Central mechanisms of perceptual filling-in

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Abstract

Human observers generally perceive a stable and coherent visual scene despite the fact that sensory information is ambiguous and often incomplete. Perceptual filling-in provides an interesting example of how the visual system realizes perceptual inferences from incomplete information. Vision scientists have a long history studying filling-in phenomena in the context of surface color filling-in. While significant progress has been achieved with behavioral experiments, little is known about the neural substrate of perceptual filling-in. We explored several hypotheses that have been considered to determine how the neural representation of edge-induced filling-in percepts arises in the brain. We argue that the visual system uses distinct extra-striate pathways for the processing of chromatic surfaces generated by edge-dependent filling-in that indirectly influence color pathways via a contour integration mechanism. Such a mechanism may play an important role in figure/ground segregation. Finally, we highlight the potential role of feedback projections that are ignored in many models despite the fact that they are as numerous as feedforward projections.

A remarkable characteristic of natural vision that is challenging to explain is our ability to perceive a stable and coherent visual scene rather quickly despite the fact that sensory information is ambiguous and often incomplete. This has led to the proposition that perception depends principally on inferential processes that take into account both the sensory input and prior knowledge (Helmholtz, 1867; Rao & Ballard, 1999; Friston, 2010; Clark, 2013). However, there are fundamental questions as to the neural and perceptual mechanisms mediating these processes. In this context, the role of perceptual filling-in may be of interest, as a possible example of perceptual inference about the state of the world from incomplete information. Here, we shall explore this idea in the context of surface color filling-in.

1. Surface appearance and perceptual filling-in.

The color appearance of a surface depends on its spectral composition but also on contextual information. With respect to filling-in, the phenomenon is typically assimilative in nature in that the contribution of remote contours results in a shift of the surface appearance toward that of the remote contour. Filling-in processes can be viewed as a fundamental ability to interpolate properties of visual stimuli across regions of the visual field when these properties are missing or different (Spillmann & de Weerd, 2003; Weil & Rees, 2011). This is a cornerstone of our visual experience in that visual stimuli appear as uniform in attributing brightness, color and texture that arises from a surrounding region. This is a natural phenomenon of which we are frequently unaware and helps to make sense of a visual scene. Nevertheless, there is current debate about the degree to which such phenomena play a role in natural vision (Shapley et al., 2019; Tyler & Solomon, 2019).

There is a long history of describing perceptual filling-in phenomena (Gerrits & Vendrik, 1970; Krauskopf, 1963; Mariotte, 1668, cited by Wade, 1998; Troxler, 1804; Walls, 1954) as its occurrence has fascinated visual scientists with the possibility of supplying clues about the functioning of the visual system. It has been considered as the main manifestation underlying the perception of a wide range of visual phenomena (Komatsu, 2006; Spillmann & de Weerd, 2003; von der Heydt, Friedman & Zhou, 2003; Weil & Rees, 2011). For example, it has been studied extensively with illusory surfaces such as in neon color spreading (Varin, 1971; van Tujil, 1975). This occurs when colored lines are intercalated with black lines and the region between the colored lines is perceived as transparent taking the coloration of the lines (Figure 1a). Another classical demonstration is the Craik-O'Brien-Cornsweet effect (COCE) that occurs when two surfaces with the same luminance are perceived to differ in brightness due to differences in the luminance gradient at their borders (Craik, 1966; O'Brien, 1958; Cornsweet, 1970) (Figure 1b). More recently, the Watercolor Effect (WCE) demonstrates an influence of remote contours on surface appearance (Pinna, Brelstaff & Spillmann, 2001; Devinck et al., 2005; Devinck & Knoblauch, 2012; Gerardin, Dojat, Knoblauch & Devinck, 2018). In the WCE, color filling-in occurs within an area enclosed by a light chromatic contour that in turn is surrounded by an adjacent darker chromatic contour. The entire enclosed area appears uniformly colored with the hue of the inner contour (Figure 1c).

While progress has been achieved with psychophysical characterization of these phenomena, a fundamental question is to determine the neural substrate of perceptual filling-in. Several hypotheses have been considered to determine how the neural representation of edge-induced filling-in percepts arises in the brain.

2. Early filtering hypothesis

The Early Filtering Hypothesis (EFH) is based on the equivalence of neural responses generated by step and gradient intensity profiles. When both types of edges are convolved with a center-surround weighting function, the resulting images are nearly identical (Ratliff & Sirovich, 1978) (Figure 2). The center-surround organization reflects the receptive field profiles in early visual processing and suggests that similar neural responses would lead human observers to perceive uniform surfaces and stimuli like the COCE similarly. However, this hypothesis does not take into account that most cells are not pure edge detectors (Sun et al., 2004). Indeed, there are two type of color sensitive cell that have been described in area V1: single- and double-opponent neurons. These cells have different spatial frequency responses suggesting that they make different contributions to color appearance (Nunez et al., 2018; Shapley et al., 2019). Single-opponent cells respond to large fields of color with spatial frequency typically <0.5 cpd and not at all to color patterns >2 cpd in parafoveal recordings around 4-5 deg eccentricity. In contrast, double-opponent cells respond to color boundaries at 2 cpd and very little <0.5 cpd at similar eccentricities (Friedman, Zhou, & von der Heydt, 2003 ; Johnson et al., 2001 ; Shapley et al., 2014 ; Thorell et al., 1984).

3. Surface/edge model

The presence of different cell profiles for chromatic processing supports the hypothesis that distinct neural channels process surface and edge percepts. In area V1, cortical responses to a uniform color surface would be expected to depend on the activity generated by single-opponent cells whereas chromatic edges would be expected to depend on double-opponent cells. Previous models of visual processing incorporate separate neural representations for edge and surface processing (Grossberg & Mingolla, 1985; Pinna & Grossberg, 2005). In area V1, the most numerous color sensitive neurons encountered are double-opponent cell (Shapley et al., 2014) whereas single-opponent cells are less numerous. This could, however, simply reflect differences in the sampling requirements to detect edges and surfaces (Schluppeck & Engel, 2002).

4. Bayesian hypothesis

While the EFH could account for why edge transients and uniform fields resemble each other, it does not explain why they are both perceived as uniform fields. Given the center-surround filtering, one might suppose that both would appear as edge-gradients. Bayesian approaches address this issue by invoking priors. Prior information would predict that both classes of stimuli would be perceived as a uniform surface in that this interpretation represents the most likely explanation for the object that generated the neural responses. For example, Brown and Friston (2012) demonstrated how the COCE could be interpreted as the consequence of Bayesian optimal perception. Such a proposal is compatible with multiple hypotheses with respect to the neural representation of filling-in, i.e., whether there is a filling-in of activity across the retinotopic map or the filled-in percept arises from activation at a later stage of processing.

5. Evidence of hierarchical processes and extra-cortical participation

Neural mechanisms in area V1 support edge and surface processing of chromatic information. An elusive question is the extent to which the neural networks underlying perceptual filling-in depend on distributed activity across extra-cortical areas. There is extensive data indicating that information is structured and processed in a hierarchical fashion in the visual system (Markov et al., 2014; Bastos et al., 2015; Michalareas et al., 2015).

The localized pair of chromatic contours that induce the WCE as well as its dependence on the contour widths is consistent with the stimulus modulating primarily double-opponent receptive fields of area V1 (Devinck et al., 2014).

On the other hand, the coloration effect in the WCE can be perceived over an extremely large visual area, reported to extend over as great as 45 deg (Pinna et al., 2001). This is much larger than the spread of neural connections in area V1 (Markov et al., 2011). In addition, the phenomenon is sensitive to the curvature of the inducing contours (Gerardin et al., 2014). These observations implicate cortical areas beyond V1 and V2 that have sufficiently large receptive fields and are sensitive to contour curvature. Taken together, the above results suggest that the WCE depends on interactions across multiple levels of processing in the visual hierarchy.

There is little neurophysiological evidence on the WCE. Coia et al. (2014) measured cortical responses using visual evoked potentials for the WCE. Their results were correlated with the psychophysical observations, but the method could not localize specific visual areas. Recently, we used functional imaging to compare responses of cortical areas to stimulus fields generated by edge-dependent filling-in and those of uniform chromaticity (Gerardin et al., 2018). Surprisingly, Multi-voxel Pattern Analyses singled out two dorsal stream areas, V3A and V3B/KO as implicated in the WCE while ventral stream areas hV4 and LO were more strongly related to processing uniform chromatic fields. The role of area LO in color processing is controversial. Brouwer and Heeger (2009) found that color could be decoded in area VO1 but not LO1 and LO2, while Seymour et al. (2016) reported color decoding in area LOC. Gerardin et al. (2018) did not attempt to localize area VO1, whose borders with hV4 and LO often show large individual differences and can be difficult to define (Hupé et al., 2012; Witthoft et al., 2014). Thus, it is quite possible that their LO included activity of VO1. In addition, Gerardin et al. (2018) found that individual differences in the perceived strength of the WCE correlated significantly with areas V3A and V3B/KO and not any other visual areas, lending additional support to the association of these dorsal stream areas with the WCE. Finally, an analysis of the effective connectivities between cortical areas V1, V3A and

LO based on Dynamic Causal Modeling (DCM) and Bayesian Model Selection supported a model in which V3A modulated V1 and LO for the WCE while the best model for processing of uniform fields involved LO modulating V1 and V3A. At the least, these analyses indicate that color appearance occurs in distinct neural networks for the processing of uniform field chromaticities and color filling-in and that processing occurs across different hierarchical levels.

A role for V3A in color filling-in may seem surprising in that this area is not classically associated with color perception. However, it has been reported to generate greater responses to color than luminance stimuli (Hadjikhani et al., 1998) and to respond also to chromatic features (Castaldi et al., 2013).

In support of its role in filling-in, neural activity of area V3A has been reported during filling-in with other visual phenomena. For example, in Troxler fading, a visible target is perceived but then it disappears after some delay, the target being replaced by the contextual information. Results with fMRI indicated that V1 and V2 show decreases in activity (Mendola et al., 2006; Weil et al., 2008) while V3A and V4v show increased activity during perceptual filling-in (Mendola et al., 2006). If the reduction in activity observed in areas V1 and V2 reflects an edge adaptation then the neuronal activity described in areas V3A and V4v (Mendola et al., 2006) could result in brightness filling-in. Such results are consistent with physiological studies. In monkeys, responses have been associated with perceptual filling-in in area V3 when receptive fields overlapped the square target placed in a texture background; their firing rates increased after prolonged fixation (De Weerd et al., 1995). In a study by von der Heydt et al. (2003), monkeys were trained to report a perceptual change with a red disk and a green ring while neuronal activity was recorded from cells with receptive fields inside the disc and at the border. The activity of neurons in area V1 and V2 with receptive fields inside the central disk did not change although a change in perceived color was indicated by the reported behavioral responses. However, neurons in the same areas with receptive fields corresponding to the borders increased in activity. In Motion-induced blindness, a visual salient target is positioned in the periphery on a moving background; the target disappears after a prolonged central fixation then reappears continuously (Bonneh et al., 2001; Bonneh et al., 2014; Devyatko et al., 2017). In fMRI experiments, responses in ventral area V4, associated with the retinotopic position of the target decreased with target disappearance while responses in area V3A, V3B and the intraparietal sulcus, associated with the retinotopic position of the background, increased with target disappearance (Donner et al., 2008). Areas V3 and V4 have also been implicated in color filling-in of afterimages induced by contours (Hong & Tong, 2017). Here, afterimage colors spread to neutral fields when constrained by contours presented after the colored image. The same adapting pattern induced multiple colored afterimages depending on the configuration of the test contours (Barkan & Spitzer, 2009, 2017; van Lier et al., 2009; Anstis et al., 2012).

Some previous imaging studies indicated a role for retinotopic activity in early visual areas such as V1 in the processing of uniform surfaces (Haynes, Lotto & Rees, 2004; Pereverzeva & Murray, 2008; Sasaki & Watanabe, 2004) and also in the processing of patterns presented at the natural blind spot (Komatsu et al., 2000, 2002; Matsumoto & Komatsu, 2005). This interpretation has been disputed (Cornelissen et al., 2006) by showing that surround induced responses in V1, in fact, depend on an extended edge response. This is consistent with physiological studies showing slower responses inside the uniform surface than for edges (Huang & Paradiso, 2008) and several studies that reported V1 responses to the edges of a surface are higher than responses to the center of a surface (Dai & Wang, 2012; Friedman et al., 2003; Zurawel et al., 2014). Optical imaging with voltage-sensitive dyes indicated edge responses to uniform fields of color and luminance in area V1 (Zweig et al., 2015). At times subsequent to the stimulus presentation, responses at the center of an achromatic surface increased while responses at the center of a chromatic surface did not change. This last study supports that achromatic and chromatic surfaces are represented differently in area V1 (Zweig et al., 2015).

6. Role of feedback processing in perceptual filling-in.

An intriguing aspect of the study by Gerardin et al. (2018) emerges from the DCM analysis. The best model that accounted for the WCE contained feedback modulation from area V3A to V1 and lateral modulation of LO. In contrast, feedback modulation from area LO to V1 and lateral modulation of V3A best described the data for uniform color fields. We hypothesize that a contour integration mechanism activates area V3A, because when we used a stimulus with a discontinuous contour, the WCE phenomenon was abolished (Devinck & Knoblauch, 2012). In addition, Coia and Crognale (2018) have shown that adaptation to a flickering contour eliminates WCE filling-in. Contour integration can also be supposed to be a necessary prerequisite in computing border ownership, a function that has been reported in cortical cells that are candidates in the processing of uniform chromatic surfaces and that are proposed to play a critical role in the initiation of filling-in (Zhou, Friedman & Devinck et al., 2006; der Heydt, 2000). Under this hypothesis for the WCE, it is the simultaneous activation of ventral stream areas associated with color processing and V1 that leads to the appearance of a uniform color filling-in. These ideas are particularly relevant in the context of previous studies that suggest an important role of feedback pathways in contextual processing (Lamme et al., 1998; Zipser et al., 1996). We hypothesize, in addition, that this feedback projection is related to figure-ground perception that is represented in area V1 (Kok & de Lange, 2014).

7. Conclusion

Cortical responses in area V1 to a uniform color surface would be expected to generate a pattern of activity across both single- and double-opponent cells whereas isolated chromatic edges would be expected to generate a pattern of activity dominated by double opponent cells. In the WCE, color filling-in requires two adjacent, continuous contours. We hypothesize that the bi-chromatic contours would signal a uniform color surface rather than just an edge. This suggests that neural responses are integrated across double-opponent cells along the path from V1 to V3A. A recent computational model, in fact, takes into account oriented double-opponent cells to compute the perceived surface from a filling-in process (Cohen-Duwek & Spitzer, 2019). This model is able to predict the filling-in phenomenon depending on distant contours such as the COCE and the WCE. However, the model is based only on hierarchically organized feedforward projections. This seems unlikely in light of our fMRI findings implicating modulation of effective connectivities from V3A to V1, i.e., in a feedback direction. Feedback connections are ignored in many models despite the fact that they are as numerous as the feedforward projections (Markov et al., 2014). In fact, there are multiple feedforward and feedback projections emanating from and targeting different cortical lamina that differ in whether they project in a focal or diffuse fashion and whether they are short or long-range (Markov & Kennedy, 2013 ; Markov et al., 2014). Laminar resolution fMRI might be able to provide evidence on a finer scale on the function of circuits underlying the WCE and other filling-in phenomena (Lawrence et al., 2019).

Taken together, these data support the hypothesis that the mechanisms underlying surface appearance are complex and require multiple levels of processing. The visual system uses separate pathways for processing of surfaces generated by a uniform chromaticity and those induced by remote contours. Thus, the neural substrates of the perception of filling-in and uniform color fields are not the same. A fundamental perspective for future research will be to clarify in greater detail the relative contributions of feedforward and feedback processes in surface perception.

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Figure Legends

Fig. 1: Examples of visual phenomena in which the appearance of surface color depends on contextual information from edges: (a) neon-color spreading, (b) the Craik-O'Brien-Cornsweet effect and (c) the Watercolor Effect.

Fig. 2: Two patterns with different intensity profiles: (a) Stimulus defined by a step intensity profile, (b) stimulus decribed with an exponential gradient typically used to generate a Craik-O'Brien-Cornsweet effect (COCE). Here, both stimuli are convolved (represented by *) with (c) a center-surround weighting function. (d) The results yield nearly identical response profiles. The solid curve indicates the response for the step profile and the dashed curve the response for the exponential gradient.

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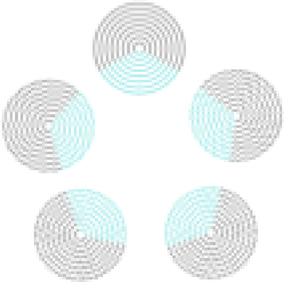
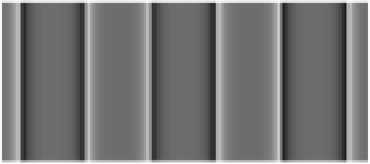
This paper measured population responses in area V1 to uniform chromatic and achromatic squares with the use of voltage-sensitive dye imaging in macaque. Results provide evidence that the response profiles are similar at the edge for both types of surfaces after stimulus onset. Subsequently, responses at the center of achromatic squares increased while responses at the center of chromatic squares remained unchanged. The results imply that surface perception is represented differently for chromatic and achromatic uniform fields.

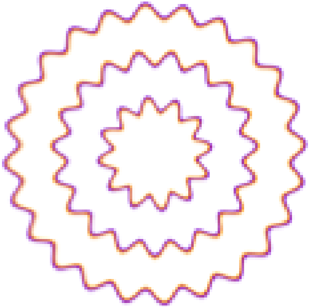
(a)

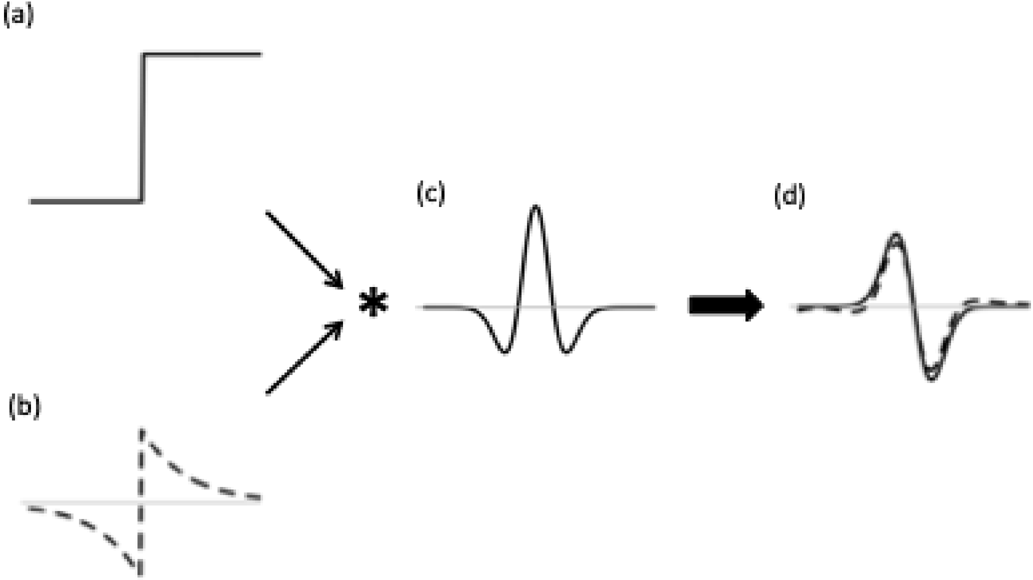


(b)



(c)




(a)
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(c)
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