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

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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.

1. 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 (Grosof, Shapley, & Hawken, 1993) and V2 (Peterhans & von der Heydt, 1989; von der Heydt & Peterhans, 1989; von der Heydt et al., 1984) 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

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defined by real or illusory edges. Examples include the Bourdon illusion (Walker & Shank, 1987, 1988), 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.

2. Methods

2.1. 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 m. 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/m^2. 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/m^2. 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

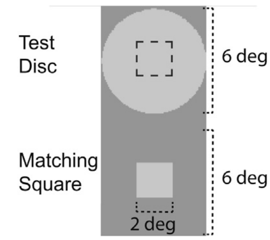

Fig. 1. The uniform disc experimental configuration. Observers adjusted the contrast of the matching square until it appeared to match the perceived modulation depth within the central area of the test disc denoted by the dashed line. Dashed and dotted lines are added for clarity here but were not in the stimulus.

Fig. 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.

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-