

Shape Perception Simultaneously Up- and Downregulates Neural Activity in the Primary Visual Cortex

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Summary

An essential part of visual perception is the grouping of local elements (such as edges and lines) into coherent shapes. Previous studies have shown that this grouping process modulates neural activity in the primary visual cortex (V1) that is signaling the local elements [1–4]. However, the nature of this modulation is controversial. Some studies find that shape perception reduces neural activity in V1 [2, 5, 6], while others report increased V1 activity during shape perception [1, 3, 4, 7–10]. Neurocomputational theories that cast perception as a generative process [11–13] propose that feedback connections carry predictions (i.e., the generative model), while feedforward connections signal the mismatch between top-down predictions and bottom-up inputs. Within this framework, the effect of feedback on early visual cortex may be either enhancing or suppressive, depending on whether the feedback signal is met by congruent bottom-up input. Here, we tested this hypothesis by quantifying the spatial profile of neural activity in V1 during the perception of illusory shapes using population receptive field mapping. We find that shape perception concurrently increases neural activity in regions of V1 that have a receptive field on the shape but do not receive bottom-up input and suppresses activity in regions of V1 that receive bottom-up input that is predicted by the shape. These effects were not modulated by task requirements. Together, these findings suggest that shape perception changes lower-order sensory representations in a highly specific and automatic manner, in line with theories that cast perception in terms of hierarchical generative models.

Results

The role of early visual regions during shape perception is ill understood, with some studies reporting activity suppression due to grouping [2, 5, 6] while others report enhancement [1, 3, 4, 7–10]. According to theories that cast perception in terms of hierarchical generative models [11–13], neural activity in lower-order sensory regions is dependent both on whether it is driven by sensory stimulation and whether this stimulation is predicted on the basis of top-down feedback signals. In this framework, early visual neurons that do not receive any bottom-up input, but that are predicted to be active because a shape is inferred at their receptive field location, are expected to show relatively enhanced neural activity [3, 4, 8, 9]. On the other hand, early visual neurons that receive bottom-up input that is congruent with the shape prediction are expected to show a relatively suppressed response [2, 6, 14].

Here, we directly test this framework within the context of illusory shape perception.

Illusory shape perception provides an ideal test bed, as the illusory shape results in both unexpected absence of visual input (at the location where the shape is perceived but retinal input is absent) and expected presence of visual input (at the location where the shape provides an explanation for the bottom-up input). We made use of the well-known illusory “Kanizsa” shapes [15], wherein circles with missing wedges (“Pac-Man” inducers) are aligned such that they can induce the perception of an illusory figure (Figure 1A). Using fMRI and population receptive field mapping [16], we quantified the spatial profile of neural activity in early visual cortex while subjects ($n = 20$) were presented with stimuli that either did (Figure 1A) or did not (Figure 1B) induce an illusory figure. Moreover, to examine whether effects of shape perception were dependent on attention, we manipulated the focus of subjects’ attention. In half of the trials, subjects had to detect the presence of an occasional illusory diamond (“figure task”; Figure 1C), placing their attentional focus on the location of the illusory shapes. In the other half of the trials, subjects had to detect two target letters (X and Z) in a rapidly presented letter stream at fixation, drawing their attention away from the illusory shapes (“letter task”).

Below, we present the spatially specific responses to these stimuli in early visual cortex in two different ways. First, we estimated the population receptive field (pRF) [16] of every voxel in early visual cortex (see Figures S1A–S1C and Supplemental Experimental Procedures available online) and used this information to transform the blood oxygen-level-dependent (BOLD) signal into the reference frame of subjects’ visual field of view (Figure S1D; Supplemental Experimental Procedures). Second, we selected groups of voxels based on the location of their receptive field and averaged over the BOLD signal measured in such voxels. In this way, we obtained separate estimates of neural activity in regions of primary visual cortex (V1) corresponding to the area of the visual field where the illusory triangles were presented (“figure region”) and regions corresponding to the Pac-Man inducers (“inducer region”; see Supplemental Experimental Procedures for details of voxel selection). These analysis strategies are complementary: while the first method allows for a characterization and visualization of neural activity concurrently for all parts of visual space, the second approach is more standard and more easily allows for statistical quantification of the experimental effects.

Reconstruction of Neural Response to Illusory Figures

We reconstructed the neural response evoked by illusory figures (Figure 1A), compared to control stimuli with the same low-level features but that did not induce an illusory figure (Figure 1B). The results showed a striking spatial dissociation (Figure 2A): neural activity for regions of V1 that corresponded to the illusory figure (but not the Pac-Man inducers; figure region) was enhanced when an illusory triangle was present, compared to when the inducers did not form an illusory figure (Figure 3A; $p < 0.001$). In other words, these V1 regions showed an increased response to the illusory figures, despite the absence of bottom-up stimulus input.

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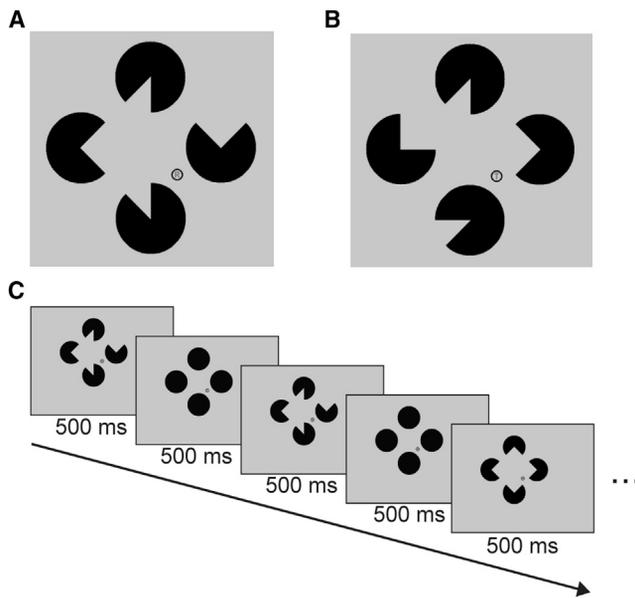


Figure 1. Experimental Paradigm

(A) Example “Kanizsa” stimulus, in which three out of four “Pac-Man” inducers were aligned such that an illusory triangle could be perceived. A fixation bull’s-eye, containing a rapid letter stream, was presented 1.5° below and to the right of the center of the configuration. In one run of the experiment, subjects performed a target letter detection task (“letter task”). (B) In control configurations, the inducers were not aligned, and consequently no illusory figure could be perceived. (C) During each trial, configurations of Pac-Man inducers alternated with black circles for 14.4 s. On a given trial, one inducer configuration was presented repeatedly for the duration of the trial. At random time points, a configuration was presented that induced the percept of an illusory diamond (rightmost frame). In one run of the experiment, subjects’ task was to detect this diamond (“figure task”). See [Figure S1](#) for analysis methods.

It can be seen that the exact retinotopic location of the activity increase was different for the four triangle types ([Figure 2B](#)). Indeed, regions of V1 corresponding to specific subdivisions of the figure region (cf. the diagrams in [Figures 3A](#) and [3C](#)) showed a stronger neural response when the illusory triangle overlaid their receptive field than when it did not ([Figure 3C](#); $p < 0.001$). Note that while previous electrophysiological studies of figure-ground segmentation often distinguish between neural activity modulation at the borders and at the center of the figure region [[7](#), [10](#)], the inherent spatial spread associated with noninvasively measured neural signals using BOLD-fMRI does not allow us to make this distinction.

Interestingly, regions of V1 corresponding to the inducers (inducer region) showed the opposite response: here, the neural response was suppressed when an illusory figure was present, compared to when it was not ([Figure 3B](#); $p = 0.0015$). This decreased response only occurred for inducers partaking in the illusion ([Figure 2](#)); the response to the Pac-Man that did not partake in the illusion was not significantly modulated by the presence of an illusory figure ($p = 0.60$). In other words, when an illusory figure was formed, inducers partaking in it (i.e., those that can be perceived as black circles partially occluded by a gray triangle) evoked a reduced neural response.

There was no effect of the illusory figures in regions of V1 with a receptive field over the nonstimulated area of the visual field that contained neither inducers, nor an illusory figure

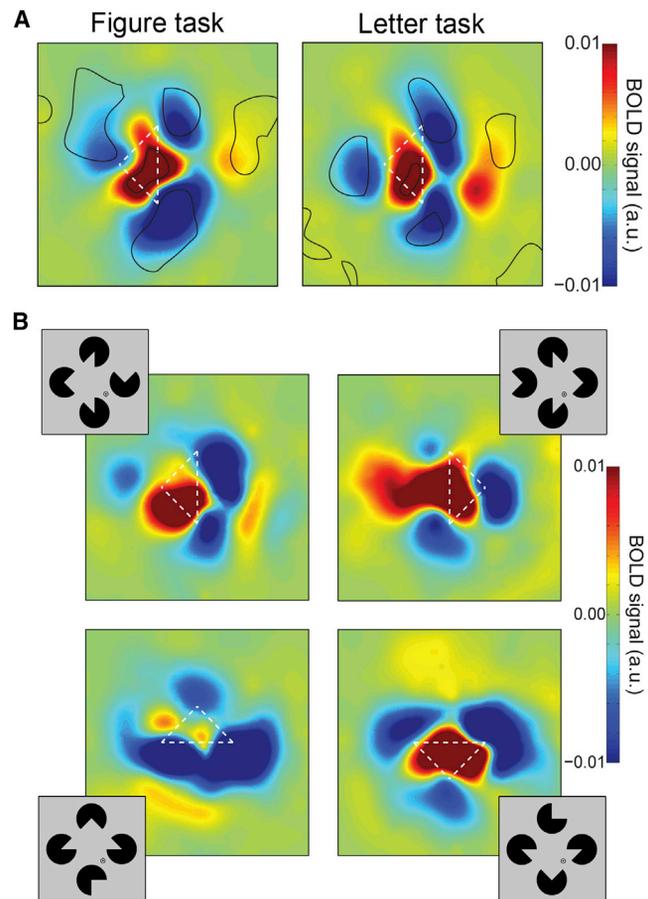


Figure 2. Illusory Shape Reconstructions from Neural Activity in V1

(A) Reconstruction of the BOLD response evoked by illusory triangle configurations versus control configurations, separately for the figure task and letter task, averaged over subjects. Images were obtained by calculating a weighted average of all voxels’ pRFs, where the weights are determined by each voxel’s response amplitude. The four different illusory triangles (see [B](#)) were combined by rotating the reconstructions of the rightward, upward, and downward triangles into the leftward-pointing triangle orientation. Dashed white triangles indicate the location of the illusory triangles. For illustrative purposes, black contours indicate boundaries of regions within which pixel values are significantly different from zero ($p < 0.05$). (B) Reconstruction of the BOLD response evoked by each of the four illusory triangle types versus control configurations, collapsed over tasks. See [Figure S2](#) for V2 results.

(“background region”; $p = 0.44$). All the effects reported above for V1 were also significantly present in secondary visual cortex (V2) (all $p < 0.01$; [Figure S2](#)). Due to the well-known increase in receptive field size when ascending the visual cortical hierarchy (which we confirm in our own data; see [Figure S1](#)), there was no sufficient retinotopic separation of figure and inducer regions for higher-order visual regions beyond V2.

Effects of Shape Perception Are Independent of Spatial Attention

Given that illusory figures have been shown to draw spatial attention [[17](#)] and that attention is known to increase neural activity in visual cortex even in the absence of bottom-up stimulation [[18](#)], one may wonder whether the V1 enhancement at the location of the figure may be the result of attentional allocation. To examine this possibility, we manipulated the

How Shape Perception Modulates Activity in V1

3

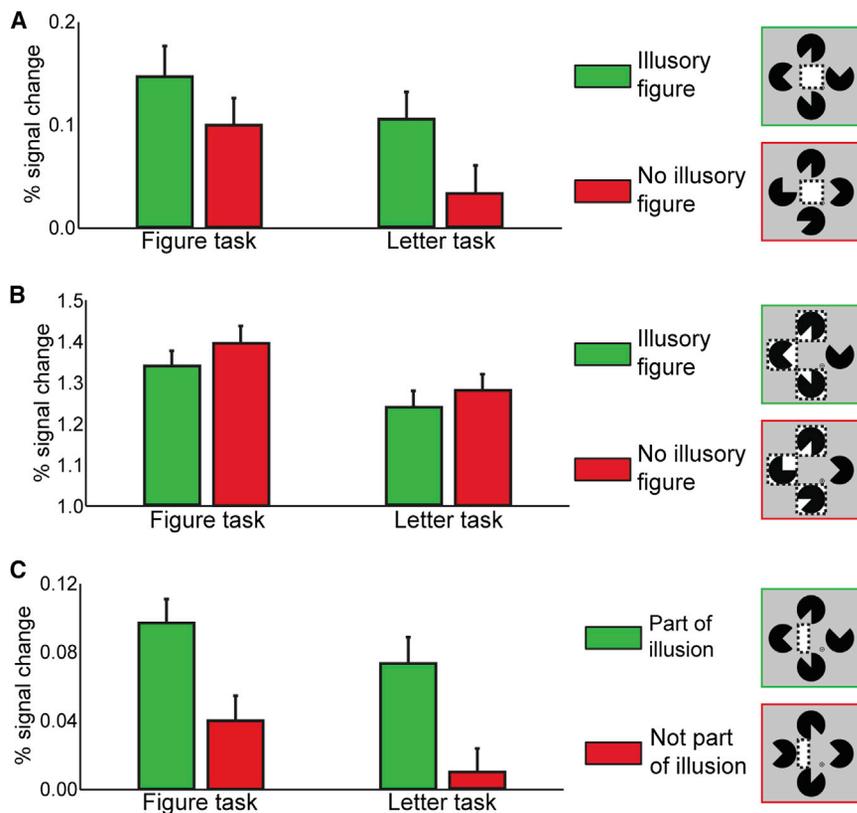


Figure 3. Opposite Neural Activity Modulations by Illusory Shape in Center and Inducer Locations in V1

(A) BOLD response in regions of V1 corresponding to the inner surface of the Kanizsa display, i.e., with receptive fields that cover the illusory triangle (indicated by dashed squares). Activity was higher when an illusory shape was present (green bars) than when it was not (i.e., in a control configuration, red bars). Fixation trials served as baseline.

(B) BOLD response in regions of V1 with a receptive field on the inducers partaking in the illusion. Activity was decreased when an illusory shape was present (green bars) compared to when it was not (red bars). Fixation trials served as baseline.

(C) BOLD response in regions of V1 corresponding to subsections of the inner surface (indicated by the dashed square), separately for Kanizsa trials in which the illusion covered their receptive field (green bars) and trials in which the illusion did not cover their receptive field (red bars). The example stimulus displays illustrate the regions of visual space probed for the contrast leftward > rightward-pointing triangles; analogous regions were selected for the other contrasts (rightward > leftward, upward > downward, and downward > upward; see [Supplemental Experimental Procedures](#) for details). Control trials served as baseline. Error bars indicate within-subject SEM. See [Figure S3](#) for results of a control experiment.

attentional state of the participants. In separate blocks of trials, subjects participated in a figure task and a letter task. In the figure task, subjects had to detect the presence of an occasional (13.3%) illusory diamond (accuracy = 85.5% ± 4.2% [mean ± SE; [Figure 1C](#)], placing their attentional focus on the location of the illusory shapes. In the letter task, subjects had to detect two letters (X and Z; 10%) in a rapidly presented letter stream at fixation (accuracy = 91.8% ± 2.0%), drawing their attention away from the illusory shapes. The effects of shape perception were not significantly modulated by task demands ([Figures 2A](#) and [S2A](#)), as indicated by a lack of interaction between task and illusion for either the increased response to the illusory triangle (V1, $p = 0.33$; V2, $p = 0.82$), or the decreased response to the inducers partaking in the illusion (V1, $p = 0.69$; V2, $p = 0.88$).

Moreover, if the illusory figures were to draw spatial attention, this might be expected to affect behavioral performance. However, performance was not influenced by the presence or absence of illusory figures in either the figure task (accuracy = 84.7% versus 86.7%, $p = 0.18$; reaction time [RT] = 574 versus 573 ms, $p = 0.91$) or the letter identification task (accuracy = 91.4% versus 92.3%, $p = 0.48$; RT = 639 versus 634 ms, $p = 0.23$).

In a control experiment ($n = 6$; see [Supplemental Experimental Procedures](#) for details) in which we withdrew attention from the shapes more strongly, we again found strong effects of shape perception on neural activity in V1, which were not modulated by the difficulty of the task at fixation that subjects were engaged in (see [Figure S3](#)). Finally, the modulatory effects of shape perception were independent of whether the fixation point was on or away from the illusory figure ($t_{19} = -1.0$, $p = 0.35$), rendering it unlikely that our results reflect an automatic spreading of attention to the figure region [[19](#)].

Discussion

Shape perception involves the grouping of local elements into coherent shapes. In this study, we examined how this constructive process modulates neural activity in V1, which is signaling the local elements. We found that feedback to V1 could be both excitatory and inhibitory, depending on the receptive field location of the V1 neurons. For regions of V1 representing the illusory figure, neural activity was increased compared to when no illusory figure was present. In contrast, regions of V1 responding to the local elements that induced the illusion showed a markedly decreased response.

According to one influential theory of shape perception, higher-level areas detecting the shape send excitatory feedback to label early visual neurons that encode the features to be grouped [[20](#)]. This is supported by results from studies on figure-ground segmentation [[1](#), [7](#), [10](#), [21](#)], illusory figure perception [[4](#), [8](#), [9](#), [22](#), [23](#)], and contour detection [[3](#), [24](#)], as well as the enhanced V1 response to the illusory figure reported here. However, suppressive effects of shape perception in early visual cortex, as reported in several other studies [[2](#), [5](#), [6](#), [25](#)] and reported here for regions of V1 responding to the inducers, are less readily explained by this theory, as top-down feedback is presumed to have excitatory effects [[20](#)]. To accommodate this finding, theories of perceptual grouping could potentially be extended to include differential top-down modulation dependent on whether a figure is perceived as being in the foreground or background [[26](#), [27](#)].

The current results can be readily explained in the context of generative theories of perception [[11–13](#)], which cast perception as an inferential process of hypothesis testing. Within this framework, the effect of feedback depends on whether or not it is met with congruent bottom-up input. This

is supported by studies reporting that valid top-down predictions reduce neural responses in sensory cortex [14, 28–32], while the unpredicted absence of bottom-up input leads to an enhanced neural response [32, 33] that carries information about the expected but absent stimulus [34]. In line with this, we report reduced responses in V1 when shape feedback is met by congruent input (in the case of the inducers) and increased responses when it is not (in case of the illusory triangle). Neurons with a receptive field on the illusory surface could show enhanced activity either because (1) they are predicted to be active by higher-order areas, (2) this prediction is violated, or (3) both. These potential explanations cannot be distinguished on the basis of the current data [35], as they would require the ability to separate prediction from prediction error responses in sensory neurons [36].

One may wonder whether spatial attention is a potential confounding factor in studies of illusory figure perception, given that illusory figures are known to draw spatial attention [17, 23] and that attention increases neural activity in early visual cortex, even in the absence of bottom-up stimulation [18]. In the current study, we tried to carefully control the attentional state of the observers and found no interaction between the effects of the illusory figures and task demands. Additionally, a control experiment wherein we manipulated the difficulty of a distracting task at fixation revealed effects of both attention and illusory figures, but no interaction between the two. In other words, the effects of the illusory figure were present both when the illusory figures were relevant and attended, or fully irrelevant with subjects performing a demanding task at fixation. The highly specific increase in activity in regions of V1 responding to the illusory surface (i.e., in absence of bottom-up input) is in line with reports from studies demonstrating highly specific top-down activations of V1 during working memory [37, 38], mental imagery [39], and stimulus expectation [34]. This body of work demonstrates the generative nature of perception, and, potentially, of cognition in general [40, 41].

The highly specific and opposing effects of shape perception reported in this study have implications for the interpretation of previous studies involving perceptual grouping. For example, McMains and Kastner [42] reported that the effect of top-down attention in early visual cortex was modulated by perceptual grouping, using stimuli similar to those used here. It would be of interest to assess the extent to which these results are driven by suppression of the inducers, excitation of the figure, or both, for the grouped stimuli.

A recent study using a bistable stimulus reported nonretinotopically specific modulations of V1 activity as a consequence of shape perception [43]. This more global (i.e., spatially nonspecific) feedback signal, which may be nonperceptual in nature [44], has previously also been observed during perceptual decisions about bistable stimuli, potentially in order to stabilize a newly established percept [45].

In conclusion, our results show that shape perception is an interactive process between higher-order visual areas and V1, wherein activity in V1 is modulated in a highly specific way according to the perceptual hypothesis provided by higher-order areas. Thereby, the current study provides empirical support for generative theories that cast perception in terms of hierarchical generative models.

Supplemental Information

Supplemental Information includes three figures and Supplemental Experimental Procedures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.05.042>.

Acknowledgments

We thank Serge Dumoulin and Ben Harvey for assistance with the pRF analysis and Nathalie Serafin with assistance during data acquisition. This study was supported by the Netherlands Organization for Scientific Research (NWO VENI, awarded to F.P.d.L.) and the James S. McDonnell Foundation (JSMF Scholar Award for Understanding Human Cognition, awarded to F.P.d.L.).

Received: April 17, 2014

Revised: May 16, 2014

Accepted: May 16, 2014

Published: June 26, 2014

References

- Lamme, V.A.F. (1995). The neurophysiology of figure-ground segregation in primary visual cortex. *J. Neurosci.* 15, 1605–1615.
- Murray, S.O., Kersten, D., Olshausen, B.A., Schrater, P., and Woods, D.L. (2002). Shape perception reduces activity in human primary visual cortex. *Proc. Natl. Acad. Sci. USA* 99, 15164–15169.
- Altmann, C.F., Bühlhoff, H.H., and Kourtzi, Z. (2003). Perceptual organization of local elements into global shapes in the human visual cortex. *Curr. Biol.* 13, 342–349.
- Lee, T.S., and Nguyen, M. (2001). Dynamics of subjective contour formation in the early visual cortex. *Proc. Natl. Acad. Sci. USA* 98, 1907–1911.
- He, D., Kersten, D., and Fang, F. (2012). Opposite modulation of high- and low-level visual aftereffects by perceptual grouping. *Curr. Biol.* 22, 1040–1045.
- Fang, F., Kersten, D., and Murray, S.O. (2008). Perceptual grouping and inverse fMRI activity patterns in human visual cortex. *J. Vis.* 8, 1–9.
- Lee, T.S., Mumford, D., Romero, R., and Lamme, V.A. (1998). The role of the primary visual cortex in higher level vision. *Vision Res.* 38, 2429–2454.
- Meng, M., Remus, D.A., and Tong, F. (2005). Filling-in of visual phantoms in the human brain. *Nat. Neurosci.* 8, 1248–1254.
- Muckli, L., Kohler, A., Kriegeskorte, N., and Singer, W. (2005). Primary visual cortex activity along the apparent-motion trace reflects illusory perception. *PLoS Biol.* 3, e265.
- Poort, J., Raudies, F., Wannig, A., Lamme, V.A.F., Neumann, H., and Roelfsema, P.R. (2012). The role of attention in figure-ground segregation in areas V1 and V4 of the visual cortex. *Neuron* 75, 143–156.
- Rao, R.P., and Ballard, D.H. (1999). Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. *Nat. Neurosci.* 2, 79–87.
- Friston, K. (2005). A theory of cortical responses. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 360, 815–836.
- Mumford, D. (1992). On the computational architecture of the neocortex. II. The role of cortico-cortical loops. *Biol. Cybern.* 66, 241–251.
- Kok, P., Jehee, J.F.M., and de Lange, F.P. (2012). Less is more: expectation sharpens representations in the primary visual cortex. *Neuron* 75, 265–270.
- Kanizsa, G. (1976). Subjective contours. *Sci. Am.* 234, 48–52.
- Dumoulin, S.O., and Wandell, B.A. (2008). Population receptive field estimates in human visual cortex. *Neuroimage* 39, 647–660.
- Senkowski, D., Röttger, S., Grimm, S., Foxe, J.J., and Herrmann, C.S. (2005). Kanizsa subjective figures capture visual spatial attention: evidence from electrophysiological and behavioral data. *Neuropsychologia* 43, 872–886.
- Kastner, S., Pinsk, M.A., De Weerd, P., Desimone, R., and Ungerleider, L.G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron* 22, 751–761.
- Flevaris, A.V., Martínez, A., and Hillyard, S.A. (2013). Neural substrates of perceptual integration during bistable object perception. *J. Vis.* 13, 17.
- Roelfsema, P.R. (2006). Cortical algorithms for perceptual grouping. *Annu. Rev. Neurosci.* 29, 203–227.
- Self, M.W., van Kerkoerle, T., Supér, H., and Roelfsema, P.R. (2013). Distinct roles of the cortical layers of area V1 in figure-ground segregation. *Curr. Biol.* 23, 2121–2129.
- Sasaki, Y., and Watanabe, T. (2004). The primary visual cortex fills in color. *Proc. Natl. Acad. Sci. USA* 101, 18251–18256.

How Shape Perception Modulates Activity in V1

5

23. Maertens, M., Pollmann, S., Hanke, M., Mildner, T., and Möller, H. (2008). Retinotopic activation in response to subjective contours in primary visual cortex. *Front. Hum. Neurosci.* 2, 2.
24. Kourtzi, Z., Tolias, A.S., Altmann, C.F., Augath, M., and Logothetis, N.K. (2003). Integration of local features into global shapes: monkey and human fMRI studies. *Neuron* 37, 333–346.
25. Zaretskaya, N., Anstis, S., and Bartels, A. (2013). Parietal cortex mediates conscious perception of illusory gestalt. *J. Neurosci.* 33, 523–531.
26. Gilad, A., Meirovithz, E., and Slovin, H. (2013). Population responses to contour integration: early encoding of discrete elements and late perceptual grouping. *Neuron* 78, 389–402.
27. Hupé, J.M., James, A.C., Payne, B.R., Lomber, S.G., Girard, P., and Bullier, J. (1998). Cortical feedback improves discrimination between figure and background by V1, V2 and V3 neurons. *Nature* 394, 784–787.
28. Alink, A., Schwiedrzik, C.M., Kohler, A., Singer, W., and Muckli, L. (2010). Stimulus predictability reduces responses in primary visual cortex. *J. Neurosci.* 30, 2960–2966.
29. Summerfield, C., Trittschuh, E.H., Monti, J.M., Mesulam, M.M., and Egner, T. (2008). Neural repetition suppression reflects fulfilled perceptual expectations. *Nat. Neurosci.* 11, 1004–1006.
30. Todorovic, A., van Ede, F., Maris, E., and de Lange, F.P. (2011). Prior expectation mediates neural adaptation to repeated sounds in the auditory cortex: an MEG study. *J. Neurosci.* 31, 9118–9123.
31. Todorovic, A., and de Lange, F.P. (2012). Repetition suppression and expectation suppression are dissociable in time in early auditory evoked fields. *J. Neurosci.* 32, 13389–13395.
32. den Ouden, H.E.M., Friston, K.J., Daw, N.D., McIntosh, A.R., and Stephan, K.E. (2009). A dual role for prediction error in associative learning. *Cereb. Cortex* 19, 1175–1185.
33. Kok, P., Rahnev, D., Jehee, J.F.M., Lau, H.C., and de Lange, F.P. (2012). Attention reverses the effect of prediction in silencing sensory signals. *Cereb. Cortex* 22, 2197–2206.
34. Kok, P., Failing, M.F., and de Lange, F.P. (2014). Prior expectations evoke stimulus templates in the primary visual cortex. *J. Cogn. Neurosci.* 26, 1546–1554.
35. den Ouden, H.E.M., Kok, P., and de Lange, F.P. (2012). How prediction errors shape perception, attention, and motivation. *Front. Psychol.* 3, 548.
36. Summerfield, C., and Egner, T. (2009). Expectation (and attention) in visual cognition. *Trends Cogn. Sci.* 13, 403–409.
37. Harrison, S.A., and Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature* 458, 632–635.
38. Serences, J.T., Ester, E.F., Vogel, E.K., and Awh, E. (2009). Stimulus-specific delay activity in human primary visual cortex. *Psychol. Sci.* 20, 207–214.
39. Albers, A.M., Kok, P., Toni, I., Dijkerman, H.C., and de Lange, F.P. (2013). Shared representations for working memory and mental imagery in early visual cortex. *Curr. Biol.* 23, 1427–1431.
40. Friston, K. (2010). The free-energy principle: a unified brain theory? *Nat. Rev. Neurosci.* 11, 127–138.
41. Koster-Hale, J., and Saxe, R. (2013). Theory of mind: a neural prediction problem. *Neuron* 79, 836–848.
42. McMains, S., and Kastner, S. (2011). Interactions of top-down and bottom-up mechanisms in human visual cortex. *J. Neurosci.* 31, 587–597.
43. de-Wit, L.H., Kubilius, J., Wagemans, J., and Op de Beeck, H.P. (2012). Bistable Gestalts reduce activity in the whole of V1, not just the retinotopically predicted parts. *J. Vis.* 12, 12.
44. Jack, A.I., Shulman, G.L., Snyder, A.Z., McAvoy, M., and Corbetta, M. (2006). Separate modulations of human V1 associated with spatial attention and task structure. *Neuron* 51, 135–147.
45. Donner, T.H., Sagi, D., Bonneh, Y.S., and Heeger, D.J. (2008). Opposite neural signatures of motion-induced blindness in human dorsal and ventral visual cortex. *J. Neurosci.* 28, 10298–10310.