VISUAL BRAIN AND VISUAL PERCEPTION:

HOW DOES THE CORTEX DO PERCEPTUAL GROUPING?

by

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Technical Report CAS/CNS-TR-96-018
Boston, MA: Boston University

Trends in Neurosciences, in press

Running Title: Perceptual Grouping by Visual Cortex

Key words: visual cortex, visual perception, boundary segmentation, LGN, V1 V2, pyramidal cell, cortical map, illusory contour, critical period, synchronization, cortical column, cortical feedback

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† Supported in part by the Office of Naval Research (N00014-95-1-0657 and N00014-95-1-0409).

‡ Supported in part by the Office of Naval Research (N00014-94-1-0597 and N00014-95-1-0409).

* Supported in part by the Office of Naval Research (N00014-95-1-0409).

Acknowledgments: The authors wish to thank Robin Locke and Diana Meyers for their valuable assistance in the preparation of the manuscript.

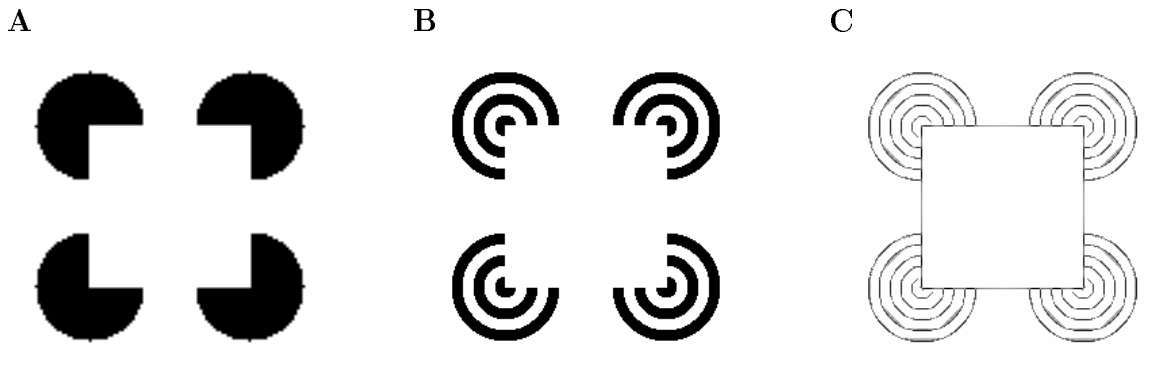

Figure 1. A Kanizsa square can be perceived (A) colinear to edge inducers and (B) perpendicular to line end inducers. (C) Model simulation of the latter type of boundary grouping.

How the brain generates visual percepts is a central problem in neuroscience. We propose a detailed neural model of how LGN and the interblob cortical stream through V1 and V2 generate context-sensitive perceptual groupings from visual inputs. The model suggests a functional role for cortical layers, columns, maps, and networks and proposes homologous circuits for V1 and V2 with larger scale processing in V2. An integrated treatment of interlaminar, horizontal, orientational, and endstopping cortical interactions and a role for corticogeniculate feedback in grouping are proposed. Modeled circuits simulate parametric psychophysical data about boundary grouping and illusory contour formation.

Although visual neuroscience is one of the most actively studied areas in biology, a gap remains in our understanding of how visual percepts arise from neurobiological properties of identified neurons. A step towards closing this gap is made herein by modeling how perceptual groupings may emerge from interactions of cells with known receptive field properties. It is well established that perceptual groupings help to segregate objects and their backgrounds in response to texture, shading, and depth cues in scenes and images[1–5]. These groupings are highly context-sensitive, as illustrated by Kanizsa square percepts (Figure 1) which can arise either colinear to inducing edges or perpendicular to inducing line ends. We show herein how the context-sensitivity of such perceptual groupings sheds light on neural data concerning the context-sensitivity of neuron responses, notably their "non-classical" receptive field properties.

Boundary Formation using Cooperating Pyramidal Cells

Long-range context-sensitive interactions are illustrated by the increasing strength of illusory contours in edge-induced Kanizsa squares (Figure 1A) as the support ratio (ratio of inducer length to total perceived edge length) increases[6], as in Figure 2A. This cooperative process builds a coherent boundary grouping that spans the gap between inducers. Cells in visual cortical area V2 respond to such illusory contours and exhibit a bipole property[7,8] whereby they fire when their receptive field lies between aligned inducers but not when they lie beyond a single inducer. This bipole property was derived from a theoretical analysis of psychophysical data about perceptual grouping[9–11] and has been further supported by subsequent psychophysical experiments[6,12].

According to the model, cooperative bipole interactions are realized in cortical layer 3 by recurrent long-range horizontal pathways among cortical pyramidal cells. In order for cooperation to build a boundary like an illusory contour, these monosynaptic excitatory connections need to converge on shared pyramidal cells with colinear or slightly curvilinear receptive fields (see Figure 3A). The horizontal connections also activate smooth stellate cells, which inhibit nearby pyramidal cells via disynaptic inhibition[13,14]. This disynaptic

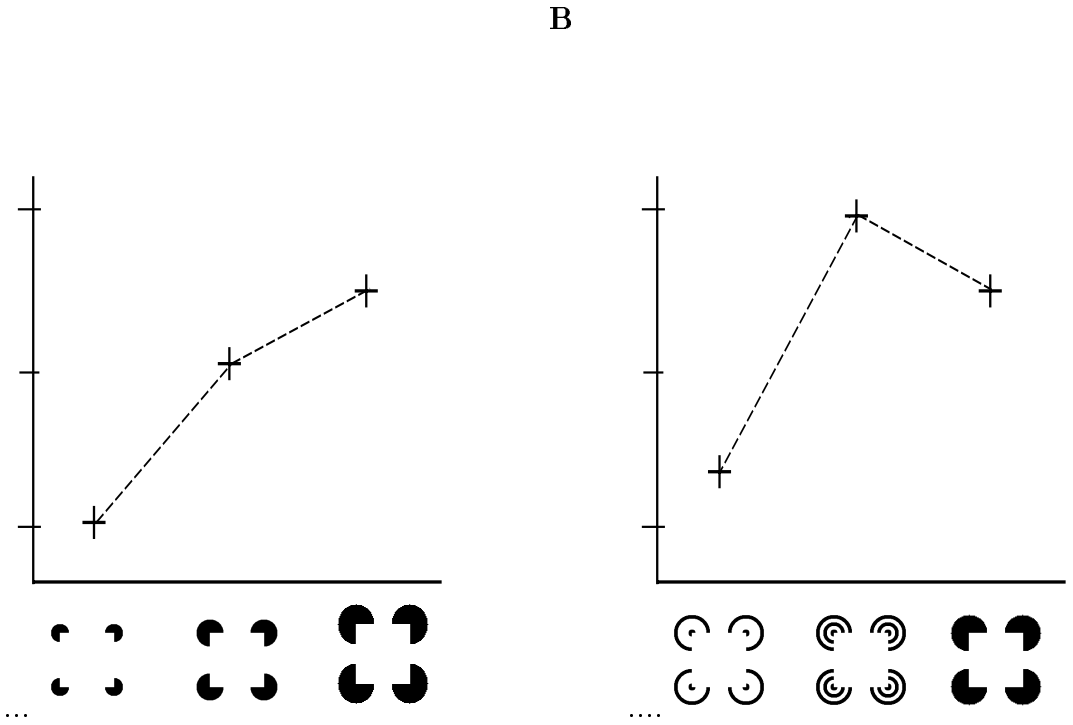

Figure 2. Model simulations of psychophysical data: (A) In response to the edge inducers in Figure 1A, illusory contour strength increases with support ratio. Support ratio is the ratio of real to total contour length. (B) For the line end inducers in Figure 1B, contour strength is an inverted U function of the number and density of line end inducers. Contour strength was determined by computing the average cell activity along the path of the illusory portion of the contour.

inhibition is proposed to control the monosynaptic excitation, and to also give rise to the bipole property. One characteristic of this control is that horizontal waves of activation resulting from spatially isolated inducers are rapidly attenuated by subsequent disynaptic inhibition. This agrees with studies showing that when a single input source drives horizontal pathways at threshold intensities *in vivo*, excitatory postsynaptic potentials (EPSPs) are generated, whereas supratheshold stimulus currents evoke disynaptic inhibition (IPSPs) that can overwhelm the EPSPs[15–19]. Bipole completion arises from model interactions between monosynaptic excitation and disynaptic inhibition when layer 3 cells receive horizontally induced EPSPs from a surrounding neighborhood of oriented cells, as in the middle of a contour. These EPSPs from convergent horizontal connections can overcome the effect of disynaptic inhibition because all the horizontal connections are proposed to converge on a single population of inhibitory interneurons (Figure 3A). Locally, it is a case of two (or more) against one. The net effect of this cooperative-competitive interaction is to convert the *outward* propagating long-range horizontal signals from pyramidal cells into the selective *inward* activation of pyramidal cells according to a bipole property.

LGN Influences on V1 Layers 4 and 6

Several other types of cooperative and competitive interactions occur in visual cortex and our model thereof. As in the brain, inputs to the model area V1 arrive at layers 4 and 6 from the model lateral geniculate nucleus or LGN[20]. LGN inputs directly activate orientationally tuned simple cells in layer 4, as has been verified by cross-correlational analysis[21] and cortical chemical and cooling inactivation experiments[22,23]. Oriented arrays of spatially displaced LGN ON and OFF cells excite mutually inhibitory simple cells that are sensitive to the

same orientation but opposite contrast polarities[24–26]. The LGN also indirectly excites and inhibits layer 4 via layer 6. Electrophysiological recordings[27–29] and antidromic activation of layer 6 corticogeniculate cells from the cat LGN[30] support the idea that layer 6 gives rise to a short-range excitatory input to layer 4 and a longer-range inhibitory interaction that is mediated by layer 4 inhibitory interneurons. The net effect is that LGN influences layer 4 via a feedforward on-center off-surround network (Figure 3B). The model proposes that this excitatory-inhibitory balance helps layer 4 cells to maintain their analog sensitivity to visual inputs of variable contrast.

Closing a Cortical Feedback Loop

Layer 4 cells, in turn, activate pyramidal cells in layer 3, which then attempt to cooperate using their long-range horizontal connections and short-range disynaptic inhibition. All the layer 3 cells that become active either via direct layer 4 inputs or by bipole cooperation then generate excitatory feedback signals to layer 6 via layer 5[31,32]. Layer 3 hereby gains access to the on-center off-surround network of connections from layer 6 to layer 4. The total interlaminar feedback loop thus proceeds in the order $4 \rightarrow 3 \rightarrow 5 \rightarrow 6 \rightarrow 4$.

Context-Sensitive Boundary Formation by Cooperation and Competition

The long-range cooperation in layer 3 can use the shorter-range on-center off-surround layer 6–to–4 signals to amplify those cell activations that are favored by the cooperative grouping while suppressing those that are not. Model layer 6–to–4 inhibition influences different orientations and positions by being distributed across a cortical hypercolumn map wherein cells sensitive to these features are spatially organized[33]. This short-range competition can relatively enhance cell responses cooperating in positional, orientational, and length-sensitive groupings by suppressing cells responding to weaker groupings, incoherent noise, or background signals. In addition, feedback amplifies cell responses without eliminating their sensitivity to stimulus strength, notably to variable contrast[34], as has been shown *in vivo*[35].

The ability of the cooperative-competitive feedback loop to maintain cell sensitivity is illustrated by computer simulations of perceptual grouping strength as a function of inducer type and spatial distribution[6,36,37]. Figure 2 simulates how contour strength increases with support ratio[6] and the density of lines[36,37], owing to increased long-range cooperation as more and more cells and their horizontal connections are activated. The existence of short-range competition interactions which balance the long-range cooperation is illustrated perceptually by the inverted U in Kanizsa square contour strength that is observed as the number and density of line-end inducers continues to increase[36,37], as in Figure 2B. The inverted U occurs in the model because the excitatory influence of each LGN input is increasingly inhibited at layer 4 by layer 6–to–4 spatial inhibition as the inducers get closer together. Thus, although more inputs activate the cooperating layer 3 pyramidal cells, each input gets smaller as the inducers get denser. This explanation functionally clarifies that the short-range layer 6–to–4 inhibition is not the same as the layer 3 disynaptic inhibition that helps to realize the bipole property.

Cortical Columns as Functional Units

These cooperative-competitive interactions play a number of other functional roles in the model that are consistent with brain data. The interlaminar feedback pathway $4 \rightarrow 3 \rightarrow 5 \rightarrow 6 \rightarrow 4$ enables cells throughout each cortical column to function together as a unit with shared properties like orientational preference that can be contextually modified by long-range cooperation and short-range competition. The role of feedback in grouping hereby gives new functional meaning to the classical observation that cortical processing has a columnar organization[20,33,38] and to data suggesting that the organization of simple, complex, and hypercomplex cells is not simply a feedforward hierarchy because whatever cell properties are elaborated in any layer may potentially influence cell responses in other layers via feedback.

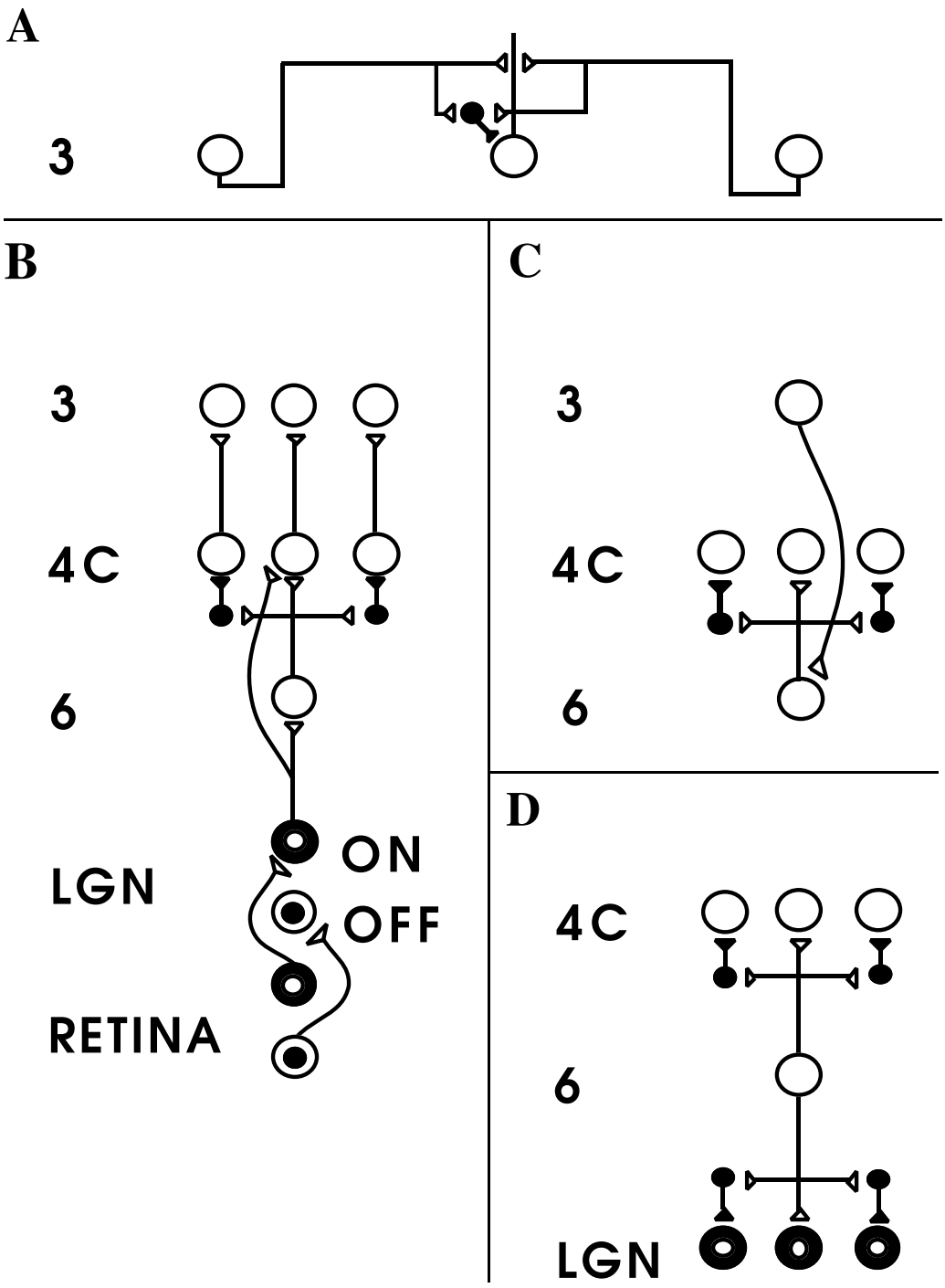

Figure 3. Caption follows on next page.

Figure 3. Model retinal, V1, and LGN circuit: Each neuron was modeled as a single voltage compartment in which the membrane potential, $V(t)$, was given by

$$C_m \frac{dV(t)}{dt} = -(V(t) - E_{EXCIT}) g_{EXCIT}(t) - (V(t) - E_{INHIB}) g_{INHIB}(t) - (V(t) - E_{LEAK}) g_{LEAK},$$

where the parameters E represent reversal potentials, g_{LEAK} is a constant leakage conductance, and the time-varying conductances $g_{EXCIT}(t)$ and $g_{INHIB}(t)$ represent the total inputs to the cell. Transient after hyperpolarization terms (AHP) were not incorporated since all groupings were allowed to reach steady state. Cortical layers and successive processing stages are indicated in the vertical direction from LGN to V1. The relative scale of horizontal interactions is roughly indicated by the length of pathways in the horizontal direction. The time-varying conductances $g_{EXCIT}(t)$ and $g_{INHIB}(t)$ were determined as follows. (A) Feedforward circuit from retina to LGN to cortical layers 4 and 6. **Retina**: Retinal ON cells have on-center off-surround organization. Retinal OFF cells have an off-center on-surround organization. **LGN**: The LGN ON and OFF cells receive feedforward ON and OFF cell inputs form the retina. **Layer 4**: Layer 4 cells receive feedforward inputs from LGN and layer 6. LGN ON and OFF cell excitatory inputs to layer 4 establish oriented simple cell receptive fields. Layer 6 cells excite layer 4 cells with a narrow on-center and inhibit them from using layer 4 inhibitory interneurons that span a broader off-surround. Like-oriented layer 4 simple cells with opposite contrast polarities compete (not shown) before generating half-wave rectified outputs that converge on layer 3 complex cells. **Layer 3**: The converging simple cell outputs enable complex cells to respond to both polarities. They hereby full-wave rectify the image. (B) Horizontal bipole interactions in layer 3: Layer 3 complex pyramidal cells monosynaptically excite one another via horizontal connections, primarily on their apical dendrites. They also inhibit one another via disynaptic inhibition that is mediated by model smooth stellate cells. Multiple horizontal connections are proposed to share a common pool of stellate cells near each target complex cell. The bipole property is hereby achieved. (C) Cortical feedback loop from layer 3 to layer 6: Layer 6 cells receive excitatory inputs from layer 3. The long-range cooperation hereby engages the feedforward layer 6–to–4 on-center off-surround network. This cooperative-competitive feedback loop can select winning groupings without a loss of analog sensitivity. (D) Top-down corticogeniculate feedback from layer 6: LGN ON and OFF cells receive topographic excitatory feedback from layer 6, and more broadly distributed inhibitory feedback via LGN inhibitory interneurons that are excited by layer 6 signals. The feedback signals pool outputs over all cortical orientations and are delivered equally to ON and OFF cells. Corticogeniculate feedback selects, gain controls, and synchronizes LGN cells that are consistent with the cortical activation that they cause, thereby acting like a type of automatic attentional focus. Layer 6–to–4 inhibition and layer 6–to–LGN inhibition both contribute to length-sensitive (endstopped) responses that facilitate grouping perpendicular to line ends.

Endstopping

Another property to which layer 6–to–4 inhibition may contribute is the endstopping effect by which the responses of oriented cells to the middle portion of a long edge are attenuated relative to cell responses at edge ends or to short edges. The cortical endstopping circuitry has been studied *in vivo* by reversible inactivation of layer 6 in V1 using the inhibitory transmitter γ-aminobutyric acid (GABA), which causes cells in layer 4 to lose their end-inhibition, as do cells in layer 3 which get input from layer 4[39,40]. This procedure has little impact on orientational selectivity *in vivo*, or in the model. An inhibitory interaction with a mean length of 2.8 ° in cat cortical area V1[27] (area 17) well matches the value predicted for the inhibitory field generating endstopping[41–43]. It is indicated below how corticogeniculate feedback may also influence endstopping.

Endstopping cannot be the only role of layer 6–to–4 inhibitory inputs since layer 6 connectivity enhances the excitability of non-length-tuned cells in layers 3 and 4[44]. The model proposes that these interactions are, more generally, part of the mechanism that helps to select correct groupings without a loss of analog or spatial sensitivity. In particular, the on-center off-surround organization from layer 4–to–6 may help to explain patch-suppressed cell responses in both cat and macaque monkey cortex. These cells respond to gratings of a specific orientation within their classical receptive field, but the response diminishes if the grating is expanded to cover the surrounding area[11,45,46]. The balance of recurrent facilitation and inhibition across hypercolumn representations of position and orientation may also help to clarify how cat and monkey cortical cells respond to discontinuities in visual input patterns[45,46]. We have included discussions of both cat and monkey data throughout this article where they are consistent.

Interactions of Areas V1 and V2

Both similarities and differences between V1 and V2 circuitry (areas 17 and 18 in the cat) play important functional roles in the model. It is known *in vivo* that cells in both V1 and V2 respond when illusory contours span closely spaced line ends[47,48], as in Figure 4A. On the other hand, cells in V1 do not respond when illusory contours span large distances, whereas cells in V2 do[7], as in Figure 4B. These facts suggest that some of the properties of V1, such as the existence of horizontal connections among pyramidal cell may be replicated in V2 at a larger scale. The model proposes that the V1 and V2 circuits are, in fact, homologous, but that V2 has longer-range interactions than V1 (Figure 5). Consistent with this proposal, a quantitative study of orientation maps (using multiunit recordings) and of cortical connections (using biocytin injections analysed in horizontal sections) show no significant differences in the proportions of excitatory and inhibitory cells and their preferred orientational contacts across areas V1 and V2, but did show a larger scale in V2 than V1[49].

As in the brain, layer 3 of the model V1 circuit activates layers 4 and 6 of the model V2 circuit[50,51]. When they interact, model V1 and V2 circuits simulate the data on offset grating stimuli from experiments on both V1 and V2 (Figures 4A and 4B). Cooperative interactions across the smaller scales in V1 enhance mutually consistent responses indicating boundary location and orientation, while larger scale cooperation in V2 supports long-range boundary completion and grouping. In addition, the same short-range inhibition that helps the model V2 to generate only well-supported long-range groupings (e.g., Figure 1C) can, as part of the homologous V1 circuit, simulate how mutually perpendicular inducers can prevent groupings in monkey area V1 (Figure 4C), which when they do form between colinear inducers improve stimulus detectability by mutual activation[52]. The same mechanisms also help to explain more global properties of Gestalt grouping (Figure 6).

Feedback from Area V1 to LGN

The model also relies on reciprocal connectivity between cortex and LGN (Figure 3D). Layer 6 in both brain and model sends topographic excitation and broader-range inhibition back to the LGN[53–55]. This feedback selects and synchronizes LGN activities that are

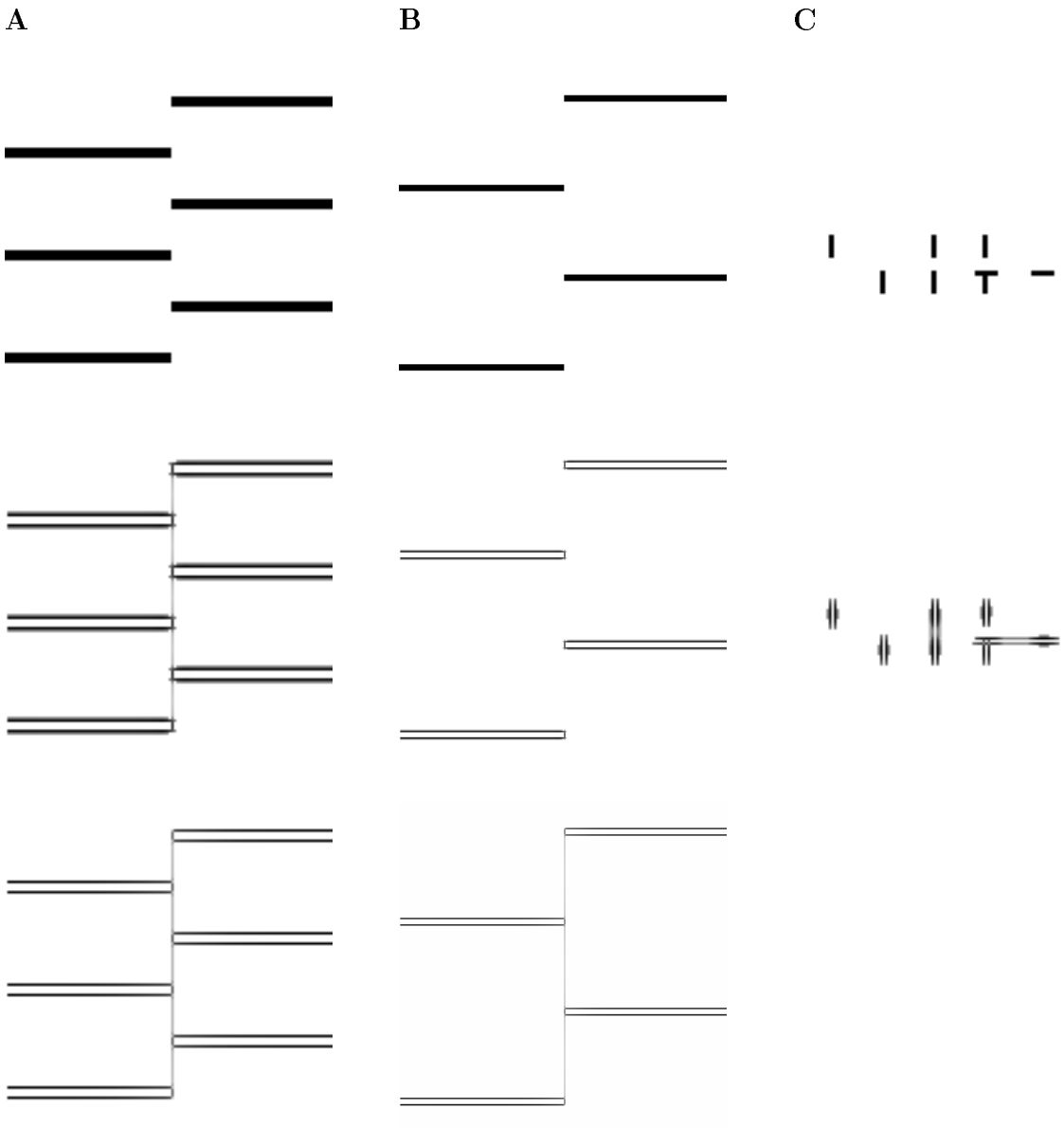

Figure 4. Simulation of the: (A) Grosof *et al.* display[47]: illusory contours between the offset gratings occur in both V1 and V2; (B) von der Heydt *et al.* display[7]: illusory contours group the line ends in V2 but not V1; (C) Kapadia *et al.* display[52]: horizontal orientations compete with the vertical grouping. The displays are in the top row, the simulated V1 responses are in the middle row, and the simulated V2 responses are in the bottom row.

consistent with cortical cell activity[56,57]. In so doing, it increases the visual information transmitted from LGN to cortex by enhancing contextually significant differences between LGN responses[58] and may influence the length tuning of LGN cells[53]. Model feedback from layer 6 cells also enhances LGN responses near line-ends, thereby strengthening the perpendicular cortical responses at line-ends that enable them to cooperatively group[26], as in Figure 1C.

A Role for Feedback in Learning?

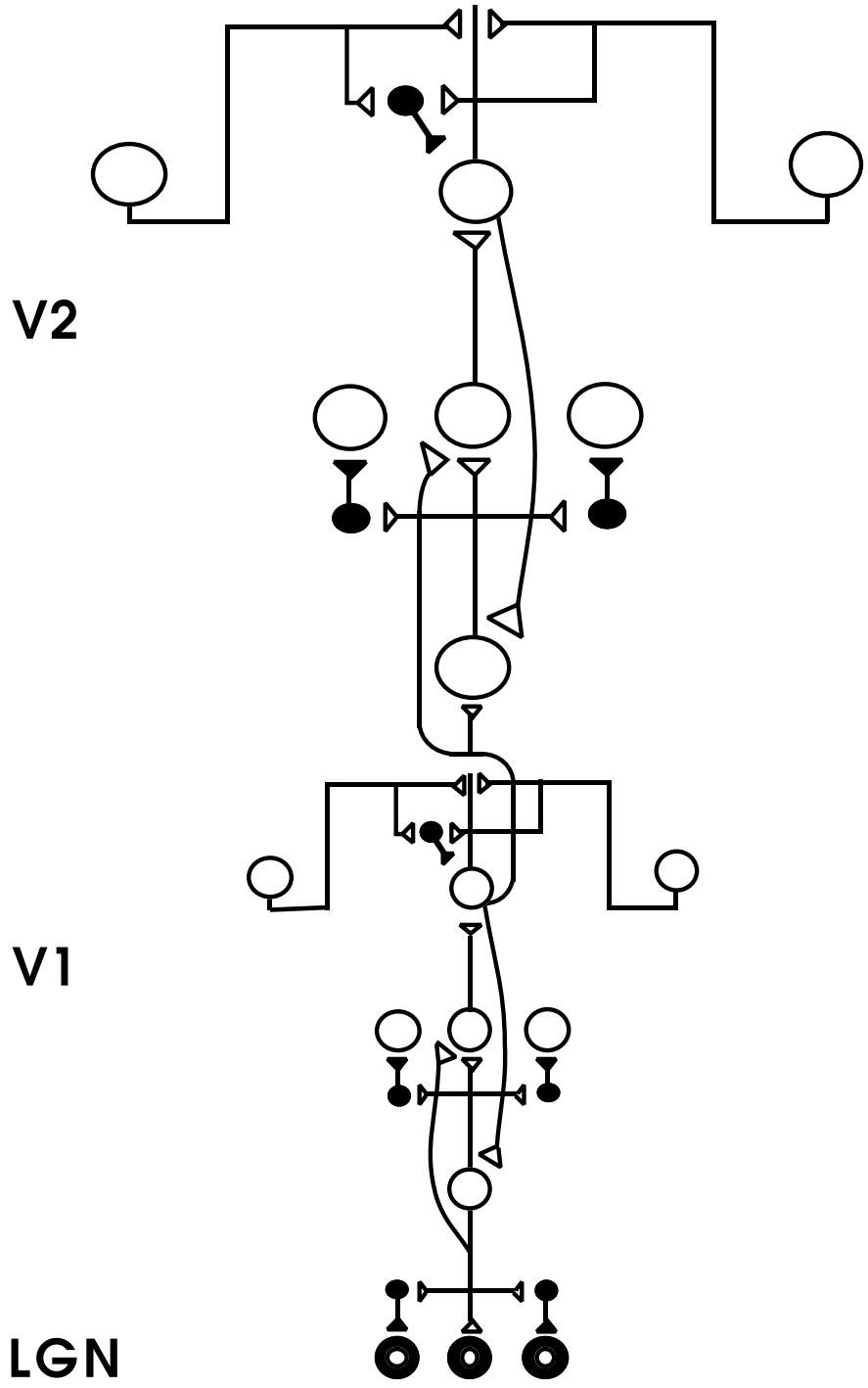

Figure 5. Schematic of LGN–V1–V2 model circuitry. The V2 circuit is proposed to replicate the main properties of the V1 circuit but at a larger spatial scale.

It has been suggested that corticogeniculate feedback helps to stabilize perceptual learning in V1, notably the adaptive tuning of disparity-sensitive cortical complex cells that occurs during the visual critical period[56]. Top-down adaptive feedback of this type seems to occur at many levels of visual and auditory processing in the brain[59]. The corticogeniculate feedback pathway may prove to be a particularly accessible system for studying how cortical learning is dynamically stabilized by feedback.

FACADE Theory and Related Vision Models

Taken together, these results suggest how multiple levels of thalamocortical organization work together to generate the emergent boundary groupings that help to form visual percepts in a context-sensitive way. The present model of boundary grouping further develops an evolving neural theory of visual perception, called FACADE theory, that has previously been used to analyse a diverse set of perceptual and neural data about both boundary and surface perception, including data on brightness, color, form, texture, depth, motion, and figure-ground perception[3,26,60–64]. The boundary formation circuits of FACADE theory are collectively called the Boundary Contour System, or BCS. The present work suggests how the combined effects of long-range cooperation, short-range competition, a cortical hypercolumn map, laminar cortical organization, interlaminar feedback pathways, and hierarchical replication of the same processing modules with different spatial scales – can robustly achieve context-sensitive properties of boundary grouping that were difficult to explain using earlier versions of the BCS. The new BCS model does so, moreover, without undermining explanations of other types of data that the theory had previously handled.

One difference between the BCS and competing perceptual grouping models is that the BCS uses feedback between its cooperative and competitive cells. Alternative models have invoked the bipole property that was introduced with the BCS, but have assumed that this property is expressed in a purely feedforward circuit[65,66]. These alternative models need to somehow deal with the fact that interlaminar feedback between layers 3, 4, and 6 does exist, and that various perceptual grouping data, notable data about visual persistence and bistable percepts, exhibit grouping formation and reset times in the hundreds of milliseconds that seem to require feedback and have, in fact, been explained using it[3,63,64]. More generally, whereas a model that uses feedback can inhibit strong signals if they are weak relative to a prescribed image context, and can amplify weak signals if they are strong relative to a prescribed image context, feedforward models have a more limited range of options. Feedback grouping models can also create coherent representations, including fast synchronous binding of signals[67–70], that feedforward models cannot.

Perhaps as a result of these advantages, feedback models have been shown capable of generating appropriate boundary groupings in response to the types of complex and noisy imagery that are created by artificial sensors, such as synthetic aperture radar, laser radar, and infrared radar sensors[71,72]. We have also found that the refined grouping mechanisms that are reported herein are capable of generating even more accurate, computationally efficient, and noise tolerant boundary groupings of radar images than did previous versions of the model. The present version of the BCS model hereby illustrates how the various levels of cortical organization — its layers, columns, maps, networks, and successive processing stages — work together to generate efficient perceptual representations of the external world, whether natural or man-made.

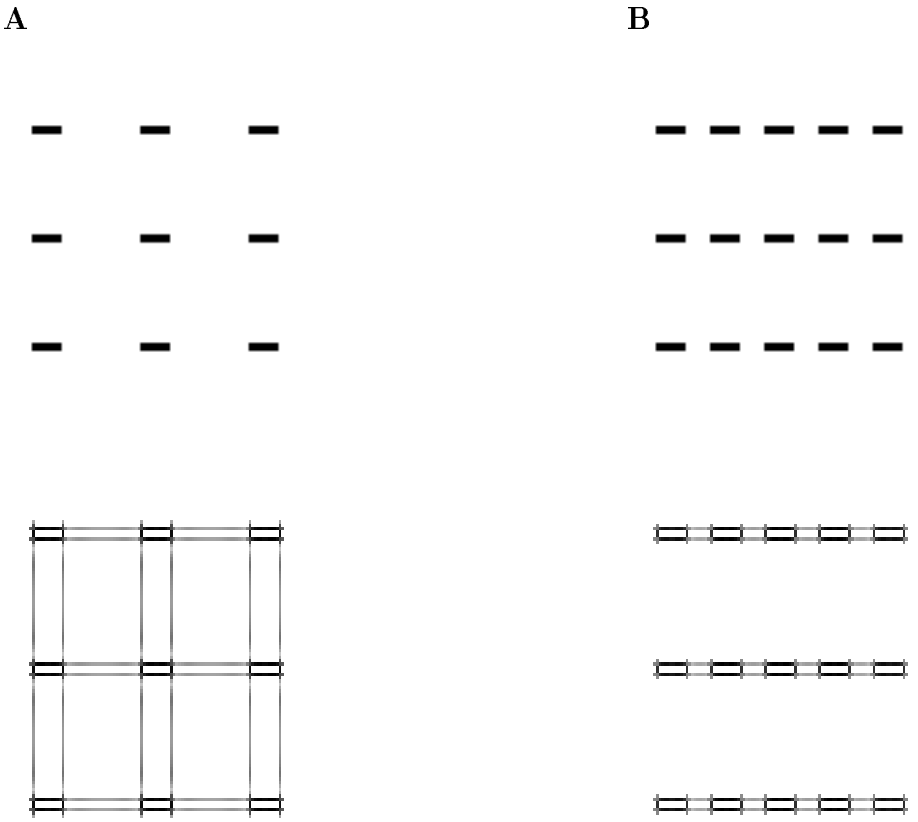

Figure 6. A) An ambiguous grouping (both vertical and horizontal) may be perceived in response to this image, and is simulated by the model. (B) Additional horizontal lines cause the grouping to become horizontal in perception and the model.

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