



# Central mechanisms of perceptual filling-in

Frédéric Devinck<sup>1,4</sup> and Kenneth Knoblauch<sup>2,3</sup>

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.

## Addresses

<sup>1</sup> Univ Rennes, LP3C, EA 1285, 35000 Rennes, France

<sup>2</sup> Univ Lyon, Université Claude Bernard Lyon 1, Inserm, Stem Cell and Brain Research Institute U1208, 69500 Bron, France

<sup>3</sup> National Centre for Optics, Vision and Eye Care, Faculty of Health and Social Sciences, University of South-Eastern Norway, Hasbergsvei 36, 3616 Kongsberg, Norway

Corresponding author:

Devinck, Frédéric ([frederic.devinck@univ-rennes2.fr](mailto:frederic.devinck@univ-rennes2.fr))

<sup>4</sup> Present address: Département de Psychologie, Université Rennes 2, 35043 Rennes Cedex, France.

**Current Opinion in Behavioral Sciences** 2019, **30**:135–140

This review comes from a themed issue on **Visual perception**

Edited by **Hannah Smithson** and **John S Werner**

<https://doi.org/10.1016/j.cobeha.2019.08.003>

2352-1546/© 2019 Elsevier Ltd. All rights reserved.

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 [1–4].

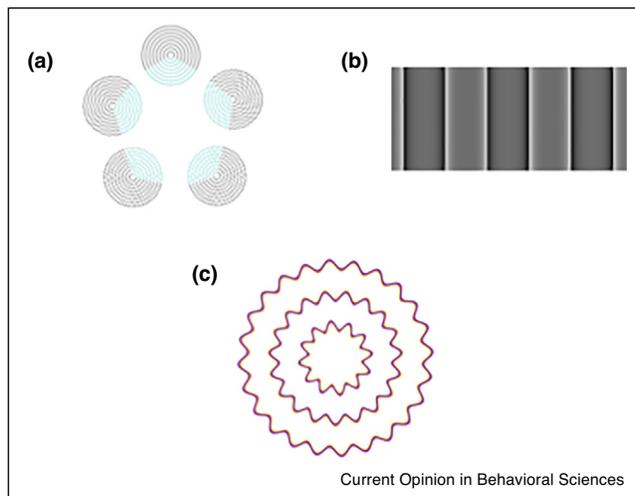
However, there are fundamental questions as to the neural and perceptual mechanisms mediating these processes. In this context, the role of perceptual filling-in may be of interest, as a possible example of perceptual inference about the state of the world from incomplete information. Here, we shall explore this idea in the context of surface color filling-in.

## 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 [5,6]. 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 [7,8].

There is a long history of describing perceptual filling-in phenomena ([9,10,82], cited by Wade [11,12,13]) 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 ([5,14,15,6]). For example, it has been studied extensively with illusory surfaces such as in neon color spreading ([16,17]). 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 [18–20] (Figure 1b). More recently, the Watercolor Effect (WCE) demonstrates an influence of remote contours on surface appearance ([21–24]). 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).

Figure 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.

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.

### 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 [25] (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 [26]. Indeed, there are two types of color sensitive cell that have been described in area V1: single-opponent and double-opponent neurons. These cells have different spatial frequency responses suggesting that they make different contributions to color appearance [7,27<sup>••</sup>]. 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  $4-5^\circ$  eccentricity. In contrast, double-opponent cells respond to color boundaries at 2 cpd and very little  $<0.5$  cpd at similar eccentricities [28–31].

### 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 [32,33]. In area V1, the most numerous color sensitive neurons encountered are double-opponent cells [30] whereas single-opponent cells are less numerous. This could, however, simply reflect differences in the sampling requirements to detect edges and surfaces [34].

### Bayesian hypothesis

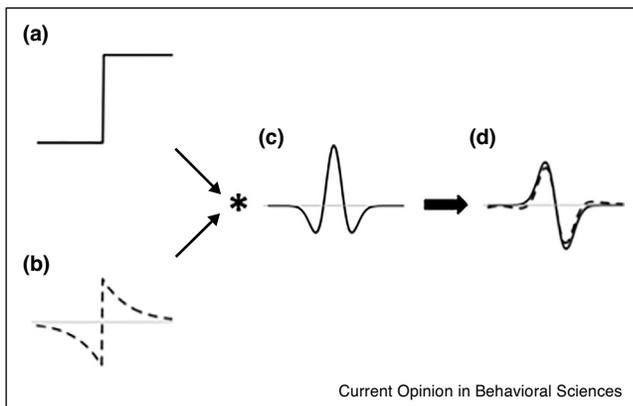
While the EFH could account for why edge transients and uniform fields resemble each other, it does not explain why they are both perceived as uniform fields. Given the center-surround filtering, one might suppose that both would appear as edge-gradients. Bayesian approaches address this issue by invoking 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 [35] 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, that is, 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.

### 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 are extensive data indicating that information is structured and processed in a hierarchical fashion in the visual system [36–38].

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 [39]. In contrast, the coloration effect in the WCE can be perceived over an extremely large visual area, reported to extend over as great as  $45^\circ$  [21]. This is much larger than the spread of neural connections in area V1 [40]. In addition, the phenomenon is sensitive to the curvature of the inducing contours [41]. These observations implicate cortical areas beyond V1 and V2 that have sufficiently

Figure 2



Two patterns with different intensity profiles: **(a)** Stimulus defined by a step intensity profile, **(b)** stimulus described 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.

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.* [42] 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 [43<sup>\*\*</sup>]. 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 [44] found that color could be decoded in area VO1 but not LO1 and LO2, while Seymour *et al.* [45] reported color decoding in area LOC. Gerardin *et al.* [43<sup>\*\*</sup>] did not attempt to localize area VO1, whose borders with hV4 and LO often show large individual differences and can be difficult to define [46,47]. Thus, it is quite possible that their LO included activity of VO1. In addition, Gerardin *et al.* [43<sup>\*\*</sup>] 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 [48] and to respond also to chromatic features [49].

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 [50,51] while V3A and V4v show increased activity during perceptual filling-in [50]. 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 [50] 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 [52]. In a study by von der Heydt *et al.* [15], 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 [53–55]. 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 [56]. Areas V3 and V4 have also been implicated in color filling-in of afterimages induced by contours [57<sup>\*\*</sup>]. 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 [58–61].

Some previous imaging studies indicated a role for retinotopic activity in early visual areas such as V1 in the processing of uniform surfaces [62–64] and also in the processing of patterns presented at the natural blind spot [65–67]. This interpretation has been disputed [68] 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 [69] and several studies that reported V1 responses to the edges of a surface are higher than responses to the center of a surface [28,70,71]. Optical imaging with voltage-sensitive dyes indicated edge responses to uniform fields of color and luminance in area V1 [72\*\*]. 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 [72\*\*].

### Role of feedback processing in perceptual filling-in

An intriguing aspect of the study by Gerardin *et al.* [43\*\*] 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 [23]. In addition, Coia and Crognale [73\*\*] 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 [80,81]. 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 [74,75]. We hypothesize, in addition, that this feedback projection is related to figure-ground perception that is represented in area V1 [76\*\*].

### Conclusion

Cortical responses in area V1 to a uniform color surface would be expected to generate a pattern of activity across both single-opponent 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 [77\*\*]. 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, that is, in a feedback direction. Feedback connections are ignored in many models despite the fact that they are as numerous as the feedforward projections [36]. 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 [36,78]. 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 [79].

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.

### Conflict of interest statement

Nothing declared.

### Acknowledgements

KK was supported by the following grants: LABEX CORTEX (ANR-11-LABX-0042) of Université de Lyon (ANR-11-IDEX-0007) operated by the French National Research Agency (ANR), ANR-11-BSV4-501, CORE-NETS, ANR-14-CE13-0033, ARCHI-CORE, ANR-15-CE32-0016, CORNET, ANR-17-NEUC-0004, A2P2MC, ANR-17-HBPR-0003, CORTICITY. FD was supported by a grant from the French National Research Agency (ANR), ANR-11-JSH-20021. We would like to thank Michel Dojat for critical discussions.

### References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

•• of outstanding interest

1. von Helmholtz H: *Handbuch der physiologischen Optik*. Leipzig: Voss; 1867.
2. Rao RP, Ballard DH: **Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects**. *Nat Neurosci* 1999, 2:79–87.
3. Friston K: **The free-energy principle: a unified brain theory?** *Nat Rev Neurosci* 2010, 11:127–138.

4. Clark A: **Whatever next? Predictive brains, situated agents, and the future of cognitive science.** *Behav Brain Sci* 2013, **36**:181-204.
  5. Spillmann L, de Weerd P: **Mechanisms of surface completion: perceptual filling-in of texture.** In *Filling-in: From Perceptual Completion to Cortical Reorganization*. Edited by Pessoa L, DeWeerd P. New-York: Oxford University Press; 2003:106-127.
  6. Weil RS, Rees G: **A new taxonomy for perceptual filling-in.** *Brain Res Rev* 2011, **67**:40-55.
  7. Shapley R, Nunez V, Gordon J: **Cortical double-opponent cells and human color perception.** *Curr Opin Behav Sci* 2019, **30**:1-7.
  8. Tyler CW, Solomon JA: **Color perception in natural images.** *Curr Opin Behav Sci* 2019, **30**:8-14.
  9. Gerrits HJM, Vendrik AM: **Simultaneous contrast, filling-in process and information processing in man's visual system.** *Exp Brain Res* 1970, **11**:411-430.
  10. Krauskopf J: **Effect of retinal image stabilization on the appearance.** *J Opt Soc Am* 1963, **53**:741-744.
  11. Wade NJ: *A Natural History of Vision*. Cambridge (MA): MIT Press; 1998.
  12. Troxler D: **Über das Verschwinden gegebener Gegenstände inner-halb unsers Gesichtskreises.** In *Ophthalmologische Bibliothek II*. Edited by Himly K, Schmidt JA. Jena: Fromman; 1804:1-53.
  13. Walls G: **The filling-in process.** *Am J Optom* 1954, **31**:329-340.
  14. Komatsu H: **The neural mechanisms of perceptual filling-in.** *Nat Rev Neurosci* 2006, **7**:220-231.
  15. von der Heydt R, Friedman HS, Zhou H: **Searching for the neural mechanism of color filling-in.** In *Filling-in: From Perceptual Completion to Cortical Reorganization*. Edited by Pessoa L, DeWeerd P. New-York: Oxford University Press; 2003:106-127.
  16. Varin D: **Fenomeni di contrasto e diffusione cromatica nell'organizzazione spaziale del campo percettivo.** *Rivista di Psicologia* 1971, **65**:101-128.
  17. van Tuijl HFJM: **A new visual illusion: neonlike color spreading and complementary color induction between subjective contours.** *Acta Psychol* 1975, **39**:441-445.
  18. Craik KJW: **Brightness discrimination, borders, and subjective brightness.** In *The Nature of Psychology*. Edited by Sherwood SL. Cambridge: Cambridge University Press; 1966:94-97.
  19. O'Brien V: **Contour perception, illusion and reality.** *J Opt Soc Am* 1958, **48**:112-119.
  20. Cornsweet T: *Visual Perception*. New-York: Academic Press; 1970.
  21. Pinna B, Brelstaff G, Spillmann L: **Surface color from boundaries: a new 'watercolor' illusion.** *Vision Res* 2001, **41**:2669-2676.
  22. Devinck F, Delahunt PB, Hardy JL, Spillmann L, Werner JS: **The watercolor effect: quantitative evidence for luminance-dependent mechanisms of long-range color assimilation.** *Vision Res* 2005, **45**:1413-1424.
  23. Devinck F, Knoblauch K: **A common signal detection model for the perception and discrimination of the watercolor effect.** *J Vision* 2012, **12**:1-14.
  24. Gerardin P, Dojat M, Knoblauch K, Devinck F: **Effects of background and contour luminance on the hue and brightness of the watercolor effect.** *Vision Res* 2018, **144**:9-19.
  25. Ratliff F, Sirovich L: **Equivalence classes of visual stimuli.** *Vision Res* 1978, **18**:845-851.
  26. Sun H, Rüttiger L, Lee BB: **The spatiotemporal precision of ganglion cell signals: a comparison of physiological and psychophysical performance with moving gratings.** *Vision Res* 2004, **44**:19-33.
  27. Nunez V, Shapley RM, Gordon J: **Cortical double-opponent cells in color perception: perceptual scaling and chromatic visual evoked potentials.** *i-Perception* 2018, **9**:1-16.
  28. Friedman HS, Zhou H, von der Heydt R: **The coding of uniform colour figures in monkey visual cortex.** *J Physiol* 2003, **548**:593-613.
  29. Johnson EN, Hawken MJ, Shapley R: **The spatial transformation of color in the primary visual cortex of the macaque monkey.** *Nat Neurosci* 2001, **4**:409-416.
  30. Shapley RM, Hawken MJ, Johnson EB: **Color in primary visual cortex.** In *The New Visual Neurosciences*. Edited by Werner JS, Chalupa LM. Cambridge, MA: MIT Press; 2014:569-586.
  31. Thorell LG, De Valois RL, Albrecht DG: **Spatial mapping of monkey V1 cells with pure color and luminance stimuli.** *Vision Res* 1984, **24**:751-769.
  32. Grossberg S, Mingolla E: **Neural dynamics of form perception: boundary completion, illusory figures, and neon color spreading.** *Psychol Rev* 1985, **92**:173-211.
  33. Pinna B, Grossberg S: **The watercolor illusion and neon color spreading: a unified analysis of new cases and neural mechanisms.** *J Opt Soc Am A Optic Image Sci Vision* 2005, **22**:2207-2221.
  34. Schluppeck D, Engel SA: **Color opponent neurons in V1: a review and model reconciling results from imaging and single-unit recording.** *J Vision* 2002, **2**:480-492.
  35. Brown H, Friston KJ: **Free-energy and illusions: the cornsweet effect.** *Front Psychol* 2012, **3**:43.
  36. Markov NT, Vezoli J, Chameau P, Falchier A, Quilodran R, Huissoud C, Lamy C, Misery P, Giroud P, Ullman S et al.: **Anatomy of hierarchy: feedforward and feedback pathways in macaque visual cortex.** *J Comp Neurol* 2014, **522**:225-259.
  37. Bastos AM, Vezoli J, Bosman CA, Schoffelen JM, Oostenveld R, Dowdall JR, De Weerd P, Kennedy H, Fries P: **Visual areas exert feedforward and feedback influences through distinct frequency channels.** *Neuron* 2015, **85**:390-401.
  38. Michalareas G, Vezoli J, van Pelt S, Schoffelen JM, Kennedy H, Fries P: **Alpha-beta and gamma rhythms subserve feedback and feedforward influences among human visual cortical areas.** *Neuron* 2016, **89**:384-397.
  39. Devinck F, Gerardin P, Dojat M, Knoblauch K: **Spatial selectivity of the watercolor effect.** *J Opt Soc Am A Optic Image Sci Vision* 2014, **31**:A1-A6.
  40. Markov NT, Misery P, Falchier A, Lamy C, Vezoli J, Quilodran R, Gariel MA, Giroud P, Ercsey-Ravasz M, Pilaz LJ et al.: **Weight consistency specifies regularities of macaque cortical networks.** *Cereb Cortex* 2011, **21**:1254-1272.
  41. Gerardin P, Devinck F, Dojat M, Knoblauch K: **Contributions of contour frequency, amplitude, and luminance to the watercolor effect estimated by conjoint measurement.** *J Vision* 2014, **14**.
  42. Coia AJ, Jones C, Duncan CS, Crognale MA: **Physiological correlates of watercolor effect.** *J Opt Soc Am A Optic Image Sci Vision* 2014, **31**:A15-A22.
  43. Gerardin P, Abbatecola C, Devinck F, Kennedy H, Dojat M, ●● Knoblauch K: **Neural circuits for long-range color filling-in.** *NeuroImage* 2018, **181**:30-43.
- 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.
44. Brouwer GJ, Heeger D: **Decoding and reconstructing color from responses in human visual cortex.** *J Neurosci* 2009, **29**:13992-14003.

45. Seymour KJ, Williams MA, Rich AN: **The representation of color across the human visual cortex: distinguishing chromatic signals contributing to object form versus surface color.** *Cereb Cortex* 2016, **26**:1997-2005.
46. Hupé J-M, Bordier C, Dojat M: **A BOLD signature of eyeblinks in the visual cortex.** *NeuroImage* 2012, **61**:149-161.
47. Witthoft N, Nguyen ML, Golarai G, Larocque KF, Liberman A, Smith ME, Grill-Spector K: **Where is human V4? Predicting the location of hV4 and VO1 from cortical folding.** *Cereb Cortex* 2013, **24**:2401-2408.
48. Hadjikhani N, Liu AK, Dale AM, Cavanagh P, Tootell RB: **Retinotopy and color sensitivity in human visual cortical area V8.** *Nat Neurosci* 1998, **1**:235-241.
49. Castaldi E, Frijia F, Montanaro D, Tosetti M, Morrone MC: **BOLD human responses to chromatic spatial features.** *Eur J Neurosci* 2013, **38**:2290-2299.
50. Mendola JD, Conner IP, Sharma S, Bahekar A, Lemieux S: **fMRI measures of perceptual filling-in in the human visual cortex.** *J Cogn Neurosci* 2006, **18**:363-375.
51. Weil RS, Watkins S, Rees G: **Neural correlates of perceptual completion of an artificial scotoma in human visual cortex measured using functional MRI.** *Neuroimage* 2008, **42**:1519-1528.
52. 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.
53. Bonneh YS, Cooperman A, Sagi D: **Motion-induced blindness in normal observers.** *Nature* 2001, **411**:798-801.
54. Bonneh YS, Donner TH, Cooperman A, Heeger DJ, Sagi D: **Motion-induced blindness and troxler fading: common and different mechanisms.** *PLoS One* 2014, **9**:e92894.
55. Devyatko D, Appelbaum LG, Mitroff SR: **A common mechanism for perceptual reversals in motion-induced blindness, the troxler effect, and perceptual filling-in.** *Perception* 2017, **46**:50-77.
56. Donner TH, Sagi D, Bonneh YS, Heeger DJ: **Opposite neural signatures of motion-induced blindness in human dorsal and ventral visual cortex.** *J Neurosci* 2008, **28**:10298-10310.
57. Hong SW, Tong F: **Neural representation of form-contingent color filling-in in the early visual cortex.** *J Vision* 2017, **17**:1-10 10. An fMRI study using MVPA that investigated color filling-in in early visual areas. Results indicated that areas V3 and V4 are implicated in form-contingent color filling-in induced by closed contours but not earlier visual areas. This suggests an extensive neural processing by extrastriate visual areas.
58. Barkan Y, Spitzer H: **Color Dove Illusion | Best Illusion of the Year Contest.** . Available online at: 2009 <http://illusionoftheyear.com/2009/05/>.
59. Barkan Y, Spitzer H: **The color dove illusion- chromatic filling in effect following a spatial-temporal edge.** In *The Oxford Compendium of Visual Illusions*. Edited by Shapiro AG, Todorovic D. New York, NY: Oxford University Press; 2017:752-755.
60. van Lier R, Vergeer M, Anstis S: **Filling-in afterimage colors between the lines.** *Curr Biol* 2009, **19**:R323-R324.
61. Anstis S, Vergeer M, Van Lier R: **Luminance contours can gate afterimage colors and « real » colors.** *J Vision* 2012, **12**:1-13 2.
62. Haynes J-D, Lotto RB, Rees G: **Responses of human visual cortex to uniform surfaces.** *Proc Natl Acad Sci U S A* 2004, **101**:4286-4291.
63. Pereverzeva M, Murray SO: **Neural activity in human V1 correlates with dynamic lightness induction.** *J Vision* 2008, **8**:1-10 8.
64. Sasaki Y, Watanabe T: **The primary visual cortex fills in color.** *Proc Natl Acad Sci U S A* 2004, **101**:18251-18256.
65. Komatsu H, Kinoshita M, Murakami I: **Neural responses in the retinotopic representation of the blind spot in the macaque V1 to stimuli for perceptual filling-in.** *J Neurosci* 2000, **20**:9310-9319.
66. Komatsu H, Kinoshita M, Murakami I: **Neural response in the primary visual cortex of the monkey during perceptual filling-in at the blind spot.** *Neurosci Res* 2002, **44**:231-236.
67. Matsumoto M, Komatsu H: **Neural response in the macaque V1 to bar stimuli with various lengths presented on the blind spot.** *J Neurophysiol* 2005, **93**:2374-2387.
68. 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.** *J Neurosci* 2006, **26**:3634-3641.
69. Huang X, Paradiso MA: **V1 response timing and surface filling-in.** *J Neurophysiol* 2008, **100**:539-547.
70. Dai J, Wang Y: **Representation of surface luminance and contrast in primary visual cortex.** *Cereb Cortex* 2012, **22**:776-787.
71. Zurawel G, Ayzenshtat I, Zweig S, Shapley R, Slovin H: **A contrast and surface code explains complex responses to black and white stimuli in V1.** *J Neurosci* 2014, **34**:14388-14402.
72. Zweig S, Zurawel G, Shapley R, Slovin H: **Representation of color surfaces in V1: edge enhancement and unfilled holes.** *J Neurosci* 2015, **35**:2103-2115.
- 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.
73. Coia A, Crognale MA: **Contour adaptation reduces the spreading of edge induced colors.** *Vision Res* 2018, **151**:135-140.
- The authors determined how the WCE and uniform chromatic fields are influenced by contour adaptation. Results indicated that color filling-in of the WCE is reduced by contour adaptation while a uniform chromatic surface is relatively unaffected. This study demonstrates the importance of contour integration in the WCE.
74. Lamme VAF, Supèr H, Spkreijse H: **Feedforward, horizontal, and feedback processing in the visual cortex.** *Curr Opin Neurobiol* 1998, **8**:529-535.
75. Zipser K, Lamme VAF, Schiller PH: **Contextual modulation in primary visual cortex.** *J Neurosci* 1996, **16**:7376-7389.
76. Kok P, de Lange FP: **Shape perception simultaneously up- and down regulates neural activity in the primary visual cortex.** *Curr Biol* 2014, **24**:1531-1535.
- This paper measured population receptive fields in V1 with fMRI for Kanisza figures. Results show that feedback modulation to area V1 is both enhancing and suppressive. Neural activity increased for the illusory figure whereas responses decreased for local elements inducing the illusory figure.
77. Cohen-Duwek H, Spitzer H: **A compound computational model for filling-in processes triggered by edges: watercolor illusions.** *Front Neurosci* 2019, **13**:225.
- This study developed a computational feedforward model to predict successfully several filling-in phenomena (the WCE and the COCE). The color of the perceived surface is calculated through a diffusive filling-in process obtained from the remote contours obtained as a result of oriented double-opponent receptive fields.
78. Markov NT, Kennedy H: **The importance of being hierarchical.** *Curr Opin Neurobiol* 2013, **23**:187-194.
79. Lawrence SJD, Formisano E, Muckli L, de Lange FP: **Laminar fMRI: applications for cognitive neuroscience.** *NeuroImage* 2019, **197**:785-791.
80. Devinck F, Hardy JL, Delahunt PB, Spillmann L, Werner JS: **Illusory spreading of watercolor.** *J Vision* 2006, **6**:625-633.
81. Zhou H, Friedman HS, von der Heydt R: **Coding of border ownership in monkey visual cortex.** *J Neurosci* 2000, **20**:6594-6611.
82. Mariotte E: **A new discovery touching vision.** *Philos Trans R Soc* 1668, **3**:668-669.