

- Nagano, M., Nakahama, K., Suzuki, Y., Sugano, S., *et al.* (2002). A transcription factor response element for gene expression during circadian night. *Nature* 418, 534–539.
14. Sassone-Corsi, P. (1994). Rhythmic transcription and autoregulatory loops: winding up the biological clock. *Cell* 78, 361–364.
 15. Masubuchi, S., Kataoka, N., Sassone-Corsi, P., and Okamura, H. (2005). Mouse Period1 (mPER1) acts as a circadian adaptor to entrain the oscillator to environmental light/dark cycles by regulating mPER2 protein. *J. Neurosci.* 25, 4719–4724.
 16. Johnson, C.H., Elliott, J., Foster, R., Honma, K., and Kronauer, R. (2003). Fundamental properties of circadian rhythms. In *Chronobiology: Biological Timekeeping*, J.C. Dunlap, J.J. Loros, and P. Decoursey, eds. (Sunderland: Sinauer Assoc.), pp. 67–106.
 17. Gery, S., Komatsu, N., Baldijyan, L., Yu, A., Koo, D., and Koeffler, H.P. (2006). The circadian gene *per1* plays an important role in cell growth and DNA damage control in human cancer cells. *Mol. Cell* 22, 375–382.
 18. Itahana, Y., Singh, J., Sumida, T., Coppe, J.P., Parrinello, S., Bennington, J.L., and Desprez, P.Y. (2003). Role of *Id-2* in the maintenance of a differentiated and noninvasive phenotype in breast cancer cells. *Cancer Res.* 63, 7098–7105.
 19. Fu, L., and Lee, C.C. (2003). The circadian clock: pacemaker and tumour suppressor. *Nat. Rev. Cancer* 3, 350–361.
 20. Hunt, T., and Sassone-Corsi, P. (2007). Riding tandem: circadian clocks and the cell cycle. *Cell* 129, 461–464.

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Visual Perception: Converging Mechanisms of Attention, Binding, and Segmentation?

Visual scenes are cluttered. Recent evidence suggests that areas as early as V1 and V2 help making sense of the scene by segmenting them into distinct objects, separating foreground and background, and binding features.

Andreas Bartels

Visual input can be highly complex, but the complexity can be much reduced when the input is segmented into distinct objects. Because objects are defined not only by their boundaries but also by properties such as specific colour, motion direction, or distance to the observer, it would make sense if the mechanisms of segmentation, feature binding and attentional selection were to converge. A recent series of experiments in monkeys and humans provides independent, but consistent evidence suggesting that this is the case. A subset of neurons in V2 indicates border-ownership of edges, and the high inter-neural synchrony found in this subset reflects membership of a special network [1,2]. The same circuitry can be directly modulated by top-down attention, thus ‘highlighting’ selected object boundaries [3,4]; similar observations have been made in V1 [5]. A new study [6] describes neurons in the upper layers of V2 that are dually responsive to both motion and colour — features that are otherwise processed in segregated pathways — and that receive top-down feedback to ‘bridge’ attentional modulation from one feature to another, thus enabling cross-feature object selection.

In a visual scene, edges or borders are ‘owned’ by an object (Figure 1A,B). This makes most borders asymmetric, as their ‘owner’ is located on just one side of the border. Illusions such as Rubin’s face–vase and the art of M.C. Escher, where single edges are co-owned by two objects, reveal that our visual system constrains borders to belong exclusively to one side: only one interpretation is allowed at a time, resulting in bi-stable percepts (where border ownership flips from one side to the other), and illustrating the dramatic consequences of border-ownership in object recognition.

Surprisingly, a neural substrate for this holistic property of figure–ground segmentation resides not only in neurons in V4, which have large receptive fields, but also in those of the primary visual cortices V1 and V2, where the neurons have tiny receptive fields (covering just 0.2 to 1 visual degrees). In addition to their selectivity for position, orientation, colour, depth or motion, neurons in these areas are additionally modulated by border-ownership: some superficial V1 neurons and most edge-responsive V2 neurons are modulated by the side of the edge ‘owner’ [2] (Figure 1C). The identity of the up-modulated neurons thus indicates the ‘side’ of the occluder, and the population of neurons reflects the outline of an object. Because the owner of a border

is always in the foreground, the ‘owned’ side also highlights what is in front and what is in the back. Indeed, in those neurons that code for depth and border-ownership, the ‘near’-side coincides with the ‘border-owner’-side [7]. The perceptual pop-out of the ‘fore’-ground is thus rooted in the neural binding of edge-ownership with depth selectivity. The violation of such a neural contingency does not go unnoticed, and may be related to the aesthetic appreciation of art work, as for instance in Magritte’s paintings, in which depth-order and occlusion are often confused.

But how are V2 neurons modulated by object properties that far exceed their small field of view? Such modulation of border-ownership can be observed in V2 for the largest possible objects on the experimenter’s screen [2]. The border-ownership responses arrive within 25 milliseconds of the stimulus response, and are thus likely to reflect feedback mediated by myelinated, fast-conducting fibers of neurons with much larger receptive fields, such as those in V4, rather than by slow, long-range horizontal connections within V2 that may mediate other contextual effects [2,8,9].

Such feedback may not just mediate spatial binding in V2, but also link colour and motion, features that are processed within V2’s anatomically segregated thin and thick stripes, respectively. A new study [6] shows that, in contrast to mid-layer neurons of V2, those in the upper and deep layers are dually responsive to both colour and motion cues. The upper and deep layers receive feedback from both colour-responsive area V4 and the motion-processing area V5/MT, and, importantly, can project information with their long axons to

the mid-layers of both the thin and thick stripes (Figure 1D). The study suggests that these neurons ‘bridge’ colour and motion information: if an observer pays attention to one attribute of an object, for example motion, the neurons ‘bridge’ this top-down modulation to enhance early processing of the other attribute, in this case colour. These neurons may thus mediate not only cross-feature attentional selection of objects (object-based binding), consistent with the integrated competition model [10], but also cross-feature binding [6]. Recent fMRI evidence indeed demonstrates the explicit conjunction coding of colour and motion as early as V1 [11]. Interestingly, voxels coding for conjunctions were separate from those coding for colour or motion, consistent with the anatomical segregation of ‘bridging’ neurons [6,11].

Is it conceivable that border ownership is mediated by the same type of circuitry that underlies bridging of basic visual features? Recent experiments show that top-down attention directly affects part of the network generating border-ownership. For example, attention directed to a partially occluded object will reduce the border-ownership response at the edge of the occluder — this boundary does not belong to the attended object and is thus signalled less clearly [3] (Figure 1C). The contrary happens when the object in the foreground is attended, which enhances its border representation. These findings confirm that attention can act on objects rather than as a spatial spotlight [3,12,13]. Importantly, however, the results show that attention modulates the same mechanism used for assigning object-boundaries, which may therefore provide the ‘interface’ for attentional object selection, which in turn may be coincident with the cross-feature ‘bridging’ mechanism described above [3,6].

A recent fMRI study used compelling stimuli (Figure 1B) to confirm that two of the above findings also hold for the human brain, namely that early visual areas (V2, and to lesser extent V1) signal object-ownership, and that this happens to a far greater extent when the stimuli are attended [4]. It is the latest of a series of fMRI studies in human showing influences of higher-level perception on early visual areas, effects likely reflecting activity of the

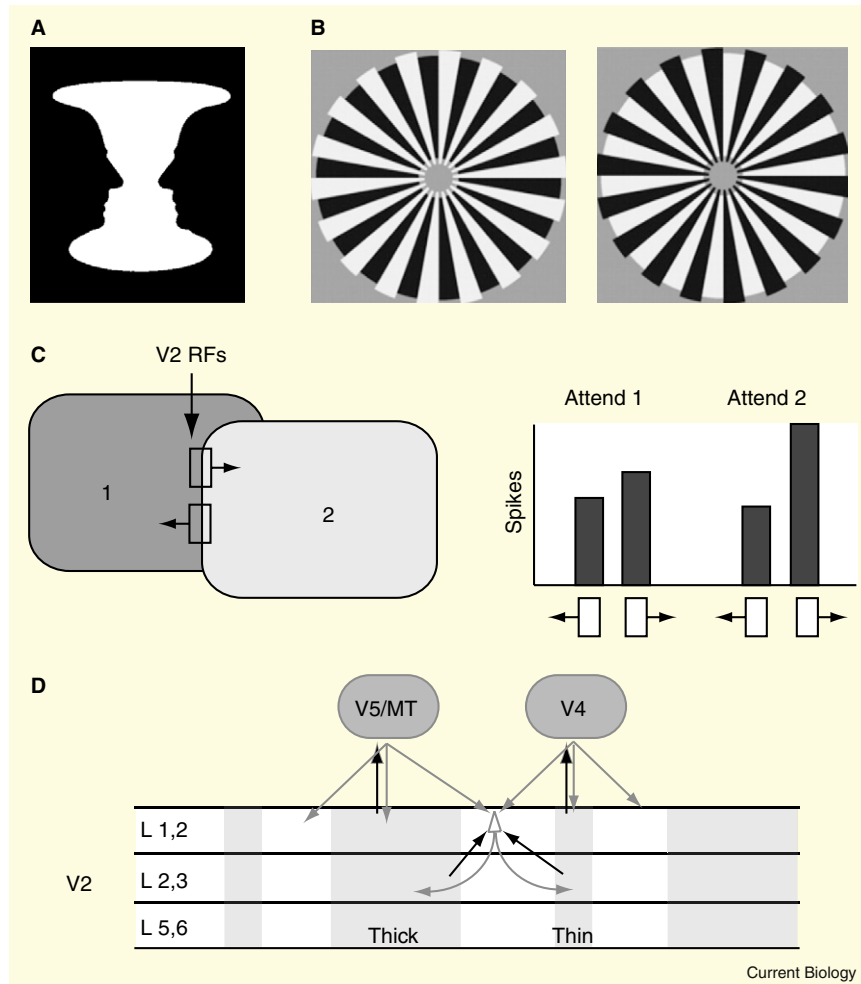


Figure 1. Scene segmentation and circuitry for feature binding.

(A) Rubin’s vase–face stimulus: the visual system allows borders to ‘belong’ to only one object, resulting in bi-stability ([19]; <http://en.wikipedia.org/wiki/File:Rubin2.jpg>). (B) Stimuli used by Fang *et al.* [4] change border-ownership by a small, clever manipulation (reproduced with permission from [4]). (C) Neurons in V2 are modulated by border ownership, which in turn is affected by object-based attention. Borders that ‘belong’ to attended objects are enhanced, as described in [3,4] (reproduced with permission from [3]). (D) Dual-responsive neurons (triangle in layer 1,2) ‘bridge’ attentional modulation across features. For example, during attention to colour of an object, V4 signals feedback to V2 enhancing both colour and motion processing in thin and thick stripes (modified with permission from [6]). We hypothesize that top-down attentional selection, object-border coding and feature binding may involve similar circuitries.

above ‘bridging’ or ‘interface’ mechanisms [11,14–16]. Note, though, that border assignment happens also in non-attended figures, and at the same (short) latency as in attended figures, indicating it does not require attention to work [3].

What is the neural code mediating border-ownership? No evidence has been found that synchronous firing ‘tags’ same-border neurons, as classic theories on the binding problem have proposed [17,18]; instead, this seems to be mediated by a plain enhancement of the neural

firing rate [1]. Nevertheless, those select neurons that are capable of coding for border-ownership have the distinct hallmark of increased synchronous firing that does not indicate same/different border coding, but that indicates that they are part of a network with far-reaching connectivity [1]. This is reminiscent of the finding by another group [5], who found that exactly that subset of neurons in V1 that was affected by top-down attentional modulation differentiated best between connected and non-connected lines

in a line-tracing task, and the same subset had more pronounced and spatially wide-spread rate-covariations compared to other neurons. Long-range connectivity and direct modulation from higher-tier visual areas is also the hallmark of cross-feature 'bridging' neurons in the upper layers of V2 [6]. Together, therefore, these studies imply a circuitry with far-reaching connectivity mediating border-ownership, feature binding and object-based attentional selection in the early visual cortex.

References

1. Dong, Y., Mihalas, S., Qiu, F., von der Heydt, R., and Niebur, E. (2008). Synchrony and the binding problem in macaque visual cortex. *J. Vis.* 8, 1–16.
2. Zhou, H., Friedman, H.S., and von der Heydt, R. (2000). Coding of border ownership in monkey visual cortex. *J. Neurosci.* 20, 6594–6611.
3. Qiu, F.T., Sugihara, T., and von der Heydt, R. (2007). Figure-ground mechanisms provide structure for selective attention. *Nat. Neurosci.* 10, 1492–1499.
4. Fang, F., Boyaci, H., and Kersten, D. (2009). Border ownership selectivity in human early visual cortex and its modulation by attention. *J. Neurosci.* 29, 460–465.
5. Roelfsema, P.R., Lamme, V.A., and Spekreijse, H. (2004). Synchrony and covariation of firing rates in the primary visual cortex during contour grouping. *Nat. Neurosci.* 7, 982–991.
6. Shipp, S., Adams, D.L., Moutoussis, K., and Zeki, S. (2009). Feature binding in the feedback layers of area V2. *Cereb. Cortex.* Jan 19 [Epub ahead of print].
7. Qiu, F.T., and von der Heydt, R. (2005). Figure and ground in the visual cortex: V2 combines stereoscopic cues with gestalt rules. *Neuron* 47, 155–166.
8. Zeki, S., and Shipp, S. (1989). Modular connections between areas V2 and V4 of macaque monkey visual cortex. *Eur. J. Neurosci.* 1, 494–506.
9. Albright, T.D., and Stoner, G.R. (2002). Contextual influences on visual processing. *Annu. Rev. Neurosci.* 25, 339–379.
10. Duncan, J., Humphreys, G., and Ward, R. (1997). Competitive brain activity in visual attention. *Curr. Opin. Neurobiol.* 7, 255–261.
11. Seymour, K., Clifford, C.W., Logothetis, N.K., and Bartels, A. (2009). The coding of colour, motion and their conjunction in human visual cortex. *Curr. Biol.* 19, 1–7.
12. O'Craven, K.M., Downing, P.E., and Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature* 401, 584–587.
13. Martinez, A., Ramanathan, D.S., Foxe, J.J., Javitt, D.C., and Hillyard, S.A. (2007). The role of spatial attention in the selection of real and illusory objects. *J. Neurosci.* 27, 7963–7973.
14. Fang, F., Boyaci, H., Kersten, D., and Murray, S.O. (2008). Attention-dependent representation of a size illusion in human V1. *Curr. Biol.* 18, 1707–1712.
15. Boyaci, H., Fang, F., Murray, S.O., and Kersten, D. (2007). Responses to lightness variations in early human visual cortex. *Curr. Biol.* 17, 989–993.
16. Murray, S.O., Boyaci, H., and Kersten, D. (2006). The representation of perceived angular size in human primary visual cortex. *Nat. Neurosci.* 9, 429–434.
17. von der Malsburg, C. (1999). The what and why of binding: the modeler's perspective. *Neuron* 24, 95–104, 111–125.
18. Engel, A.K., and Singer, W. (2001). Temporal binding and the neural correlates of sensory awareness. *Trends Cogn. Sci.* 5, 16–25.
19. Rubin, E. (1915). *Synsoplerede Figuren* (Copenhagen: Gyldendal).

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Plant Evolution: Measuring the Length of the Day

How has the ability of plants to measure the length of the day evolved? The finding that the genome of the unicellular alga *Chlamydomonas reinhardtii* contains a gene homologous to, and functionally conserved with, the *Arabidopsis* gene *CONSTANS* might provide part of the answer.

Ove Nilsson

For many plants, except those that are growing close to the equator, and especially for those growing at higher latitudes, it is important to adapt their life cycles and growth to the varying day lengths and temperatures that occur over the year. This photoperiodic regulation of growth has been studied in detail over the last 90 years (recently reviewed in [1]). Many annual plants, which complete their life cycle within one year, display photoperiodic regulation of flowering. These plants can be divided into long day plants and short day plants. Long day plants, such as the well-characterized plant *Arabidopsis thaliana*, sense the increasing day length during spring and this triggers flowering early in the year. In contrast, short day plants, such as rice, sense the decreasing day lengths occurring at the end of summer in

order to time their flowering with the fall. However, it is not only flowering that is under photoperiodic control. For instance, perennial plants like trees that grow in the temperate regions of the world initiate growth cessation and bud set as a response to the shortening days after summer, and certain potato cultivars display a short-day-induced tuberization. For all these plants, correct day-length-sensing is vital for the life cycle of the plant, ensuring both flowering at the right time of the year (at the same time as other members of the species) and avoidance of frost damage to the developing seed. Trees also need to set bud in time to be able to develop frost hardiness before winter arrives.

So how then can the plant measure the length of the day? Most of what we have learned about the molecular mechanism underlying this regulation has been gained through studies

in *Arabidopsis thaliana*. The central module responsible for the day-length-sensing is composed of the two genes *CONSTANS* (*CO*), encoding a B-box zinc-finger protein [2], and the major target of *CO*, *FLOWERING LOCUS T* (*FT*), encoding a transcription cofactor that stimulates flowering [3–6] (recently reviewed in [7]). *CO* mRNA accumulation displays a diurnal variation, controlled by the circadian clock [8,9]. Under both long and short days, *CO* mRNA starts to accumulate around 10–12 hours after dawn. This means that, under short days, *CO* mRNA accumulation will occur in the night, but as the days get longer a point will be reached when *CO* mRNA starts to accumulate at the end of the day, in the light. An important feature of this system is that the *CO* protein is rapidly degraded in the dark, meaning that no *CO* protein activity will be present in short days [10]. However, when *CO* expression occurs in the light (as in long days), the *CO* protein is stabilized and can activate *FT*, leading to flowering [10]. Both *co* and *ft* mutant plants are unable to measure the length of the day and will therefore flower at about the same time in long and short days [11], stressing the importance of the *CO-FT* module for day-length-sensing. In a short day