1 Long-range Cortical Connections Give Rise to 2 a Robust Velocity Map of V1

3 Phillip Sheridan (corresponding author)

4 *School of Information and Communication Technology, Griffith University,*
5 *University Drive, Meadowbrook, Qld, Australia, p.sheridan@griffith.edu.au*

6 Abstract

7 This paper proposes a two-dimensional velocity model (2DVM) of the primary vi-
8 sual cortex (V1). The model's novel aspect is that it specifies a particular pattern
9 of long-range cortical temporal connections, via the Connection Algorithm, and
10 shows how the addition of these connections to well-known spatial properties of V1
11 transforms V1 into a velocity map. The map implies a number of organisational
12 properties of V1: 1) the singularity of each orientation pinwheel contributes to the
13 detection of slow-moving spots across the visual field; 2) the speed component of
14 neuronal velocity selectivity decreases monotonically across each joint orientation
15 contour line for parallel motion and increases monotonically for orthogonal motion;
16 3) the cells that are direction selective to slow-moving objects are situated in the
17 periphery of V1; and 4) neurons in distinct pinwheels tend to be connected to neu-
18 rons with similar tuning preferences in other pinwheels. The model accounts for
19 various types of known illusionary perceptions of human vision: perceptual filling-
20 in, illusionary orientation and visual crowding. The three distinguishing features of
21 2DVM are: 1) it unifies the functional properties of the conventional energy model
22 of V1; 2) it directly relates the functional properties to the known structure of the
23 upper layers of V1; and 3) it implies that the spatial selectivity features of V1 are
24 side effects of its more important role as a velocity map of the visual field.

25 Keywords: Gabor filter, contextual modulation, velocity model, primary visual
26 cortex, orientation pinwheels, motion streaks

27 1 Introduction

28 The most casual observations of biological vision systems invariably lead to
29 the conclusion that the ability to predict an object's velocity is fundamental to
30 vision. In simple terms, in the absence of motion in the animal world, nobody
31 eats or gets eaten. Ever since the Cambrian explosion, that period of earth
32 history where the number of phylum increased from four to 38 and when the

33 genetic code for vision first appeared, velocity estimation from visual inputs
34 has been driving an evolutionary arms race [1].

35 1.1 *Visual Perception of Motion*

36 The intensity of vision research over the past few decades has reflected the
37 importance of understanding how biological vision systems reliably perceive
38 motion. Although computational models of velocity have undergone substan-
39 tial development, empirical experiments continue to reveal new properties of
40 the vision system that are not accounted for by these models. Central to this
41 and other papers is the concept of the receptive field (RF) which we interpret
42 as: a position in the visual field that, if a stimulus is placed there, will excite
43 a population of neurons in V1. Experiments on single neuron responses of
44 cats to certain types of motion reported in [2] produced surprising response
45 properties of V1 cells to two types of object motion: the first type had objects
46 moving quickly parallel to the RF's orientation (parallel motion); the second
47 type had the objects moving slowly orthogonally to the RF's orientation (or-
48 thogonal motion). Although they reported that cells had the same temporal
49 frequency response to both types of motion, to the former type, cells tended to
50 be selective to motion direction and band pass selective to spatial frequency,
51 while to the latter, the same cell tended to be non-selective to motion direction
52 and low pass selective to spatial frequency.

53 Two investigations of the orientation tuning curves of simple and complex
54 cells in response to moving and flashing bars of different lengths produced
55 results that were seemingly at odds with each other. The conclusion reported
56 in [3] was that the orientation tuning curve was always unimodal (i.e. it ex-
57 hibited just a single peak corresponding with the cells optimal orientation)
58 whereas the shape of the orientation curve was markedly dependent on the
59 length of the bar, the curve sharpening with increasing length. These results
60 implied that, if the bar length was reduced to a moving spot, the optimal
61 direction was unchanged and remained orthogonal to the longer axis of the
62 RF. In contrast, results reported [4] that the optimal direction for a small spot
63 was generally orthogonal to that of a long bar. Hence, a cell responded to two
64 perpendicular axes of movement: the first for long bars, which was perpendic-
65 ular to the preferred orientation, i.e. perpendicular to the long axis of the RF
66 (orientation component); the second for short bars or spots, parallel to the
67 preferred orientation (axial component). At an intermediate bar length, the
68 two axes of movement might coexist. Two distinct models were employed to
69 account for these apparent divergent results [5].

70 A third category of intriguing experiments investigated the perception of visual
71 illusions. Results reported in [6] showed that long, drifting lines could activate

72 a V1 neuron even when the RF of that neuron was covered by a mask many
73 times the size of the RF (perceptual filling in). Another set of experimental
74 results reported in [7] revealed the perception of illusory orientation. When
75 a moving bar orientated obliquely to its parallel motion was presented to an
76 observer, two related phenomenon were demonstrated: 1) with the bar length
77 held constant, the perceived orientation approached the parallel direction of
78 motion as the speed increased; 2) with the speed held constant, the perceived
79 orientation approached the actual orientation of the bar with increasing bar
80 length. Consequently, they concluded that V1 neurons did not act as feature
81 detectors that isolate individual stimulus attributes. A third visual illusion is
82 a variation on the visual crowding phenomenon reported in [8].

83 1.2 Overview of Model

84 It has been shown that models representing variations on the standard energy
85 model [9] and [10] successfully demonstrated the inter-dependency between
86 attributes of orientation, spatial frequency, temporal frequency, length, speed
87 and direction. These spatial characteristics are used to predict purely func-
88 tional aspects of V1 neurons. The model presented in this paper, named 2-D
89 Velocity Model (2DVM), extends this energy paradigm by relating neuronal
90 function to the structure of Layer 2/3 of V1 via a novel Long Range Corti-
91 cal Connection Algorithm. Two important structural aspects of Layer 2/3 of
92 V1 are central to 2DVM: 1) a local structure of patches of neurons known as
93 pinwheels describe a pattern of neuronal orientation preferences and spatial
94 frequency preferences; 2) a global structure is implied by the pattern of con-
95 nectivity of long-range cortical connections between pinwheels. 2DVM thus
96 represents a structural as well as a functional velocity model of the primary
97 visual cortex.

98 The properties of 2DVM, to be discussed later, are summarized as follows:

- 99 • *Functional properties that 2DVM was designed to account for include:*
 - 100 • Velocity selectivity: different cells in a local map respond optimally to
 - 101 stimuli moving at unique velocities;
 - 102 • Suppression/facilitation: responses of cells lying along an orientation con-
 - 103 tour line are suppressed by cells in the same relative position in local
 - 104 maps orthogonal to the cells preferred orientation and tend to be excited
 - 105 by cells in the same relative position in local maps aligned with the cell's
 - 106 preferred contour line;
 - 107 • Orthogonal pair selectivity: cells are selective to orthogonal velocity pairs,
 - 108 fast moving in the parallel direction and slow moving in the orthogonal
 - 109 direction;
 - 110 • Orientation selectivity: different cells within a local map respond prefer-

111 essentially to stimuli of different orientation. Cells responding to stimuli of
 112 the same orientation lie along iso-orientation lines radiating from a cell
 113 with no preferred orientation, known as the singularity;
 114 • Spatial frequency selectivity: different cells lying along an orientation con-
 115 tour line of a local map respond preferentially to different spatial frequency
 116 where the singularity has a preference for the lowest spatial frequencies;
 117 • Bar length selectivity: cells are selective to bar length.
 118 • *Structural properties that 2DVM was designed to account for include:*
 119 • At the global scale, the location of each pinwheel is associated with a
 120 position in the visual field;
 121 • At the local scale, each point in a pinwheel is associated with a particular
 122 orientation, frequency and velocity.

123 In addition to the intended design effects, the model also produced the follow-
 124 ing:

- 125 • *Side effects of the model's design that coincide with known properties of V1*
 126 *include:*
 - 127 • Neurons tend to be direction selective to parallel motion;
 - 128 • Neurons tend to be non-direction selective to orthogonal motion;
 - 129 • Perceptual filling in: drifting lines can activate a V1 neuron even when
 130 the neuron's associated RF is occluded by a mask many times its size;
 - 131 • Illusionary orientation: when a perceived orientation of a stimulus is at-
 132 tracted towards the direction of its motion.
- 133 • *Side effects of the model's design that predict structural properties of V1*
 134 *that are as yet untested by empirical experiments:*
 - 135 • The speed component of neuronal velocity selectivity decreases monoton-
 136 ically across each joint orientation contour line for parallel motion and
 137 increases monotonically for orthogonal motion;
 - 138 • The neurons that are direction selective to slow-moving objects are situ-
 139 ated in the periphery of V1.

140 *Assumption:* Theory predicts that when an image moves with sufficient speed
 141 across the visual field, the captured image (or neural image) becomes smeared
 142 due to the temporal integration properties of the retinal receptors. [11]. The
 143 perception of these effects, such as the patterns produced by waving a sparkler
 144 against the night sky, is known as motion streaks. 2DVM's design is predicated
 145 on the assumption that motion streaks are projected into V1.

146 Three key features of 2DVM are: 1) it unifies the functional properties of the
 147 conventional energy model of V1; 2) it directly relates the functional properties
 148 to the known structure of the upper layers of V1; and 3) it makes predictions
 149 about as yet untested hypotheses of V1.

151 This paper is structured as follows: in Section 2 we outline the background
 152 information that underpins the development of 2DVM, in Section 3 we provide
 153 the mathematical formulation of the model, and Section 4 focuses on what
 154 the model does by presenting simulation results for key response properties
 155 of 2DVM. Section 5 discusses implications of the model and the paper is
 156 summarized and concluded in Section 6.

157 **2 Background**

158 In this section we provide the background information that underpins the de-
 159 velopment of 2DVM. The spatial responses to oriented stimuli of neurons in
 160 the primate V1 have been known for some time [12]. Since then, it has been
 161 generally accepted that these tuning functions of RFs were largely context in-
 162 dependent [13]. More recent research has demonstrated contextual influences
 163 from the region close to the RF [14], [15], [16]. The near surround region of an
 164 RF can modify RF responses through suppression, [17] by collinear facilita-
 165 tion [18] and by cross-orientation facilitation effects [19], [15], [20]. While the
 166 mechanisms underlying the modulating effects of suppression and facilitation
 167 immediately surrounding the region of an RF are pretty well understood, the
 168 modulating effects of long-range influences have not as yet received the same
 169 degree of attention. However, the evidence for long-range contextual modu-
 170 lation is increasing, e.g. [21], [22], [23], [24], and has important implications
 171 for the organization of V1. The Local-Global Map hypothesis [25] states that
 172 orientation pinwheels constitute fundamental building blocks in Layer 2/3,
 173 which together describe the global organization of cortical cell response prop-
 174 erties. This concept was further developed in [26] where an abstraction of the
 175 orientation pinwheels, called local maps, that tile V1 at the scale of the pin-
 176 wheel demonstrate how functional units of contextual modulation are related
 177 to orientation pinwheels. It was hypothesized that these local maps might also
 178 have significance for other response properties in V1. The velocity model pre-
 179 sented in this paper extends the Local-Global Map hypothesis to show how
 180 the spatial properties predicted by the local map are fundamental building
 181 blocks to a velocity map of V1.

182 2DVM draws heavily on the concept of the Gabor function to implement this
 183 velocity map. The response properties of neurons in V1 have been shown to be
 184 well modelled by convolving the input image with a family of Gabor functions
 185 [27]. Further, research has shown that the upper layers of Area V1 are modelled
 186 well by a multi-dimensional Gabor space [28]. Most of the multi-dimensional
 187 Gabor space models of V1 described to date employed short-range convolu-

188 tions at the scale of the RF [29], [30], [31], [32]. By contrast, 2DVM extends
 189 the Gabor space paradigm by incorporating both long-range and short-range
 190 contextual modulation. Although there are many inputs via short-range con-
 191 nections from cells close to a particular local map, the inputs via long-range
 192 connections from distant ones are the means by which the high velocity selec-
 193 tivity embodied in this model is achieved.

194 3 Methods

195 This section presents a formal mathematical description of 2DVM. We will
 196 first describe the basic spatial model that employs one cycle of a plaid pat-
 197 tern to produce a Gabor response function. Then we will show how this can
 198 be extended to include temporal suppression and facilitation to describe a
 199 computational velocity model of V1.

200 3.1 Base (Spatial) Model

The classic Gabor response function is the product of a sinusoidal, known as the carrier (car), and a Gaussian, known as the envelope (env). 2DVM employs a variant of the classic Gabor function, named One-Cycle-Plaid-Gabor function (OCP-Gabor). The (car) of OCP-Gabor is a plaid pattern. This is the product of a pair of orthogonally orientated sinusoidal gratings. Fig. 1 displays an example of a plaid pattern, where the top two images are the orthogonal sinusoidal components of the plaid and the bottom left image is the plaid that results from the product of those top two images. A plaid pattern can be defined formally as follows:

$$\begin{aligned}
 S_{ew} &= \cos(2\pi F_{ew}(x \cos(\omega_0) + y \sin(\omega_0)) + \phi_{ew}) \\
 S_{ns} &= \cos(2\pi F_{ns}(x(-\sin(\omega_0)) + y \cos(\omega_0)) + \phi_{ns}) \\
 201 \quad car(x, y, F_{ew}, F_{ns}, \omega_0, \phi_{ew}, \phi_{ns}) &= S_{ew} S_{ns} \tag{1}
 \end{aligned}$$

$env(x, y, \theta, \sigma_{ew}, \sigma_{ns},) = Kexp(-\pi(\sigma_{ew}^2(x - x_0)_\theta^2 + \sigma_{ns}^2(y - y_0)_\theta^2))$, where

$$(x - x_0)_\theta = (x - x_0) \cos(\theta) + (y - y_0) \sin(\theta)$$

$$(y - y_0)_\theta = -(x - x_0) \sin(\theta) + (y - y_0) \cos(\theta)$$

202 The response function of OCP-Gabor, $g()$, is then:

$$203 \quad g(x, y, \theta, \sigma_{ew}, \sigma_{ns}, F_{ew}, F_{ns}, \omega_0, \phi_{ew}, \phi_{ns}) = env \times car \tag{2}$$

204 where:

- 205 • F_{ew}, F_{ns} : spatial frequencies of the east-west (ew) and north-south (ns) sinusoidal carrier
- 206
- 207 • ω_0 : angle of orientation of the plaid pattern
- 208 • ϕ_{ew} and ϕ_{ns} : phase of the east-west (ew) and north-south (ns) components
- 209 of the plaid carrier
- 210 • K : scale of the magnitude of the Gaussian envelope
- 211 • θ : rotation angle of Gaussian envelope
- 212 • $(\sigma_{ew}, \sigma_{ns})$: scale of the two axes of the Gaussian envelope
- 213 • (x_0, y_0) : location of the peak of the Gaussian envelope

214 Fig. 1, displays an example of the OCP-Gabor where the bottom left image
 215 represents the carrier and the bottom right represents the product of the
 216 carrier with a Gaussian envelope. Note that this is subtly but importantly
 217 different from the classical Gabor function. While both the single sinusoidal
 218 carrier and one cycle of the plaid result in an OCP-Gabor function that has
 219 an orientation and spatial frequency preference, a one cycle plaid also induces
 220 a preference for bar length. This preference is a mathematical consequence of
 221 choosing the envelope so that it covers one cycle in the preferred direction of
 222 orientation. We note that our choice of the Gaussian parameters restricts the
 223 effect of the plaid to one cycle in the orthogonal direction. Consequently, the
 224 resulting Gabor function is only selective to one cycle of the plaid and not
 225 selective to the full plaid pattern. Therefore, OCP-Gabor does not contradict
 226 the well-known result that MT neurons are selective to the motion of complete
 227 plaid patterns and V1 neurons are not [33].

We define a Gabor field, $GF()$, as the convolution of an input signal, $i(x, y)$, with a OCP-Gabor response function as follows:

$$GF_{i, \theta, \sigma_{ew}, \sigma_{ns}, F_{ew}, F_{ns}, \omega_0, \phi_{ew}, \phi_{ns}}(x, y) = i(x, y) * g(x, y, \theta, \sigma_{ew}, \sigma_{ns}, F_{ew}, F_{ns}, \omega_0, \phi_{ew}, \phi_{ns})$$

228 With this OCP-Gabor field defined, we now assemble a family of Gabor fields
 229 employing the following notation:

- 230 • $roi(p, q)$: represent a disc of a fixed radius centred on p and q
- 231 • I : a set of input signals (visual field)
- 232 • Ω : finite and discrete set of coordinate pairs (p, q)
- 233 • Θ : a set of orientation angles represented as real values
- 234 • B : a set of Gaussian scales represented as real values.
- 235 • Φ : $((0, \pi/2), (0, -\pi/2), (\pi/2, 0), (-\pi/2, 0))$, a set of four ordered pairs of real
- 236 values that represent the phase of the east-west and north-south components
- 237 of the plaid carrier

From this we define a mapping:

$$2DVM : (I, \Omega, \Theta, B, \Phi) \Rightarrow R^4$$

238 as

$$2DVM(i, p, q, \theta, \sigma_{ew}, \sigma_{ns}, F_{ew}, F_{ns}, \phi_{ew}, \phi_{ns}) = \sum_{x, y \in roi(p, q)} GF_{i, \theta, \sigma_{ew}, \sigma_{ns}, F_{ew}, F_{ns}, \omega_0, \phi_{ew}, \phi_{ns}}(x, y) \quad (3)$$

240 Throughout the remainder of this paper, we will adopt the convention that ω_0
241 has the same value as θ with $x_0 = y_0 = 0$.

242 Although the 2DVM output space possesses four dimensions (two prescribing
243 the internal spatial layout of the local maps, and two prescribing the spatial
244 layout of the collection of local maps), it can be represented very naturally in
245 two dimensions. This is similar to Layer 2/3 of Area V1, which is conceptually
246 a multi-dimensional space but it is organized physically as a two-dimensional
247 sheet of neurons [34], [35], [36]. Layer 2/3 appears as a patchwork of struc-
248 tures known as orientation pinwheels or local maps, a structure that is in-
249 tegral to this model. Each orientation pinwheel has a singularity from which
250 iso-orientation contour lines project. The term singularity identifies the conflu-
251 ence of the pinwheel's iso-orientation contours and thus possesses no preferred
252 orientation. Each orientation pinwheel is associated with an RF [37]. When
253 an orientated stimulus is presented to the visual field, orientation pinwheels
254 associated with the RF that the stimulus input signal is projected onto will a
255 evoke strong response along the preferred iso-orientation contour [38]. Layer
256 2/3 of Area V1 is composed of approximately 10,000 orientation pinwheels [39].
257 Fig. 2 depicts this organizational structure where it can be observed that the
258 orientation contours span 180 degrees. We adopt the convention in this paper
259 that when we refer to the physical collection of neurons that are organized as
260 a pinwheel-like structure we employ the term 'pinwheel' and when we refer to
261 the properties attributed to these neurons, we use the term 'local map'. It was
262 suggested in [25] that these pinwheel contour lines be modelled by a uniform
263 spread of angles over 360 degrees. Taking a local map in isolation, the contour
264 lines of the pinwheels possess 180 degree symmetry (Fig. 2). However, in the
265 context of the global map and for the purposes of the velocity model of this
266 paper, we require an additional property that is implied in a figure reported in
267 [40] and displayed in Fig. 2, one of 90 degree symmetry globally. To this end,
268 we divide a circle into four quadrants. Label the four sectors as West, North,
269 East and South to reflect their relative positions to each other. In the West
270 sector, we place the contour lines depicted in the left half of Fig. 2 so that the
271 angle of each contour line as determined by the coordinate system coincides
272 with its preferred orientation. In the East sector, (right half of Fig. 2) the an-
273 gle of each contour line as determined by the coordinate system is orthogonal
274 to its preferred orientation. Note that the North and South sectors are devoid

of contour lines and that the West and East segments of every straight line passing through the singularity represent orthogonal orientations. This is an important property of our model that we will return to shortly. A discrete form of these relations is depicted in Fig. 3 with the following interpretation:

- The singularity is depicted by the darkened cell in the centre
- Each of the cells containing a pair of numbers represents a point along a contour line where:
 - the first number represents its position out from the singularity
 - the second number represents the angle (degrees) of the contour line it lies on
- The cells that contain a dash (–) are inactive.

In 2DVM, we associate each pair of numbers in the cells of Fig. 3 with a particular OCP-Gabor function in the following manner: the specified angle of each cell determines the angle of orientation of the carrier and envelope, ω_0 of Eq. 2. The other number of the pair, which specifies the cell's position out from the singularity, determines the values of the four parameters, two governing the plaid's spatial frequency and two, the Gaussian's spread, as follows: let $1/k$ denote a spatial frequency for some positive integer k . Let F_{ew}^i and F_{ns}^i represent the F_{ew} and F_{ns} and let σ_{ew}^i and σ_{ns}^i represent the σ_{ew} and σ_{ns} respectively of Eq. 2, of the i th cell out from the singularity. Let the F_{ew} and F_{ns} values in the West sector be given by:

$$F_{ew}^i = 1/(k2^i), F_{ns}^i = 1/(k2^{-i})$$

$$\sigma_{ew}^i = k2^{i+1}, \sigma_{ns}^i = k2^{-(i+1)}$$

and their counterparts in the East sector be given by:

$$F_{ew}^i = 1/(k2^{-i}), F_{ns}^i = 1/(k2^i)$$

$$\sigma_{ew}^i = k2^{-(i+1)}, \sigma_{ns}^i = k2^{(i+1)}$$

This specification of parameters has the effect of associating a unique OCP-Gabor response function with each cell of a local map. A few examples of the OCP-Gabor function associated with cells of a local map are displayed in Fig. 4 where each of the six images represents an intensity map of an OCP-Gabor function. In this figure, the six sub-images all display distinct preferences: *Top*: left for the narrow light/dark edge of a long motion streak; right for its associated wide light/dark edge; *Middle*: left has preference for the narrow light/dark edge of a shorter motion streak; right is its associated low pass wide light/dark edge; *Bottom*: left for the light/dark edge of a horizontal pair of spots; right is its associated light/dark vertical edge; *top two pairs*: for horizontal orientation; *bottom pair*: no orientation preference; *left-hand filters of top two pairs*: band-pass; *right-hand filters of those*: low-pass; *bottom of three*

313 *pairs*: will give the strongest relative response to the lowest spatial frequency.
 314 These spatial preferences are consistent with the empirical results derived in
 315 [41]; [42].

316 In summary of the main features of the spatial aspects of 2DVM, we observe
 317 that: 1) the novel aspect of the spatial component is that it employs a plaid
 318 function as the carrier of its OCP-Gabor functions; 2) the global organization
 319 of the model is a tiling of pinwheels that mimic the topological organization
 320 of the visual field.

321 3.2 *Velocity (Temporal) Extension*

322 Our base model is a purely spatial model of Layer 2/3. The cells of the local
 323 maps have been designed to be selective to orientation, spatial frequency and
 324 bar length. In addition, the parallel component of each cell is a band-pass
 325 filter for frequency and the orthogonal component is a low-pass filter. 2DVM
 326 transforms this spatial model into a velocity model using a novel Connection
 327 Algorithm. To this end, consider a pattern of inter-local map connectivity
 328 described as follows: each cell along each contour of each local map possesses
 329 connections to cells in the same relative position in four other local maps.
 330 The four connected local maps are determined by the orientation line and its
 331 distance from its singularity, i.e. the two quantities specified in the cells of
 332 Fig 3. The end points of each set of four connections are determined by the
 333 following Connection Algorithm.

334 **Connection Algorithm** Given a cell (current cell) lying on a particular
 335 orientation contour line of a particular local map (current local map):

- 336 (1) Enumerate the cells along the contour line out from the local map's sin-
 337 gularity.
- 338 (2) Let n represent the number of cells in the orientation contour line and p
 339 the position of the current cell out from the singularity.
- 340 (3) Enumerate the local maps on either side of the current local map that lie
 341 along a line passing through the singularity and orientated as the cell's
 342 orientation contour line.
- 343 (4) Count $(n+p)$ local maps out from the current local map in both directions
 344 and connect the current cell to a cell in a similar position in each of these
 345 two local maps.
- 346 (5) Enumerate the local maps on either side of the current local map that lie
 347 along a line passing through the singularity and orientated orthogonally
 348 to the cell's preferred angle of orientation.
- 349 (6) Count $(n-p+1)$ local maps out from the current local map in both direc-
 350 tions and connect the current cell to a cell in a similar position in each

of these two local maps.

An example of the connectivity pattern generated by the Connection Algorithm is depicted in Fig 5. The figure displays the simplest case of the connections associated with a single contour line that consists of five cells. An important feature of the connectivity pattern established by this algorithm is that it relates the global distribution of local maps to the local structure of each local map in a disciplined manner. Specifically, if we consider the sequence of cells that span a given joint contour line of a local map, it can be observed that the cell located at the left-hand end is connected to the local map furthest away in the parallel direction. (In Fig. 5, note the yellow line connecting Cell 5A to 1A.) The second cell from the end is connected to the second furthest local map in the parallel direction. This pattern is continued for each subsequent cell along the line across the singularity to the opposite end of this joint contour line. At the extreme right-hand end of this sequence, the last cell is connected to the closest local map in the parallel direction. (In Fig. 5, see red line connecting 5E to 4E.) As the mirror image of the connectivity pattern also applies, each cell possesses four-way connectivity, thus the local map's connectivity possesses 90 degree symmetry.

The model also specifies these connections as being excitatory over one unit of time. That is, each cell at the current time receives inputs, through these connections, from four cells at the preceding time slice, two from the parallel direction and the other two from the orthogonal direction. The parallel connections transmit the response to a moving bar's narrow edges and the orthogonal connections transmit the responses to a moving bar's long edges. The non-singularity edge detectors have aspect ratios greater than one, while the singularity has an aspect ratio value of one and a preference for the lowest spatial frequencies in its local map. In our model, each singularity is associated with four OCP-Gabor filters, each associated with a phase pair, (ϕ_{ew}, ϕ_{ns}) , as specified in Φ . Although the net effect is a non-preferential spatial orientation response, the effects on the velocity maps are significant. Individually, each filter will respond differently to the edge bordering a light/dark or dark/light pair of spots aligned horizontally or vertically. The role of this set of four Gabor filters in our model is to detect slow-moving spots that would otherwise be undetectable by the filters with aspect ratios greater than one. The need to include this property results from the anatomical evidence that shows that intrinsic connections to and from singularities are predominantly of short-range, whereas long-range intrinsic connections arise between iso-orientation domains [43]; [44].

Another issue the Connection Algorithm addresses is keeping track of the individual stimuli when multiple stimuli move across the visual field at the same velocity, such as each bird in a flock or each plane flying in a formation, the correspondence problem. Our model deals with this by employing the well-

known phenomenon of suppression/facilitation. Surround suppression is the name given to the inhibitory modulating effects of similarly-orientated stimuli in the near surround of an RF. Collinear facilitation is the facilitatory effect that co-orientated stimuli situated in the near surround of an RF can have on the neuron associated with that RF. We specify an additional set of inhibitory/excitatory connections with the Connection Algorithm to address this aspect of the correspondence problem. Specifically, as well as propagating the signal to a local map in the subsequent time slice, the additional connections also propagate the signal to the local map at the same time slice. The cells lying along parallel contour lines are propagated in an inhibitory manner while cells along aligned contour lines are propagated in an excitatory manner. The parallel components induce surround suppression and the aligned components induce collinear facilitation. In order to ensure that only internal members of a group of stimuli are suppressed/facilitated, the weights of these connections are determined dynamically depending on the state of the surround area. There are many ways in which these weights can be formulated [29]. In this paper, we employ a simple mathematical tool to produce a maximum weight (inhibitory/excitatory) when the two incoming signals are perfectly balanced achieving a value of $1/4$. The weight's magnitude decreases with increased imbalance. This connection weight is expressed mathematically as:

Let r_1 represent the response received from one of the orthogonal connections and r_2 the response from the opposite connection. The weight is given by $((r_1/(r_1 + r_2))(r_2/(r_1 + r_2)))$. It can be observed that this product is a maximum, with a value of 0.25, when $r_1 = r_2$ and is a minimum when r_1 or $r_2 = 0$.

The final local step for each cell receiving inputs from two distinct time slices, before summing these inputs, is to apply the function $pLog()$ to the inputs, which returns the logarithm of the input if the input is greater than one and zero otherwise. The effect of $pLog()$ ensures that unusually large values do not exert too large an influence on the velocity computation. The final global step is to perform a half-wave rectification on the signal. This process has the effect of ignoring any small values and is a component of many models of V1 [2].

3.3 Summary of Velocity (Temporal) Connections

The Connection Algorithm was employed to specify two sets of inter-local map connections within V1. One set connected local maps across time slices in a purely excitatory manner. The other set connected local maps within the same time slice and was a combination of inhibitory orthogonal connections and

excitatory parallel connections. The combined effects of the spatial selectivity properties with the time-synchronized excitatory connections transmitting the outputs of bar/edge detectors from the base spatial model are summarized as follows. The presentation of a stimulus to an RF will evoke a response by the cells in the RF's associated local map. However, the strongest response will be by the cell whose preferred orientation and preferred spatial frequency is closest to that of the presented stimulus. The temporal connections will then propagate these responses to the population of local maps according to the connectivity pattern previously described. If the stimulus then moves to another RF in the visual field in the next unit of time, a similar response at this new local map will be made. At this point in time, the local map's cells receive inputs via their connections and this value is summed with its current value. All non-zero values represent a measure of the stimulus change in location (distance and direction) over one unit of time. Of these, the cell with the peak response establishes the stimulus velocity at the current time. Moreover, as a result of the 90 degree symmetry of connectivity, the cell with the strongest response will represent an estimate of four possible stimulus velocities.

The key features of the temporal aspect of 2DVM are: 1) the Connection Algorithm, which specifies a pattern of connectivity between cells in distinct local maps; 2) this pattern also specifies the global organization of V1.

3.4 *Implementation*

In this section, we briefly discuss an important feature of the particular implementation of 2DVM employed to generate the simulation results reported in the next section. Although the organization of V1 can be represented in polar coordinates, a more convenient and efficient data structure is Spiral Honeycomb Image Algebra (SHIA) [45], [46]. SHIA is finite and discrete, allowing it to more closely model the properties of the layered structure of V1. These two properties allow SHIA to eloquently capture and manipulate the multi-dimensional aspects of the layers of V1 that are awkwardly achieved in polar coordinates. Another attractive feature of SHIA pertinent to 2DVM is that it facilitates the interactions inherent in the global-local structure. That is, both the relationships between cells as part of the global map and the cell as part of a local map are captured with an algebraic operation of vector multiplication. This feature is particularly useful when manipulating the pattern of inter-local map connectivity as described above. Note, the shape displayed in the boundary of the local and global maps of 2DVM is a side-effect of the hexagonal data structure and is not directly pertinent to the modelling presented in this paper. Consequently, the reader is cautioned not to be side-tracked by an unintended meaning of the patterns produced by these borders.

472 The implementation of 2DVM that produced the results reported in this paper
473 along with Java source code is available in a software package named VisioLab
474 from the following website: <http://www.ict.griffith.edu.au/sheridan/>.

475 4 Simulation results

476 In this section we present simulation results to demonstrate various aspects of
477 2DVM. In the first subsection we show that 2DVM achieves its key design goal
478 of modelling V1 as a velocity map. The second subsection presents simulation
479 results that demonstrate how the model addresses three types of visual illusion
480 important to human vision.

481 4.1 *Velocity Selectivity*

482 The results below demonstrate three important features of the model: 1) or-
483 thogonal pair selectivity: cells are selective to orthogonal velocity pairs, fast
484 moving in the parallel direction and slow moving orthogonally, 2) velocity
485 tuning varies monotonically across joint iso-contour lines, and 3) direction se-
486 lectivity: where cells that respond to parallel motion tend to be selective to
487 direction while cells responding to orthogonal motion do not.

488 Two figures presented in this section, 6 and 7, display distinct velocity re-
489 sponses but have a common format. As this common format is somewhat
490 complex, the reader is advised to carefully consider the remainder of this para-
491 graph to understand the intended features of the simulation results displayed.
492 Each row of three sub-images of each figure has the following interpretation:
493 the image on the left, the fractal-like border of the dark region represents the
494 boundary of the simulated visual field, and the circles identify the location of
495 49 simulated RFs that we denote with rf in the model. The image displays two
496 oriented bars which are half a cycle of a sinusoid of frequency $1/32$ cycles/pixel
497 wide. This frequency is set to the singularity's preferred spatial frequency. The
498 bar, labelled A, is positioned at one of the rfs and represents the initial position
499 of the simulated stimulus. The bar, labelled B, represents its new location one
500 unit of time later. Therefore, we interpret the difference of the two locations
501 as velocity. For example, the upper left image of Fig. 6 represents a change of
502 stimulus position from the rf located at the 10 o'clock position to 4 o'clock.
503 Note that this distance represents the length of the straight line segment con-
504 necting the two rfs and intersects three other rfs . Consequently, we say that in
505 this case the stimulus has moved a distance spanning five rfs . The challenge
506 of simulating a motion streak is dealt with using an elongated bar. We define
507 fast moving as more than two rfs . Consequently, when the motion is more

508 than two rfs, we choose to represent this as an orientated bar parallel to the
509 direction of motion.

510 The parameterization of 2DVM employed to generate the results discussed in
511 this section is: number of local maps = 49; number of cells in a local map
512 = 49; singularity spatial frequency = $1/32$ cycles/pixel. For this parameter-
513 ization, the second and third images of each row display the model output
514 from the associated input. In these images, the fractal-like borders identify
515 the boundaries of the simulated global velocity map and simulated local map.
516 The centre image displays the activation levels of the cells of a particular local
517 map. For example, in the middle image Row 1 of Fig. 6 it can be observed
518 that the cell with the highest activation level within the local map has value
519 11.1 and is located in the 9 o'clock position two cells out from the centre cell.
520 All other cells of that local map possess values less than 6.0. The right image
521 depicts the global output signal (49 local maps) and is an intensity map where
522 the brightness of a pixel represents the activation level: light pixels indicate
523 high activation and dark pixels indicate low activation. All 49 local maps are
524 displayed with each map's singularity depicted by a mark. For example, in
525 the right image of Fig. 6 Row 1, observe that the most activated local map
526 is centred on the mark in the 4 o'clock position of the global map. The ac-
527 tivation values of this local map are displayed in the centre image where, it
528 can be seen, the brightest pixel in the global map corresponds to the cell with
529 activation value 11.1. The pixels displaying low brightness correspond to the
530 activation levels in the range (2.3, 5.8). All other cells of the global map are
531 dark, which mean their activation levels are close to zero.

532 Although 2DVM can be applied to an arbitrary number of rfs, the examples
533 have been parameterized to 49 rfs and therefore 49 local maps. It can also be
534 observed that this parameterization implies that each local map is also com-
535 posed of 49 cells, 24 of which are identified with orientation contour lines. In
536 the simulated velocity map, the singularities correspond on a one-to-one basis
537 with the rf of the visual field and possess the same spacing as the rf. This
538 spacing property is purely intended to facilitate the reader's ability to relate
539 each local map with the appropriate rf and is not a property of the model it
540 depicts. The local maps are organized such that the speed component of veloc-
541 ity tuning varies monotonically across a joint orientation contour line whereas
542 direction varies according to a cells preferred orientation. This local-global
543 structure is revealed in our investigation of the following four pairs of velocity
544 scenarios.

545 The first set to be considered is that of a stimulus moving horizontally at the
546 highest detectable speed as displayed in Fig. 6 Row 1, and of a bar moving
547 orthogonally at the slowest detectable speed as displayed in Fig 6 Row 2.
548 The image in Row 1, left, of Fig 6 indicates that the stimulus bar is in an
549 rf at the left edge of the field. After one unit of time, the image indicates

550 that the stimulus has arrived at an rf at the right-hand edge of the field.
 551 The activation levels on the local map associated with this rf (middle image)
 552 indicate that the cell with the highest value (11.1, shaded for clarity) is located
 553 at the left end of the horizontal contour line. The intensity values of this local
 554 map and the other 48 local maps are displayed in the global velocity map,
 555 right. In this parameterization of the model, there are four cells, not counting
 556 the singularity, lying along the joint horizontal contour line. The fact that
 557 the most activated cell (value 11.1) lies at the end of the contour line means
 558 that, according to our model, the stimulus has either moved four rfs in the
 559 parallel direction or one rf orthogonally. To illustrate this point, consider the
 560 velocity scenario depicted in Row 2 of Fig. 6. In the left sub-image, it can
 561 be observed that the stimulus has moved one rf orthogonally to the cell's
 562 preferred orientation. The middle and right sub-images indicate that the most
 563 activated cell is the same one as displayed in Row 1. Therefore, this particular
 564 cell has responded to both a fast-moving spot in the parallel direction and a
 565 slow-moving bar in the orthogonal direction and thus constitutes evidence in
 566 support of one of the intended design features of the model. The most activated
 567 local maps in the middle images of Rows 1 and 2 also provide examples of
 568 cells that are selective to motion direction. Recall that each cell in the model
 569 receives inputs from up to four distinct local maps. However, because this
 570 particular local map does not possess neighbouring local maps horizontally to
 571 its right or orthogonally above, all the cells lying along this contour line will
 572 be selective to motion direction.

573 Our second set of velocity scenarios to be discussed is displayed in Rows 3 and
 574 4 of Fig. 6. These two scenarios explore the case where the stimulus is moving
 575 slightly slower horizontally and slightly faster vertically than was discussed
 576 in the first set. More specifically, comparing these two motion scenarios, the
 577 simulated horizontal motion depicted in Row 3 left spans four rfs, while the
 578 vertical motion depicted in Row 4 left spans three rfs. The most activated
 579 cell in the local map in both rows lies on the horizontal contour line one cell
 580 left of the singularity (shaded). Accordingly, the most activated cell in each of
 581 the two global maps is the one corresponding to the biggest value of the local
 582 maps. In other words, the cell on the horizontal contour line one cell left of
 583 the singularity has responded to both of these distinct velocities. Importantly,
 584 no other cell in either global map has responded to these two velocities. Once
 585 again, the intended design feature of the model—that a cell responds to fast
 586 parallel motion and slow orthogonal motion—has been illustrated. As was the
 587 case with our first pair of velocity scenarios, the local map on the third row
 588 possesses only one neighbouring local map to its right thus the active cell is also
 589 selective to parallel motion. However, this cell is not selective to orthogonal
 590 motion because there are local maps on both its orthogonal sides.

591 The third pair of velocity scenarios to be considered is displayed in Rows
 592 1 and 2 of Fig. 7. These scenarios explore the case where, once again, the

horizontal motion is slightly slower and the vertical motion is slightly faster than the case discussed in the previous scenario pair. The first row depicts the stimulus initially located one rf to the left of the centre while the second row depicts the stimulus initially located in an rf at the bottom of the field. In both rows the stimulus is positioned one unit of time later in the rf to the right of the centre. Thus Row 1 depicts the simulation of slow horizontal motion over a distance spanning three rfs, while Row 2 depicts the simulation of fast vertical motion spanning four rfs. Observe that, in contrast to the first two pairs of scenarios, here the faster speed is vertical and the slower is horizontal. Therefore, according to the design of our model and the pinwheel configuration that it mimics as displayed in Fig. 2, we should expect that the contour line displaying the highest activation should be the one projecting horizontally to the right of the singularity. These expectations are confirmed as can be observed in the local map of each row. Moreover, the cell with the highest response to these two velocities is on the horizontal contour line one cell out from the singularity. It can also be observed that this scenario pair provides an example of a cell that is non-selective to both parallel and orthogonal motion, as there exist local maps at all required distances.

The fourth pair of velocity scenarios to be discussed is displayed in Rows 3 and 4 of Fig. 7. This is the reverse of the first scenario set in that the simulation of the highest detectable velocity is vertical and the slowest detectable velocity is horizontal. Once again, according to the design of our model and the pinwheel configuration that it mimics (Fig. 2), we expect that the cell exhibiting the highest activation should be at the opposite end of the horizontal contour line to that of the active cell in the first scenario. The local maps displayed in Rows 3 and 4 of this figure confirm this expectation.

To summarize these simulation results: the speed component of velocity tuning decreases monotonically across the joint contour line from left to right for horizontal motions, and increases monotonically for vertical. Given the parameterization of the model employed (49 rfs and 49 local maps) we assert that the four velocity scenarios presented constitute all possible detectable speeds in a horizontal and vertical direction. Although we have only presented velocity variation for stimulus moving horizontally and vertically, the response pattern observed in the velocity map will be identical for all other detectable directions of motion differing only in the orientation contour line that is activated [47].

An aside regarding spatial properties may be useful here. As it is well known that Gabor space models are selective to orientation and frequency, we make this claim for 2DVM without explicitly presenting simulation results. However, our claim that 2DVM is selective to stimulus length requires justification. We assert that this property is a consequence of the OCP-Gabor. In particular, the length of a cycle of the plaid in the parallel direction is proportional to

the length of the stimulus that it is selective to. Simulation experiments were conducted where stimuli of various lengths were presented to two different plaid functions. A representative sample of the data from these experiments are presented in the graphs of Fig 8, where it can be observed that the empirical results are consistent with the theoretical expectations of the OCP-Gabor function.

4.2 Illusionary Effects Induced by the Model

In this section we present results that demonstrate how 2DVM models three types of visual illusions experienced by the human vision system.

The first type, visual crowding, is the inability to recognize objects in a clutter and represents a fundamental limit on conscious visual perception and object recognition [48]. One manifestation of this phenomenon is an observer's inability to distinguish individual items in a moving clutter. 2DVM mimics this effect in two ways: 1) a sequence of slow-moving stimuli aligned in orthogonal motion; and 2) fast-moving stimuli aligned in parallel motion. Two simple examples that simulate this effect are presented in Fig. 9, which displays three stimuli aligned in orthogonal motion, and Fig. 10, which displays three stimuli aligned in parallel motion. In both cases, the response to the middle stimulus has been suppressed and consequently did not initiate a velocity response. The result is that the velocity of the remaining two stimuli were correctly identified, albeit at the expense of not 'seeing' the middle stimulus.

The second type is known as perceptual filling-in. An experiment reported in [6] involved measuring the response of cortical cells of V1 to RFs associated with the blind spot created by the optic disc in the retina. Orientated moving bars were presented to the visual field and the cortical cells of V1 associated with the optic disc accurately interpolated the position of the bar at the time the bar passed over the blind spot. They also artificially produced a blind spot by obstructing an RF and found that in all cases the cells associated with the occluded RF responded in the same way as when the RF was not occluded. We have simulated this experiment in 2DVM by taking two disjointed bars that were aligned and passing them over the model's simulated visual field. The results produced were consistent with the data reported in [6]. These results are displayed in Fig. 11, where it can be observed that the local map associated with the gap between the two bars responded with a similar velocity to the local maps on either of its sides. This illusionary velocity resulted from the effects of collinear facilitation at the rf as the two co-aligned bars passed over the region.

The third type is that of illusionary orientation induced by fast moving stimuli,

673 motion streak. (Discussed in Section 1.) A simulation of this effect is displayed
674 in Fig 12, where it can be observed that the longer the length of the motion
675 streak the greater is the illusory orientation. In particular, the top left sub-
676 image depicts a stationary bar oriented at 30 degrees counter clockwise from
677 the vertical. Its associated local map (right) reveals that the maximum energy
678 occurs, as expected, on the contour line of 30 degrees (no motion streak). The
679 middle row represents simulated motion of the bar depicted in the first row.
680 The simulated motion streak takes the form of a parallelogram, which would
681 result from the smearing caused by the bar's motion. The associated local
682 map (right) indicates that the maximum energy occurs at both the contour
683 line of 30 degrees and 60 degrees. This means that the perceived orientation
684 is somewhere between 30 degrees and 60 degrees. The bottom row of the fig-
685 ure simulates increased speed as revealed by the elongated parallelogram. The
686 local map of this scenario reveals that the maximum energy unambiguously
687 occurs on the contour line of 60 degrees. Together, the three pairs of images
688 demonstrate that illusory orientation is induced by increased speed.

689 5 Discussion

690 In this section we interpret the model and simulation results, then discuss how
691 these might impact future investigations of V1.

692 5.1 *Role of Visual Illusion*

693 Surround suppression, as a spatial characteristic, has been recognized since
694 the 1970s [49]. Although it is still a debate as to where in the vision system
695 the surround suppression actually takes place, experiments reported in [50]
696 demonstrated that it resulted from inhibition in the visual cortex. Collinear
697 facilitation, as a spatial characteristic, has been recognized since the 1980s [18].
698 The suppression/ facilitation effects of surround suppression and collinear fa-
699 cilitation in classical models of Area V1 tend to account for purely spatial
700 properties [29], [51]. They also hypothesized that the spatial function of these
701 effects was to produce a pop-out effect and as such, direct attention to impor-
702 tant features in the visual field. Although 2DVM possesses the pop-out effect,
703 we hypothesize that the critical role of suppression/ facilitation is not merely
704 pop-out but to enhance robustness in the velocity map. In particular, sur-
705 round suppression and collinear facilitation address the correspondence prob-
706 lem associated with determining velocities of individuals moving in the same
707 direction as a group. This is important because a vision system's inability
708 to adequately address the correspondence problem in the context of velocity
709 estimation would tend to introduce errors. This also has implications for the

710 neural mechanism that underpins visual crowding.

711 5.2 Predictions of 2DVM

712 We observe that the OCP-Gabor space model presented in this paper has
713 implications for the manner in which contextual modulation in general, and
714 velocity in particular, manifest in V1. The parameterization of the OCP-Gabor
715 functions accounted for the empirically-derived data that described the veloc-
716 ity preference bandwidth response on points within local maps. However, the
717 same parameterization implies four predictions not yet tested empirically. The
718 foregoing computational analysis of long-range contextual modulation and ve-
719 locity in V1 leads to an interesting prediction about the structure of the local
720 maps in V1 and, in particular, the storage of contextual modulation param-
721 eters within these local maps. The model parameters σ_{ew} , σ_{ns} , F_{ew} and F_{ns}
722 of $2DVM(i, p, q, \theta, \sigma_{ew}, \sigma_{ns}, F_{ew}, F_{ns})$, in Equation 3, imply a spatial structure
723 for the storage of long-range contextual information, i.e. a spatial structure
724 that is measurable at the scale of a local map.

725 *Prediction 1:* The middle range of velocity selectivity should take place in
726 the neighbourhood of local map singularities, whereas the extreme velocity
727 selectivity (fastest and slowest) should be stored and processed by neurons
728 located furthest from singularities. This represents only one plausible potential
729 parameterization of 2DVM, as noted in Section 3. The core prediction is that
730 different velocity ranges will be stored in different regions within each local
731 map. One way this prediction could be tested empirically is with methods
732 similar to standard optical imaging experiments by expanding the size of the
733 orientation field from one RF to the entire visual field.

734 *Prediction 2:* It is a well-known fact that many V1 cells are selective to mo-
735 tion direction [2]. However, there is an open question as to why this is so.
736 Indeed, numerous experiments aimed at explaining why certain cells have a
737 direction selectivity have been reported [37]. In an investigation reported in
738 [52] intracellular recordings from V1 simple cells favoured models of direc-
739 tion selectivity based on excitation from the lateral geniculate nucleus (LGN)
740 rather than cortical inhibition. They concluded that it seemed unlikely that
741 inhibition from the null direction was the primary mechanism for creating
742 direction selectivity.

743 The cells modelled in 2DVM possess a mix of direction and non-direction
744 motion selectivity. However, the structural modelling of 2DVM implies a clear
745 prediction of which neurons are direction selective and why this occurs. 2DVM
746 predicts that direction selectivity for slow-moving objects should only occur
747 in neurons in local maps near the periphery of the global map. Direction

selectivity requires that local maps must have at least one null direction. The only way this can occur for slow-moving objects is if the local map is near the periphery of the global map. The converse should also apply. That is, direction selectivity to slow-moving objects should be a rare occurrence for neurons situated in local maps near the global map’s centre. The model’s explanation for direction selectivity for fast-moving objects is similar. But its prediction as to the location of such neurons is less precise. 2DVM indicates that the greater the velocity, the greater the separation of local maps. If the required separation means that the local maps are on different sides of the global map, then selectivity must ensue. Consequently, 2DVM predicts that the higher a neuron’s peak velocity response, the more likely it is to be selective to motion direction.

Prediction 3: The Connection Algorithm presented in this paper prescribed a pattern of connectivity between cells located in different local maps with similar tuning properties. Although this pattern of connectivity underpins the design features of the model, it also raises two other inter-related issues. On the one hand, it implies a hypothesis about the V1 connectivity that is empirically untested. The specific testable prediction is that individual cells within orientation pinwheels are connected to specific cells in neighbouring pinwheels that have similar tuning preferences. On the other hand, if the prescribed connections exist in V1, then one would also expect that small variations to the pattern should only result in small effects in the accuracy of the velocity map. This expectation could be tested computationally with the use of genetic algorithms to investigate whether the pattern represents a computationally convergent property.

Prediction 4: Although the Velocity Model presented in this paper predicts two-dimensional (2-D) motion, it says nothing about 3-D motion. It seems very likely that the property of smooth velocity variation across a joint contour line has implications for the perception of 3-D motion and how the two eyes work together to produce this perception.

5.3 Limitations

The mathematical formulation of 2DVM and its implementation as presented in this paper are scale independent. However, the simulation results that were presented represented only a minimal non-trivial parameterization of the RF space. That is, we reported on the case where the number of RFs is 49 and the size of a local map is 49 cells. Although these results demonstrated the features of 2DVM on a small scale and on synthetically generated images, no evidence was provided that the model applies at the actual scale of V1 or on natural images. This would entail a parameterization of many more local

787 maps, possibly up to 10,000, which is the estimated number of orientation
788 pinwheels in V1 [39]. Such a parameterization would involve a more elaborate
789 consideration of the simulated visual field and a realistic distribution of RFs.
790 While this was outside the scope of this paper, it would constitute a worthy
791 investigation that might reveal other properties of the functional architecture
792 of V1. For example, an interesting hypothesis is a connection between motion
793 streaks and the perception of Glass patterns [53]. Although it is expected
794 that 2DVM would produce a velocity response to Glass patterns, the current
795 implementation possesses insufficient local maps to explore this hypothesis.

796 Another reason for implementing 2DVM with a realistic number of local maps
797 is to be able to interpret the velocities of 2DVM in terms of the more com-
798 monly used dimensions, degrees per second, as employed in the literature. The
799 current choice of dimensions, rfs per unit of time, is appropriate in the current
800 context but it lacks a connection to the way velocity perception is measured
801 in psychophysical experiments with humans.

802 This paper focused on the design issues of the model. However, it did not
803 provide any insight as to how such a model might actually be implemented
804 in cortical architecture. For a discussion of this issue, the reader is referred to
805 [54].

806 5.4 *Points of Controversy*

807 The first point of controversy pertains to the motion streak hypothesis, which
808 states that motion streak patterns are not only projected into V1, as assumed
809 in this paper, but they are also used by the vision system to predict direction of
810 motion. Psychophysical experiments aimed at investigating the motion streak
811 hypothesis have produced a mixed bag of results. Evidence that rejected the
812 motion streak hypothesis was reported in [55]; [56]. However, other experi-
813 ments on single neuron responses of cats to certain types of motion supported
814 this hypothesis [2]; [9]; [10]; [57]; [58]; [59]; [60]; [61]. Given that motion streaks
815 are projected into V1, the results of this paper support the conclusion that
816 they are also used to determine direction of motion. In addition, the results of
817 this paper also demonstrate how motion streaks contribute to the V1 neurons
818 estimate of stimulus speed. Consequently, 2DVM proposes a stronger version
819 of the motion streak hypothesis, i.e. motion streaks are used by the vision
820 system to predict velocity.

821 A second point of controversy relates to the question of whether or not the fun-
822 damental role of V1 neurons represents individual feature attribute detectors.
823 Most of the earlier work in this area cited in this paper supports this proposi-
824 tion. However, the results reported in [7], concluded that V1 neurons did not

825 represent individual feature attribute detectors. Although 2DVM agrees with
826 that conclusion up to the formulation of velocity, it markedly diverges from
827 their conclusion at that point by asserting that V1 neurons are velocity de-
828 tectors and these, taken together, form a velocity map of the visual field. The
829 reason for the attention given to the idea that individual neurons in V1 are
830 primarily feature detectors may have its roots in historical matters. That is,
831 the technology of the day with its limitations may have constrained the types
832 of hypotheses that were feasible to investigate at the time. Many significant
833 discoveries were made over this 50 year period. In the interests of further dis-
834 cussion, we draw on an analogy to put these discoveries in perspective. Just as
835 the stone blocks that make up the great pyramids of Egypt, with their precise
836 engineering and placement, are individually significant in their own right, so
837 also are the individual spatial and temporal selective properties of V1 neu-
838 rons. However, as the importance of the individual stone blocks pales when
839 compared with the pyramid structure as a whole, it may also turn out that
840 the individual spatial and temporal properties pale into insignificance when
841 placed in the context of V1 considered as a whole, i.e. a velocity map. Such a
842 paradigm shift in the role of V1 would require considerable empirical evidence
843 before being embraced by the vision community. Empirical proof is currently
844 lacking but maybe now is the time to start looking for the required evidence.

845 6 Summary and Conclusion

846 At the outset of this paper, we discussed the fundamental importance of ve-
847 locity estimation in biological vision. The novelty of 2DVM is in indicating
848 the importance of V1s role in this process. Our model demonstrates how the
849 tessellated pattern of orientation pinwheels, together with a pattern of long-
850 range connections between these as specified by the Connection Algorithm,
851 implies a global-local velocity map of the upper layers of V1. The statement
852 is elaborated in the following three points:

- 853 (1) The observable architecture of the orientation pinwheels arranges spa-
854 tial selectivity properties in a manner that is consistent with the spatial
855 aspects of velocity computation.
- 856 (2) The inter-orientation pinwheel connectivity, as specified in the Connec-
857 tion Algorithm, over the time domain transforms the spatial properties
858 into a velocity map of V1.
- 859 (3) The input signal to 2DVM is a representation of the entire visual field.
860 This implies that the velocity response outputs are reliable estimates up to
861 the constraints imposed by the resolution of the representation.

862 2DVM was formulated in two stages. First, the base model emerged directly
863 from known spatial properties of V1 cells, such as orientation tuning and

frequency tuning. These properties were captured in an OCP-Gabor space.
 Second, in the extension to the base model, a pattern of temporal connections was specified via the Connection Algorithm. The primary purpose of the temporal connections was to account for the empirically observable response properties of V1 cells to two types of object motion: the first type is to objects moving quickly parallel to the RF's orientation (parallel motion); the second type is to objects moving slowly orthogonally to the RFs orientation (orthogonal motion). The simulation results presented in this paper demonstrated that 2DVM successfully achieved its design goal of accounting for V1 cell responses to these two types of 2-D motion. In addition, simulation results also demonstrated how the model accounted for various types of visual illusion and thereby suggested mechanisms that may account for this phenomenon in the human vision system. In particular, results indicated how the well-known contextual modulation effects of spatial suppression/facilitation contributed to the vision systems ability to achieve robustness in the velocity map. It was also argued that the occurrence of illusory orientation associated with stimuli moving quickly obliquely to its direction of motion is a consequence of motion streaks. The addition of the temporal connections to the model implied a significant role for singularities in the velocity map. Recall that each singularity (confluence of all iso-orientation contour lines in a local map) is associated with four OCP-Gabor filters in the model. Although the net effect of these filters on the spatial orientation is a non-preferential orientation response, it was shown that singularities contributed to the detection of slow-moving spots that would otherwise be undetectable by the non-singularity cells of a local map. The net effect of the model's formulation also produced two modelling outcomes consistent with empirically-derived data: 1) to parallel motion, the model indicated that cells tended to be selective to motion direction and band pass selective to spatial frequency; 2) to orthogonal motion, the model indicated the same cell tended to be non-selective to motion direction and low pass selective to spatial frequency.

The intended design features of the model for known empirical results aside, the model also produced three hypotheses that would warrant the focus of future research. First, the speed component of neuronal velocity selectivity decreases monotonically across each joint orientation contour line for parallel motion and increases monotonically for orthogonal motion. Second, the cells that are direction selective to slow-moving objects are situated in the periphery of V1. Third, neurons in distinct pinwheels tend to be connected to neurons with similar tuning preferences in other pinwheels.

2DVM has extended all other cited models of V1 by demonstrating how many of the functional properties of V1 emerge from known structural properties. This paper has also contributed to the discussion on the role motion streaks played in the vision process. In particular, we have extended the motion streak hypothesis by arguing that motion streaks are integral to the vision system's

estimates of velocity and not merely, as previously conjectured, contributors to direction detection. We also demonstrated how motion streaks contributed to the phenomenon of illusionary orientation in the human vision system. Further, this paper demonstrated that the long-range cortical connections within Layer 2/3 of V1, when combined with the neuronal spatial tuning properties, result in a robust velocity map of the visual field. Consequently, it is the conclusion of this paper that the spatial selectivity features of V1 are side-effects of its more important role as a velocity map of the visual field and that empirical experiments aimed at investigating this are warranted.

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The source code that implements 2DVM is available in a software package named VisioLab from the following website: <http://www.ict.griffith.edu.au/sheridan/>

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Fig. 1. Displays the components of an OCP-Gabor filter. Upper left is a horizontally-orientated sinusoid while upper right is a vertically-orientated sinusoid. Lower left is the product of these two sinusoids. Lower right is the product of the plaid (lower left) with a Gaussian and illustrates an OCP-Gabor filter.

Fig. 4. Displays examples of OCP-Gabor response functions as intensity maps. In Rows 1 & 2, the left images are horizontally phase-shifted for edge selectivity while the right are vertically phase shifted. Row 1 shows the highest vertical and lowest horizontal frequencies while Row 2 shows slightly lower vertical and slightly higher horizontal frequencies. The bottom pair (Row 3) has two sinusoidal components with equal frequency: left provides preference for the light/dark edge of a horizontal pair of spots; right is its associated light/dark vertical edge.

Fig. 5. This is an example of the connections generated by the Connection Algorithm. The circles (numbered) represent local maps; the five cells within each local map (we name A to E) represent the horizontal contour line of the map, with the darkened centre cell (C) indicating the singularity. The lines connecting individual cells in one map to another represent the temporal cortical connections as generated by the algorithm. NOTE: There is only one map with connections to all the others—the 'Destination Map' (Map 5). Further, note the symmetry of how the lines connect with specific cells in each direction. For instance, Cell 5A connects horizontally to cell 1A and vertically to Cell 6A; Cell 5B connects horizontally to Cell 2B and vertically to Cell 7B. (Diagram numbered and coloured for ease of explanation only.)

Fig. 6. Shows 4 velocity scenarios. Left images depict a stimulus at two points in time. The circles identify the rfs. The right images depict 49 local maps as intensity maps, with each singularity marked. Bright pixels represent high activating neurons and dark pixels, low. The brightest, circled, are shown as local maps (centre) with the numbers representing activation levels. Row 1 depicts the fastest horizontal motion, Row 2, the slowest vertical motion, Row 3, the second fastest horizontal motion, and Row 4, the second slowest vertical motion. The highest activating cells are shaded.

Fig. 7. Shows 4 velocity scenarios. The left-images depict a stimulus at two points in time. The circles identify the rfs. The right images depict 49 local maps as intensity maps, with each singularity marked. Bright pixels represent high activating neurons and dark pixels, low. The brightest, circled, are shown as local maps (centre) with the numbers displaying activation levels. Row 1 depicts the second slowest horizontal motion, Row 2, the second fastest vertical motion; Row 3, the slowest horizontal motion and Row 4, the fastest vertical motion. The highest activating cells are shaded.

Fig. 8. Displays the response profiles of two different OCP-Gabor functions to stimuli of differing lengths. It can be observed that the OCP-Gabor function with parallel frequency of 1/128 reaches its optimum tuning at a stimulus of approximately 60 units and the 1/192 parallel frequency OCP-Gabor function is tuned to 96 units.

Fig. 9. Example of simulation results of the suppression effects on a group of slow-moving stimuli. The upper two images display the groups position at two distinct times and jointly they depict velocity. The circles indicate rfs. The three orientated bars represent orthogonal motion. Upper left indicates that these three stimuli are at the right-hand edge of the visual field. Upper right depicts their position one unit of time later. The 2DVM response to this velocity is displayed in the lower two images. The local map (left) displays the activation levels associated with the middle stimulus. The global map (right) reveals the suppression effect on the other two stimuli.

Fig. 10. Example of simulation results of the suppression effects on a group of fast-moving stimuli. The upper two images display the groups position at two distinct times and jointly they depict velocity. The circles indicate rfs. The three orientated bars represent parallel motion. Upper left indicates that these three stimuli are near the upper edge of the visual field. Upper right depicts their position one unit of time later. The 2DVM response to this velocity is displayed in the lower two images. The local map (left) displays the activation levels associated with the middle stimulus. The global map (right) reveals the suppression effect on the other two stimuli.

Fig. 11. Example of simulation results of the facilitation effects of two stimuli separated by a gap and moving at the same velocity. The upper two images display the groups position at two distinct times and jointly depict velocity. The circles indicate rfs. The two oriented bars separated by a gap represent orthogonal motion. The 2DVM response to this velocity is displayed in the lower two images. The local map (left) displays the activation levels associated with the gap. The global map (right) displays the facilitation effect on that local map.

Fig. 12. Depicts illusionary orientation associated with increasing velocity induced by motion streaks. Each pair of sub-images represents a bar orientated at 30 degrees. The left images represent the projection of the bar onto the rf. The right images represent the local maps associated with the activated rf. Top pair: (left) zero velocity; (right) orientation contour line (OCL) at 30 degrees most activated; Middle: (left) small motion streak indicates a moderate speed; (right) OCL at 30 degrees and 60 degrees equally activated; Bottom: (left) longer motion streak indicating a higher velocity; (right) OCL at 60 degrees most activated.