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Emergent Filling In Induced by Motion Integration Reveals a High-Level Mechanism in Filling In

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Abstract

The visual system is intelligent—it is capable of recovering a coherent surface from an incomplete one, a feat known as perceptual completion or filling in. Traditionally, it has been assumed that surface features are interpolated in a way that resembles the fragmented parts. Using displays featuring four circular apertures, we showed in the study reported here that a distinct completed feature (horizontal motion) arises from local ones (oblique motions)—we term this process *emergent filling in*. Adaptation to emergent filling-in motion generated a dynamic motion aftereffect that was not due to spreading of local motion from the isolated apertures. The filling-in motion aftereffect occurred in both modal and amodal completions, and it was modulated by selective attention. These findings highlight the importance of high-level interpolation processes in filling in and are consistent with the idea that during emergent filling in, the more cognitive-symbolic processes in later areas (e.g., the middle temporal visual area and the lateral occipital complex) provide important feedback signals to guide more isomorphic processes in earlier areas (V1 and V2).

Keywords

motion perception; visual attention; filling in; motion integration; motion aftereffect; modal completion; amodal completion; middle temporal (MT) visual area; lateral occipital complex (LOC); V1; V2

The visual system is intelligent—it is capable of recovering a coherent surface from an incomplete one, a feat known as *perceptual completion* or *filling in*. A noted example is the Kanizsa square (Fig. 1a), in which four notched circles induce a subjective square shape with a sharp contour and enhanced luminance relative to the background (Kanizsa, 1979). Because the completed object has the same “mode” (i.e., contour and surface brightness) as if a real square were present, this process is termed modal completion (Michotte, Thines, & Crabbe, 1964). In amodal completion, the completed object is occluded and thus lacks visible attributes (e.g., the notched circles are perceptually completed as occluded disks). Conceivably, to perceive Kanizsa-like subjective figures, the visual system has to interpolate critical missing links from the given fragmented image so that contour and surface can be completed, modally or amodally. Traditionally, surface features are interpolated in a way that resembles the fragmented parts. In moving visual phantoms (Fig. 1b), for instance, in

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which a low-contrast moving grating is divided by an empty orthogonal gap, the gap is perceptually completed with the same pattern, color, speed, and direction of movement as the inducing grating, albeit more dimly (Tynan & Sekular, 1975).

In the study reported here, we used a novel configuration that combined these two illusions. Using this configuration, we showed that in both modal and amodal completion, the interpolation processes can generate a solution distinct from the fragmented parts. Specifically, we presented a translationally moving diamond perceived through four circular apertures, as shown in Figure 1c (see also Video S1 in the Supplemental Material available online). Integrating the four apertures allowed the boundary contour and motion direction to be filled in, which resulted in a vivid percept of a diamond moving leftward or rightward. Because the filling-in motion percept from integration was distinct from the local motion percept (uphill or downhill motion), we call this type of perceptual completion *emergent filling in*.

Emergent filling in affords a unique opportunity to examine the long-standing debate over isomorphic versus symbolic mechanisms of filling in: The isomorphic theory argues that filling in is achieved through point-wise neural representation of visual features in retinotopic visual areas (Gerrits & Vendrik, 1970), whereas the symbolic theory contends that contour and surface interpolations, which are based on the contrast information at the surface border, take place at higher areas (Gregory, 1972). Emergent filling in of motion implies that both early retinotopic areas and late nonretinotopic areas make essential contributions. Specifically, because of their small receptive fields, neurons in early visual cortex can measure only the component of motion perpendicular to a contour that extends beyond their receptive fields (e.g., uphill or downhill motion in our configuration) and thus cannot recover the true motion—this is known as the aperture problem in motion perception (Marr & Ullman, 1981). Downstream, the middle temporal visual area (MT or V5) solves this problem by integrating directional responses from V1 (Pack & Born, 2001). The collaboration between these regions highlights the synergetic interactions between local isomorphic processes (e.g., contour interpolation) and global symbolic processes (e.g., structure and global motion extraction) in enabling emergent filling in.

If there is indeed neural emergent filling in, one would expect to observe adaptation effects from the filling-in motion that are not due to spreading of local motions from the circular apertures in our displays. Moreover, if higher-level symbolic processes (e.g., in MT, V5, and the lateral occipital complex, LOC) play a critical role in guiding more isomorphic process (e.g., in V1 and V2), one would further expect that the adaptation effects specific to filling in, if observed, should be modulated by selective attention, as opposed to traditional filling in, which is relatively automatic, independent of attention (M. Meng, Remus, & Tong, 2005; Sasaki & Watanabe, 2004).

To test these ideas, we adapted observers in the integrated condition to the motion displays in which a diamond shape appeared to move behind four circular apertures. Immediately after the motion display ended, we measured the motion after-effect outside of the apertures using a dynamic test: a random dot kinetogram (RDK), which consisted of a random series of dots that rapidly appeared and disappeared. Because aftereffects from local motion in the apertures could potentially transfer to the test region (Bex, Metha, & Makous, 1999; Lalanne & Lorenceau, 2006; X. Meng, Mazzoni, & Qian, 2006; Price, Greenwood, & Ibbotson, 2004; Snowden & Milne, 1997; Weisstein, Maguire, & Berbaum, 1977), we also adapted observers to control displays that had the same local apertures but could not be integrated to generate emergent filling in (the nonintegrated condition; see Fig. 1c).

We found a much stronger adaptation effect in the integrated (with filling in) condition than in the nonintegrated (without filling in) condition. The difference between the magnitude of the effects in the two conditions therefore reveals that the motion aftereffect was not confounded by transfers from nearby apertures but was solely due to adaptation to the emergent, perceived filling-in motion; we term this a *filling-in motion aftereffect*. The filling-in motion aftereffect was observed in both our modal- and amodal-completion conditions, but, notably, was reduced when the attentional load of a fixation task was increased during adaptation. This suggests that the symbolic processes in later areas might provide important feedback signals to guide isomorphic processes in earlier areas (Halgren, Mendola, Chong, & Dale, 2003), which critically depend on attention. Because the filling-in motion aftereffect was only present when we used dynamic tests and disappeared when we used static tests, the effect was likely a high-level one, involving MT and V5 (Culham et al., 1998; Nishida, Ashida, & Sato, 1994). Moreover, the filling-in motion aftereffect was reduced when the surface filling in was removed and only contour filling in remained; this suggests the contribution of both surface filling in and contour filling in (see Fig. S1 in the Supplemental Material). In short, adaptation to emergent filling-in motion can generate an attention-dependent, high-level motion aftereffect.

Method

Observers viewed displays inducing modal and amodal completion in a passive-adaptation experiment and an attentional-load experiment, in which the task varied between easy and difficult.

Observers

Six observers participated in the passive-adaptation experiment (in both the amodal and modal conditions), and 8 observers participated in the attentional-load experiment (4 in the modal condition and 4 in the amodal condition). One observer was author Z. L.; the others, who were naive to the purpose of the study, were drawn from the University of Minnesota community and received monetary compensation for their time. All had normal or corrected-to-normal vision and signed a consent form approved by the university's institutional review board.

Stimuli and apparatus

The stimuli were presented on a gamma-corrected 22-in. CRT monitor (Hewlett-Packard p1230; refresh rate = 100 Hz, resolution = 1024×768 pixels) using MATLAB (The MathWorks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

The adapting display consisted of four circular apertures (diameter = 4° , center-to-center distance = 6° , luminance = 23.4 cd/m^2) set in a black background and placed equidistantly around a central fixation cross (center-to-center distance = 4.24° ; Fig. 1c). In the integrated condition (see Video S1 in the Supplemental Material), a diamond (size = 8.24° , speed = $11.68^\circ/\text{s}$) appeared to move leftward or rightward behind the apertures. Thus, within each individual aperture, a sequence of motion in an uphill-downhill (or downhill-uphill motion) cycle was perceived; there were 150 frames in each cycle (with 2 frames between each reversal of direction). In the non-integrated condition (see Video S2 in the Supplemental Material), for each trial, the starting frame for each of the four apertures was randomly chosen from among the 150 frames of the cycle; the direction sequences were randomly distributed among the apertures with half moving uphill-downhill and half moving downhill-uphill. As a result, a coherently moving diamond could not be perceived.

On average, the local motion signals in each aperture were the same across the integrated and nonintegrated conditions. In both conditions, the objects in motion could induce amodal or modal completion. In the amodal condition, the objects had flickering surfaces consisting of half white patches (size = $0.16^\circ \times 0.16^\circ$, luminance = 26.7 cd/m^2) and half black patches, randomly distributed for each frame. In the modal condition, the objects had uniform black surfaces. Flickering was removed in the attention task to reduce attentional capture, by fixing the distribution of white and black patches throughout each trial.

The test display was an RDK (Britten, Shadlen, Newsome, & Movshon, 1992) that appeared within an imaginary circular aperture (diameter = 3.17°) centered on the fixation cross, with no spatial overlap with the adapting apertures (contour-to-contour distance = 0.66°). On each video frame, a fraction of dots (size = $0.12^\circ \times 0.12^\circ$, luminance = 19.1 cd/m^2 on a black background, density = 30 dots per deg^2/s) were randomly chosen and plotted at a displacement of 0.18° from the positions three frames (30 ms) earlier to generate apparent motion ($6^\circ/\text{s}$); the other dots were plotted at random locations. The probability that a dot exhibited coherent motion was determined by the level of motion coherence assigned to that trial.

The fixation crosses (length = 0.39° , width = 0.12°) were presented in a rapidly changing stream (rapid serial visual presentation). In the passive-adaptation experiment, the fixation cross's color cycled through red, green, and yellow (two items per second). In the attentional-load experiment, the color for each cross could be red, green, or blue, and the shape could be an intact cross, an upper cross (missing the lower part), or a lower cross (missing the upper part). In the easy task, red items, regardless of the shape, were the targets; in the difficult task, upper crosses in red and lower crosses in green, never the reverse, were the targets. Each target was presented for 25 frames, followed by a gray cross for 750 frames (i.e., two items per second).

Procedure

Subjects sat approximately 57 cm from the monitor with their heads positioned in a chin rest in a dimly lit room while an experimenter was present. Motion sensitivity in each individual observer was calibrated prior to the adaptation phase. Sensitivity was measured using an RDK (duration = 800 ms) with eight coherence levels (with 2%, 5%, 10%, 15%, 20%, 30%, 40%, and 60% of the dots moving coherently) and two directions (leftward and rightward), randomized across 160 trials in four blocks. Observers indicated the motion direction of the RDK by clicking the left or right button of a mouse. For each individual observer, a logistic function was fitted to the responses to obtain the amount of coherence for asymptotic performance (the average of the absolute coherence levels for 97% "rightward" and 97% "leftward" responses), which we defined as 1 unit of normalized coherence. Stimuli with 100%, 50%, and 25% of normalized coherence and two directions (leftward and rightward) served as test stimuli in the adaptation phase.

Following sensitivity calibration, observers in the passive-adaptation experiment were adapted to four types of stimuli in a blocked design, a full crossing of integrated versus nonintegrated and modal versus amodal conditions, with the order randomized within observers. For each type of stimulus, observers adapted to two directions, leftward motion and rightward motion, in two blocks, with at least 2 min of rest in between. The order of adaptation directions was counterbalanced across observers. Each block started with an initial adaptation trial (50 s) followed by 47 top-up adaptation trials (5 s each). Each adaptation trial was followed immediately by an RDK test lasting 200 ms. The next adaptation trial began once the observer indicated the motion direction of the test through nonspeeded mouse clicking.

The attentional-load experiment was similar to the passive-adaptation experiment, except for the addition of a detection task during adaptation, a reduction in the number of top-up trials (from 47 to 35), and unequal numbers of trials for each test level. During adaptation, observers were asked to fixate on the central cross, which changed color every 500 ms, and press a key as quickly and accurately as possible when the cross became a target. During the easy task, the cross was a target when it turned red. In the difficult task, the cross was a target when the upper half turned red or the lower half turned green. In the initial trial, 9 to 11 targets appeared; in each top-up trial, 1 to 2 targets appeared. Easy and difficult tasks were blocked. The order of adaptation directions and task difficulty was counterbalanced across observers. For the RDK test, to make it difficult for observers to guess the distribution of the numbers of trials for each coherence level, we randomly distributed the six test stimuli across 36 trials in each block (such that there were 2 to 10 trials for each stimulus per block).

Results

Dynamic motion aftereffect due to the filling-in motion

Adaptation effects were observed in both the amodal- and modal-completion conditions. After looking at the fixation cross and adapting to the task-irrelevant surrounding motion in one direction, observers were more likely to perceive the RDK moving in the opposite direction. Figure 2 shows motion-direction adaptation: The motion response function showed a greater shift leftward (i.e., there were more “rightward” responses) following leftward adaptation than following rightward adaptation. This motion aftereffect in the nonintegrated condition replicates a now widely reported “phantom” motion aftereffect (Weisstein et al., 1977), both of which reflect transfer of motion aftereffects from adapting locations to unadapted locations. It is important to note that in both the amodal- and modal-completion conditions, the adaptation effect in the integrated condition was much larger than that in the nonintegrated condition, despite the fact that the same adapting stimuli appeared in the individual apertures. Such a difference between the integrated and nonintegrated conditions thus reflected an adaptation effect to emergent filling in and likely involved both contour filling in and surface filling in (see also Fig. S1).

To quantify the strength of the adaptation effect, we used as an index the difference between the leftward and rightward adaptation in points of perceived null motion—the amount of motion coherence for which observers were equally likely to respond “leftward” or “rightward.” Because the patterns between the amodal- and modal-completion conditions were similar (the difference in adaptation effect between the integrated and nonintegrated conditions was 0.14 and 0.16, respectively), paired $t(5) = 0.28$, $p = .78$, the data are combined here. The mean shift of null points following leftward relative to rightward adaptation was 0.33 ($SEM = 0.04$) units of normalized motion coherence for the integrated stimuli, which is significantly larger than 0.18 ($SEM = 0.06$) for the nonintegrated stimuli, $t(5) = 3.29$, $p = .022$. In terms of actual, nonnormalized coherence, the shift was greater for the integrated stimuli ($M = 0.19$, $SEM = 0.03$) than for the nonintegrated stimuli ($M = 0.12$, $SEM = 0.04$), $t(5) = 4.33$, $p = .008$. However, because the points of perceived null motion are logistically fitted, this is not an assumption-free approach. To quantify the adaptation effect in a more objective manner, we first calculated the percentage of “rightward” responses across all coherence levels tested for each condition, and we then compared the difference in the percentage of “rightward” responses following leftward and rightward adaptation, which therefore served as an objective, quantitative index of the adaptation effect. As Table 1 shows, for the integrated stimuli, leftward adaptation (relative to rightward adaptation) resulted in more “rightward” responses after adapting to the integrated

stimuli ($M = 24.8\%$, $SEM = 4.3\%$) than to the nonintegrated stimuli ($M = 10.1\%$, $SEM = 4.9\%$), $t(5) = 5.55$, $p = .012$.

Filling-in motion aftereffect depends on attention

Does the motion adaptation effect arising from perceptual completion depend on attention to the adaptation stimuli (whether to the local apertures or to the completed percept)? To address this question, we compared the adaptation effects due to completion (i.e., the difference between aftereffects in the integrated and the nonintegrated conditions) between the easy and the difficult fixation tasks (Lak, 2008). In both the amodal- and modal-completion conditions, we consistently found that the adaptation effect due to completion was much bigger in the easy fixation task than that in the difficult one (Table 1). To quantify this, we again calculated the percentage of “rightward” responses across all coherence levels tested for each condition and used as an index the difference in the percentages of “rightward” responses following leftward and rightward adaptation. In the easy task, for the integrated stimuli, leftward adaptation (relative to rightward adaptation) resulted in more “rightward” responses to the integrated stimuli ($M = 24.3\%$, $SEM = 7.9\%$) than to the nonintegrated stimuli ($M = 0.03\%$, $SEM = 6.5\%$), $t(7) = 2.57$, $p = .037$. However, in the difficult task, leftward adaptation to the integrated stimuli resulted in more “rightward” responses ($M = 13.9\%$, $SEM = 8.6\%$) than “leftward” responses, similar to leftward adaptation to the nonintegrated stimuli ($M = 15.3\%$, $SEM = 4.6\%$), $t(7) = -0.25$, $p = .812$. The difference in adaptation between integrated and nonintegrated stimuli is thus robust in the easy task ($M = 21.5\%$, $SEM = 7.8\%$) but essentially absent in the difficult task ($M = -1.4\%$, $SEM = 5.3\%$).

Discussion

Interpolation processes during perceptual completion usually follow the features from the available parts to fill in the gaps. In this study, using motion apertures, we showed that filling in of motion direction could be distinct from local motion directions, hence the term emergent filling in. Moreover, adaptation to this emergent filling-in motion, either modally or amodally, generated a motion aftereffect in a region outside of the adapting apertures when a dynamic test was used. This motion aftereffect was much reduced when the same local adapting motion signals were presented in the apertures but could not be integrated to fill in the test region. This contrast demonstrates a motion aftereffect due to emergent filling in. The filling-in motion aftereffect was reduced when the surface filling in was removed with only contour filling in remaining, which suggests the contribution of both surface filling in and contour filling in (see Fig. S1). By manipulating the attentional load of the central fixation task during adaptation, we further showed that the filling-in motion aftereffect was dramatically reduced when the central fixation task demanded more attention than when it demanded less attention.

The attention modulation observed is in contrast with previous findings showing an early, isomorphic mechanism for completion. For example, in psychophysical studies, it has been shown that both modal and amodal completion appear to be obligatory and occur preattentively (Davis & Driver, 1994; He & Nakayama, 1992; Rauschenberger & Yantis, 2001; Rensink & Enns, 1998), before object-based attention selection (Moore, Yantis, & Vaughan, 1998) and surface-based attention selection (Davis & Driver, 1997), and at least for amodal completion before perceptual grouping by shape similarity (Palmer, Neff, & Beck, 1996). A recent functional MRI (fMRI) study also suggests that filling in of visual motion from the phantom illusion in V1 and V2 could occur independently of attention (M. Meng et al., 2005), similar to color filling in (Sasaki & Watanabe, 2004). The distinction of attention modulation between our study and these previous studies suggests the important

role of high-level symbolic processes (e.g., in MT, V5, or LOC) in emergent filling in, possibly by providing feedback signals to guide isomorphic processes in early visual cortex. In principle, attention modulation of motion aftereffects can be traced to attention effects on the interpolation processes, or on the representation of emergent motion, or both. Because motion integration in MT is sensitive to attention (Cook & Maunsell, 2004), attention effects on the interpolation processes are likely to play an important role.

The idea that during emergent filling in, high-level symbolic processes provide feedback signals to guide isomorphic processes in early visual cortex is intriguing. Over the last two decades, many studies have provided evidence in support of the isomorphic theory, which has led to the belief that perceptual completion is hardwired in early visual cortex to provide an anticamouflage device for discovering hidden objects (Komatsu, 2006; Pessoa, Thompson, & Noe, 1998; M. L. Seghier & Vulleumier, 2006). For example, evidence from psychophysics (Davis & Driver, 1994, 1998; He & Nakayama, 1992; Pillow & Rubin, 2002; Rensink & Enns, 1998; Smith & Over, 1975; Weisstein et al., 1977), modeling (Grossberg, 1994; Li, 1998), neuropsychology (Mattingley, Davis, & Driver, 1997), neurophysiology (De Weerd, Gattass, Desimone, & Ungerleider, 1995; Fiorani, Rosa, Gattass, & Rocha-Miranda, 1992; Lee & Nguyen, 2001; Roe, Lu, & Hung, 2005), and fMRI (M. Meng et al., 2005; Sasaki & Watanabe, 2004) generally reveals a low-level mechanism in V1, V2, or both that is responsible for completion, but not a cognitive, symbolic mechanism (Dennett, 1992; Gregory, 1972).

Previous studies using fMRI have shown that modally completed feature surfaces sometimes activate high-level regions—for example, LOC has been shown to activate in response to modally completed Kanizsa figures (Mendola, Dale, Fischl, Liu, & Tootell, 1999) independent of the contour (Stanley & Rubin, 2003), and associative areas in the dorsal pathway (the caudal region of the intraparietal sulcus and LOC) have shown activation to modally completed surfaces from the Craik-O'Brien-Cornsweet illusion (Perna, Tosetti, Montanaro, & Morrone, 2005), dependent on the edges. However, such activation might be due to feedforward activity from V1 and V2 (M. Seghier et al., 2000), and even without invoking filling in at all (Cornelissen, Wade, Vladusich, Dougherty, & Wandell, 2006). In general, previous research showing early mechanisms of perceptual completion has invoked spreading of contour and features as a mechanism of integration, which could be achieved through horizontal connections in early visual cortex (Gilbert, 1992). For instance, the long-range integration seen in Kanizsa figures can be computed in early visual cortex via a cascade of activity percolating through a chain of lateral connections (Gilbert, Das, Ito, Kapadia, & Westheimer, 1996; Ullman, 1976). Because of the aperture problem in motion perception (Marr & Ullman, 1981), the emergent filling-in phenomenon relies on higher-order integration processes that extract complex global structures from local information.

It is debated whether modal completion and amodal completion involve the same contour- and surface-completion mechanisms (Kellman & Shipley, 1991; Murray, Foxe, Javitt, & Foxe, 2004). Given the large projecting angle between adjacent inducing edges (roughly 90°) in the current study, the completed shape in the amodal-completion condition might be more angular (i.e., closer to a corner) than the completed shape in the modal-completion condition (Singh, 2004). In addition, the filling-in motion surface in the test region in the modal-completion condition, compared with that in the amodal-completion condition, might invoke neural representations of motion in early visual cortex (M. Meng et al., 2005). Despite these potential differences in contour and surface, similar filling-in motion aftereffects and similar attention modulation effects were observed across amodal- and modal-completion conditions, which suggests that the mechanism responsible for the filling-in motion aftereffect is insensitive to the differences between modal and amodal completions but sensitive to emergent filling in.

In our configuration, the temporal vector sum motion direction remained constant in the integrated condition but changed in the nonintegrated condition because of phase randomization. Could the larger motion aftereffect in the integrated (i.e., with filling in) condition compared with the nonintegrated (i.e., without filling in) condition be due to this difference? A subsequent control experiment showed that adapting motion with directions balanced over time is just as effective in producing motion aftereffects (see Fig. S2 in the Supplemental Material). Would completed motion, in particular in the modal-completion condition, attract attention more than non-completed motion would, or could it be that observers simply imagined motion in the integrated condition but not in the non-integrated condition?

These attention and imagination confounds, although valid concerns in previous studies on motion aftereffects (Snowden & Milne, 1997; Weisstein et al., 1977), could not explain our data. Subjectively, in the passive-adaptation experiment, in which observers simply fixated on the central cross while it changed color, the motion in the nonintegrated condition actually appeared more attention capturing than that in the integrated condition. As for the imagination confound, a global net leftward or rightward motion was apparent in the nonintegrated condition and thus the suspected engagement of motion imagination would similarly apply. Objectively, in the attentional load experiment, we deliberately controlled the attentional load of the central fixation task and made the motion stimuli completely task irrelevant. With a central fixation task continuously demanding close inspection in both the integrated and nonintegrated conditions, attention was controlled; yet in both the modal- and amodal-completion conditions, a significant motion-aftereffect difference between the integrated and nonintegrated conditions was still observed when the attentional load was low. Similarly for the imagination confound, with the central fixation task continuously loading observers' attention, the imagination factor was controlled.

These results suggest that not all interpolation processes are the same; some rely more on low-level mechanisms, whereas others rely more on high-level mechanisms, which potentially differentiates filling-in mechanisms. For example, filling in at the blind spot or retinal scotomas is instantaneous, with the contour and feature to be filled in readily available from the surrounding retinotopic areas in V1 and V2. Similarly, filling in during Troxler fading and stabilized retinal images could be achieved through such retinotopic mechanisms. Perceiving Kanizsa-like subjective figures usually requires integrating spatially disjoined parts to provide the contour and surface features to be filled in. If the integration process could be computed through an early mechanism, such as in Kanizsa figures, then the mechanism of perceptual completion may be mainly an early one (Shimojo, Kamitani, & Nishida, 2001). If, in contrast, the integration process must be computed through a late mechanism, such as in motion integration across apertures, then the mechanism of perceptual completion would rely heavily on later mechanisms. This framework might help to unite the vast filling-in phenomena in the literature. Further studies of the emergent filling-in phenomenon are likely to yield more insight regarding the mechanisms involved in filling in.

Supplemental Material

Additional supporting information may be found at <http://pss.sagepub.com/content/by/supplemental-data>

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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References

- Bex PJ, Metha AB, Makous W. Enhanced motion aftereffect for complex motions. *Vision Research*. 1999; 39:2229–2238. [PubMed: 10343804]
- Brainard DH. The psychophysics toolbox. *Spatial Vision*. 1997; 10:433–436. [PubMed: 9176952]
- Britten KH, Shadlen MN, Newsome WT, Movshon JA. The analysis of visual motion: A comparison of neuronal and psychophysical performance. *Journal of Neuroscience*. 1992; 12:4745–4765. [PubMed: 1464765]
- Cook EP, Maunsell JH. Attentional modulation of motion integration of individual neurons in the middle temporal visual area. *Journal of Neuroscience*. 2004; 24:7964–7977. [PubMed: 15356211]
- Cornelissen FW, Wade AR, Vladusich T, Dougherty RF, Wandell BA. No functional magnetic resonance imaging evidence for brightness and color filling-in in early human visual cortex. *Journal of Neuroscience*. 2006; 26:3634–3641. [PubMed: 16597716]
- Culham, J.; Nishida, S.; Ledgeway, T.; Cavanagh, P.; von Grünau, M.; Kwas, M.; Raymond, J. Higher-order effects. In: Mather, G.; Verstraten, FAJ.; Anstis, S., editors. *The motion aftereffect: A modern perspective*. Cambridge, MA: Massachusetts Institute of Technology; 1998. p. 85-124.
- Davis G, Driver J. Parallel detection of Kanizsa subjective figures in the human visual system. *Nature*. 1994; 371:791–793. [PubMed: 7935838]
- Davis G, Driver J. Spreading of visual attention to modally versus amodally completed regions. *Psychological Science*. 1997; 8:275–281.
- Davis G, Driver J. Kanizsa subjective figures can act as occluding surfaces at parallel stages of visual search. *Journal of Experimental Psychology: Human Perception and Performance*. 1998; 24:169–184.
- Dennett, DC. Filling in versus finding out: A ubiquitous confusion in cognitive science. In: Pick, HL., Jr; van den Broek, P.; Knill, DC., editors. *Cognition: Conceptual and methodological issues*. Washington, DC: American Psychological Association; 1992. p. 33-49.
- De Weerd P, Gattass R, Desimone R, Ungerleider LG. Responses of cells in monkey visual cortex during perceptual filling-in of an artificial scotoma. *Nature*. 1995; 377:731–734. [PubMed: 7477262]
- Fiorani M Jr, Rosa MG, Gattass R, Rocha-Miranda CE. Dynamic surrounds of receptive fields in primate striate cortex: A physiological basis for perceptual completion? *Proceedings of the National Academy of Sciences, USA*. 1992; 89:8547–8551.
- Gerrits HJ, Vendrik AJ. Simultaneous contrast, filling-in process and information processing in man's visual system. *Experimental Brain Research*. 1970; 11:411–430. [PubMed: 5496938]
- Gilbert CD. Horizontal integration and cortical dynamics. *Neuron*. 1992; 9:1–13. [PubMed: 1632964]
- Gilbert CD, Das A, Ito M, Kapadia M, Westheimer G. Spatial integration and cortical dynamics. *Proceedings of the National Academy of Sciences, USA*. 1996; 93:615–622.
- Gregory RL. Cognitive contours. *Nature*. 1972; 238:51–52. [PubMed: 12635278]
- Grossberg S. 3-D vision and figure-ground separation by visual cortex. *Perception & Psychophysics*. 1994; 55:48–121. [PubMed: 8036093]
- Halgren E, Mendola J, Chong CDR, Dale AM. Cortical activation to illusory shapes as measured with magneto-encephalography. *NeuroImage*. 2003; 18:1001–1009. [PubMed: 12725774]
- He ZJ, Nakayama K. Surfaces versus features in visual search. *Nature*. 1992; 359:231–233. [PubMed: 1528263]
- Kanizsa, G. *Organization in vision: Essays on gestalt perception*. New York, NY: Praeger; 1979.
- Kellman PJ, Shipley TF. A theory of visual interpolation in object perception. *Cognitive Psychology*. 1991; 23:141–221. [PubMed: 2055000]

- Komatsu H. The neural mechanisms of perceptual filling-in. *Nature Reviews Neuroscience*. 2006; 7:220–231.
- Lak A. Attention during adaptation weakens negative after-images of perceptually colour-spread surfaces. *Canadian Journal of Experimental Psychology*. 2008; 62:101–109. [PubMed: 18572987]
- Lalanne C, Lorenceau J. Directional shifts in the barber pole illusion: Effects of spatial frequency, spatial adaptation, and lateral masking. *Visual Neuroscience*. 2006; 23:729–739. [PubMed: 17020629]
- Lee TS, Nguyen M. Dynamics of subjective contour formation in the early visual cortex. *Proceedings of the National Academy of Sciences, USA*. 2001; 98:1907–1911.
- Li Z. A neural model of contour integration in the primary visual cortex. *Neural Computation*. 1998; 10:903–940. [PubMed: 9573412]
- Marr D, Ullman S. Directional selectivity and its use in early visual processing. *Proceedings of the Royal Society of London B: Biological Sciences*. 1981; 211:151–180.
- Mattingley JB, Davis G, Driver J. Preattentive filling-in of visual surfaces in parietal extinction. *Science*. 1997; 275:671–674. [PubMed: 9005854]
- Mendola JD, Dale AM, Fischl B, Liu AK, Tootell RB. The representation of illusory and real contours in human cortical visual areas revealed by functional magnetic resonance imaging. *Journal of Neuroscience*. 1999; 19:8560–8572. [PubMed: 10493756]
- Meng M, Remus DA, Tong F. Filling-in of visual phantoms in the human brain. *Nature Neuroscience*. 2005; 8:1248–1254.
- Meng X, Mazzoni P, Qian N. Cross-fixation transfer of motion aftereffects with expansion motion. *Vision Research*. 2006; 46:3681–3689. [PubMed: 16824574]
- Michotte, A.; Thines, G.; Crabbe, G. Les compléments amodaux des structures perceptives [Amodal complements of perceptual structures]. Louvain, France: Studia Psychologica Louvain, Publications Universitaires de Louvain; 1964.
- Moore CM, Yantis S, Vaughan B. Object-based visual selection: Evidence from perceptual completion. *Psychological Science*. 1998; 9:104–110.
- Murray MM, Foxe DM, Javitt DC, Foxe JJ. Setting boundaries: Brain dynamics of modal and amodal illusory shape completion in humans. *Journal of Neuroscience*. 2004; 24:6898–6903. [PubMed: 15295024]
- Nishida S, Ashida H, Sato T. Complete interocular transfer of motion aftereffect with flickering test. *Vision Research*. 1994; 34:2707–2716. [PubMed: 7975308]
- Pack CC, Born RT. Temporal dynamics of a neural solution to the aperture problem in visual area MT of macaque brain. *Nature*. 2001; 409:1040–1042. [PubMed: 11234012]
- Palmer SE, Neff J, Beck D. Late influences on perceptual grouping: Amodal completion. *Psychonomic Bulletin & Review*. 1996; 3:75–80. [PubMed: 24214805]
- Pelli DG. The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*. 1997; 10:437–442. [PubMed: 9176953]
- Perna A, Tosetti M, Montanaro D, Morrone MC. Neuronal mechanisms for illusory brightness perception in humans. *Neuron*. 2005; 47:645–651. [PubMed: 16129395]
- Pessoa L, Thompson E, Noe A. Filling-in is for finding out. *Behavioral and Brain Sciences*. 1998; 21:781–802.
- Pillow J, Rubin N. Perceptual completion across the vertical meridian and the role of early visual cortex. *Neuron*. 2002; 33:805–813. [PubMed: 11879656]
- Price NS, Greenwood JA, Ibbotson MR. Tuning properties of radial phantom motion aftereffects. *Vision Research*. 2004; 44:1971–1979. [PubMed: 15149830]
- Rauschenberger R, Yantis S. Masking unveils pre-amodal completion representation in visual search. *Nature*. 2001; 410:369–372. [PubMed: 11268213]
- Rensink RA, Enns JT. Early completion of occluded objects. *Vision Research*. 1998; 38:2489–2505. [PubMed: 9798011]
- Roe AW, Lu HD, Hung CP. Cortical processing of a brightness illusion. *Proceedings of the National Academy of Sciences, USA*. 2005; 102:3869–3874.

- Sasaki Y, Watanabe T. The primary visual cortex fills in color. *Proceedings of the National Academy of Sciences, USA*. 2004; 101:18251–18256.
- Seghier M, Dojat M, Delon-Martin C, Rubin C, Warnking J, Segebarth C, Bullier J. Moving illusory contours activate primary visual cortex: An fMRI study. *Cerebral Cortex*. 2000; 10:663–670. [PubMed: 10906313]
- Seghier ML, Vulleumier P. Functional neuroimaging findings on the human perception of illusory contours. *Neuroscience & Biobehavioral Reviews*. 2006; 30:595–612. [PubMed: 16457887]
- Shimojo S, Kamitani Y, Nishida S. Afterimage of perceptually filled-in surface. *Science*. 2001; 293:1677–1680. [PubMed: 11533495]
- Singh M. Modal and amodal completion generate different shapes. *Psychological Science*. 2004; 15:454–459. [PubMed: 15200629]
- Smith A, Over R. Tilt aftereffects with subjective contours. *Nature*. 1975; 257:581–582. [PubMed: 1165782]
- Snowden RJ, Milne AB. Phantom motion aftereffects: Evidence of detectors for the analysis of optic flow. *Current Biology*. 1997; 7:717–722. [PubMed: 9368753]
- Stanley DA, Rubin N. fMRI activation in response to illusory contours and salient regions in the human lateral occipital complex. *Neuron*. 2003; 37:323–331. [PubMed: 12546826]
- Tynan P, Sekular R. Moving visual phantoms: A new contour completion effect. *Science*. 1975; 188:951–952. [PubMed: 1138365]
- Ullman S. Filling-in gaps: Shape of subjective contours and a model for their generation. *Biological Cybernetics*. 1976; 25:1–6.
- Weisstein N, Maguire W, Berbaum K. A phantom-motion aftereffect. *Science*. 1977; 198:955–958. [PubMed: 929181]

Fig. 1.

Illustrations of filling in (perceptual completion) and the used in the present study. In the Kanizsa square illusion (a), four notched circles induce perception of a square shape that has a sharp contour and greater luminance than the background. A still frame from the moving-visual-phantom illusion is shown in (b). In this illusion, a low-contrast moving grating is divided by an empty orthogonal gap. The gap is perceptually completed with the same pattern, color, speed, and direction of movement as the inducing grating, albeit more dimly. In the present study, we used a novel configuration that combined these two illusions. Four types of adapting displays (c) were used. Each display showed four shapes that moved leftward or rightward behind four circular apertures set in a black background. The arrows illustrate the local motion direction of the object in each aperture (this direction was changed across trials). In the integrated conditions, the movement induced the percept of a diamond shape. In the nonintegrated conditions, the movement did not induce a coherent shape percept. In the amodal conditions, the moving objects were composed of flickering black and white patches, which resulted in the induced shape being perceived as occluded and thus completed only perceptually. In the modal conditions, the moving objects had the same color as the black background and thus appeared to occlude portions of the apertures.

Fig. 2.

Results from the passive-adaptation experiment for both the (a) amodal- and (b) modal-completion conditions. The probability that observers would indicate rightward motion is plotted as a function of normalized motion coherence of the test stimuli and the type of motion that subjects were adapted to. Negative motion coherence indicates leftward motion; positive motion coherence indicates rightward motion. Each data point represents the average for 6 observers; a logistic function has been fitted to the data point in each condition.

Table 1

Mean Magnitudes of the Motion Aftereffect in the Passive-Adaptation and Attentional-Load Experiments

Experiment	Integrated condition	Nonintegrated condition
Passive adaptation ($n = 6$)	24.8 (4.3)	10.1 (4.9)
Attentional load: easy task ($n = 4$)	24.3 (7.8)	2.8 (6.5)
Attentional load: difficult task ($n = 4$)	13.9 (8.6)	15.2 (4.6)

Note: Standard errors of the mean are given in parentheses. The magnitude of the motion after-effect was measured as the difference between the percentage of “rightward” responses following leftward adaptation and the percentage of “rightward” responses following rightward adaptation.