-edges condition (cond. 9) and significantly so for 2 of 3 participants ($tDS(7, 80) = 8.17$, $p < 0.01$ for participant #1, $tDS(7, 80) = 3.85$, $p < 0.01$ for participant #2, though $tDS(7, 80) = 2.39$, NS for participant #3; fig. 6). This result is consistent with the idea that the pac-men used in the two-illusory-edges alone condition contributed to the percept of a complete enclosed illusory surface. Another critical comparison is between attenuation for the all-illusory-edge object (cond. 3) compared to the three-partial-illusory edges (cond. 10). The only difference between these two conditions is that 2 of the pac-men were replaced with half circles, though perceptually this change affected whether the central figure appeared closed (cond. 3) or not (cond. 10). The perceived contrast was always significantly weaker for the all-illusory-edge object ($tDS(7, 80) = 8.79$, $p < 0.01$ for participant #1, $tDS(7, 80) = 3.85$, $p < 0.01$ for participant #2, $tDS(7, 80) = 5.52$, $p < 0.01$ for participant #3; fig. 6), which again is consistent with the strength of attenuation depending on whether the central figure is perceived as a complete closed 4-sided illusory figure.

DISCUSSION

Results of the current study support a strong version of form-cue invariance, in that complete, closed, four-sided figures, no matter how constructed, are effective at segmenting center from surround, as evidenced by the induced reduction in perceived contrast within the central figure. Further, the presence of illusory edges, even when incomplete, can be strong enough to induce a reduction in contrast perception; adding real edges to achieve a fully closed figure did not significantly affect the results (fig. 5). Last, changing some of the pac-men that induce illusory contours to half circles reduces the induction from the surround. This result is consistent with eliminating the perceptual cues to closure of the central square. In sum, the results show that perceived contrast within the central square is reduced regardless of how the square is constructed so long as the stimulus configuration implies closure, as expected if the neural representation of an object is insensitive to the component cues that define the individual sub-parts of the object.

Previous behavioral evidence shows some consistency, but also divergence, in the visual representation of real and illusory edges. For instance, many visual illusions transfer across edge types, though the strength may differ when the inducing stimulus is a real edge compared to an illusory edge. Stronger tilt aftereffects are seen following adaptation to real edges compared to illusory edges (Berkley et al., 1994; Paradiso et al., 1989), the Bourdon illusion is stronger when the target triangles are defined by illusory edges compared to real luminance edges (Walker & Shank, 1987; Walker & Shank, 1988b), and improved orientation discrimination transfers across illusory and real contours, but only when the training occurs with illusory edges (Vogels & Orban, 1987). Models of divergent neural processing have proposed (1) separate local feature detection pathways that are later pooled at a neural locus of contour perception (Finkel & Edelman, 1989; Peterhans & von der Heydt, 1989; von der Heydt & Peterhans, 1989), (2) a cognitive feedback stage of perceptual organization that contributes to the final illusory contour percept (e.g., Gregory, 1972), or (3) a combination of both (Spillmann & Dresch, 1995). The current results do not address whether divergent neural pathways representing real and illusory edges exist, but they do

indicate that real and illusory edges defining an object may not be treated any differently in the integration process. In this sense, each illusory edge “sheds its cloak” so the neural representations of real and illusory edges are combined to construct the representation of an object.

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Figure 1.

The uniform disc experimental configuration. Observers adjusted the contrast of the matching square until it appeared to match the perceived modulation depth within the central area of the test disc denoted by the dashed line. Dashed and dotted lines are added for clarity here but were not in the stimulus.

Figure 2.

Illustration of the test disc for all 10 experimental conditions, showing variations in how the central square was defined by different combinations of real and illusory contours.

Figure 3.

The perceived modulation depth (vertical axis) as a function of stimulus modulation depth, for participant #1. The dotted line corresponds to the veridical match. The circles, squares, and diamonds correspond to the uniform disc (cond. 1), the full-real contour object (cond. 2), and the full-illusory contour object (cond. 3), respectively. Error bars, where visible, are one standard error of the mean.

Figure 4.

Each bar shows the mean matched contrast averaged across the four test contrast levels for one individual participant. A priori comparisons, and their respective significance, are shown above the bars in each panel (* = $p < 0.05$, ** = $p < 0.01$). Error bars are one standard error of the mean.

Figure 5.

Each bar shows the mean matched contrast averaged across four test contrast levels for one participant. The dashed line denotes the matched contrast for the uniform control. A priori comparisons, and their respective significance, are shown above the bars in each panel (* = $p < 0.05$, ** = $p < 0.01$, ns = not significant). Error bars are one standard error of the mean.

Figure 6.

Each bar shows the mean matched contrast averaged across four test contrast levels for one individual participant. The dashed line denotes the matched contrast for the uniform control. A priori comparisons, and their respective significance, are shown above the bars in each panel (* = $p < 0.05$, ** = $p < 0.01$, ns = not significant). Error bars are one standard error of the mean.