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Central mechanisms of perceptual filling-in

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24 **Abstract**

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

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44 A remarkable characteristic of natural vision that is challenging to explain is our
45 ability to perceive a stable and coherent visual scene rather quickly despite the
46 fact that sensory information is ambiguous and often incomplete. This has led
47 to the proposition that perception depends principally on inferential processes
48 that take into account both the sensory input and prior knowledge (Helmholtz,
49 1867; Rao & Ballard, 1999; Friston, 2010; Clark, 2013). However, there are
50 fundamental questions as to the neural and perceptual mechanisms mediating
51 these processes. In this context, the role of perceptual filling-in may be of
52 interest, as a possible example of perceptual inference about the state of the
53 world from incomplete information. Here, we shall explore this idea in the
54 context of surface color filling-in.

55

56 **1. Surface appearance and perceptual filling-in.**

57

58 The color appearance of a surface depends on its spectral composition but also
59 on contextual information. With respect to filling-in, the phenomenon is
60 typically assimilative in nature in that the contribution of remote contours results
61 in a shift of the surface appearance toward that of the remote contour. Filling-in
62 processes can be viewed as a fundamental ability to interpolate properties of
63 visual stimuli across regions of the visual field when these properties are
64 missing or different (Spillmann & de Weerd, 2003; Weil & Rees, 2011). This is
65 a cornerstone of our visual experience in that visual stimuli appear as uniform in
66 attributing brightness, color and texture that arises from a surrounding region.
67 This is a natural phenomenon of which we are frequently unaware and helps to
68 make sense of a visual scene. Nevertheless, there is current debate about the
69 degree to which such phenomena play a role in natural vision (Shapley et al.,
70 2019; Tyler & Solomon, 2019).

71 There is a long history of describing perceptual filling-in phenomena
72 (Gerrits & Vendrik, 1970; Krauskopf, 1963; Mariotte, 1668, cited by Wade,

73 1998; Troxler, 1804; Walls, 1954) as its occurrence has fascinated visual
74 scientists with the possibility of supplying clues about the functioning of the
75 visual system. It has been considered as the main manifestation underlying the
76 perception of a wide range of visual phenomena (Komatsu, 2006; Spillmann &
77 de Weerd, 2003; von der Heydt, Friedman & Zhou, 2003; Weil & Rees, 2011).
78 For example, it has been studied extensively with illusory surfaces such as in
79 neon color spreading (Varin, 1971; van Tujil, 1975). This occurs when colored
80 lines are intercalated with black lines and the region between the colored lines is
81 perceived as transparent taking the coloration of the lines (Figure 1a). Another
82 classical demonstration is the Craik-O'Brien-Cornsweet effect (COCE) that
83 occurs when two surfaces with the same luminance are perceived to differ in
84 brightness due to differences in the luminance gradient at their borders (Craik,
85 1966; O'Brien, 1958; Cornsweet, 1970) (Figure 1b). More recently, the
86 Watercolor Effect (WCE) demonstrates an influence of remote contours on
87 surface appearance (Pinna, Brelstaff & Spillmann, 2001; Devinck et al., 2005;
88 Devinck & Knoblauch, 2012; Gerardin, Dojat, Knoblauch & Devinck, 2018). In
89 the WCE, color filling-in occurs within an area enclosed by a light chromatic
90 contour that in turn is surrounded by an adjacent darker chromatic contour. The
91 entire enclosed area appears uniformly colored with the hue of the inner contour
92 (Figure 1c).

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

97

98 **2. Early filtering hypothesis**

99

100 The Early Filtering Hypothesis (EFH) is based on the equivalence of neural
101 responses generated by step and gradient intensity profiles. When both types of

102 edges are convolved with a center-surround weighting function, the resulting
103 images are nearly identical (Ratliff & Sirovich, 1978) (Figure 2). The center-
104 surround organization reflects the receptive field profiles in early visual
105 processing and suggests that similar neural responses would lead human
106 observers to perceive uniform surfaces and stimuli like the COCE similarly.
107 However, this hypothesis does not take into account that most cells are not pure
108 edge detectors (Sun et al., 2004). Indeed, there are two type of color sensitive
109 cell that have been described in area V1: single- and double-opponent neurons.
110 These cells have different spatial frequency responses suggesting that they make
111 different contributions to color appearance (Nunez et al., 2018; Shapley et al.,
112 2019). Single-opponent cells respond to large fields of color with spatial
113 frequency typically <0.5 cpd and not at all to color patterns >2 cpd in parafoveal
114 recordings around 4-5 deg eccentricity. In contrast, double-opponent cells
115 respond to color boundaries at 2 cpd and very little <0.5 cpd at similar
116 eccentricities (Friedman, Zhou, & von der Heydt, 2003 ; Johnson et al., 2001 ;
117 Shapley et al., 2014 ; Thorell et al., 1984).

118

119 **3. Surface/edge model**

120

121 The presence of different cell profiles for chromatic processing supports the
122 hypothesis that distinct neural channels process surface and edge percepts. In
123 area V1, cortical responses to a uniform color surface would be expected to
124 depend on the activity generated by single-opponent cells whereas chromatic
125 edges would be expected to depend on double-opponent cells. Previous models
126 of visual processing incorporate separate neural representations for edge and
127 surface processing (Grossberg & Mingolla, 1985; Pinna & Grossberg, 2005). In
128 area V1, the most numerous color sensitive neurons encountered are double-
129 opponent cell (Shapley et al., 2014) whereas single-opponent cells are less

130 numerous. This could, however, simply reflect differences in the sampling
131 requirements to detect edges and surfaces (Schluppeck & Engel, 2002).

132

133 **4. Bayesian hypothesis**

134

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

147

148 **5. Evidence of hierarchical processes and extra-cortical participation**

149

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

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

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

168 There is little neurophysiological evidence on the WCE. Coia et al.
169 (2014) measured cortical responses using visual evoked potentials for the WCE.
170 Their results were correlated with the psychophysical observations, but the
171 method could not localize specific visual areas. Recently, we used functional
172 imaging to compare responses of cortical areas to stimulus fields generated by
173 edge-dependent filling-in and those of uniform chromaticity (Gerardin et al.,
174 2018). Surprisingly, Multi-voxel Pattern Analyses singled out two dorsal stream
175 areas, V3A and V3B/KO as implicated in the WCE while ventral stream areas
176 hV4 and LO were more strongly related to processing uniform chromatic fields.
177 The role of area LO in color processing is controversial. Brouwer and Heeger
178 (2009) found that color could be decoded in area VO1 but not LO1 and LO2,
179 while Seymour et al. (2016) reported color decoding in area LOC. Gerardin et
180 al. (2018) did not attempt to localize area VO1, whose borders with hV4 and LO
181 often show large individual differences and can be difficult to define (Hupé et
182 al., 2012; Witthoft et al., 2014). Thus, it is quite possible that their LO included
183 activity of VO1. In addition, Gerardin et al. (2018) found that individual
184 differences in the perceived strength of the WCE correlated significantly with
185 areas V3A and V3B/KO and not any other visual areas, lending additional
186 support to the association of these dorsal stream areas with the WCE. Finally,
187 an analysis of the effective connectivities between cortical areas V1, V3A and

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

194 A role for V3A in color filling-in may seem surprising in that this area is
195 not classically associated with color perception. However, it has been reported
196 to generate greater responses to color than luminance stimuli (Hadjikhani et al.,
197 1998) and to respond also to chromatic features (Castaldi et al., 2013).

198 In support of its role in filling-in, neural activity of area V3A has been
199 reported during filling-in with other visual phenomena. For example, in Troxler
200 fading, a visible target is perceived but then it disappears after some delay, the
201 target being replaced by the contextual information. Results with fMRI
202 indicated that V1 and V2 show decreases in activity (Mendola et al., 2006; Weil
203 et al., 2008) while V3A and V4v show increased activity during perceptual
204 filling-in (Mendola et al., 2006). If the reduction in activity observed in areas
205 V1 and V2 reflects an edge adaptation then the neuronal activity described in
206 areas V3A and V4v (Mendola et al., 2006) could result in brightness filling-in.
207 Such results are consistent with physiological studies. In monkeys, responses
208 have been associated with perceptual filling-in in area V3 when receptive fields
209 overlapped the square target placed in a texture background; their firing rates
210 increased after prolonged fixation (De Weerd et al., 1995). In a study by von der
211 Heydt et al. (2003), monkeys were trained to report a perceptual change with a
212 red disk and a green ring while neuronal activity was recorded from cells with
213 receptive fields inside the disc and at the border. The activity of neurons in area
214 V1 and V2 with receptive fields inside the central disk did not change although
215 a change in perceived color was indicated by the reported behavioral responses.
216 However, neurons in the same areas with receptive fields corresponding to the

217 borders increased in activity. In Motion-induced blindness, a visual salient
218 target is positioned in the periphery on a moving background; the target
219 disappears after a prolonged central fixation then reappears continuously
220 (Bonneh et al., 2001; Bonneh et al., 2014; Devyatko et al., 2017). In fMRI
221 experiments, responses in ventral area V4, associated with the retinotopic
222 position of the target decreased with target disappearance while responses in
223 area V3A, V3B and the intraparietal sulcus, associated with the retinotopic
224 position of the background, increased with target disappearance (Donner et al.,
225 2008). Areas V3 and V4 have also been implicated in color filling-in of
226 afterimages induced by contours (Hong & Tong, 2017). Here, afterimage colors
227 spread to neutral fields when constrained by contours presented after the colored
228 image. The same adapting pattern induced multiple colored afterimages
229 depending on the configuration of the test contours (Barkan & Spitzer, 2009,
230 2017; van Lier et al., 2009; Anstis et al., 2012).

231 Some previous imaging studies indicated a role for retinotopic activity in
232 early visual areas such as V1 in the processing of uniform surfaces (Haynes,
233 Lotto & Rees, 2004; Pereverzeva & Murray, 2008; Sasaki & Watanabe, 2004)
234 and also in the processing of patterns presented at the natural blind spot
235 (Komatsu et al., 2000, 2002; Matsumoto & Komatsu, 2005). This interpretation
236 has been disputed (Cornelissen et al., 2006) by showing that surround induced
237 responses in V1, in fact, depend on an extended edge response. This is
238 consistent with physiological studies showing slower responses inside the
239 uniform surface than for edges (Huang & Paradiso, 2008) and several studies
240 that reported V1 responses to the edges of a surface are higher than responses to
241 the center of a surface (Dai & Wang, 2012; Friedman et al., 2003; Zurawel et
242 al., 2014). Optical imaging with voltage-sensitive dyes indicated edge responses
243 to uniform fields of color and luminance in area V1 (Zweig et al., 2015). At
244 times subsequent to the stimulus presentation, responses at the center of an
245 achromatic surface increased while responses at the center of a chromatic

246 surface did not change. This last study supports that achromatic and chromatic
247 surfaces are represented differently in area V1 (Zweig et al., 2015).

248

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

250

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

272

273 **7. Conclusion**

274

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

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

304 clarify in greater detail the relative contributions of feedforward and feedback
305 processes in surface perception.

306

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308

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316

317 **Figure Legends**

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

322
323 Fig. 2: Two patterns with different intensity profiles: (a) Stimulus defined by
324 a step intensity profile, (b) stimulus described with an exponential
325 gradient typically used to generate a Craik-O'Brien-Cornsweet effect
326 (COCE). Here, both stimuli are convolved (represented by *) with (c)
327 a center-surround weighting function. (d) The results yield nearly
328 identical response profiles. The solid curve indicates the response for
329 the step profile and the dashed curve the response for the exponential
330 gradient.

331

332

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363
364 **This study developed a computational feedforward model to predict**
365 **successfully several filling-in phenomena (the WCE and the COCE).**
366 **The color of the perceived surface is calculated through a diffusive**
367 **filling-in process obtained from the remote contours obtained as a**
368 **result of oriented double-opponent receptive fields.**

- 369
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375

376 **The authors determined how the WCE and uniform chromatic fields are**
377 **influenced by contour adaptation. Results indicated that color filling-**
378 **in of the WCE is reduced by contour adaptation while a uniform**
379 **chromatic surface is relatively unaffected. This study demonstrates**
380 **the importance of contour integration in the WCE.**

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An fMRI study demonstrating that WCE color filling-in engages neural pathways distinct from those generated by a field of uniform chromaticity. Filling-in color was best classified by dorsal stream areas V3A and V3B/KO, while a field of uniform chromaticity was best classified by ventral stream areas hV4 and LO. A DCM analysis revealed feedback modulation from V3A to V1 and LO for color filling-in and from LO to V1 and V3A for fields of uniform chromaticity.

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509 **square under the hypothesis that perceptual responses to these**
510 **stimuli were dominated, respectively, by double- and single-opponent**
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588 **This paper measured population responses in area V1 to uniform**
589 **chromatic and achromatic squares with the use of voltage-sensitive**
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591 **profiles are similar at the edge for both types of surfaces after**
592 **stimulus onset. Subsequently, responses at the center of achromatic**
593 **squares increased while responses at the center of chromatic squares**
594 **remained unchanged. The results imply that surface perception is**
595 **represented differently for chromatic and achromatic uniform fields.**

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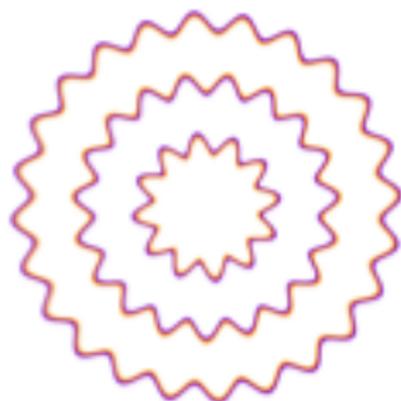
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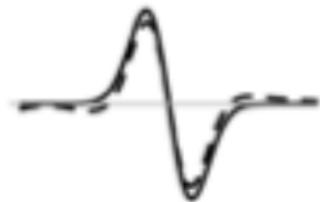
(a)



(c)



(d)



(b)

