

Neural Basis of Pattern Vision

Daniel C Kiper, Institute of Neuroinformatics, University of Zurich, Switzerland
Matteo Carandini, Institute of Neuroinformatics, University of Zurich, Switzerland

CONTENTS

Introduction

Pattern vision as image filtering

Contextual effects on pattern vision

Spatial representation of visual patterns

Pattern vision beyond primary visual cortex

The perception of patterns

From the retina to the cerebral cortex, the early stages of the visual system decompose the visual scene into a number of relevant features, while discarding redundant information. Successive stages of the visual system perform an increasingly complex analysis of the visual scene.

in turn send their own spikes to the cerebral cortex, in a large area called the primary visual cortex, or area V1. Area V1 is a key center of visual processing, whose outputs are sent to numerous other visual cortical areas and to the rest of the cortex. (See A00402; A00331)

INTRODUCTION

0375.001 The visual system analyzes the two-dimensional images projected on the retinas, and from these images extracts informative features. These features allow the perception of form and texture, and enable the observer to distinguish and recognize objects and ultimately construct an internal three-dimensional representation of the world. The computations that extract the informative features constitute ‘pattern vision’.

0375.002 Pattern vision is achieved by a succession of neural operations performed by the early stages of the visual pathway. These operations have been studied extensively by recording the activity of individual neurons in cats and in primates such as macaque monkeys (See A00357; A00628). Studies in these animals have revealed principles that probably apply to humans as well. Indeed, recent studies employing functional magnetic resonance imaging (fMRI) in humans have confirmed a tight relationship between neural activity and the perceptual aspects of pattern vision.

Anatomy of the Visual System

0375.003 The early stages of visual processing are illustrated in Figure 1 (See A00628). The optics of the eye focus images onto the retina. Through a network of retinal cells, electrical signals generated by photoreceptors are transmitted to retinal ganglion cells. These cells produce spikes of electrical activity, which are carried by the optic nerve to the lateral geniculate nucleus (LGN). The neurons of the LGN

PATTERN VISION AS IMAGE FILTERING

0375.004 Neurons in the visual system respond to the distribution of light presented in a particular region of the visual field – the neuron’s ‘receptive field’ (See A00000). The study of the receptive fields of visual neurons is fundamental to our understanding of visual function, and provides the basis for the current knowledge about pattern vision. In particular, receptive fields can be seen as filters through which cells view the visual scenes; filtering is a well-known concept in engineering and computer science. Image filtering by the receptive fields in the early stages of the visual system is illustrated in Figure 2 (See A00628). Starting with a visual stimulus (a), we follow the operation of successive stages in the retina (b, c) and in the primary visual cortex (d, e). We illustrate the operation of each stage through a ‘neural image’, a map of the responses that would be obtained if an array of identical cells were looking at the physical image in all possible positions. In a neural image, gray indicates no response, whereas white and black indicate higher and lower responses.

Image Filtering in the Retina

0375.005 Photoreceptors in the retina have small receptive fields (Figure 2b, lower panel), and transform light into electricity. The gain of this transformation depends on the prevalent light conditions, a phenomenon known as ‘light adaptation’. Thanks to

light adaptation, rather than signaling absolute light intensity, photoreceptors encode the strength of light relative to the average in the recent past in that local region of the retina. This relative measure of light is called 'contrast', and it entails discarding information about absolute light levels. The advantage of computing contrast is illustrated in the neural image given by the responses of the whole array of photoreceptors (Figure 2b, top). This neural image uses the full available range of responses (represented as white to black), even though the visual stimulus was illuminated by dim light (Figure 2a). We are mostly oblivious to light adaptation, but can become briefly aware of it by stepping from a dark room into bright daylight or vice versa.

0375.006 Retinal ganglion cells have receptive fields organized in a center-surround fashion, and respond to the difference between the intensity of light in the center and in the surround (See A00000). Cells in our example are on-center (Figure 2c, lower panel), so they are optimally stimulated by a light spot on a dark background: they thus give a negative response to the mole just to the right of the person's nose, which is darker than the surrounding skin (Figure 2c, top). Center-surround receptive fields enhance contours such as those at the edges of the face, the mouth and the eyes. By extracting these features, they discard information about light intensity in uniform regions. Uniform regions, such as the cheek or the dark area behind the face in our example, stimulate both the center and the surround, whose contributions average out (resulting in gray regions in the neural image, Figure 2c, top).

Image Filtering in Primary Visual Cortex

0375.007 While the receptive fields of LGN neurons are similar to those of retinal ganglion cells, the receptive fields of neurons of cortical area V1 are radically different (See A00628; A00000; A00402). Most V1 cells show receptive field properties that are absent at earlier stages, including selectivity for stimulus orientation and direction of motion (See A00376). In particular, because of their orientation selectivity, V1 cells respond strongly to bars and edges of the appropriate orientation.

0375.008 The receptive field of 'simple' V1 neurons is composed of separate 'on' and 'off' elongated regions (Figure 2d, lower panel). The optimal stimulus to obtain a positive response is one that stimulates the 'on' regions with positive intensity while stimulating the 'off' regions with negative intensity. In our example, this happens near the

mouth, the eye, and the eyebrow (Figure 2d, top). In contrast, the edge of the face is mostly vertical, so it stimulates the 'on' regions and the 'off' regions at the same time. The inputs from these regions cancel out, and the resulting response of the cell is zero (gray in the neural image). The eyebrow is mostly horizontal, and evokes a negative response flanked by two positive responses, evoked by the regions above it and below it. Indeed, just like cells in earlier stages of the visual pathway, simple cells are sensitive to the precise location of a stimulus within their receptive field, and to the 'polarity' of a stimulus, i.e. whether the stimulus is brighter or darker than the background. This dependence on stimulus location and polarity is overcome by V1 'complex' cells. Complex cells have receptive fields where 'on' and 'off' regions overlap. For example, the 'on' region of our model complex cell takes up the whole receptive field (Figure 2e, lower panel). As a result, the cell gives roughly the same positive response to a bar presented anywhere within its receptive field, whether it is lighter or darker than the background. The neural image produced by complex cells (Figure 2e, top) shows responses corresponding to the location of horizontal features such as the mouth, eye, and eyebrow. Complex cells such as the one in Figure 2e can be thought of as summing the positive outputs of many simple cells such as that in Figure 2d, whose receptive fields are elongated in the same direction, and whose spatial location is displaced. By summing positive outputs from displaced simple cells, complex cells would overcome the dependence on stimulus location and polarity shown by simple cells. Invariance for location and polarity might be useful to maintain continuous responses in spite of small eye movements.

The neural images in Figure 2d and e illustrate 0375.009 only two of the many concurrent representations that are formed in our primary visual cortex when we look at a stimulus such as that in Figure 2a. Indeed, the primary visual cortex contains cells selective for the full range of orientations and for a variety of spatial scales (See A00402; A00356). An example of this variety is illustrated in Figure 3 for four simple cells selective for different combinations of orientation and spatial scale. The two cells in the left quadrants are selective for horizontal orientations, whereas the two cells in the right quadrants are selective for vertical orientations. The two cells in the top quadrants are selective for lower spatial scales than the two cells at the bottom. These cells respond to very different features in the visual stimulus (Figure 3c). The cell in the top right quadrant gives a negative response to the edge of

the face, where the 'on' region is strongly stimulated by the dark background, and the lighter skin stimulates the 'off' region. None of the other cells responds well to these features. In contrast, the cell in the lower right quadrant responds strongly to features such as the mouth and eyebrows, which are missed by the other cells.

0375.010 In summary, cells in the primary visual cortex extract relevant elements of the visual image such as contours, lines and edges, at a variety of spatial scales. For the image in Figure 3a, simple and complex cells stimulated by the edges of the face will give a strong response. Those centered on the background or on uniform parts of the face will remain mostly silent. Thus, the primary visual cortex extracts the face's edges and the contours of the face's various features. Simple cells provide an accurate description of the location of these features, as well as the indication of their polarity. For example, they indicate that the face is brighter than the background. The combined activity of simple and complex cells can yield a stable, faithful representation of the objects present in the environment.

CONTEXTUAL EFFECTS ON PATTERN VISION

0375.011 We have described responses of visual neurons as entirely determined by the instantaneous distribution of light on their receptive field. In fact, these responses also depend on factors such as the previous history of stimulation, the overall contrast within the receptive field, and the distribution of contrast in the surrounding regions. These factors mostly affect the responses of neurons in the visual cortex.

Pattern Adaptation

0375.012 Prolonged exposure to a visual pattern perturbs visual perception, reducing the perceived contrast and altering the appearance of subsequently viewed patterns. A classic example of this alteration can be experienced by looking at a pattern made of oblique bars for 30s or so and then looking at a pattern made of vertical bars. The vertical pattern will appear briefly as if it were tilted in the opposite direction to the preceding pattern. Effects of this kind are termed 'pattern adaptation'. A simple explanation for the perceptual effects of pattern adaptation states that, first, perception is the result of a weighted sum of the outputs of sensory neurons, and second, that pattern adaptation fatigues the neurons that respond most

strongly. By causing these neurons to respond less strongly than they normally would, adaptation biases perception away from the adapting pattern.

The physiological substrate of pattern adaptation 0375.013 appears to lie in the primary visual cortex and in subsequent cortical areas. The responses of V1 neurons are sharply reduced after only a few seconds of stimulation, in a manner that could account for the perceptual effects. In contrast, the responses of neurons in the LGN and in the retina are essentially unaffected.

Pattern adaptation reflects a self-calibration 0375.014 mechanism in the visual cortex. This mechanism is continuously at work to adapt the responses according to the prevailing statistics in the stimulus. Its goal might be to increase the independence of subsequent neuronal responses, so that the response at a given time cannot be predicted by an earlier response. This makes maximal use of the resources, as it uses neuronal responses to encode the information that is not redundant over time. We tend to notice this calibration mechanism only when it misbehaves: when a prolonged stimulus is turned off, the calibration mechanism is caught off-guard, and visual perception is briefly perturbed.

Interactions Between Superimposed Patterns

In addition to interacting in the time domain, different patterns interact when they are presented 0375.015 simultaneously. An example of this kind of interaction can be seen by superimposing two oriented patterns: for example, superimposing an orthogonal mask on an oriented test pattern impairs the perception of the test pattern. This phenomenon is known as 'masking', and reduces the apparent contrast of the test pattern. The physiological correlate of masking appears to lie in mechanisms present in the retina and especially in the primary visual cortex. These mechanisms control the responsiveness of neurons and depend on overall contrast in a visual region centered on the receptive field. When two patterns are superimposed, overall contrast is increased, and neuronal responsiveness is reduced. This reduction in responsiveness has been observed in visual neurons of cats and monkeys, as well as in the electroencephalogram (EEG) obtained from visual cortex of humans.

The current interpretation of masking effects involves inhibition between V1 neurons that have 0375.016 overlapping receptive fields but are selective for different orientations. Two superimposed patterns

differing in orientation stimulate two sets of neurons, which inhibit each other and thus respond less than to a single pattern. This explanation, however, is being challenged and may not be entirely correct.

Interactions Between Spatially Displaced Patterns

0375.017 Patterns do not have to be spatially superimposed to interact with each other. Strong interactions can also be observed between patterns that are spatially segregated. Perceptually, these interactions can be suppressive or enhancing, depending on stimulus configuration. The physiological substrate of these interactions between spatially separate visual patterns seems to lie in area V1 and in the successive cortical areas. The responses of V1 neurons are influenced by stimuli presented in the regions surrounding their receptive field. This influence is commonly considered to originate in 'lateral inhibition', reciprocal inhibitory connections between pools of V1 neurons with displaced receptive fields.

0375.018 Among the phenomena that would be explained by lateral inhibition is 'surround suppression'. Oriented patterns situated in the region surrounding the receptive field of a V1 neuron can substantially reduce the responses of the neuron, especially if their orientation is similar to that preferred by the neuron. For example, the responses of a V1 neuron to an optimally oriented bar can decrease if the bar is made to extend beyond the receptive field of the neuron. Cells showing this property are often called 'end-stopped'. One of the roles of surround suppression might be to enhance the independence of V1 neurons. The statistics of images commonly encountered by the visual system are such that contours and edges tend to be surrounded by other contours and edges. For example, in Figure 3 the horizontal contour given by the mouth is close to the vertical contour given by the edge of the face. Without surround suppression, knowing that a V1 neuron is strongly activated would also say something about the nearby neurons: they would be more likely to be active than other neurons. This lack of independence between neurons would be wasteful, as it would encode redundant information.

0375.019 In addition to suppression, interactions between different regions of the receptive field can in some conditions involve enhancement. This enhancement may result from a sort of double inhibition: if one reduces the activity of a population of

neurons that normally inhibits another population, the activity of the second population may be enhanced.

Anatomically, the interactions between different regions are thought to be mediated by local circuits as well as by long fibers running parallel to the cortical surface, which connect V1 cells over distances of several millimeters. Long-range connections tend to link cells that share the same preferred orientation. Moreover, they preferentially connect cells along an axis that corresponds to the cells' preferred orientation. 0375.020

SPATIAL REPRESENTATION OF VISUAL PATTERNS

Area V1 contains a full representation of the visual field, with nearby regions in the visual field corresponding to nearby regions in area V1. This kind of representation is called 'retinotopic'. Retinotopy is derived by a similar organizations in the retina, optic nerve and LGN; it coexists with other organizational principles that group cells according to characteristics such as orientation preference and ocular dominance (See A00356). Retinotopy can be observed in Figure 4a, which illustrates an idealized visual stimulus resembling a bull's-eye, and the corresponding map of responses across area V1 in one hemisphere (Figure 4b). This representation of the visual stimulus is heavily distorted: just like the retina and the LGN, area V1 devotes most of its cells to the center of fixation (fovea). Indeed, while the portion of the bull's-eye that is inside the first solid ring takes up a tiny portion of the surface of the stimulus, the region that represents it occupies about half of area V1. Another major difference between the stimulus and the corresponding map of activity is the geometrical arrangement of the features. Concentric circles and radial lines in the stimulus become vertical and horizontal stripes of activity in the cortical map. This geometrical distortion could be important to help the rest of the brain recognize objects regardless of their distance and of their orientation. Indeed, as we move closer to an object, its size on the retina is scaled up. If we tilt our head (or the object), the object's image on the retina rotates around the fovea. Thanks to the transformation operated by the cortex, such scalings and rotations become simple translations, which may be easier to analyze for the subsequent stages of visual processing. 0375.021

A striking example of the consequences of cortical magnification is illustrated in Figure 5. In this 0375.022

simulation, a mathematical model was fed a photograph of a room (a) and generated a prediction of the distribution of responses across the primary visual cortex in one hemisphere (b). The model simulates an observer who focuses her eyes on the letter 'O' on an eye chart (see detail) located at the back of the room. The representation in V1 is amazingly distorted. Most of the cortical surface devoted to the stimulus is taken up by the eye chart, and particularly by the letter 'O' and by the nearby letters. Barely any cortical space is given to the rest of the room, even though it occupies by far the largest portion of the visual stimulus.

PATTERN VISION BEYOND PRIMARY VISUAL CORTEX

0375.023 Area V1 is by no means the only visual area in the cerebral cortex: in primates there are tens of visual areas, each containing a full representation of the visual field (See A00402; A00331). These areas receive input directly or indirectly from V1. From what we understand, different areas emphasize the analysis of different aspects of the visual world. In particular, areas V2, V4 and IT appear to be closely related to the perception of visual patterns.

Cortical Area V2

0375.024 The next stage of visual processing after V1 is performed in the secondary visual area, V2. The precise role of V2 is unknown; some differences between the responses of V2 and of V1 have been found, but most receptive field properties are similar in both visual areas. At equivalent positions in the visual field, the receptive fields of V2 cells are slightly larger than in V1. A functional property that has been demonstrated for V2 cells is their ability to respond to illusory contours, contours that are defined by figural clues rather than by lines or edges. Such contours could result from partially occluded objects, and the capacity to interpolate them is necessary to segment the visual scene into various objects. On the other hand, there are suggestions that also V1 cells can respond to such contours, so it is not clear that this property is specific to V2.

Cortical Area V4

0375.025 The properties of V4 cells are even less well understood than those at earlier stages, but several results suggest that V4 cells have an important

role in pattern vision. First, receptive fields in V4 are considerably larger than in V1 or V2 (See A00331), making V4 cells suitable for the analysis of large areas of the visual field. Large receptive fields could set the stage for the detection and identification of whole objects. Second, V4 transmits information to the inferior temporal (IT) cortex, a cortical region that is known to be crucial for object recognition (see below). Third, a number of studies have shown that the activity of V4 cells is strongly modulated by attention. The response of a V4 cell to a given stimulus is high if the stimulus has a behavioral relevance (i.e. if the observer is paying attention to it), and low otherwise. Fourth, the foveal representation is even more enhanced in V4 than it is in either V1 or V2. This would seem reasonable if V4 were to be concerned with pattern vision rather than with attributes of the whole visual field. Finally, recent physiological results, although controversial, add further support to a role of V4 in pattern vision. Although most V4 neurons, like those of V1 and V2, are selective for the orientation of a visual stimulus, a number show a preference for stimuli that differ from the bars and edges that seemed optimal to stimulate cells at earlier levels. For example, some V4 neurons respond better to stimuli made of concentric rings, or of radially oriented line segments, than to simpler bar and edge stimuli. Thus, individual V4 cells seem able to encode visual patterns more complex than those encoded by individual cells at earlier levels. Taken together, these facts strongly suggest that V4 is important for pattern vision.

Inferotemporal Cortex

0375.026 In the cortical areas of the inferior temporal lobe, neurons prefer stimuli even more complex than those described in area V4. These cells often produce their highest activity for stimuli that have complex, irregular shapes, or for stimuli made of numerous features arranged in complex patterns. There are, for example, neurons in the anterior IT cortex that respond selectively to faces, or to other body parts (See A00359). The responses of IT neurons are often invariant relative to stimulus position within their receptive field. For familiar objects, they can even be invariant relative to the angle of view. A given neuron could thus respond to an object regardless of the object's rotation, even though the object's two-dimensional projection on the retinas varies considerably in these conditions. These neurons are therefore important for the perception of complex patterns, a function necessary to achieve object identification.

0375.027 The role of IT cortex in complex pattern perception and object perception is supported by lesion studies. Humans and monkeys with IT cortex lesions are severely impaired in object recognition tasks. They fail to recognize familiar objects, and are incapable of learning new ones. A particular example of such a loss is the incapacity to recognize faces, a condition called 'prosopagnosia'. This condition is thought to result from lesions to the parts of IT cortex specialized in the analysis of faces. Studies of the neurons' receptive fields and those of cortical lesions thus converge to indicate that IT cortex has an important role in pattern vision.

THE PERCEPTION OF PATTERNS

0375.028 We have seen that visual stimulation activates neurons at numerous stages in the visual pathway. In the responses of these neurons we have also found counterparts for perceptual effects such as pattern adaptation, masking, and the interactions between spatially displaced patterns. These results suggest a link between the responses of cortical neurons and the perception of visual patterns.

Neural Activity and Pattern Vision

0375.029 Other links between the responses of cortical neurons and the perception of visual patterns have been demonstrated by lesion studies and by stimulation experiments. Studies have been made of people with lesions of the visual cortex due to disease or to accident, for example patients with gunshot wounds after the First World War. These studies established that the absence of a part of visual cortex yielded some deficit in visual perception. Stimulation experiments employ localized injections of current to stimulate small groups of cortical neurons, and have been mostly performed on surgical patients or on blind volunteers. Electrical stimulation of the visual cortex leads to the perception of illusory visual stimuli.

0375.030 More recently, a strong link between neural activity and pattern vision has been demonstrated using fMRI. This imaging technique is not invasive, and allows the experimenter to measure brain activity in people who are awake, while they make perceptual decisions on the presence or absence of a visual stimulus. Using this method it has been shown that the detection of visual patterns relies on neurons in V1 and in subsequent areas of the visual cortex. The activity of these neurons predicts the performance of the participants and even correlates with perceptual decisions on a trial-by-trial basis.

When making a difficult perceptual judgment, participants make a number of mistakes, such as indicating that a pattern is present when it is absent (false alarms), or that it is absent when it is present (misses). The responses of visual cortical neurons correlate with the perceptual decision of the participant rather than with the physical stimulus. Responses in visual cortex determine if the person will perceive the stimulus or not.

The Binding Problem

0375.031 Most of the theoretical and experimental work described above implies that the early stages of the visual system decompose an image into features, or components. Our visual perception, however, is one of unity and coherence, not a juxtaposition of independent elements. This suggests that at some stage of the visual pathways the image components must be bound together to form a coherent perception. To date, the solution to this problem is largely unknown (See A00345). In an attempt to provide an answer to this question, it was proposed that the neuronal substrate that glues different features together is found in the temporal pattern of neuronal activity. In that view, two cells coding for features belonging to the same object would synchronize their activity. The synchronicity of cell firing would thus serve as a tag for a given object, which is propagated through the various stages of visual processing. The so-called 'binding by synchrony' hypothesis received some experimental support with the discovery of cells in the visual cortex of cats and monkeys that, for example, synchronize their activity when they are simultaneously activated by a single bar, and not when activated by two distinctly separate bars. Whether this synchronization reflects the process of 'binding' is the subject of intense debate and experimental scrutiny and there is, to date, no consensus on its validity.

Further Reading

- Barlow HB and Mollon JD, eds (1982) *The Senses*. Cambridge, UK: Cambridge University Press.
- De Valois RL and De Valois K (1988) *Spatial Vision*. Oxford: Oxford University Press.
- Harris CS (1980) *Visual Coding and Adaptability*. Mahwah, NJ: Laurence Erlbaum.
- Hubel DH (1988) *Eye, Brain and Vision*. New York: Scientific American Library.
- Rodieck RW (1998) *The First Steps in Seeing*. Sunderland, MA: Sinauer.
- Wandell B (1995) *Foundations of Vision*. Sunderland, MA: Sinauer.

Wurtz RH and Kandel ER (2000) Central visual pathways. In: Kandel ER, Schwartz JH and Jessell TM (eds) *Principles of Neural Science*, pp. 523–547. New York: McGraw-Hill.

Wurtz RH and Kandel ER (2000) Perception of motion, depth and form. In: Kandel ER, Schwartz JH and Jessell TM (eds) *Principles of Neural Science*, pp. 548–571. New York: McGraw-Hill.

Glossary

Contrast The strength of light relative to the average. The average is measured in the recent past in a local region of the retina.

End-stopping The property of some V1 neurons whose responses are reduced when visual stimuli extend beyond their receptive field.

Lateral inhibition Reciprocal inhibition between (groups of) neurons performing similar operations.

Lateral geniculate nucleus A part of the thalamus that receives signals from the eye and sends them to the visual cortex.

Light adaptation The mechanism by which retinal photoreceptors adjust to the average absolute light intensity and encode a relative measure of light (contrast).

Masking The suppressive interaction of two visual patterns.

Neural image The image obtained by plotting the responses of an array of identical cells with receptive fields covering the physical image.

Pattern adaptation The phenomenon whereby prolonged exposure to a visual pattern perturbs visual perception.

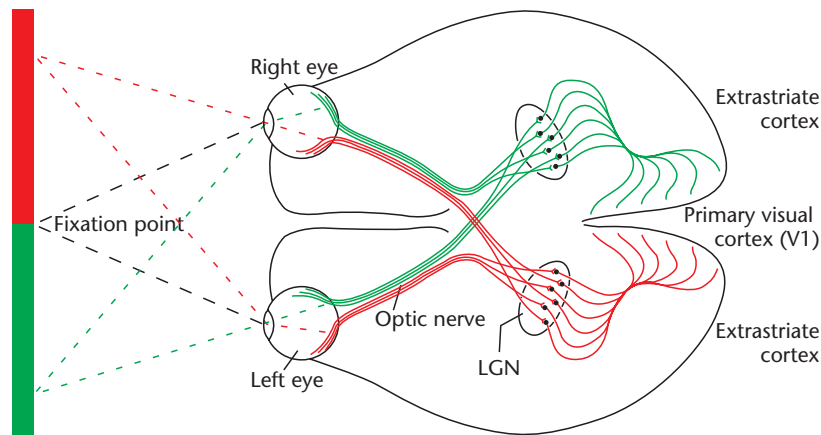
Prosopagnosia The inability to recognize faces.

Retinotopy A full representation of the visual field, with nearby regions in the visual field corresponding to nearby regions in the representation.

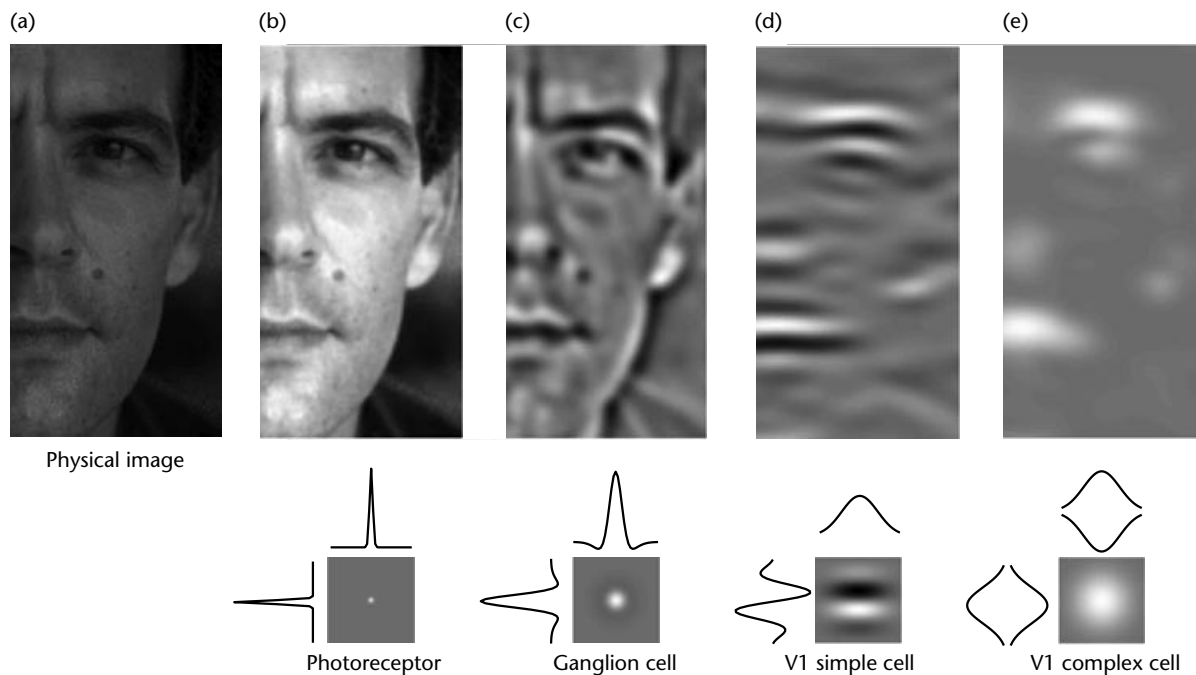
Spike Action potential.

V1 Primary visual cortex.

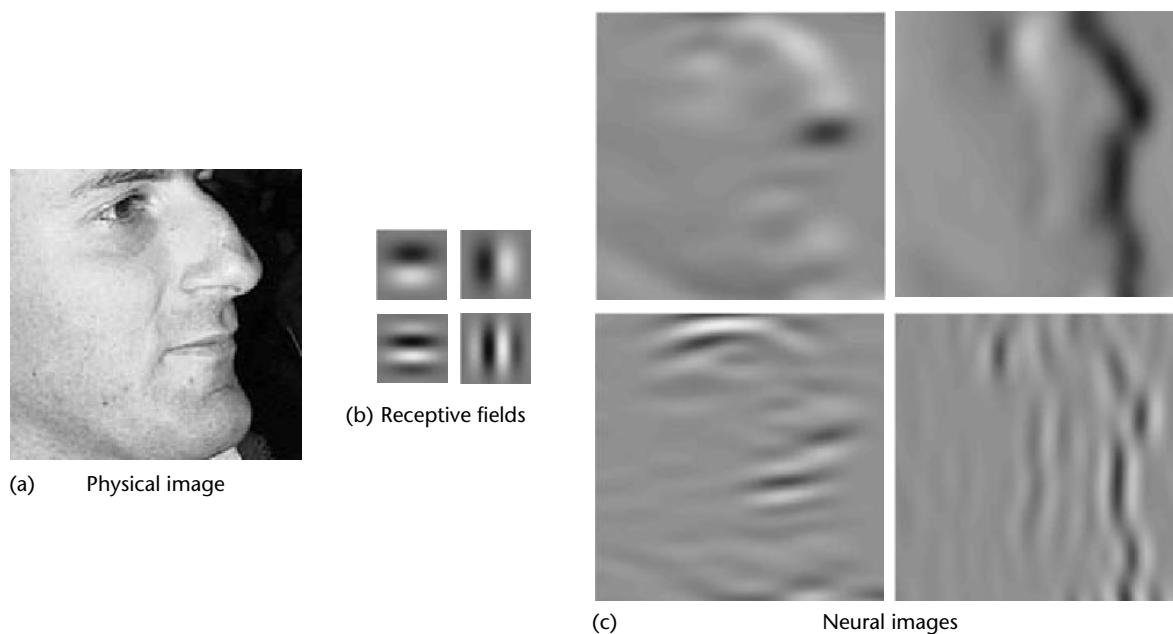
Keywords:



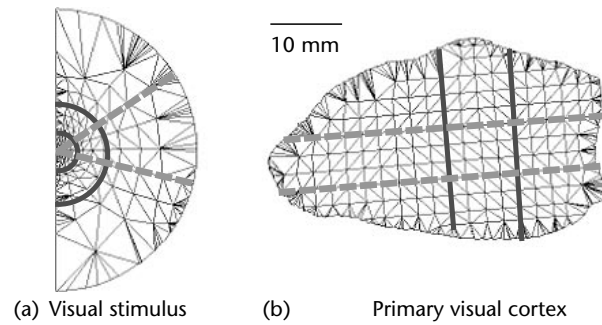
0375f001 **Figure 1.** Basic organization of the visual pathways. Images originating in the left and right visual hemifields are projected onto opposite parts of each retina. Retinal ganglion cells connect through the optic nerve to the Lateral geniculate nucleus (LGN). Neurons in the LGN then project to the primary visual cortex. The visual information is further analyzed in an array of subsequent visual areas. Note that the left visual hemifield is analyzed in the right cerebral hemisphere, and vice versa.



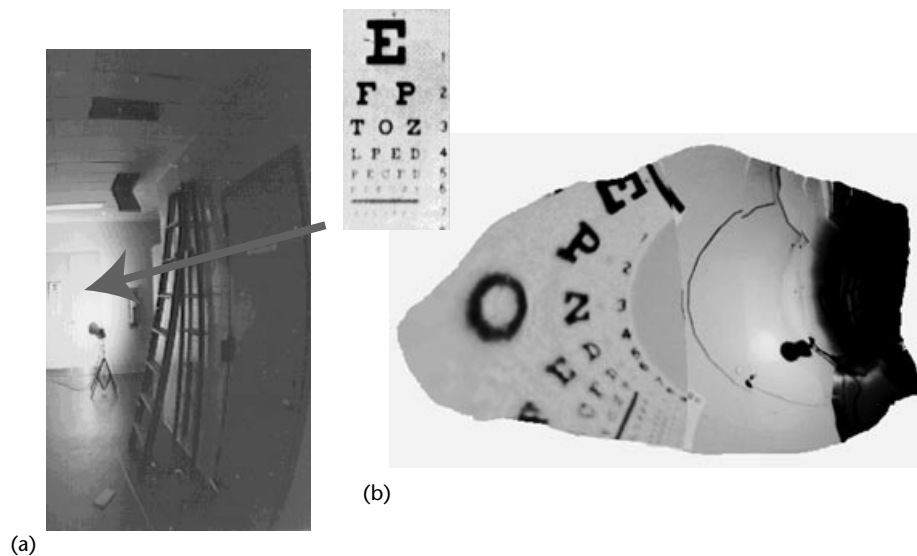
0375f002 **Figure 2.** Receptive fields and neural images in the retina and primary visual cortex (V1). (a) A physical image obtained in conditions of dim illumination. (b–e, top row) Receptive fields of a photoreceptor, an on-center ganglion cell, a horizontally tuned V1 simple cell and a horizontally tuned complex cell. (b–e, bottom row) Neural images



0375f003 **Figure 3.** Neural images in V1. (a) Physical image. (b) The two-dimensional receptive fields of eight simple cells, each sensitive to vertical, horizontal, or oblique orientations. The top set encodes orientations at a lower spatial scale than the bottom set. (c) The neural images resulting from the analysis of the image shown in (a) by the two sets of cells shown in (b). Each cell extracts one particular orientation at a given spatial scale. Adding together the eight images in (c) would result in a coarse but faithful representation of the physical image (a).



0375f004 **Figure 4.** Retinotopy in primary visual cortex. Mathematical model of the transformation between a visual stimulus (a) and area V1 in one hemisphere (b). Solid and dashed lines indicate the transformation of concentric and radial features in the visual stimulus into vertical and horizontal lines of activity in V1. From Frederick C and Schwartz EL (1990) Conformal image warping. *IEEE Computer Graphics and Applications* (March): 54–61.



0375f005 **Figure 5.** Application of the model in Figure 4 to simulate the representation in area V1 of the image of a room. In the back of the room is an eye chart (see detail), and the retina is centered on the letter O. The representation in cortex greatly magnifies the letters in the eye chart at the expense of the rest. From Schwartz EL, Merker B, *et al* (1988) Applications of computer graphics and image processing to 2D and 3D modeling of the functional architecture of visual cortex. *IEEE Computer Graphics and Applications* (July): 13–23.

Encyclopedia of Cognitive Science - author queries

Article 375 [Kiper & Carandini]

Introduction

Anatomy of the visual system

paragraph 1, sentence 4 'These cells produce spikes, ...' - OK to add 'of electrical activity' after 'spikes'?

Figure 2

Caption, penultimate sentence '...responses of a given cell as it is moved over a whole image' - suggest change 'is moved over' to 'scans'.

Figure 3

Caption, (b) - 'eight simple cells' - not clear - 'four' in related text. Last sentence - again, 'eight images' OK?

Figures 4, 5 (was 4a,b)

Has permission been obtained to reproduce these in both print and electronic formats?