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Research Article

A Survey of Architecture and Function of the Primary Visual Cortex (V1)

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The largest visual area, known as the primary visual cortex or V1, has greatly contributed to the current understanding of mammalian and human visual pathways and their role in visual perception. The initial discovery of orientation-sensitive neurons in V1, arranged according to a retinotopic mapping, suggested an analogy to its function as a low-level feature analyser. Subsequent discoveries of phase, spatial frequency, color, ocular origin, and direction-of-motion-sensitive neurons, arranged into overlapping maps, further lent support to the view that it performs a rich decomposition, similar to signal processing transforms, of the retinal output. Like the other cortical areas, V1 has a laminar organization with specialization for input from the relayed retinal afferents, output to the higher visual areas, and the segregation of the magno (motion) and parvo (form) pathways. Spatially lateral connections that exist between neurons of similar and varying properties have also been proposed to give rise to a computation of a bottom-up saliency map in V1. We provide a review of the selectivity of neurons in V1, laminar specialization and analogies to signal processing techniques, a model of V1 saliency computation, and higher-area feedback that may mediate perception.

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1. INTRODUCTION

The primary visual cortex (V1) contains orientation-tuned neurons, arranged in a retinotopic map, which have become the hallmark of early cortical computation in the primate visual system. Prior to the discovery of such neurons, the important role of V1 in the human visual system was known in the early twentieth century through patients who suffered total or partial loss of vision depending on the extent of damage to that area. The systematic correspondence between affected V1 area and regions of the field of view led Holmes [1] to deduce the retinotopic organization before the advent of *in vivo* extra cellular recording. Since then, anatomical examinations have shown that the visual signals from the retina enter the visual cortex mainly through V1, which in turn feeds the higher visual areas [2, 3]. The primary visual cortex thus plays an important role in visual perception in humans.

Attention was first drawn to the primary visual cortex by the discovery of edge and line "detector" neurons by Hubel and Wiesel in the late 1950s (see [4] for a review of their early work). These detector neurons are organized into smoothly changing maps of preferred orientation parallel to the surface of V1. Subsequently, V1 neurons selectively responding to a variety of other stimuli, such as color, spatial frequency, eye of origin, motion, and even visual disparity between the two eyes were found. We provide a short review of key information about the function and architecture of V1 that may be used to build a blueprint of this crucial stage of the human visual system. We hope that this may assist efforts to reverse engineer the early human visual system or to transfer successful cortical strategies to computer vision and signal processing algorithms. Despite the large number of studies on V1, probably one of the most examined out of all the other visual areas, significant controversy still exists on the extent of the computation that V1 performs. For this purpose, our review will include mainly established experimental facts about V1 and we only briefly mention controversial areas. Owing to the huge amount of literature on V1, we selectively provide references for facts that cannot be found in standard textbooks. Further details can be found in Winder's review [5] and Olshausen and Field's examination of what is still unknown about V1 [6]. In addition, we also present some more recent experimental data that have significant implications on the computational function of V1.

The human visual system consists of anatomically distinct processing areas. The areas which exclusively process

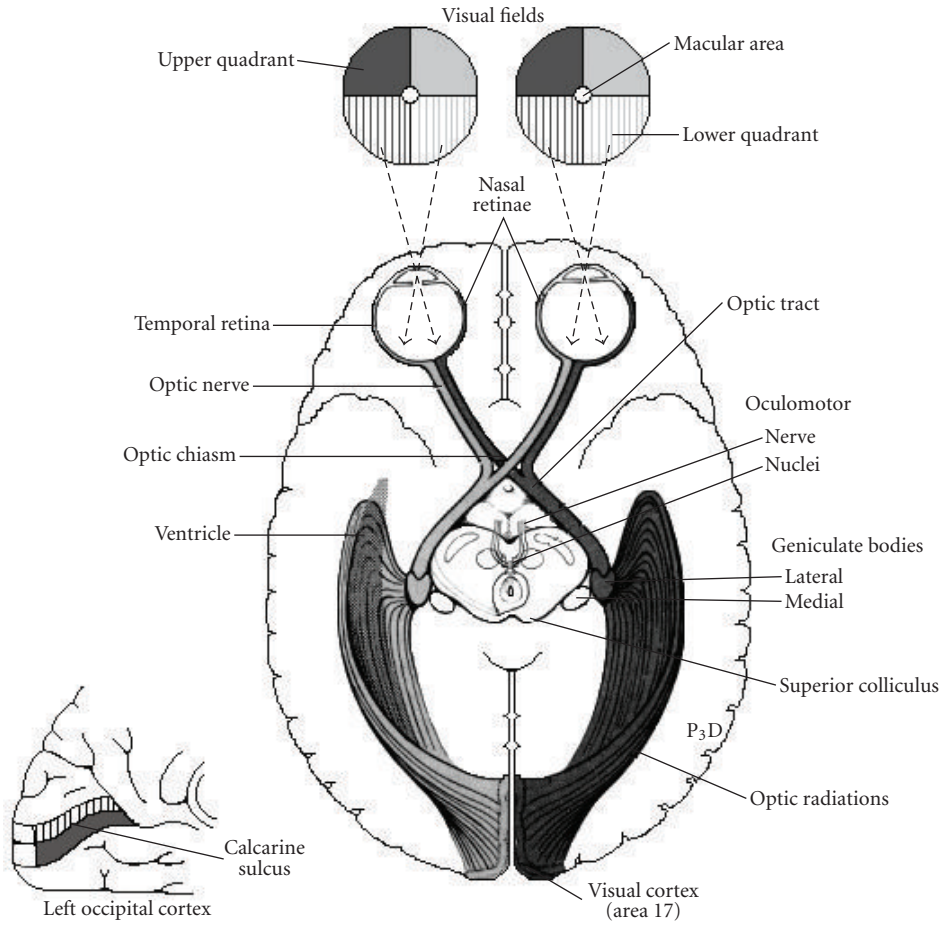

Figure 1: Illustration of the optic nerve, lateral geniculate nucleus (LGN) and V1 (area 17 in the figure), obtained from [7].

visual information are found in the visual cortex and are called V1, V2, V3, V4, V5/MT, MST, and so on. These cortical areas are interconnected with a high degree of regularity and precision [8]. The parallel connections from V1 to multiple higher cortical areas indicate that the human visual system employs a hierarchical processing strategy [9], whereby the higher cortical areas are interconnected with a mixture of parallel and serial two-way connections. We first provide a brief overview of the human visual system (illustrated in Figure 1). The retina contains an array of photoreceptors, which samples the field of view, and ganglion cells which process the visual signal prior to transmission through the optic nerve. Even at the earliest stages of visual processing in the retina, anatomically distinct classes of neurons with different processing properties create two separate streams of information for motion and form. The optic nerve carries the visual signal to the thalamus where it is relayed by the lateral geniculate nucleus (LGN) to the primary visual cortex.

The neurons in the LGN and V1 maintain an anatomical and functional segregation of cells involved in the two streams, although some interconnections exist at the boundaries of these anatomical regions in the LGN and V1. From V1, the two streams of information are separated into parallel neural connections to higher cortical areas, clearly demonstrating the existence of two parallel processing "pathways" in the human visual system, termed dorsal and ventral pathways. The dorsal pathway consists of V1 → V2 → V5 → parietal lobe and is also called the "where" pathway as it is involved in object localization (action and spatial) tasks. The ventral pathway consists of V1 → V2 → V3 → V4 → temporal lobe, which is also called the "what" pathway involved in object recognition tasks [10]. The segregation of these two parallel processing streams is far from being distinct as there are numerous two-way interconnections between the cortical areas, including V1 [11]. A common property of neurons across visual stages is that each cortical neuron responds only to a small area of the visual field, called the receptive field (RF) of the neuron, and the size of this area increases with visual stages from V1 onwards, suggesting that information is integrated over larger areas of the field of view in the higher areas of the visual cortex. Depending on the context, the notion of receptive fields may also encompass the computational function of the neuron. Those of linear neurons

can be expressed as a linear combination of its inputs, which is analogous to the finite impulse response (FIR) of linear filters.

1.1. Anatomical structure

The primary visual cortex anatomically corresponds to Brodmann's area 17 and is visually identifiable as a distinctive stripe caused by the myelinated neurons in its fourth layer. For this reason, it is also called the striate cortex. The neurons of V1 are arranged into a thin slightly folded two-dimensional sheet with six separate layers. At an approximate surface area of 8 mm × 6 mm and a thickness of 1.7 mm [12], V1 is the largest area in the visual cortex. The retinotopic organization of the neurons indicates that V1 uses the spatial location of stimuli in the field of view to organize its analysis and this may have important implications on its function. Wandell [12] estimates the number of neurons in primate V1 to be at least 150 million which puts the ratio of V1 neurons to retinal ganglion output cells at 100 : 1. Even after allowing for the compression performed by the ganglion cells prior to transmission over the bandwidth-limited optic nerve, V1 produces more outputs than visual inputs leading to an overcomplete representation of the visual field [13]. Each neuron makes in the order of thousands of short-range interconnections with other neurons in V1 [12]. Neuron density and the number and destination of connections vary in the six layers of V1 (further details can be found in [14]).

2. SUBCORTICAL INPUTS

As in many other visual areas, the properties of neurons in V1 can be better understood by investigating the transformations of the visual signals that occur in the earlier stages of the visual system. The major feedforward input to V1 consists of afferent nerve axons from the lateral geniculate nucleus which itself relays signals from the retina. A simplistic view of the function of these two early stages can be summarized as visual sensing, information encoding, and transmission from the frontal end of the skull to the visual cortex at the occipital (back) end. We provide a brief summary of these early subcortical computation and refer the reader to reviews such as [15, 16] for more detail.

As an outgrowth of the brain, the retina contains a variety of neurons, such as ganglion, amacrine, and bipolar cells among others, in addition to the light-sensing photoreceptors. Incoming light across the visual field $I(x)$ is sampled as a function of spatial location x by the photoreceptors and transformed to outputs $O(x)$ by the retinal ganglion cells. The photoreceptors and ganglion cells vary in size and visual properties according to their eccentricity from the center of the retina where the fovea is found. The family of so-called P-type ganglion cells, constituting about 85% of the total population, is predominantly found in the foveal region and possesses high spatial resolution while responding sluggishly to changes. On the other hand, the periphery contains M-type cells which only make up 10% of ganglion cells and which have poorer spatial resolution but higher temporal resolution.

An analogy to the computation performed by the P-type ganglion cells in the fovea is a linear transform, $O(x) = \int K(x,x')I(x')dx'$, with adaptable dynamic range which depends on light levels and is adaptable over a time scale of less than 30 seconds. In daylight, the transform is similar to isotropic spatial bandpass filtering with a peak sensitivity of around 3–5 cycles per visual degree. The kernel of the transformation can be approximated by a difference of two Gaussians, for example, $K(x,x') \propto Ae^{-(x-x')^2/(2\sigma^2_{\text{center}})} - Be^{-(x-x')^2/(2\sigma^2_{\text{surround}})}$, with space constants $\sigma_{\text{center}} < \sigma_{\text{surround}}$ and weights $A > B > 0$ (or $A < B < 0$), which replicates the interaction between the central and surround subfields of receptive fields observed in extracellular recordings. In dim light, this transform changes to a lowpass filter or Gaussian-like smoothing filter $K(x,x') \propto e^{-(x-x')^2/(2\sigma'^2)}$. The adaptivity of the transform can be theoretically understood by assuming that the aim of the retinal computation is to transmit as much information as possible from the photoreceptors to the brain with limited information transmission capacity at the retinal output—the optic nerve composed of output fibers from the retinal ganglion cells [17, 18]. The adaptation of the transform to light levels corresponds to different efficient codes for different input signal-to-noise levels. Applying the efficient coding principle to color coding leads to the red-center green-surround receptive fields of the neurons [19]. Hence, let the color input be $I(x,c)$ for cone type c = red, green, blue, a cell with the red-centre-green-surround receptive field gives output $O \propto \int dx' Ae^{-(x-x')^2/(2\sigma^2_{\text{red}})} I(x', \text{red}) - \int dx' Be^{-(x-x')^2/(2\sigma^2_{\text{green}})} I(x', \text{green})$ with weights $A > B > 0$ (or $A < B < 0$), and spatial constants $\sigma_{\text{red}} < \sigma_{\text{green}}$.

The segregation between the two main types of M and P ganglion cells output is preserved both in the optic nerve and in the lateral geniculate nucleus. The axons of P-type ganglion cells project to the upper four layers of the LGN while the axons of the M-type cells project to the lower two layers. Allard [20] and Kaplan and Benardete [21] believe that M cells are responsible for the perception of movement while P cells help in the perception of form and color with their higher spatial acuity. Theoretically, the receptive fields of the M cells could be understood by assuming that their role is to extract input information as fast as possible (rather than as much as possible by P cells), given limited information transmission capacity [22].

The lateral geniculate nucleus relays information from ganglion cells in the retina to the visual cortex. So the receptive fields of the neurons (defined as the effective transform of the visual inputs from the photoreceptors to the cell outputs, whatever intermediate processing there is) are similar to those of the retinal ganglion cells. Massive cortical feedbacks (ten times as much as feedforward to V1) from V1 and V2 to LGN provide more connections to the LGN than any other source of input including the retina [23]. LGN cells are not orientation-selective by themselves [24] but have been observed to become orientation-selective with feedback from V1 [25]. The function of the LGN is poorly understood beyond being viewed as a relay station.

3. TWO ASPECTS OF ORGANIZATION AND FUNCTIONS IN V1

Much of the initial investigations into the function and organization of neurons in V1 were carried out by single- and multiple-cell extra cellular recording of their outputs to given, albeit simple, visual stimuli. While different families of neurons tuned to features such as orientation, spatial frequency, phase of symmetry, color, ocular origin, and direction of motion were discovered and their responses to simple stimuli adequately characterized, the organization of these neurons on a larger scale and the lateral interactions between neurons in response to larger stimuli were less amenable to systematic *in vivo* characterization. Fortunately, population recording techniques such a functional magnetic resonance imaging (fMRI) and optical imaging of the cortical surface have plugged the gap to reveal the organization of the neurons into overlapping retinotopic maps for different features [26]. Computational modelling techniques have also significantly matured to propose plausible mechanisms for lateral interactions [27].

The huge interest in characterizing the functional properties of neurons in V1 arises from the short distance in terms of synaptic connections, typically at least 4, from photoreceptors in the retina and the compact spatial localization of the photoreceptors inputs contributing to the receptive fields of the neurons, which are usually no larger than 1 or 2 degrees of visual angle. Hubel and Wiesel [28] identified three types of neurons: simple, complex, and hyper complex. A simple neuron performs a linear combination of its visual inputs and the population response of these neurons can be approximated by a linear filtering of the visual signal by their FIR masks, the signal processing analogy to biological receptive fields, followed by a nonlinear pointwise transform that is more or less monotonous with threshold and saturating behavior, that is, response $= f(\int K(x,x')I(x')dx')$ with nonlinearity $f(\cdot)$. According to the "energy" model [29], the output of two simple cells in quadrature (90° phase difference) with a squaring nonlinear function $f(\cdot)$ can be summed to provide quasi-position-invariant responses of complex neurons within their receptive fields. Hypercomplex neurons respond to the end-stopping of lines. V1 contains a consequential number of cell types with different classes of receptive fields and visual properties. The detailed and overcomplete representation of the visual field through the huge population of neuronal responses in V1 earned the latter its name "sorting office" of visual signals [30].

The presence of extensive lateral connections between neurons and the discovery of a class of inhibitory V1 interneurons [31] which do not directly receive visual input prompted a reexamination of the predominantly feedforward role of neural circuits in V1, and in particular the nature of the receptive field. The classical Receptive Field (cRF) was measured by Hubel and Wiesel [28] with point light sources and bars. Such simple visual stimuli did not elicit any response beyond a certain distance from the center of the RF. However, the lateral connections and inhibitory interneurons hint at significant interactions between the computation of nearby feedforward neurons. This interaction causes each cell's response to be significantly influenced by stimuli outside its classical receptive field in a region called its context or surround. Consequently, a neuron's response can clearly signal global properties of input on a spatial scale much larger (e.g., of a typical visual object) than the classical receptive field [32–34]. Such a global property clearly has exciting computational implications. One could also view the classical receptive field as arising from the feedforward processing of LGN inputs in V1, while the second contextual influence of stimuli outside the cRF as arising from the recurrent or lateral processing in V1. For clarity, we will first discuss the former before the latter.

3.1. Organization of individual cells in V1

V1 cells respond selectively to different input features [35], such as orientation, color, scale, spatial phase, direction of motion, and ocular origin. The selectivity of the neurons to specific features of visual stimuli, such as orientation, spatial phase, and scale, is achieved by the spatially defined linear function of the receptive fields. Selectivity to different types of stimuli such as colour and ocular origin is achieved by selecting the origin of the visual signals, for example, rod and cone photoreceptors on the retina, left or right eye. Livingstone and Hubel [36] found that V1 cells are usually simultaneously tuned to more than one of these features, which is not surprising considering that they only perform a linear combination of their visual inputs. For instance, simultaneous tuning to both orientation and direction of motion is common. However, V1 neurons are usually more strongly tuned to one specific feature than others.

The retinotopic map of the primary visual cortex is a well-known feature. However, the correspondence between neuron location and the retinotopic location of their receptive fields is only evident over scales greater than 1.2 mm parallel to the surface of V1 [37]. At smaller scales, neurons are organized by columns specializing in different stimuli. The selectivity of V1 neurons to different feature dimensions causes several overlapping maps to coexist parallel to the surface of V1 [37].

Hubel and Wiesel [28] discovered that the preferred orientation of neurons remained more or less constant through the layers of V1 perpendicular to the surface. The column of cortical tissue is considered as a functional unit. The preferred orientation of the neurons varies systematically in a stepwise manner along the surface of V1 with occasional breaks and reversal of direction. Similar columnar organizations of selectivity have since been found for other feature dimensions such as color and ocular dominance (the differential sensitivity to inputs from different eyes) [38]. A hypercolumn is argued to contain a complete representation of orientation and ocular dominance selectivity [35], color selectivity (see Figure 2), as well as spatial frequency selectivity [39]. De Valois et al. [39] argue that a complete integration region (CIR), covering roughly a 1 mm square area of cortical space, contains about 100 000 cells, among which roughly 32 000 cells have narrow spatial frequency tuning

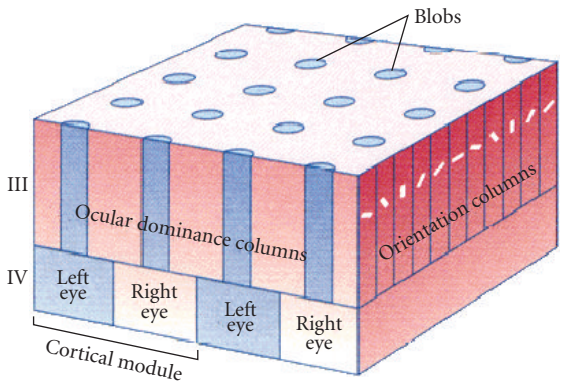

Figure 2: Illustration of a hypercolumn containing neurons selective to orientation, ocular dominance, and color, obtained from [40].

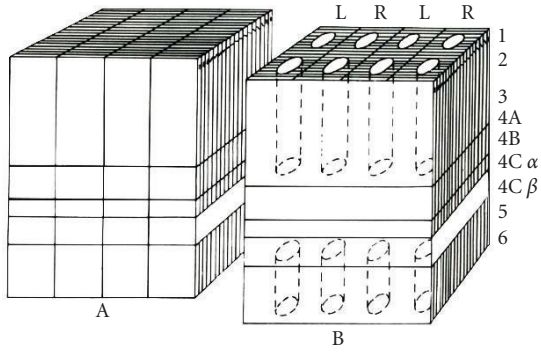

Figure 3: Ice cube model of the V1 area. The function and selectivity of cells remain more or less similar across the laminar layers and vary gradually along the surface. Cytochrome-oxidase staining reveals columns of colour sensitive cells in layer 2/3, obtained from [42].

over a range of about 3 octave of peak spatial frequencies and 20 orientations for a particular region of space. The discovery of columnar organizations prompted the emergence of the "ice cube" model of V1 (illustrated in Figure 3).

Freeman [41] performed a multiparameter study of the organization of neurons within columns of the primary visual cortex of the cat. In particular, Freeman investigated whether pairs of adjacent neurons were related by common visual properties such as preferred orientation, spatial frequency, or spatial phase. Similarly to the original experiments of Hubel and Wiesel [28], Freeman found that preferred orientation was the most similar in adjacent neurons. Spatial frequency was the next most common property, while the property that varied the most between adjacent neurons was spatial phase. This led Freeman to the hypothesise that V1 may use a strategy of pooling the response of neurons with different spatial phases to achieve phase invariance.

Figure 4 shows the connections from the LGN to V1, the intralaminar (intralayer) connections in V1, and the projections from V1 to the upper areas of the cortex. V1 is divided into six different layers according to the relative density of neurons, interconnections, and external connections from the LGN and to other visual areas [12]. Minor differences in the layers may cause further subdivisions. Layer 1 contains relatively few neurons and does not perform any major processing. The incoming LGN connections consist of two separate bundles originating from the magnocellular and parvocellular layers and project to two neighboring but different subregions in sublayer 4C of V1 called layers 4Ca and 4Cb, respectively. The magnocellular pathway flows from layer 4Ca to 4B and then projects to the "thick stripes" of V2 and V5. The parvocellular pathway flows through layer 4Cb and then projects to the "blobs" and "interblobs" in layers 2 and 3. The "thick stripes" of area V2 and the "blobs" and "interblobs" of layer 2/3 in V1 are qualitative descriptions of regions revealed by staining of cortical tissue with cytochrome oxidase. The latter is a metabolic enzyme which participates in the electron transport chain in the brain. The distinctive blobs contain cells that are color-selective and are tuned to both a broad range of orientations and to low spatial frequencies. In comparison, cells in the interblobs are the opposite with no color selectivity, high selectivity to particular orientations and high spatial frequencies [36]. The presence of two types of regions in layer 2/3 and their separate projections to different regions of V2 (also revealed by cytochrome-oxidase staining) prompted the view that the parvo "what" pathway specializes into two subpathways in V1: parvo-B deals exclusively with colour and Parvo-I deals with orientation and high acuity perception [30]. The distinction between the properties of the cells in the blobs and the interblobs has been blurred by new research that revealed cells in the interblobs tuned to both color and orientation [38].

3.1.1. *Orientation selectivity*

Orientation-selective cells were the first type of feature detectors identified by Hubel and Wiesel [28] in V1. Three kinds of orientation-selective cells were actually found: simple, complex, and hypercomplex. Simple cells respond selectively to lines or edges at particular orientations. Their population response is obtained by linearly filtering the visual input by their RFs as in 2D signal processing. The filter can be approximated by a 2D Gabor function, for example, filter $\propto \exp(-x^2/2\sigma_x^2 - y^2/2\sigma_y^2)\cos(2\pi f x + \phi)$, illustrated in Figure 5, which is oriented along the y-axis, with width σ_x and length $\sigma_y > \sigma_x$, is tuned to optimal spatial frequency f and has a receptive field phase of symmetry ϕ (a phase of 0° or 90° makes the cell tuned to a bar or edge, resp.). The response of a simple cell is therefore also dependent on the spatial phase ϕ' of the stimulus, that is, the precise location of the line with respect to the RF, with optimal response at $\phi' = \phi$. The phase of the RF also affects its symmetry along the axis of the cell's preferred orientation. In the V1 area of cats, the majority of simple cells were found to have RF centers separated by less than 1° of visual angle and the majority of those were also found to have RF centers offset by less than

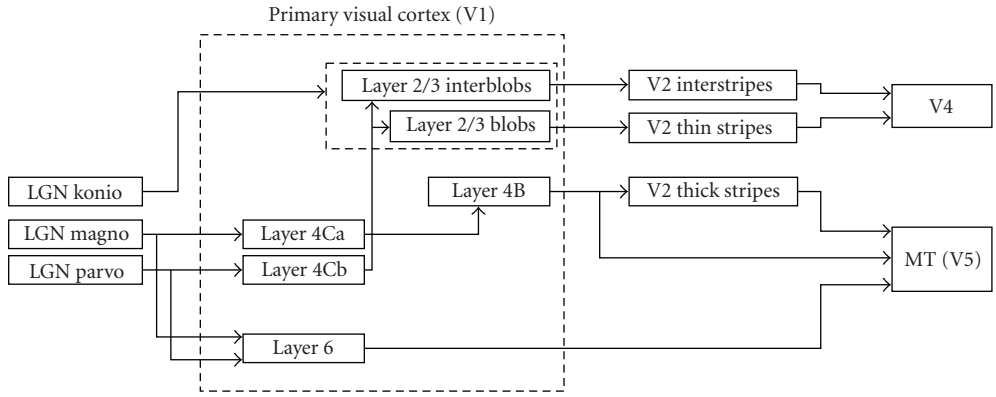

Figure 4: Connections from LGN, interlayer connections and projections to other cortical areas. Note that layer 4C has been separated into 4Ca and 4Cb, adapted from [30, 43].

a quarter of RF sizes [44]. This indicates a considerable degree of overlap of RFs. On the other hand, complex cells also selectively respond to lines or edges at particular orientations but their response is insensitive to the position of the line or edge within the RFs. A standard view [45] is that they receive inputs from simple cell subunits of different phases. They are abundant in layer 2/3 [30] and have also been reported in layer 6. A drifting sine grating stimulus would elicit a half-wave rectified modulation in the mean firing rate of a simple cell, and an approximately constant firing rate in a complex cell.

Although Hubel and Wiesel [35] initially discovered that V1 cells were tuned to the same orientation in a column, the degree of orientation selectivity was found to vary as one goes deeper into the column and the layers of V1 [46]. This is a property of the laminar specialization of V1. As the primary site of visual input from the LGN to V1, layer 4C appears to have broad orientation tuning. According to Ringach et al. [46] (who used grating stimulus to assess orientation selectivity), the neurons in layer 4C have the shortest average response time (45 milliseconds) in V1 to retinal stimulus. The longest average response time is found in layer 2 (70 milliseconds) where orientation tuning width (defined as half-width at $1/\sqrt{2}$ height) is the narrowest at 20° on average, and layer 6 (65 milliseconds) which possesses marginally sharper orientation tuning than layer 4C, whose tuning width is at 25° on average. The authors propose that the increased delay in response time in layers 2 and 6 indicate significant lateral interactions between V1 cells to sharpen orientation selectivity. De Valois et al. [47] have earlier reported that orientation bandwidth in macaques at half-height of the maximum response ranges from 6° to 360° (unoriented) with a median near 40°. There are also cells untuned or poorly tuned to orientation, they tend to be tuned to color and are in the CO blobs [36], which are associated with cells tuned to lower spatial frequencies [48].

Figure 6 shows the arrangement of preferred orientation on a layer parallel to the surface of V1 in the cat. The pinwheel arrangement (angularly varying) of selectivity around central singularities is common in mammalian V1. The sharp breaks in this orderly arrangement, called fractures, correspond to important landmarks in the maps of other visual features such as the shift in eye of origin in ocular dominance maps.

3.1.2. Color selectivity

Three classes of cones (color photoreceptors) exist in the retina, selective to long (L), middle (M), and short (S) wavelengths of light corresponding to red, green, and blue colors, respectively. As mentioned earlier, retinal ganglion cells and LGN cells combine color opponency (red-green and blue-yellow) and spatial opponency (center surround) in a red-center green-surround fashion [50], called *single opponency*. In V1, many cells are mainly tuned to either color or orientation [36], while some are tuned to both [38]. Cells tuned to color tend to have a double-opponency organization, for example, the center of the receptive field has the red-green opponency while the surround has the green-red opponency [36]. Using physiological and psychophysical data in his arguments, Lennie [9] proposes that a cortical neuron responds to multiple types of stimuli (e.g., binocular disparity, color, orientation, phase, etc.) and "pure" neurons which respond selectively to one type only of stimulus do not exist.

Outside of the central 2.5° of vision, Livingstone and Hubel [36] found 15% of V1 cells to be color-selective and nonorientation-selective. Inside the central 2.5° of vision, this percentage of color-selective and nonorientation-selective cells increases to over 20%. The percentages of color-selective and orientation-selective cells were similar. Thus, 47% and 23.4% of cells were found to be color-selective in the foveal and nonfoveal zone of vision in V1, respectively.

Landisman and Ts'o [38] have found that cytochrome-oxidase blobs in V1 contain predominantly one type of color opponent cells, either red-green or blue-yellow [51]. Blobs dedicated to red-green color opponency were 3 times more numerous than blue-yellow blobs [51]. However, areas of

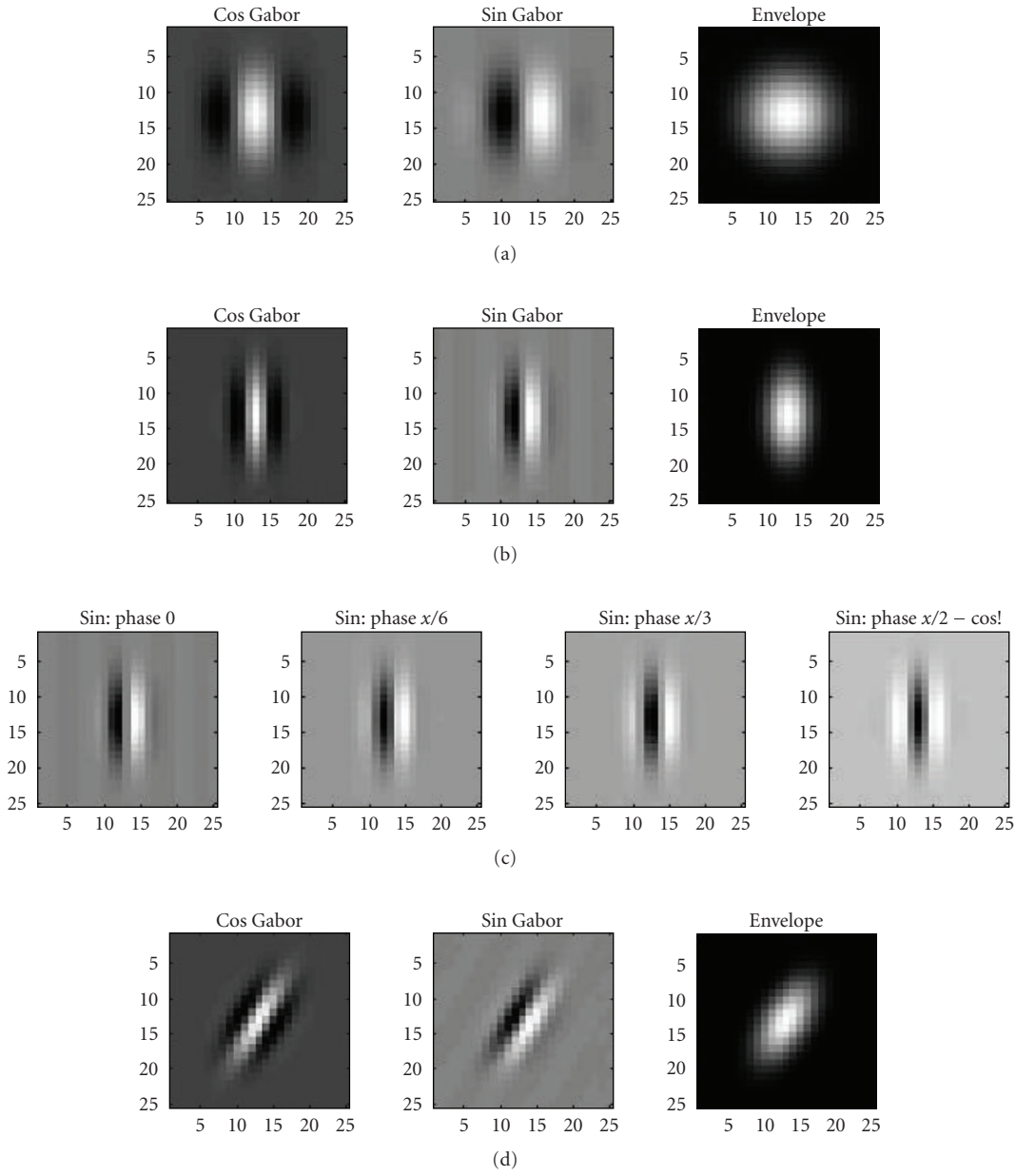

Figure 5: Gabor patches, illustrating effects of parameter changes, notably angular selectivity (elongation), phase, and rotation. (a) $\sigma_x = \sigma_y$; (b) $\sigma_x = \sigma_y/2$; (c) left to right, increasing phase shift and Gabor transformed from antisymmetric to symmetric.

color-selective neurons, called color patches, revealed by optical imaging[1] of neurons can extend beyond blobs and can even encompass two blobs. When two CO blobs of different color opponencies are found in a colour patch, the interblob region contains cells responding to both red-green and blue-yellow color opponencies information in an additive manner. These additive dual-opponency responses are present in 44% of color patches identified in the experiment. Inside color patches, cells are recorded to be more color-selective and unoriented.

3.1.3. *Scale selectivity*

De Valois et al. [39] have found that LGN cells have broad spatial frequency tuning while V1 cells have bandpass characteristics. From the top to the bottom of layer 4C (a to b) of V1, Hawken and Parker [52] have found a gradual decrease in RF size and contrast sensitivity. The findings agree with the common knowledge that the LGN mainly projects to layer 4C: LGN M and P cells project to sublayers 4Ca and 4Cb,

[1] High-resolution imaging of areal differences in tissue reflectance due to changes in blood oxygenation caused by neural activity.

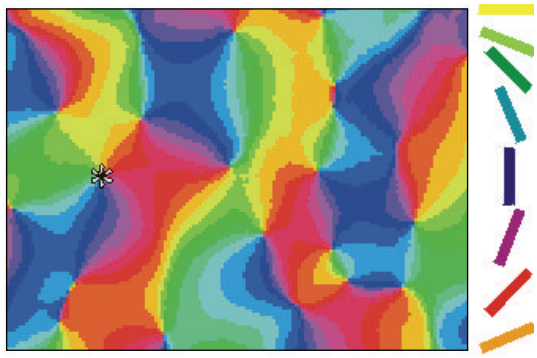

Figure 6: Orientation selectivity map (approximately a 3 mm × 3.5 mm area on cortical surface) from a layer of cat V1 parallel to the surface. The star indicates a singularity in the center of the pinwheel organization. Some neurons in the pinwheel center possess closely overlapping and tight orientation selectivity, obtained from [49].

respectively. Neurons in layers 4C subsequently project to the upper layers of V1. The specificity of the two pathways appears to be maintained in layer 4C.

Bredfelt and Ringach [53] have observed that spatial frequency tuning varies dynamically over a limited range as stimuli are presented. More specifically, the bandpass selectivity of cells increases with time after initial response by about a fraction of an octave, although it is hard to discern by the quality of data. Then increasing low-frequency attenuation causes the peak of the tuning curve to shift towards higher frequencies by 0.62 ± 0.69 octaves. The authors found that feedback models agree better with their observations than feedforward models. More specifically, the delayed strengthening of a suppressive feedback loop could explain the delayed attenuation at low frequencies of the spatial tuning curve.

De Valois et al. [39] proposed that the primary visual cortex performs a 2-dimensional frequency filtering of the visual input signal with neurons which are jointly tuned in orientation and spatial frequency. Simple cells in the foveal region were found to have spatial frequency bandwidths at half amplitude from 0.4 octaves to greater than 2.6 octaves, with a peak in the number of cells at 1.2–1.4 octaves. The peak spatial frequency of the simple cells varied from 0.5 cycles per degree to greater than 16.0 cycles per degree. The frequency tuning bandwidth is around 1.5 octaves [54, 55].

3.1.4. Direction of motion and speed selectivity

During Hubel and Wiesel's original experiments, the two pioneers observed direction-selective cells which fired more vigorously for oriented stimuli moving in a particular direction than other directions, including the opposite [4]. In contrast to orientation-selective cells with separable receptive fields that can be expressed as a product of functions of space and time, respectively, direction-selective cells have spatiotemporal receptive fields oriented both in space and time [56]. Directionally selective simple cells exhibit a gradual spatial shift (translation) over time of their spatial receptive field function. Computational models have proposed that direction selectivity can be built by a linear combination of lagged nondirection-selective cell responses [57]. Some complex cells also exhibit direction selectivity but interpretation of the nonlinear nature of their receptive fields requires second-order analysis (for further details, see [58]). The direction of motion was found to be always perpendicular to the preferred orientation of the cell for simple stimuli such as gratings [59]. Given the relatively small size of their RF compared to the typical size of objects on the retina, directionally selective cells are theoretically only able to detect the component of local motion perpendicular to the border of an object. However, it has been found that some neurons can signal global motion [60], possibly by lateral interactions with other types of neurons. Some neurons are selective to the speed of the stimulus independently of spatial frequency [61]. A pooling of responses across neurons with similar speed tuning but different spatial frequency tuning has been proposed to account for this property which plays an important role in the motion processing magno pathway.

3.1.5. Plasticity

The recent studies on the spatiotemporal characteristics of V1 neurons [53, 56] have shown the dynamical changes that can occur in their receptive fields. Adaptation to fixed stimuli over timescales of a few seconds to a few minutes has also been known to temporarily affect the receptive fields of the neurons by depression (fatigue) [62, 63] and also enhancement [64]. Dragoi et al. [65] investigated the effects of bottom-up rapid adaptation and temporal interactions while viewing natural images under normal conditions. The authors found that brief adaptation at the millisecond timescale to stimulus near the preferred orientation of the cell causes the preferred orientation to move away from that of the adapting stimulus and increases the bandwidth of the tuning curve, while adaptation to stimulus orthogonal to the preferred orientation does not change the latter and sharpens orientation tuning. The authors have also shown that top-down influences from a higher-level representation of the future location of a target cause a change in the orientation tuning of V1 neurons.

3.1.6. Models and computational understanding of the feedforward V1

Li and Atick [66, 67] and Li [68, 69] have shown that the receptive fields in V1 can be understood as part of an efficient code that removes the pair-wise or second order correlation between signals in two pixels. This efficient code, which is orientation selective, multiscale, and so forth, is related to the center-surround receptive field in the retina in the sense that they are both comparably efficient codes for removing such signal redundancy in inputs. This framework explains and predicts how the selectivity of V1 cells to different features

should be correlated. For instance, the framework explains that cells tuned to color are tuned to lower spatial frequencies and often not tuned to orientation, that cells tuned to higher spatial frequencies are often binocular, and that cells tuned to orientations are also tuned strongly or weakly to motion direction. The multiscale efficient coding framework also explains that if the spatial frequency tuning bandwidth is about 1.6 octaves as those observed in the cortex [54, 55], then the neighboring cells tuned to the same spatial frequency have receptive fields with 90° phase difference (phase quadrature), as in physiological data [70]. It also predicts the cell response properties to color, motion, and depth, and also how cells' receptive fields adapt to environmental changes.

Olshausen and Field [71] used independent component analysis (ICA) to find the minimum independent set of basis images that can be used to represent patches of 16×16 pixels from images of natural scenery. The basis images were again found to be similar to V1 receptive fields. These findings support the theory that V1 RFs evolved in the human brain to efficiently detect and represent visual features. Simoncelli and Heeger [57] modeled the response of V1 complex cells by averaging responses over a pool of simple cells of the same orientation and RF spatial phase, but different and nearby RF centers. Hyvärinen and Hoyer [72] modified the ICA approach of Olshausen and Field [71] to account for the complex cells whose responses exhibit phase-invariant and limited shift-invariant properties. Miller et al. have modelled and simulated how feedforward pathways from LGN and V1 intra-cortical circuitry contribute to the cell's response and tuning properties such as contrast-invariant tunings to orientation [30, 73].

3.2. Interaction between V1 cells and global computation

The traditional view of cortical processing is a pyramid where visual information is integrated over successively larger spatial regions from the base (V1) to the top (V4,V5) of the pyramid. However, information can be integrated laterally or recurrently over long distances at the early stages of processing like V1. It has been found that a neuron's response to stimulus within its receptive field (RF) can be influenced by stimuli surrounding the classical RF. In particular, the response of orientation-tuned neurons to an optimally oriented bar in its RF is suppressed by an effect called isoorientation inhibition, by up to 80% when identically oriented bars surround the RF. This suppression is weaker when surround bars are randomly oriented, and is the weakest when the surround bars are orthogonally oriented [75]. When an optimally oriented low-contrast bar within the RF is flanked by collinear high-contrast bars outside the RF, such that the center and the surround bars could be part of a smooth line or contour, the response can be enhanced by a few times [76]. However, Polat et al. [77] have shown that high-contrast stimuli in a neuron's RF, flanked by high-contrast stimuli along its preferred orientation, whether oriented at or orthogonal to its preferred orientation, inhibits the neuron's response. These contextual influences are fast, occur within 10–20 milliseconds after initial cell response, and exist in cat and monkeys, whether they are awake or anaesthetized.

Classical receptive fields were mapped by measuring the response of individual cells to a moving high-contrast light source (point or bar) and plotting the responses with respect to the 2D position of the light source. The more recent *reverse-correlation technique* probes the phenomenological receptive field by correlating the cell's response with a grating of variable size centered upon the classical receptive field [78]. The size of the grating to elicit the highest response from the cell is called "summation field" (SF) since the response may be affected by lateral connections between multiple V1 neurons.

The resulting SF sizes are 2.3 times bigger than the average size of classical RFs found by Barlow et al. [79]. They depend on the contrast of stimuli, and is on average more than 100% larger in low-contrast than in high-contrast conditions [80]. To gratings larger than the SF, the neural response (average firing rate) falls but becomes asymptotic to a level typically higher than spontaneous firing rate.

Angelucci et al. [78] found that monosynaptic horizontal connections within area V1 are of an appropriate spatial scale to mediate interactions within the SF of V1 neurons and to underlie contrast-dependent changes in SF size. They additionally suggested that the spatial scale of feedback connections from higher visual areas is commensurate with the full spatial range of interactions between SF and the surround.

Using a recombinant adenovirus containing a gene for green fluorescent protein to image neural connections, Stettler et al. [81] found lateral connections in V1 to be slightly larger in diameter than previously believed and much denser than feedback connections from V2, apparently contradicting results from of Angelucci et al. [78]. Lateral connections were found to stretch almost 4° of visual angle in diameter from the center of the injection[2] which is much larger than the average RF[3] size of 0.5°. In the central 1 mm diameter of the injection, the lateral connections were nonspecific, whereas on the outside of the central 1 mm diameter, the connections had bell-curve-like densities with the centers located on neurons with similar orientation preference. Feedback connections stretched to 2.5° in diameter from V2 and originated from neurons with diverse orientation preferences. Bosking et al. [82] showed that the lateral connections projected further along the axis of the receptive field than in the orthogonal direction. Long-range connections project mostly to neurons with similar orientation preference [83] and are mostly excitatory [76], while short-range connections are mostly indiscriminate of orientation preference and are commonly inhibitory [84].

Kagan et al. [74] measured the classical RF and summation fields of macaque V1 (summarized in Table 1). Moving bright and dark (relative to background) orientation bars were used to measure the classical RF size of V1 cells. The cells were further subcategorized as simple, complex and

[2] Which occurred over a 0.2 mm diameter.
[3] Measured by minimum stimulus bar which elicited a response.

Table 1: Dimensions of summation fields and classical receptive fields in macaque V1. The number of cells is in parentheses. ± values are standard deviations. Monocontrast cells respond either to light or dark bars but not both. This table was obtained from [74]. Note that 1° = 60 minutes of arc (minarc).

	SF minarc			cRF minarc		
Layer	Simple	Complex	Monocontrast	Simple	Complex	Monocontrast
2/3	22 ± 3 (5)	23 ± 10 (49)	7 ± 2 (5)	48 ± 11 (5)	26 ± 12 (49)	7 ± 2 (5) (74)
4	12 ± 7 (18)	28 ± 11 (74)	18 ± 8 (7)	29 ± 16 (18)	32 ± 13 (74)	18 ± 8 (7)
5/6	8 ± 5 (9)	49 ± 33 (29)	19 ± 12 (3)	19 ± 12 (9)	56 ± 338 (29)	17 ± 11 (3)
All	13 ± 8 (33)	31 ± 18 (178)	14 ± 8 (17)	29 ± 16 (33)	35 ± 21 (178)	14 ± 8 (17)

monocontrast. The latter responded either to bright or dark bars but not both. Expanding gratings were also used to measure SF size. However, they used a rectangular grating whose length (in the direction of preferred orientation of the neuron) was restricted to the neuron's optimal length to a bar. This may not affect a neuron's classical RF but may limit the effect on SF by lateral interactions with other neurons as hypothesised by Angelucci et al. [78].

4. COMPUTATIONAL MODELS OF V1 FUNCTIONS

4.1. Signal processing analogies

There are several strands of research in what might be called "classical" signal processing methodologies that bear close parallels to the visual processing found in biology. For example, the scheme of Burt and Adelson [85] which triggered much work into wavelet-based image compression bears a striking resemblance both to Laplacian of Gaussian models of retinal receptive fields [86] and difference of Gaussians [87, 88], used as a model of retinal receptive field processing. Another related branch of spatial processing operators that may be traced back to retinal models is that of scale-space representations, a branch of research that stretches back to the biologically inspired work of Marr and Hildreth [89] on edge detection, and from which a path can be traced through the work of Witkin [90], Koenderink [91], and Lindeberg [92] to the relatively recent, very successful SIFT method of keypoint detection [93]. We provide a summary of the properties of different signal processing techniques in Table 2.

Table 2: Characteristics of signal processing analogies.

	Compact spatial support	Complex	High angular selectivity	Multiscale
Gabor	*n*	*y*	*n*	*y*
Shiftable transform	*y*	*y*	*y*	*y*
Steerable filter	*y*	*y*	*n*	*n*
Deformable filter	*y*	*y*	*y*	*y*
Multirate Steerable filter	*y*	*y*	*y*	*y*

Accepted methodologies in current use that bear close resemblance to the spatial computations performed by V1 include the multirate filter-bank [94] approach which evolved primarily along the needs of image compression [95] and event detection and characterization [96], and the requirements of scale-and-orientation invariant measures in computer vision.

As mentioned in Section 3.1.1, Gabor functions remain the most widely used mathematical descriptions of spatial receptive field patterns. Gabor functions have the distinct advantage, from a modeling point of view, that they are very adaptable with a small number of parameters. Initially proposed as a phase-invariant way of decomposing and thereby localizing a signal in time-frequency space [97], Gabor functions have found wide application not only in speech and image processing, but also in visual neuroscience, where two-dimensional versions were constructed as very successful approximations to cortical simple-cell receptive fields by Marcelja [98], and both popularized in complex form by Daugman [99] and successfully applied to characterizing the variegated patterns of the human iris for identity recognition by him in [100]. Spatial Gabor functions, often with phases intermediate to cos and sin oscillatory forms, are widely used in visual psychophysics, where they are termed Gabor *patches* (illustrated in Figure 5). Note that alternative two-dimensional complex wavelet definitions that are arguably functionally better suited to visual processing [101] were first suggested by Granlund [102]. Granlund's efforts also included the earliest applications to texture analysis [103] of such V1-inspired methods.

Despite the optimization of space, frequency, and orientation localization of 2D Gabor functions [99], there are some computational issues in their efficient application to areas such as image compression. One of these is lack of easily specified orthogonality. Another issue is the potential instability in reconstructing an image perfectly from projections onto Gabor functions sampled on regular grids. Finally, despite optimizing a space-frequency localization product, Gabor envelopes do not have strictly compact support in either time or frequency space. Daubechies, motivated by these problems [104] and inspired by a seminal paper by Mallat [105] linking wavelet decompositions to multiresolution spaces and to efficient filtering structures with decimation, succeeded in constructing very efficient orthogonal wavelets

of compact support [106]. Daubechies' initial wavelet constructions, together with spline wavelets, symmlets, and so forth, have been very successful in the domain of image compression.

Multirate filter-bank structures are brutally efficient devices for performing orthogonal image decompositions, because of their close alliance with digital filtering. However, despite the early and good successes in singularity detection and characterization, a problem arises when attempting to use such decompositions for more general visual pattern recognition, where the shifting of coefficient power between subbands presents practical complications. A property that is missing in maximally decimated filter-bank structures as typified by decompositions employing a single mother wavelet is therefore *shift invariance*. Inspired by Granlund's approach employing locally one-dimensional Hilbert transformers, Simoncelli et al. [107] addressed these shortcomings by proposing *shiftable* multiscale transforms, where completeness is relaxed to achieve greater coefficient stability in the subbands. Freeman and Adelson [108] also formalized and popularized the notion of steerability, closely tied to the principle of overcompleteness, as a means of synthesizing intermediate orientation channels from a set of fixed two-dimensional filters. These ideas were further refined by Perona [109] to more general kernels for early image processing, though many of these are not thought to be of particularly direct relevance to V1-level mechanisms.

An important distinction between the multirate filtering approaches placed on firm theoretical footing by Daubechies and Mallat, and their extension to 2D, is that the number of highpass subbands is usually quite low, often 3 for each scale of decomposition, corresponding to a low angular selectivity response. This is despite biological evidence, as described in Section 3.1.1, on the angular tuning curves of V1, and even, as pointed out by Perona [109], despite the growing body of evidence suggesting that many of the most promising methods for edge detection [110], stereo algorithms, and even compression at that time were using increased numbers of angular channels for each scale. For V1-like responses, Freeman's construction paradigm [108] partly alleviated this, allowing for a general nonseparable design paradigm where angular selectivity may be tuned arbitrarily through specifying polar separable filter constructions.

An alternative construction that achieves both lower overcompleteness (and therefore is more efficient), yet also displays good shift-invariance and higher angular selectivity is the dual-tree complex wavelet transform (DTCWT) pioneered by Kingsbury [111], illustrated in Figure 7. This complex transform has found applications in motion estimation, interpolation, denoising, and keypoint detection [112]. One problem with the original DTCWT transform is that despite its higher angular selectivity, the highpass channels do not lend themselves to easy orientation steering (i.e., altering only the angular tuning of the filtered response using outputs of filters at only a single scale). A recent modification of the tree [113] yields near rotation invariance, and consequently orientation steerability within any one scale (see Figure 8). This makes the patterns of coefficients very stable

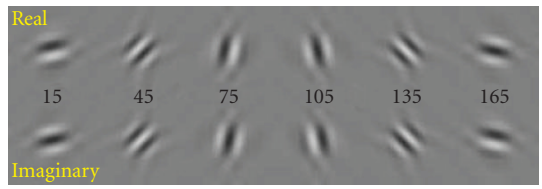

Figure 7: Impulse responses of original construction of Kingsbury's complex dual-tree wavelets.

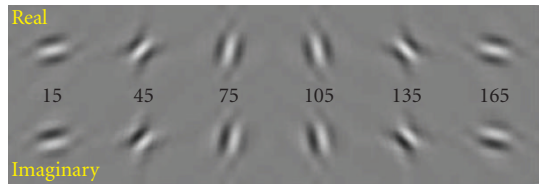

Figure 8: Impulse responses of original construction of Kingsbury's modified complex dual-tree wavelets. Note that as direction is altered, the number of cycles per envelope remains approximately constant, which is directly associated with the property of approximate rotation invariance.

under rotations, yet keeps the redundancy less than that of the fully shiftable, rotationally steerable framework of an undecimated construction, such as Freeman and Adelson's. Variations on these constructions have been pursued by Selesnick [114].

As mentioned earlier, the DTCWT has found applications in image denoising. Perhaps one of the best performing denoising systems is based on the steerable complex pyramid of Portilla et al. [115], where very high angular selectivity is used, by employing as many as 12 orientation channels. Another interesting demonstration of denoising by structural detection using the steerability properties of a steerable wavelet decomposition was suggested by Bharath and Ng [116]. Ng and Bharath have also shown that color opponent wavelet decompositions based on complex steerable wavelets permit the detection of perceptual boundaries [117], that is, both edges and line-line structures, even at single scales.

The parallels to V1 computation in the scale-space paradigm are formulated in terms of partial derivatives of a multiscale image representation, in which the original image lies "embedded" at the finest scale of this representation. First and pure second-order linear Cartesian derivatives are similar to symmetric and antisymmetric receptive fields of V1 neurons, although it is quite common in scale-space approaches to use isotropic Gaussian kernels as the scale-space generator.

The scale-space image representation also lends itself elegantly to defining derivatives in scale, which can be used to, for example, determine optimal scales for processing an image, by using the general principle that the scale/spatial location at which one finds a maximum magnitude of spatial derivative response provides an indication of the "optimal" scale for processing: see Seo and Yoo's [118] superb

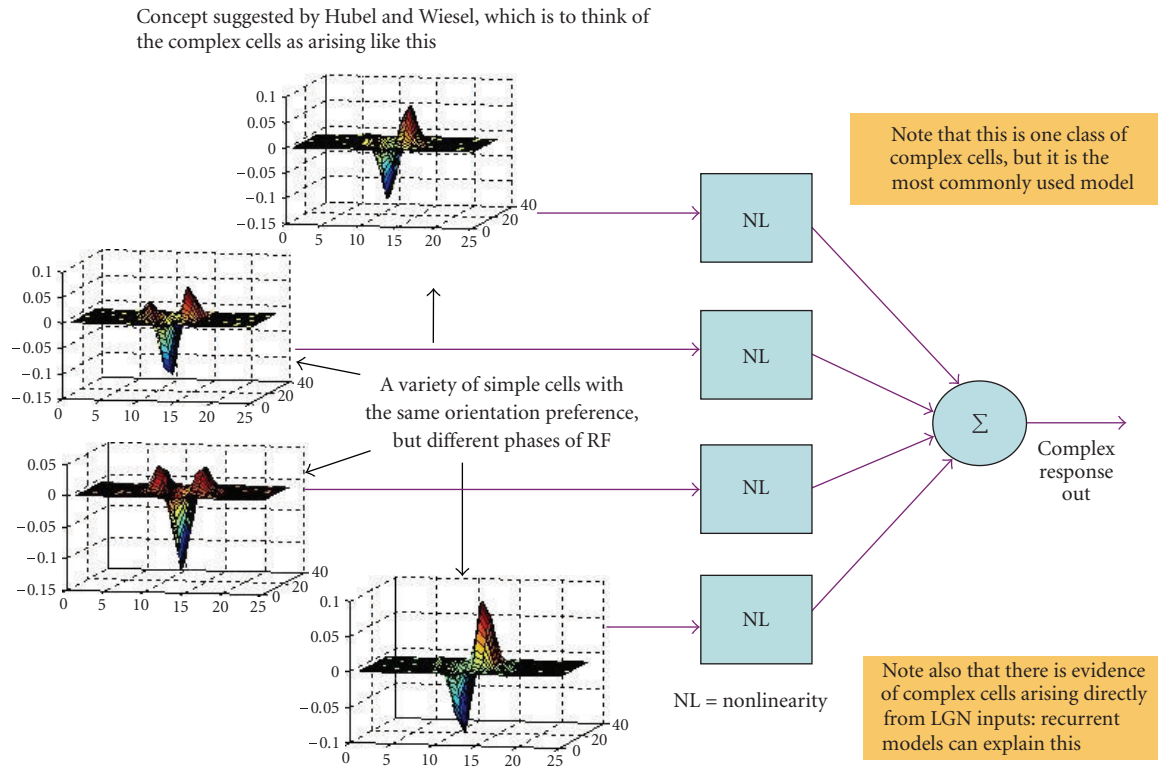

Figure 9: Generalized use of nonlinear combination of receptive fields over linear parameter variation to construct invariant feature measure. Note that the number of linear filters depends on parameter characteristics and sharpness of its tuning. For phase-invariant responses from quadrature filters, this reduces to two linear operators/directions.

illustration of this principle. See also [119] for a practical application in medical blood vessel segmentation.

The primary operators of both the scale-space and filter-bank paradigms are *linear* and these bear close relevance indeed to the spatial properties of many V1 receptive fields. However, the majority of V1 receptive fields is actually of a complex nature, by which is meant that usually display spatially phase-invariant properties [120], or other, possibly unspecified nonlinearities. Interestingly, there is a generic model for how such properties arise in biological vision, which is efficiently mirrored by signal processing. Thus, in order to "achieve" phase-invariant responses at one angle of orientation, one may use the model shown in Figure 9 (modified from [121]).

Note that for two phases of response that are in exact quadrature, the number of linear operators feeding into the nonlinearity in order to generate a phase-invariant response reduces to two, which are the in-phase and quadrature components. Note also, however, that an interesting generalization also emerges: in order to generate a phase- and orientation-invariant measure of the edge likelihood, one may "pool" responses over all phases and orientations, an interesting generalization.

It is clear that although there are close analogies to spatial processing operators in image processing and computer vision, there remain distinctions in existing spatial processing paradigms: temporal responses in existing image processing frontends are usually $\delta_1(k)$ functions (with k being frame/time index), whereas there are well-defined velocity tuning characteristics to most V1 neurons. This, we believe, represents a rich source of inspiration for operator design, and presents technical challenges, due to existing bandwidth shortcomings.

4.2. Theory and model of intracortical interactions in V1

There have been various attempts to model the intracortical interactions and contextual influences in V1 [122–125]. Since a network with recurrent interactions can easily have all kinds of stability problems, it is difficult to make a well-behaved model that does not generate unrealistic or hallucinative responses to input stimuli, even when the model focuses only on a subset of the contextual influences such as collinear facilitation [123]. Because of this, many models, for example [124, 125], do not include explicit geometric or spatial relationships between visual stimuli, and thus have limited power to link physiology with visual behavior.

Recently, aided by a dynamically well-behaved model, including cells tuned to various orientations and different spatial locations and both suppressive and facilitative contextual influences as in physiology, Li [27, 32–34, 126] proposed that contextual influences enable V1 to generate a saliency map based on visual input defined mainly by stimulus

contrast. The model consists of recurrent pairs of excitatory and inhibitory neurons with weighted connections to the output of orientation-selective complex cells and color-opponent centre-surround cells that simulate among others the effect of isoorientation inhibition, collinear enhancement, and color contrast to produce a saliency map; with locally translation-invariant neural tuning properties and intracortical interactions, V1 responses highlight the locations where translation invariance or homogeneity in input breaks down on a global scale. These locations can be at texture boundaries, at smooth contours, or at pop- out targets (such as red among greens or vertical among horizontals) in visual search behavior. The recurrent computation of the neurons in the model which produces a saliency response is analogous to a *max* operation on different feature saliency maps, whereas other models of saliency such as Itti et al. [127] have used *sum* operators. This theory links V1 physiology/anatomy with visual behavior such as texture segmentation [128], contour integration [129], and pop-out and asymmetries in visual search [130, 131], which have often been thought of as complex global visual behavior dealt with beyond V1. The model proposes that V1 performs the initial stage of the visual segmentation task through the saliency map, and such segmentation has been termed preattentive segmentation in the psychological community. It is termed "segmentation without classification (recognition)" in [33], which relates to the bottom-up segmentation in computer vision. This theory/model has generated testable predictions, some of which have been experimentally confirmed, such as color-orientation interference in texture segmentation [132] and the relationship between border saliency and figure-ground saliency effects [133].

In particular, saliency maps are believed to provide a fast mechanism to direct the focus of attention of the visual processing system and eye-fixations without having to wait for slower feedback information from the higher-level cognitive areas of the visual cortex. Saliency maps are useful for controlling pan-tilt zoom cameras and retinomorphic cameras capable of simultaneous image processing at different resolutions.

5. CONCLUSION

Neurophysiological and anatomical experiments have provided new insights into the functions of V1 neurons. The response of V1 cells has been shown to be more dynamic than previously believed. In particular, the spatial selectivities of V1 cells have been shown to undergo a temporal refinement process of the tuning curve from medium to high frequencies [53]. The underlying mechanism of V1 selectivity has also been shown to be more than a feedforward weighted-sum filtering (either linear or non-linear) of stimuli from the receptive fields [78]. Lateral connections between V1 neurons and feedback connections from higher cortical areas have been shown to affect the response of V1 cells, and more importantly, determine the role of V1 in high-level visual functions beyond feature detection and representation. The following material could be useful for further readings on the primary visual cortex. Wandell [12] provides a textbook style introduction to physiology and psychophysics of vision in general. Lennie [9] provides a review of V1 together with a proposal for its role in visual feature analysis in the context of functions of extrastriate areas. Martinez and Alonso [120] reviewed the properties and models regarding complex and simple cells. Schluppeck and Engel [134] reviewed and reconciled the conflicting evidence about color processing in V1 from optical imaging and single-unit recording data. Angelucci et al. [135] review the anatomical origins of intracortical interactions in V1, while Lund et al. [136] review the anatomical substrate for the functional columns. Reid [137] reviews V1 in a textbook chapter for neuroscience. Frégnac [138] reviews the dynamics of functional connectivities in V1 at both molecular and network levels.

We do not cover in this review the topic of development processes of V1, and only briefly cover plasticity and learning. However, the dynamical changes in the properties of V1 neurons and the plasticity of their responses to the immediate history of stimulus presentation, over timescales of milliseconds, in addition to the fact that the majority of retinal signals enter the visual cortex through V1, indicate that V1 may play a large role in the plasticity and adaptability of the overall perceptual process of seeing. Chapman and Stryker [139] review the development of orientation selectivity in V1, while Sengpiel and Kind [140] review the role of neural activities in development. The material in this review on the intra-cortical interactions and contextual influences are relatively recent, thus further developments and revised points of views on these aspects are expected. Furthermore, there is much interest regarding the possible role of V1 in higher-level cognitive phenomena. These phenomena include alternative or unstable perceptions (e.g., binocular rivalry when subjects perceive one image of the two different and inconsistent images presented to the two eyes), attentional blindness, visual awareness, or consciousness [141, 142].

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