

# Reappraising the Functional Implications of the Primate Visual Anatomical Hierarchy

JAY HEGDÉ and DANIEL J. FELLEMAN

The primate visual system has been shown to be organized into an anatomical hierarchy by the application of a few principled criteria. It has been widely assumed that cortical visual processing is also hierarchical, with the anatomical hierarchy providing a defined substrate for clear levels of hierarchical function. A large body of empirical evidence seemed to support this assumption, including the general observations that functional properties of visual neurons grow progressively more complex at progressively higher levels of the anatomical hierarchy. However, a growing body of evidence, including recent direct experimental comparisons of functional properties at two or more levels of the anatomical hierarchy, indicates that visual processing neither is hierarchical nor parallels the anatomical hierarchy. Recent results also indicate that some of the pathways of visual information flow are not hierarchical, so that the anatomical hierarchy cannot be taken as a strict flowchart of visual information either. Thus, while the sustaining strength of the notion of hierarchical processing may be that it is rather simple, its fatal flaw is that it is overly simplistic. *NEUROSCIENTIST* 13(5):416–421, 2007. DOI: 10.1177/1073858407305201

**KEY WORDS** *Feedback, Feed-forward, Thalamocortical relay, Pure vision, Recurrent processing*

The anatomical pathways of neural processing have been best understood in the macaque monkey. In the macaque visual system, the image information that leaves the retina, or “bottom-up,” “feed-forward,” or “ascending” information, travels to the lateral geniculate nucleus (LGN) of the thalamus, from where it is relayed to the primary visual cortex or V1 (also referred to as the striate cortex). From V1, feed-forward information travels to area V2 and many other visual areas in the extrastriate cortex. In general, the laminar patterns of feed-forward connections are complementary to the laminar patterns of feedback (descending) connections, that is, the connections in the opposite direction (Fig. 1A).

These and many other criteria can be used to determine which area sends feed-forward information to, and receives feedback information from, which other area or areas. In most cases, the two types of connections are reciprocal, so that an area that sends feed-forward connections to another area also receives feedback connections from it (Felleman and Van Essen 1991).

By keeping track of the “sender” and “receiver” status of each pair of areas and iterating this analysis over all possible pairwise comparisons, it is possible to

organize the visual system into an anatomical hierarchy. Table 1 provides an exercise that illustrates this principle.

The retina and the LGN respectively constitute the first two levels of the visual anatomical hierarchy, with 10 or more additional levels in the visual cortex. V1 is the first cortical (and the third overall) level of the hierarchy, followed by V2. A simplified version of this anatomical hierarchy is shown in Figure 1B (for a complete version, see Felleman and Van Essen 1991; Lewis and Van Essen 2000). The anatomical hierarchy is most clear-cut at the lower levels, up to the level of about visual area 4 (V4) and the middle temporal area (MT), because the sender–receiver distinction is clear-cut up to this level of the hierarchy.

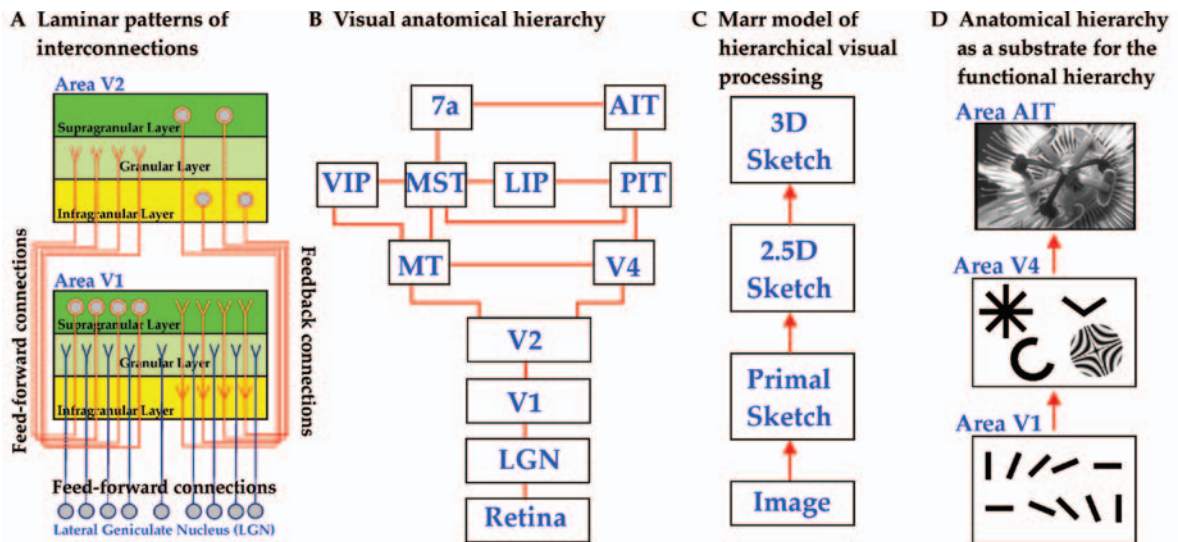
The visual hierarchy is believed to be broadly similar in other primates including humans (Grill-Spector and Malach 2004; Kaas 2004). Also, the overall functional organization of other neocortical sensory modalities, such as the auditory and somatosensory systems, is analogous to that of the visual system (Felleman and Van Essen 1991; Kaas and Collins 2001). Thus, studies of the functional organization of the macaque visual system have important implications for other systems.

There is some minor debate about whether there exists a unique, well-defined visual anatomical hierarchy or whether multiple, internally consistent hierarchies can be defined using the same anatomical data (Ungerleider and Haxby 1994; Hilgetag and others 1996). However, there is little debate that the visual system is hierarchically organized according to principled anatomical criteria. On the other hand, the functional implications of the anatomical hierarchy are far less clear, as we will outline in this article.

From the Department of Psychology, University of Minnesota, Minneapolis, Minnesota (JH); and the Department of Neurobiology and Anatomy, University of Texas Medical School, Houston, Texas (DJF).

JH is supported by the ONR grant N00014-05-1-0124 to Dr. Daniel Kersten. DJF is supported by the Whitehall Foundation and Vision Core Grant P30 EY-10618.

**Address correspondence to:** Jay Hegdé, Department of Psychology, 75 East River Parkway, University of Minnesota, Minneapolis, MN 55455 (e-mail: hegde@umn.edu).



**Fig. 1.** Anatomical and functional hierarchies in the macaque visual system. The human visual system (not shown) is believed to be roughly similar. *A*, A schematic summary of the laminar patterns of feed-forward (or ascending) and feed-back (or descending) connections for visual area V1. The laminar patterns vary somewhat from one visual area to the next. But in general, the connections are complementary, so that the ascending connections terminate in the granular layer (layer 4) and the descending connections avoid it. The connections are generally reciprocal, in that an area that sends feed-forward connections to another area also receives feedback connections from it. The visual anatomical hierarchy is defined based on, among other things, the laminar patterns of these interconnections among the various areas. See text for details. *B*, A simplified version of the visual anatomical hierarchy in the macaque monkey. For the complete version, see Felleman and Van Essen (1991). See text for additional details. AIT = anterior inferotemporal; LGN = lateral geniculate nucleus; LIP = lateral intraparietal; MT = middle temporal; MST = medial superior temporal; PIT = posterior inferotemporal; V1 = visual area 1; V2 = visual area 2; V4 = visual area 4; VIP = ventral intraparietal. *C*, A model of hierarchical processing of visual information proposed by David Marr (1982). *D*, A schematic illustration of the presumed parallels between the anatomical and functional hierarchies. It is widely presumed not only that visual processing is hierarchical but also that the anatomical hierarchy provides a substrate for, and therefore parallels, the hierarchical processing.

**Table 1.** Connectivity of Areas/Regions in a Hypothetical Visual System

Cortical Area/ Subcortical Nucleus	Receives Ascending Input from	Sends Ascending Output to
A	B, D	B
B	A, F	A
C	D, G	D
D	C, E, F, G	A, C, E, F
E	D, F	D, F
F	D, E, H	B, E, D
G	H, I	C, D, H
H	G, I	F, G
I	J	G, H
J	K	I
K	Retina	J

Only the ascending connections are shown. Given these connectivity data, can you arrange these areas into a hierarchy? The answer is shown below. Does the hierarchy remain the same if the input source for K is unknown? What happens if other inputs and/or outputs are unknown? (Answer: This data set results in the same hierarchical structure shown in Figure 1B, with the names of the visual areas/regions substituted as follows: A = 7a; B = AIT; C = VIP; D = MST; E = LIP; F = PIT; G = MT; H = V4; I = V2; J = V1; K = LGN.)

### Conventional Wisdom About the Functional Implications of the Anatomical Hierarchy

It would appear rather straightforward to assume that the functional organization of the visual system somehow directly reflects the underlying anatomical hierarchy. In its extreme form, there are two facets to this assumption. One is that the visual processing itself is hierarchical, and the other is that the hierarchy at the functional level parallels that at the anatomical level.

The notion that visual processing is hierarchical has been around since before the anatomical hierarchy was elucidated. Marr (1982) was one of the early and influential proponents of hierarchical processing in vision (Fig. 1C). He proposed that during the early stages of visual processing, the visual system extracts information about the local image elements (i.e., the basic “building blocks” or primitives) of the visual scene, such as the local contrast, orientation, and so on, to construct a raw “primal sketch” of the visual scene. In intermediate stages of processing, the visual system constructs a representation of object surfaces (or “2½-D sketch”) using the information about the primitives that was extracted during the previous stage. Finally, the visual system constructs a full representation of the visual scene (or “3-D sketch”) by combining the various elements of the 2½-D sketch. Many modern models also propose similar processing hierarchies (see Palmer 1999).

At first blush, the presumed parallels between the functional and the anatomical hierarchies appear to be supported by a large body of evidence (for reviews, see Felleman and Van Essen 1991; Ungerleider and Haxby 1994; Van Essen and Gallant 1994). For instance, classical receptive fields (CRFs) at a given eccentricity generally get larger, and response latencies generally get longer, at progressively higher levels of the anatomical hierarchy. However, it is clear that these properties neither directly reflect the hierarchical pattern of connections nor by themselves determine the functional properties of the neuron (Felleman and Van Essen 1991; Bullier and others 2001; Tucker and Fitzpatrick 2004). The most direct support for hierarchical processing comes from the fact that neurons in progressively higher levels of the hierarchy represent progressively more complex properties of the image. Many complex CRF characteristics that have been reported at higher levels appear to be absent or less prevalent at lower levels of the anatomical hierarchy (Felleman and Van Essen 1991; Ungerleider and Haxby 1994; Van Essen and Gallant 1994).

Altogether, there is little doubt that visual processing progresses in a simple-to-complex fashion from lower to higher levels of the hierarchy. But the issue, at least in our context, is whether this progression is hierarchical and whether it parallels the anatomical hierarchy. Previous studies that collectively seemed to show hierarchical differences among visual areas do not settle this issue, because they have generally explored one visual area at a time using stimuli and experimental paradigms optimized for the given area. Therefore, the extent to which the apparent differences among the areas reflect genuine functional differences versus differences in methodology is unclear. What is called for is a direct comparison of the functional properties at different hierarchical levels using the same set of tests.

### Direct Tests of Hierarchical Processing

Recently, Hegdé and Van Essen (2007) compared shape representation in visual areas V4 and V2, and to some extent in area V1, using the same, relatively large set of 2-D shape stimuli of low-to-intermediate complexity. As noted above, these three areas clearly belong to three different levels of the anatomical hierarchy (Fig. 1B; see also Felleman and Van Essen 1991). Previous work has established that these three areas play key roles in low-to-intermediate levels of shape processing (Connor 2004). Therefore, direct comparisons of shape processing among these three areas are good candidates for testing functional parallels to the anatomical hierarchy: If the processing is truly hierarchical, V1 neurons should be preferentially responsive to the simple stimuli (e.g., oriented bars and gratings) and unresponsive to, or generally nonselective for, more complex stimuli such as arcs, intersections, and angles. Neurons in V2 and V4 should be progressively more selective for the more complex stimuli, and these selectivity patterns should change in a stepwise fashion from V1 to V2 to V4.

Instead, the authors found a very complex, and clearly nonhierarchical, pattern of shape selectivity across the three

areas. Briefly, they found that shape selectively greatly overlapped among the three areas, with V1 neurons showing not only the expected selectivity for simple stimuli but also unexpected selectivity for complex shapes. The reverse was true for neurons in V2 and V4. Thus, all three areas played largely overlapping, and nonhierarchical, roles in the processing of the shape stimuli tested.

Note that what these results show is that the visual processing is not *necessarily* hierarchical, and not that it is *never* hierarchical. Indeed, it does (and always will) remain possible that the processing of some visual features changes in a hierarchical fashion across some visual areas (see, e.g., Thomas and others 2002). But the lesson in our context is that the visual processing is not always hierarchical and, therefore, does not necessarily parallel the anatomical hierarchy.

### Why Is Visual Processing Not Strictly Hierarchical?

It might seem surprising that the anatomical hierarchy, even when it is clear-cut, is not clearly reflected at the functional level. After all, the connections that underlie the anatomical hierarchy have undeniable functional consequences. So why does the function of the visual system seem not to reflect them?

The answer, as detailed in the next section, is simply that there is much more to the visual system than just the anatomical hierarchy. For one thing, the laminar patterns of connectivity that help determine the anatomical hierarchy are not necessarily related to the microcircuitry that helps determine the functional properties of visual neurons and vice versa. As Felleman and Van Essen (1991) pointed out, “the physiological properties [such as] increases in classical receptive field size and more advanced receptive field selectivities . . . may largely reflect the contributions of ascending pathways and of circuitry intrinsic to each area” (p 41). In other words, the functional properties of visual neurons do not vary hierarchically across the various levels of the anatomical hierarchy because the hierarchical connections are not the sole determinant of the functional properties of visual neurons.

### Anatomical Hierarchy as a Flowchart of Visual Information

If the visual anatomical hierarchy by itself cannot be taken as a blueprint for hierarchical processing, can it be taken as a flowchart that delineates how the visual information flows from one part of the visual system to another? The answer is that the hierarchy only partially accounts for the overall flow of information. There are four main interrelated reasons for this.

*1. Recurrent processing.* Conventional hierarchical models of vision formulate visual processing as a unidirectional ascent through the visual hierarchy that results in a unique representation of the visual world. But it is increasingly clear that that feedback and lateral interactions, collectively referred to as recurrent or re-entrant processing, play a crucial role in visual information processing



**Fig. 2.** The importance of recurrent processing in visual perception. This two-tone (“Mooney”) image is uninterpretable based on image information (i.e., bottom-up or feed-forward processing) alone. But given prior knowledge of the visual scene (for which see Fig. 4), the image is easy to interpret. Recurrent processing brings to bear such top-down influences as prior knowledge and the behavioral context to help constrain the interpretation of the visual image.

(Bullier and others 2001; Hochstein and Ahissar 2002). For instance, when an image is ambiguous (see Fig. 2), the visual system must bring to bear, through recurrent processing, prior knowledge of the visual world to help disambiguate it. Importantly, there is no reason to suspect that the recurrent processing itself follows a hierarchical pattern.

Note that recognizing the importance of recurrent processing also means recognizing that the functional properties of a visual neuron are not solely determined by its CRF. In other words, the contributions of the image context, mediated among others by the lateral connections with the non-classical surround, and the behavioral context, mediated by feedback connections, also play crucial roles. Although the visual anatomical hierarchy explicitly incorporates the feedback connections (Felleman and Van Essen 1991), the functional significance of these pathways remains to be fully elucidated.

It is worth noting that there are visual tasks that seem to require little or no recurrent processing, notwithstanding the general importance of recurrent processing to visual perception. For instance, detection tasks such as determining whether a given natural image contains an animal can be performed so fast (within 150 ms) as to allow little or no time for recurrent processing. Although it is true that the visual system can do much without recurrent processing (see VanRullen and Thorpe 2001 and the references therein), recurrent processing is important when the visual image is ambiguous, complex, or (as is often the case with natural visual scenes) both.

**2. Other pathways of information flow.** The cortical anatomical hierarchy relies solely on the interconnections between the various cortical areas. But it is clear that in addition to these cortico-cortical (CC) pathways

(Fig. 3A), information also flows between cortical areas through cortico-thalamo-cortical (CTC) pathways. Specifically, many extrastriate cortical areas send output to the pulvinar, a collection of nuclei in the thalamus, which in turn sends inputs to other cortical areas (Fig. 3B).

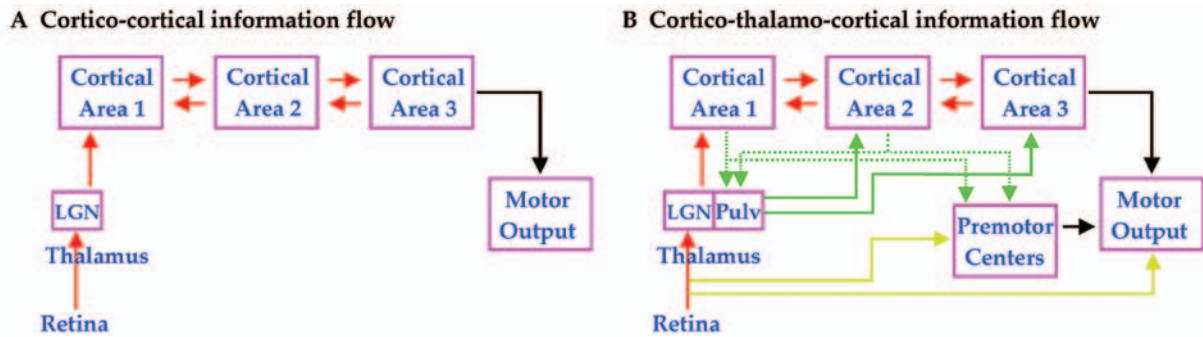
It is unclear whether this CTC relay can by itself activate or “drive” the postsynaptic neuron in the next cortical area or whether the CTC connections play a more modulatory role, with the CC connections acting as the driving inputs (Sherman and Guillery 2006). It is also unclear whether the CTC pathways also follow any hierarchical pattern, much less the same hierarchical pattern as the CC connections. That is, it is unknown whether, for a given extrastriate visual area such as V2, the CTC connections project to the same areas as the CC connections. If they do not, this will add another layer of complexity to the pattern of information flow in the visual system. But even if they do follow the same hierarchical pattern, the fact remains that the cortico-cortical connections, and the anatomical hierarchy based on them, provide an incomplete picture of the flow of visual information.

**3. Dynamic information processing.** Based on the anatomical hierarchy, the information flow would appear to follow an obligatory sequence of preset connections. But recent studies of functional connectivity, most notably using functional magnetic resonance imaging (Bassett and Bullmore 2006; Lee and others 2006), show that only a subset of the existing anatomical connections are activated at any given time, typically in a task-dependent manner. Moreover, in no known instance are the patterns of functional connectivity strictly hierarchical.

The dynamicity of the visual system also has a more explicitly temporal dimension, in that the functional properties of visual neurons change over time. These changes are often adaptive, in that they optimize the response of neurons to some visual feature, and can occur on different time scales. Indeed, perception itself is a relatively quick form of plasticity, with perceptual learning and development at the slower end of the spectrum of adaptive changes that the visual system is subject to (Kourtzi and DiCarlo 2006). The hierarchical view of visual processing does not acknowledge, much less explain, these dynamic properties.

**4. Vision in an integrated multisensory and behavioral context.** Viewing visual representation as an end unto itself ignores the fact that vision has evolved to subservise the behavioral goals of the animal (Churchland and others 1994). Thus, the visual processing of a given image, such as that in Figure 4, will vary depending on the behavioral goal. That is, the processing of the image must necessarily be different depending on whether the task is to identify the person in the picture, to determine if it is a man or a woman, to determine the brand of the coffee cup in the person’s hand, or simply to determine the slope of the grassy knoll in the background.

There is also increasing evidence that the different sensory and motor modalities are not as independent of each other as previously thought. It is clear that many



**Fig. 3.** Schematic comparison of cortico-cortical (CC) and cortico-thalamo-cortical (CTC) pathways of information flow in the macaque visual system. *A*, The CC pathway, such as that shown in Fig. 1B, redrawn to facilitate comparisons with the CTC pathway. In the CC pathway, the retinal signals are relayed by the thalamus (specifically, the LGN) to the primary visual cortex (denoted here as Cortical Area 1). The CC pathway assumes that once the visual information is relayed to the cortex, all subsequent processing leading up to the motor output occurs in the cortex. For clarity, only three cortical areas are shown here. *B*, The CTC pathway subsumes the CC pathway, but incorporates many additional connections. These include a transthalamic pathway (green arrows) by which information flows from one cortical area to the next via the pulvinar (labeled Pulv) in the thalamus. Dotted green arrows = cortico-thalamic signals; solid green arrows = thalamo-cortical signals. The CC pathways are shown in red. Branches of the retinal afferent are shown in yellow. The inputs to the motor system, which derive from both the CC and CTC pathways, are shown in black. Redrawn after Sherman and Guillery (2006).



**Fig. 4.** Natural images are rarely unambiguous. Although two-tone images such as that shown in Figure 2 illustrate a special type of image ambiguity, many other types of image ambiguity are ubiquitous in natural visual scenes. Occlusion, shadows, visual clutter, and changes in illumination and the observer's viewpoint are among the many factors that introduce uncertainty to natural visual scenes. Because image ambiguities cannot be resolved by feed-forward processing alone, the visual system must use prior knowledge of the visual world and of the behavioral context to resolve the behaviorally relevant image ambiguities.

cortical areas once thought of as purely visual areas receive nonvisual input (Ghazanfar and Schroeder 2006). Indeed, all cortical areas may be multisensory to one extent or another. Therefore, visual processing affects, and is affected by, other sensorimotor modalities.

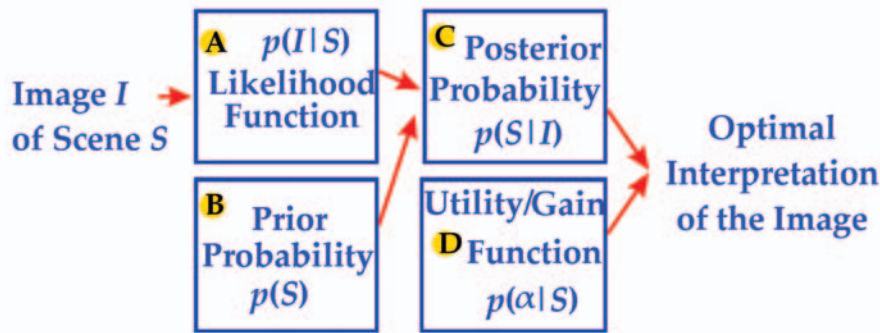
It is conceivable that a grand anatomical hierarchy of all sensory and motor systems can be constructed with the anatomical rules used by Felleman and Van Essen

(1991). However, understanding the functional significance of the various intermodal and intramodal pathways in such a grand hierarchy will pose an even greater challenge to future investigations.

### Bayesian Inference as an Alternative Framework for Understanding Visual Processing

Its many flaws notwithstanding, the hierarchical view of visual processing has endured. The reason for this, apart from the seductive simplicity of the view, is that there has been nothing with which to replace it.

We still do not have an alternative neural model, but there is something on the computational horizon that holds considerable promise of an eventual comprehensive neural model. The Bayesian estimation theory provides a unifying framework for understanding brain function, especially the sensorimotor aspects of it (see Doya and others 2007). To illustrate it in the context of visual perception, the Bayesian framework posits that the visual system infers the likely interpretation of a given image by evaluating various underlying probabilistic factors such as the image information, the prior knowledge of the visual world, and the behavioral context (Fig. 5). That is, this framework recognizes that the visual system cannot and need not construct a veridical, complete internal representation of the visual world, and that visual perception is not a deterministic process, but a probabilistic, inferential process (Kersten and others 2004). Note that this framework addresses the computational shortcomings of the hierarchical model, in that it explicitly allows for the system to evaluate all available bottom-up and top-down information in a dynamic manner. It has the additional advantage that it is known to explain many aspects of brain function (Doya and others 2007).



**Fig. 5.** Vision as inference: the Bayesian framework of visual perception. This framework posits that the visual system arrives at a likely interpretation of a given image  $I$  of a visual scene  $S$  by jointly evaluating the various relevant probability distributions. These include the likelihood of the image given the scene (box A), the prior probability of a given scene (box B), and the behavioral context (box D). Posterior probability (box C) is the product of the likelihood function and prior probability. For a more rigorous treatment, see Kersten and others (2004). Although this figure shows perception in a flow-chart format, the Bayesian framework does not presume perception to be a strictly serial process.

However, the Bayesian framework is not yet a neural model. In other words, the framework currently helps explain the computations that underlie various brain functions, but not how the brain implements these computations. It is almost entirely unclear, for instance, which parts of the visual system play which role in which inference, or how the brain selects what to attend to or which aspect of the vast body of prior knowledge is relevant to the task at hand.

Nonetheless, the Bayesian framework helps highlight that vision should not be viewed as a rigid, image-driven process but as one that dynamically tests hypotheses about the external world and evaluates possible courses of action, using both the current image information as well as past experiences.

## References

- Bassett DS, Bullmore E. 2006. Small-world brain networks. *Neuroscientist* 12:512-23.
- Bullier J, Hupe JM, James AC, Girard P. 2001. The role of feedback connections in shaping the responses of visual cortical neurons. *Prog Brain Res* 134:193-204.
- Churchland PS, Ramachandran VS, Sejnowski TJ. 1994. A critique of pure vision. In: Koch C, Davis DL, editors. *Large-scale neuronal theories of the brain*. Cambridge (MA): MIT Press. p 23-60.
- Connor CE. 2004. Shape dimensions and object primitives. In: Chalupa LM, Werner JS, editors. *The visual neurosciences*. Cambridge (MA): MIT Press. p 1080-9.
- Doya K, Ishii S, Pouget A, Rao RPN, editors. 2007. *Bayesian brain: probabilistic approaches to neural coding*. Cambridge (MA): MIT Press.
- Felleman DJ, Van Essen DC. 1991. Distributed hierarchical processing in the primate cerebral cortex. *Cereb Cortex* 1:1-47.
- Ghazanfar AA, Schroeder CE. 2006. Is neocortex essentially multisensory? *Trends Cogn Sci* 10:278-85.
- Grill-Spector K, Malach R. 2004. The human visual cortex. *Annu Rev Neurosci* 27:649-77.
- Hegd  J, Van Essen DC. 2007. A comparative study of shape representation in macaque visual areas V2 and V4. *Cereb Cortex* 17:1100-16.
- Hilgetag C-C, O'Neill MA, Young MP. 1996. Indeterminate organization of the visual system. *Science* 271:776-7.
- Hochstein S, Ahissar M. 2002. View from the top: hierarchies and reverse hierarchies in the visual system. *Neuron* 36:791-804.
- Kaas JH. 2004. The evolution of the visual system in primates. In: Chalupa LM, Werner JS, editors. *The visual neurosciences*. Cambridge (MA): MIT Press. p 1563-72.
- Kaas JH, Collins CE. 2001. The organization of sensory cortex. *Curr Opin Neurobiol* 11:498-504.
- Kersten D, Mamassian P, Yuille A. 2004. Object perception as Bayesian inference. *Annu Rev Psychol* 55:271-304.
- Kourtzi Z, DiCarlo JJ. 2006. Learning and neural plasticity in visual object recognition. *Curr Opin Neurobiol* 16:152-8.
- Lee L, Friston K, Horowitz B. 2006. Large-scale neural models and dynamic causal modeling. *NeuroImage* 30:1243-54.
- Lewis JW, Van Essen DC. 2000. Corticocortical connections of visual, sensorimotor, and multimodal processing areas in the parietal lobe of the macaque monkey. *J Comp Neurol* 428:112-37.
- Marr D. 1982. *Vision*. San Francisco (CA): WH Freeman and Co.
- Palmer SE. 1999. *Vision science. Photons to phenomenology*. Cambridge (MA): MIT Press.
- Sherman SM, Guillery RW. 2006. *Exploring the thalamus and its role in cortical function*. 2nd ed. Cambridge (MA): MIT Press.
- Thomas OM, Cumming BG, Parker AJ. 2002. A specialization for relative disparity in V2. *Nat Neurosci* 5:472-8.
- Tucker TR, Fitzpatrick D. 2004. Contributions of horizontal and vertical circuits to the response properties of neurons in the primary visual cortex. In: Chalupa LM, Werner JS, editors. *The visual neurosciences*. Cambridge (MA): MIT Press. p 733-46.
- Ungerleider LG, Haxby JV. 1994. "What" and "where" in the human brain. *Curr Opin Neurobiol* 4:157-65.
- Van Essen DC, Gallant JL. 1994. Neural mechanisms of form and motion processing in the primate visual system. *Neuron* 13:1-10.
- VanRullen R, Thorpe SJ. 2001. The time course of visual processing: from early perception to decision-making. *J Cogn Neurosci* 13:454-61.