A Model of Color Vision Based on Cortical Reentry

It is known that the perceived color of an object depends on the context in which it is viewed, its reflectance properties and the spectral distribution of the illuminating light. What is not known, however, is how the visual system functions so that color percepts depend upon the integration of local and contextual cues. While phenomenological theories of color vision exist, robust neurally based theories consistent with psychophysical observations are sparse. In the present study we develop such a theory and establish its self-consistency by computer simulations of cerebral cortical areas involved in color perception. The simulations test the hypothesis that long-range reciprocal connections within and between cortical areas mediate a dynamic process of reentry that integrates contextual cues into the color percept. When stimuli similar to those used in psychophysical testing of contextual influence were used, firing patterns consistent with psychophysical data on color constancy and color induction in humans were observed. Selective disruption of reciprocal inter- or intra-areal connections reduced the correspondence between the model’s responses and the psychophysical data. The findings are consistent with the proposal that reentrant interactions within and between cortical areas provide a major basis for the context-sensitive aspects of color vision.

The perception of the color of an object is not solely dependent upon the wavelength distribution of light reflected from it. Rather, it is synthesized within the central nervous system as a result of the interaction of this distribution with the wavelength distribution of reflected light from surrounding parts of the visual scene. Two examples of this context dependency of color perception are color constancy, in which the perceived color of an object remains approximately constant independent of the wavelength distribution of the illuminant, and color induction, in which the perceived color of an object can be changed by surrounding it with an object of another color. Traditional investigations of color vision have focused intensively on the local properties of the visual system concerned with color. Among the major contributions to this aspect of the theory of color vision was the postulation, by Young and Helmholtz, that color is analyzed to some degree in a segregated manner from other visual attributes such as form, motion and depth. Additional contributions, the effect of context was not explicitly taken into consideration. However, since the striking demonstration of color constancy effects by Land (1964), various investigators have concerned themselves increasingly with the contextual aspects of color vision. This has led to a number of computational or algorithmic approaches to the study of color constancy (Land and McMann, 1971; Buchsbaum, 1980; Hurlbert and Poggio, 1988; Gershon and Jepson, 1989; Forsyth, 1990). Although several authors have presented models of color constancy based on retinal adaptation (D’Zmura and Lennie, 1986; Brainard and Wandell, 1992), psychophysical studies of lesion patients (Land et al., 1983) and normal subjects (Arend and Reeves, 1986; Valberg and Jange-Malecki, 1990) clearly implicate cortical processes in this phenomenon.

Studies of the visual cortex have revealed the existence of functionally segregated areas and a high degree of intra- and inter-areal connectivity (Zeki and Shipp, 1988; Felleman and Van Essen, 1991). It has been demonstrated by means of lesion studies (Heywood et al., 1987; Zeki, 1990; Walsh et al., 1992), electrophysiology (Livingstone and Hubel, 1984; Ts’o and Gilbert, 1988) and psychophysics (Livingstone and Hubel, 1987) that color is analyzed to some degree in a segregated manner from other visual attributes such as form, motion and depth. These and other studies (Schiller et al., 1990; Heywood et al., 1992; Merigan and Maunsell, 1993; Barbur et al. 1994) provide considerable evidence that the chromatic and achromatic aspects of the color percept have different cortical locations. The chromatic aspect of color vision has been associated with a specific visual pathway starting with the parvocellular layers of the LGN and continuing via the cytochrome oxidase-rich blobs of V1 and thin stripes of V2 into area V4 (e.g. Zrenner et al., 1990). The evidence suggests that regions up to V2 are involved with the local aspects of color vision (Livingstone and Hubel, 1984; Ts’o and Gilbert, 1988; Lennie et al., 1990; Walsh et al., 1992) and that area V4 plays a role in constructing the contextual effects of color (Zeki, 1983a,b; Schein and Desimone, 1990; Walsh et al. 1993). In addition to the pathways up to V4, area IT has been shown to be involved in color vision (Dean, 1979; Heywood et al., 1988; Komatsu et al., 1992; Horel, 1994; Heywood et al., 1995), although its exact functional role is not known. These various observations give rise to two main questions: (i) Given that the contextual aspects of color vision have a major cortical component, what is the role of the extensive collections of intra- and inter-areal connections in mediating contextual influences? (ii) What role does area IT play in chromatic vision? In the present paper we provide a theoretical analysis aimed at clarifying answers to these questions.

It has previously been proposed that the dense, reciprocal connectivity within and among areas of the cerebral cortex subserves a dynamic process of reentry which consists of ongoing, parallel signaling between and within brain areas (Edelman, 1987, 1993). Previous modeling studies have shown how this process can subserve properties such as the synchronization of firing between distant neurons (Sporns et al., 1989), figure-ground segregation (Sporns et al., 1991) and cortical integration and binding (Tononi et al., 1992). The proposal on which the present theoretical study rests is that reentry also leads to the integration of context during the construction of the color percept. Using images obtained via a CCD camera and video digitizer as input to computer
simulations, we describe and analyze a model incorporating anatomical and physiological properties of certain parts of the visual cortex. We show how reciprocal connections within and among areas can give rise to neuronal responses consistent with the properties of human color vision. In simulations performed using the model, we show how color can be represented by firing patterns within a population of neurons, each neuron of which is broadly tuned with respect to color and responds to white. These results indicate that the representation of a large number of colors does not require neurons having sharply tuned chromatic response functions and a null response to white. The model can generate unique firing patterns for stimuli unique in their hue or saturation, and these firing patterns vary in a continuous manner when hue and saturation are continuously varied. The response of the model to a set of psychophysically based tests concerned with color constancy and color induction illustrates that the neural circuits simulated in the model are sufficient to mediate the integration of contextual cues into the color percept. Selective perturbations of the different reciprocal pathways illustrate their role in producing color constancy and color induction. Taken together, these experiments illustrate that, within the context of the model, reentry mediated by the modeled cortical circuitry produces firing patterns consistent with the phenomena of color constancy and color induction.

Materials and Methods
All simulations were run on Neumachine, a special-purpose transputer-based parallel computer, built at the Neurosciences Institute, using the Cortical Network Simulator (Reeke et al., 1990). This program allows the user to design models consisting of multiple areas representing different brain regions. Each region contains multiple neural units of different types. Each unit, modeled as a leaky integrator, is assumed to represent a group of interconnected neurons, and is characterized by a specific set of parameters. The level of activity corresponding to each unit can be viewed as representing the average firing rate of this collection of cells, and its response properties can be considered as representative of a typical response of a cell within the group. The model contained a total of \(-65,000\) units and \(7,000,000\) connections. General features of the model are presented here; specific details are given in Appendix A.

Dynamics
At each computer iteration or cycle, the state of each unit is characterized by an activation variable \(a(t)\). Each unit \(i\) receives individual connections of one or more connection types from other units. Connections can be set to be either voltage-dependent or voltage-independent. The total contribution of input to unit \(i\) from voltage-independent connections, \(A_i^{VI}(t)\), is given by

\[
A_i^{VI}(t) = \sum_{j=1}^{N_i} c_{ij} s_j(t)
\]

where \(c_{ij}\) is a scale factor applied to all connections of type \(i\), \(M\) is the total number of different connection types projecting to unit \(i\), \(c_{ij}\) is the strength of the connection between a presynaptic unit \(j\) and unit \(i\) (negative values imply an inhibitory hyperpolarizing, as opposed to a shunting, connection), \(s_j(t)\) is the activity level of unit \(j\) at time \(t\) and \(N_i\) is the total number of connections to unit \(i\) of type \(i\).

The total contribution from voltage-dependent connections, \(A_i^{VD}(t)\), is given by

\[
A_i^{VD}(t) = \sum_{m=1}^{M} \sum_{j=1}^{N_i} \left( A_i^{VI}(t) + \omega_j(t) \right) c_{ij} s_j(t)
\]

where \(\omega_j(t)\) is a decay coefficient which determines how much activity is carried from one simulation step to the next and \(\sigma(\xi) = 1 - \text{sech}(\xi/T)\) is an increasing sigmoidal function whose slope is determined by \(T\). This function assures a connection whose effect depends upon the postsynaptic voltage: as the postsynaptic voltage increases, the connection has an increasing effect, but if the postsynaptic voltage is zero, the connection has no effect.

The activity level of unit \(i\) is given by

\[
s_i(t + 1) = \phi(A_i^{VI}(t) + A_i^{VD}(t) + \omega_i(t) + n_i(t))
\]

where \(n_i(t)\) is a noise value added to the activity level at each cycle and \(\phi\) is a limiting function given by

\[
\phi(x) = \begin{cases} 
1 & \text{if } x \geq 1 \\
0 & \text{otherwise} \\
x & \text{if } 0 < x < 1 
\end{cases}
\]

A cycle of the simulation consists of calculating the current value of \(s_i\) for each unit within the model according to Equation 1. Each stimulus was presented to the model for 40 simulation cycles. This was empirically determined as sufficient to allow the activity levels \(s_i\) to settle to relatively stable values. After each stimulus presentation, the model was allowed to run for five cycles with no input, a period adequate to allow the units' activation levels to decay to the resting noise level.

Stimuli
All stimuli presented to the model were obtained as signals from a CCD camera and video digitizer. To approximate the spectral properties of the cone photoreceptors, three sets of spectral filters were used in front of the camera while acquiring the stimuli. The filters used were all from the Kodak photographic range. The L cone response was approximated by filter number 102, the M cone response by the collection of filters CC50G, CC50C and CC10G, and the S cone response by filters 1A and 39. These were chosen empirically by matching the cone spectral responses (Wyszecki and Stiles, 1982) to the spectral responses of the filters given by the Kodak technical manual (Eastman Kodak, 1990.) This produces three gray level images for each stimulus, each one corresponding to the response of one of the cone types. The properties of the filters were chosen to match the spectral absorption properties of human cones. Although the filters do not match the cone absorption exactly, they have approximately the same peaks and amounts of overlap between the different cone types. After obtaining the raw images, several steps were involved in producing the images used as input to the model. First, the center portions (448 × 448 from 638 × 478) of the raw images were spatially averaged to produce three images of size 64 × 64 pixels. After spatial averaging, the images were scaled by a factor determined by each channel's response to an achromatic stimulus (Munsell NG) such that each channel had the same response to the achromatic stimulus.

The stimuli used consisted of various shapes made from Munsell matte paper illuminated using two 500W quartz halogen lights. The color of the illuminant was changed using lighting filters from the Bogen Cine range of cool colors (FP207) and warm colors (FP208). This enabled a wide range of stimuli, varying in both reflectance and illumination, to be used and reported. As mentioned earlier, there is considerable evidence concerning the separation of chromatic and achromatic aspects of the color percept within the brain. Although the brain regions thought to be involved in the construction of the chromatic axis are reasonably well characterized, the neural basis of achromatic perception is not as well localized. For example, a lesion study of specific layers of the LGN (Schiller et al., 1990) indicates that brightness perception can be mediated by both the parvocellular and magnocellular layers of the LGN. For this reason, it was decided to ignore the achromatic axis in the study and use isoluminant stimuli. This was achieved by preparing stimuli made from Munsell papers of a specific value \(6\), using stimuli from a plane of constant value through the Munsell color solid, and by assuring, with a light meter, that all illuminants used had the same luminance. Gross adjustments in luminance were achieved by using neutral density filters (Bogen Cine-FP204) or, for small changes, by altering the voltage supply to the lights. The specific form of the stimuli used will be discussed in the presentation of each experiment.

General Architecture and Major Features
A major goal of the present study was to investigate the possible role of reentrant interactions within the visual cortex in mediating context
dependent phenomena. Although there is evidence implicating V4 in mediating long-range effects of color vision, the involvement of earlier areas and backward connectivity from V4 to earlier areas cannot be excluded. A detailed anatomical model of the cortical hierarchy up to V4 was therefore constructed and analyzed. The gross connectivity of the model is shown in Figure 1.

As can be seen, the model consists of a number of areas, each corresponding to an area within the visual cortex. Obviously, this does not imply that the modeled areas have structural and functional characteristics identical to those in the primate visual system. Instead, only those properties assumed to be directly related to color vision were modeled. To reflect this simplification, we adopt the convention of indicating real areas in Roman type (e.g. V4) and modeled areas in italics (e.g. V4).

The LGN contains six cell types corresponding to the color opponent, center-surround cells seen in the parvocellular layers of the LGN (Derrington et al., 1984). Region V1/V2 can be considered as modeling the functional role of areas V1 and V2 in color vision. Regions V1/V2 and V4 are each modeled as containing four maps of excitatory and inhibitory units, with units in the individual maps being tuned respectively to respond maximally to red, yellow, green or blue stimuli. Note that while, for descriptive purposes, these maps are considered in the model as separate collections of units, in reality, the maps would be interspersed and their units would spatially coexist within the cortex. The method by which chromatic receptive field tuning is achieved is still an open question and as this study was not explicitly concerned with this problem, the proposal of De Valois and De Valois (1993) was utilized. The justification for this choice is examined further in Discussion.

The four maps in V1/V2 and V4 are linked via extensive patterns of reciprocal connectivity both within and between themselves. It is this pattern of reciprocal connectivity that subserves the reentrant interactions proposed to underlie contextual integration. The connection patterns were such as to replicate the functional connectivity observed in V4 (Schein and Desimone, 1990). This implies large, silent surrounds with chromatic specificities giving rise to isochromatic inhibition and opponent facilitation (e.g. a cell excited by red in its classical receptive field is inhibited by red and facilitated by green in its non-classical surround). To achieve this functional connectivity, excitatory units receive long-range intrinsic connections from units of the opposite chromatic specificity and inhibitory units receive long-range connections from excitatory units of the same chromatic specificity. In addition, all intrinsic excitatory connections are voltage-dependent. Thus cells are only affected by stimulation of the surround when they are driven by a stimulus in their receptive field. The anatomical arrangement of these connections within V1/V2 and V4 corresponds to the long-range patchy connections observed in the supragranular layers of visual cortex (Yoshioka et al., 1992; Lund et al., 1993; Levitt et al., 1994b). In addition, units in V1/V2 receive voltage-dependent connections from V4 corresponding to the backward connections observed in visual cortex (Fellman and Van Essen, 1991; Rockland et al., 1994). The patchy nature common to forward connections and intra-areal connections is not seen in backward connections (for a review see Salin and Bullier, 1995). To 

reflect this, all backward connections were such that each V4 unit projects back with equal strength to all units from which it received connections. This results in a more diffuse pattern of connectivity than is the case with the forward and intrinsic connections.

In the present paper, a potential functional role of IT in color vision is proposed, namely to provide a representation in neural space of the constructed color. This is obtained by remapping the activity of each of the four mapped sets of V4 cells onto space within IT. Briefly, each IT unit receives 16 connections from the center part of each V4 map. The strengths of these connections follow four gradients: the gradients from the red and green V4 units run in opposite directions to each other and orthogonal to the gradients from the blue and yellow units, which themselves run in opposite directions. Full details of this mapping is given in Appendix A. Although this designated area is labeled IT, it is in no way meant to model the complete functionality of the inferior temporal cortex.

The major features of the model are summarized here; further details of the exact parameters used are given in Appendix A. Among the most important features of the model are the following.

1. **Hierarchical organization**: as in the visual system, the model was constructed in a hierarchical manner such that, in the progression from lower to higher areas, the receptive fields became larger and their tuning properties changed. For example, in the progression from the LGN to V1/V2 the units changed from being tuned to respond to differences in cone signals to being tuned to the axes of perceptual color space.

2. **Topographic mapping**: each modeled area, except IT, was topographically mapped with respect to the input image. As observed in the visual cortex, this topography became less strict as the progression to higher areas was made.

3. **Intra-area connections**: forward connections were organized in such a way as to determine classical receptive field properties, such as chromatic tuning, of units in the higher area. In general, this means that a large region of a lower area projected to a smaller region of a higher area resulting in a progressive increase in classical receptive field size when going from lower to higher areas. Specificity of the forward connections resulted in a change in chromatic tuning properties from lower to higher areas. In accord with the observed anatomy, the backward connections had much less chromatic specificity than either forward or intra-area connections.

4. **Local circuitry**: the modeled cortical areas (V1/V2 and V4) consisted of four types of excitatory and inhibitory units tuned to respond maximally to red, yellow, green and blue, the axes of the perceptual color space. The local patterning of excitatory and inhibitory connections between units tuned to the same spectral region determined the dynamic operating range for these units.

5. **Intra-area connections**: areas V1/V2 and V4 had an extensive pattern of long-range horizontal connections that provided the anatomical basis of the observed influences beyond the classical receptive field (Schein and Desimone, 1990). The connections were such

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**Figure 1.** Diagram of gross connectivity in the full model. Each box represents a particular modeled area. Lines represent patterns of connections; straight lines refer to cortico-cortical connections both forward and backward, and circular lines represent long-range, intra-areal connections. The local circuitry within each area is not represented in this figure (see text and Appendix A for details). Filled arrowheads refer to voltage-independent connections and open arrowheads to voltage-dependent connections. The size of the filled triangles connected to the arrows represents the degree of convergence of the forward and backward connections between V1/V2 and V4. The size of the filled squares represents the spread of the modeled long-range, intrinsic connections in both cortical regions. The data constraining the extent of these various connections are summarized in Table 5 of Appendix A. The spatial dimensions of each area are in units; differences in these values from area to area are discussed in Appendix A.
This method provides a way of representing the activity pattern of a population of neurons as a vector. In short, each unit in the population makes a contribution to the resultant vector in the direction of its preferred stimulus with a length proportional to its activity at that time. The resultant population vector characterizes the activity pattern of the complete population and enables comparisons to be made between the model's responses to different stimuli. A similar procedure has been utilized in analyzing the response of IT cells to the presentation of faces (Young and Yamane, 1992).

The majority of the results in the next section will be presented as population vector representations of the activity pattern within IT. These are obtained by summing all vectors calculated by taking the average response of each unit over the last 10 cycles from the 40 cycles used for each stimulus presentation and multiplying that value by a unit vector in the preferred direction of that unit. The space chosen in which to represent the results is the so-called perceptual space as defined by the opponent axes of green-red and yellow-blue (cf. the uniform appearance diagram of Abramov et al. (1990)). Details of the calculation of the preferred directions of IT units within this space are given in Appendix B.

The angle of the population vector represents the constructed hue and the length of the vector represents saturation. Note that this length is not a function of activity level but rather is dependent upon the pattern of activity within IT. Saturation reflects how far a stimulus is from achromatic. This has a direct correspondence to the representation of saturation within the model. An achromatic stimulus does not produce a null response within IT but rather a symmetric response pattern around the center position with a vector sum of approximately zero. As a stimulus becomes more saturated, this activity pattern becomes less symmetric and skewed in the direction of the constructed hue. The more saturated the color, the larger the skewness of the activity pattern and the longer the population vector. In this manner, saturation is represented directly by the length of the vector.

The maximum theoretical length of a resultant population vector was used to normalize the axes used to represent the results. To calculate this value, we assumed that the position of a unit within the 16 × 16 matrix of units making up IT defines the preferred direction of that unit and thus a maximum vector length would be produced if all the units in one half of IT were fully active (s1 = 1) and all the units in the other half of IT were silent (s1 = 0). Since we are assuming an idealized spatial positioning of preferred directions, the response pattern so produced would be symmetrical in the half that is active and produce a resultant vector that is at right angles to the line dividing the active and silent halves of IT. The length of this vector is given by

\[ |r_{\text{max}}| = 2 \sum_{x=1}^{16} \sum_{y=1}^{16} \cos\left(\tan^{-1}\left(y/x\right)\right) = 84.8 \]
where \( N_s \times N_f = 8 \) inasmuch as \( IT \) is modeled as a \( 16 \times 16 \) array of units and one-quarter of \( IT \) contains \( 8 \times 8 \) units. In all the results presented in terms of population vectors, the resultant vectors are normalized by dividing by this value. Data points then represent the fraction of this theoretical maximum that the model produces.

To calculate the population vector for a particular stimulus, we used the average activity of a unit over 10 simulation cycles. In their study of cells in motor cortex, Georgopoulos et al. (1988) used a variety of averaging methods to calculate each cell's contribution to the resultant vector. They found that all such methods gave reasonable results, with some clearly better than others. We replicated such a comparison with our model and found that the averaging method used had only minor effects on the results.

Measures of Constancy and Induction

In order to compare the model's results to psychophysical data and to compare the results of different models, for example after simulated lesions, quantitative measures of color constancy and color induction produced by the model are needed. The vectors used in obtaining these measures are illustrated in Figure 2. Figure 2a illustrates a hypothetical constancy diagram, with circles produced by the model's response to 10 stimuli under white light, under colored light with non-contextual background and under colored light with a contextual background. The diagram is of the same form as figures used later in the paper to document the model's response in color constancy experiments. Figure 2b illustrates hypothetical population vectors produced by the model in response to a yellow stimulus both in a void and when surrounded by a homogeneous red background.

The measure of constancy used is

\[
K_i = 100 \times \frac{(v_{wi} - v_{di}) \cdot (v_{wi} - v_{di})}{(v_{wi} - v_{di})^2}
\]

where \( v_{wi} \) and \( v_{di} \) are the population vectors produced by the model when presented with stimuli \( i \) in the Mondrian and void conditions respectively. \( v_{wi} \) is the population vector produced by the model with stimulus \( i \) in the reference condition (white light and contextual background). Thus, the value \( K_i \) represents the size of the shift towards constancy expressed as a percentage of the amount required for perfect constancy.

The measure of color induction used is given by

\[
I_i = \frac{|p_s - p_d|}{|p_s|}
\]

where \( p_s \) and \( p_d \) are the population vectors produced by the model for the stimulus with no surround and the stimulus with a surround of radius \( d \) respectively. In the basic experiments testing induction, an achromatic (Munsell N6) center stimulus is utilized. In this case \( p_s \) is almost zero and the measure of induction used is simply the length of the population vector produced.

Results

Chromatic Tuning within \( IT \)

The pattern of forward connectivity into \( IT \) provided units with an even spread of preferred directions throughout the hue circle. Figure 3a shows the distribution of preferred directions of units in \( IT \). The pinwheel pattern centered at the origin illustrates that the distribution of preferred directions is relatively even. Note that in addition to producing a population of units with an even spread of preferred hues, the pattern of forward connectivity also produces a 'chromatopic' map within \( IT \): units close to each other respond maximally to similar hues.

As discussed in the previous section, population vectors calculated from the response of \( IT \) are used to characterize the results. An example of an average activity pattern in \( IT \) and the corresponding population vector is shown in Figure 3b.

Local Properties

We perceive color as a continuum. To test the ability of the model to produce firing patterns consistent with this perceptual ability, it was tested with the standard 10 Munsell papers (Munsell 10R 6/6-10RP 6/6), having a constant chroma and value and differing only in hue, as well as with Munsell papers having constant hue and value but differing in chroma. [The Munsell system uses a three part code to specify the reflectance properties of a colored object. For example, the notation 10R 4/6 describes an object with Munsell hue 10R, Munsell value 4/ and Munsell chroma /6, which roughly corresponds to saturation. For a full description of the Munsell color notation refer to Wyszecki and Stiles (1982).] The model was presented with stimuli consisting of a colored square on a black background viewed under white light. The response of the model to these stimuli is shown in Figure 4.

The results in Figure 4 show how the response varies in a constant manner as the stimuli are varied in hue only, producing the hue circle around the origin and as they are varied in chroma only, producing the various saturation lines radiating away from the origin.

Contextually Influenced Properties

Color Constancy

In order to test the hypothesis that long-range intra-cortical connections in \( V4 \) and \( V1/V2 \) and cortico-cortical connections between \( V4 \) and \( V1/V2 \) can mediate contextual integration, experiments were conducted using stimuli similar to those used to test color constancy. Physiological experiments on monkeys using a color constancy paradigm showed that cells in area \( V4 \) responded in accord with the color observed by the experimenter whereas cells in area \( V1 \) responded to the major wavelength component of light in the cell's receptive field (Zeki, 1983b). To illustrate that units in the model exhibit similar properties, the response of two unit types in both \( V1/V2 \) and \( V4 \) were recorded while being presented a stimulus under white light and colored light both with and without a contextual surround. In all of the experiments discussed in this section, the Mondrian-like contextual surround consisted of a \( 5 \times 5 \) checkerboard made up of squares of with equal Munsell values but varying chromas. Figure 5 shows the average response of red and green units when presented with a stimulus of Munsell 10R 6/6 under white light and illuminant 122 (fern green).

The data reveal a clear difference in the responses of units in \( V1/V2 \) and \( V4 \). Under white light, red units in both \( V1/V2 \) and \( V4 \) respond strongly and green units show a weak response. When the illuminant is changed to fern green and the stimulus is viewed in the void condition, the response of the red units drops and the response of the green units rises in both cortical regions. Under this condition, all units show firing which is purely dependent on the wavelength distribution of light in their receptive fields. When a contextual surround is added, a clear difference between the response properties of \( V1/V2 \) and \( V4 \) units is seen. Units in \( V1/V2 \) show very little alteration in their firing levels when a contextual surround is added; they continue to fire in correlation with the local properties of the visual scene. Units in \( V4 \), however, change their firing levels when a contextual surround is added. Red units increase their firing
Figure 3. Characterization of region IT. In both figures color is used as a heuristic indicator of value, not to represent actual or perceived color. (a) Distribution of preferred direction of units. The position in the diagram represents the position within IT and the color represents the preferred direction of that unit. The angles refer to angles in the space defined in Appendix B, with 0 corresponding to the Y (yellow) axis. Note that black squares refer to units with a regression curve giving \( r^2 < 0.85 \); these units are not used when calculating subsequent population vectors. (b) Example of an average activity pattern and resultant (unnormalized) population vector for a stimulus of 10Y 6/6 on a black background under white light. The individual vectors contributed by each IT unit are shown in green and the resultant population vector in red. Note that the axes are shortened to show the individual vectors in more detail and therefore the population vector is not shown at its full length.

Figure 4. Responses of the model to various stimuli of constant chroma (Munsell 6) but varying hue (Munsell 10R, 10YR through 10GP) and constant hue (Munsell 10R, 10Y, 10G and 10B) but varying chroma (Munsell 2, 4, 6, 8 and 10 for 10R, 10G and 10B, and 2, 4, 6 and 8 for 10Y). The points shown represent the end points of the normalized population vectors calculated from the response of IT.
Figure 5. Response of red (solid lines) and green (dotted lines) units in V1/V2 (top) and V4 (bottom) under white light (left) and under fern green light in both the void condition (center) and with a Mondrian-like surround (right). The lines give the average activation of 64 V1/V2 units and 16 V4 units at the center of the topographic maps when presented with a stimulus of Munsell 10R 6/6. The x-axis represents cycles of the simulation.

Figure 6. Results of color constancy experiments for five different illuminants. In each case the black line shows the results for the non-void condition under white light; the green line shows the void condition under colored light; the red line shows the non-void condition with a Mondrian-like background under colored light; and the orange line shows the non-void condition with a background of Munsell N6. The points shown represent the end points of the normalized population vectors. The difference between the black and green circles represents the color shift that occurs as the result of changing the color of the illuminant. For perfect color constancy the red or orange circle should overlay the black circle. The deviation from this situation represents the deviation from ideal color constancy.
while green units decrease their activation levels and fire more in accordance with what is seen under white light than would be predicted from the local cues in the visual scene. These properties of the model agree with the observed physiology (Zeki, 1983b).

To characterize the model's color constancy behavior more fully, experiments were conducted imitating psychophysical investigations on color constancy (Arend and Reeves, 1986; Valberg and Lange-Malecki, 1990; Arend et al., 1991; Lucassen and Walraven, 1993). Each experiment consisted of presenting the 10 standard stimuli to the model under three different viewing conditions: (i) with a Mondrian-like background (non-void viewing condition) under white light; (ii) with a black background under colored light; and (iii) with a Mondrian-like background under colored light.

Figure 6 shows the results of five experiments with five different illuminants that produce color shifts towards different parts of the perceptual color space. The model shows qualitatively similar results to those seen psychophysically. In particular: (i) when the illuminant color is changed and the stimuli viewed in a void, the constructed color changes; (ii) when a background context is added, the color circles shift back from those produced in the void condition towards those produced with white light. In the psychophysical data, when a contextual background is added, the color matches move from those obtained in the void condition towards those obtained under white light; (iii) the shift that is observed when a context is added does not produce ideal constancy in any situation; (iv) the shape of the color circle produced in the void condition can change when the illuminant is colored; and (v) when context is added, the shape of the color circle is not altered dramatically from that seen in the void condition but its center point is shifted. These last two points are also seen in the psychophysical data of Lucassen and Walraven (1993).

In order to compare our results quantitatively with data on human psychophysics, the amount of constancy achieved by the model was quantified using the measure, $K_r$, described in Materials and Methods. The data in a number of quantitative psychophysical studies of color constancy were analyzed using the same measure. A comparison between the average constancy values achieved by the model and those observed psychophysically is given in Table 1. The model of Courtney et al. (1995), which investigates the possible role in color constancy of interactions between retinal and cortical mechanisms, shows an average degree of constancy of 20%.

The degree of constancy varies with the stimulus used, the particular illuminant and the observer. The quantitative psychophysical data show considerable variance in the values of color constancy, from zero or even negative values (Arend and Reeves, 1986; Arend et al., 1991), to values approaching 80% of perfect constancy (Valberg and Lange-Malecki, 1990; Lucassen and Walraven, 1993). As shown in Table 1, the results in the present study gave values in the mid-range of those reported by various authors. It is important to note that our model only attempted to model cortically mediated aspects of color constancy. Non-central mechanisms, such as retinal adaptation or the interaction of the color stream with the rest of the brain, could change the degree of constancy observed.

The psychophysical data from the study of Lucassen and Walraven (1993) showed effects not seen in the results presented so far. With one particular illuminant (cyan) their results show a flattening of the color circle due to the use of stimuli which approached the physical limit of the monitor used to produce them. Since we use actual pieces of Munsell paper rather than simulated images, this cannot occur. However, if our illumination level or model parameters were changed to produce saturation in either the camera input or unit responses, then a similar effect of a flattening of the color circle was seen (data not shown). More importantly, when context was added to such saturated stimuli, the resultant model response produced a flattened color circle that was shifted with respect to the void condition towards the circle seen under white light (data not shown). This agrees, qualitatively, with the psychophysical data of Lucassen and Walraven for the cyan illuminant.

In addition to Mondrian-like backgrounds, recent psychophysical experiments have shown that a uniform achromatic background can also produce color constancy effects (Arend and Reeves, 1986; Valberg and Lange-Malecki, 1990; Arend et al., 1991). Figure 6 shows the results from a similar experiment conducted with the model. This experiment was identical to the color constancy experiments described above except the Mondrian surround was replaced by a uniform achromatic surround (Munsell N6). The results agree with the psychophysical findings in that a similar degree of constancy occurs with either a Mondrian or a uniform achromatic surround.

### Color Induction

Another major contextual effect of color vision is color induction or simultaneous color contrast (Jameson and Hurvich, 1959; Kinney, 1962) in which an object appears to be of the opposing color to an inducing surround. To test the model's ability to produce this basic property of the color vision system, an
experiment was conducted replicating a basic color induction paradigm. The stimuli presented to the model consisted of an achromatic square (Munsell N6) surrounded by a field of one color (the inducing color) viewed under white light. The results of this experiment are shown in Figure 7a. The figure shows induction effects in that an achromatic stimulus produces responses consistent with the color opposing the inducing surround.

A number of studies have also been conducted investigating the effects of more complex inducing surrounds on the level of induction and we replicate one of those here. The experiment conducted was to investigate the effect on induction of surround radius and distance to surround. The experiment consisted of two parts. In the first part the distance to the surround ($r_d$) was fixed at zero (i.e. no test-to-surround gap) and the surround radius ($r_s$) was varied. In the second part the surround radius was fixed at full field width and the distance to the surround, and therefore the size of the gray ring separating the stimulus and the inducing surround was varied. The results, shown in Figure 7, agree with the psychophysical observations (Kinney, 1962; Walraven, 1973; Tiplitz Blackwell and Buchsbaum, 1988; Wesner and Shevell, 1992; Singer and D'Zmura, 1994) in that increasing the size of the surround increases the induction effect, while increasing the stimulus to surround distance decreases the induction effect.

Role of Reentry
The results presented in the previous sections show how the model produces responses consistent with the phenomena of color constancy and simultaneous color contrast. The model consists of three reentrant pathways mediated by the long-range intrinsic connections within $V1/V2$ and within $V4$, and the backward connections from $V4$ to $V1/V2$. In order to assess the role of these different circuits in affecting the model's response, selective lesion experiments were performed in which the connections underlying one reentrant circuit were perturbed and the effect on color constancy and color inductions observed.

Figure 8a shows the effect on constancy of cutting each of the three different sets of connections for the standard stimuli under fern green light (no. 122). Figure 8b summarizes the effect on constancy of the different lesions as measured with 50 different stimuli, made up of the 10 standard stimuli under five different illuminants. Note that in order to avoid any potential artifacts due to uneven distribution of hues in the contextual surround a
homogeneous surround of Munsell N6 was used in these experiments.

Figure 9 shows the effect of lesions on induction with a background of 10R 6/6 surrounding a stimulus of 10Y 6/6. In each case the amount of induction measured as a percentage of that shown by the intact model is plotted against surround radius. In this manner, the graph illustrates the effect of the particular lesions as a function of surround size.

A number of conclusions can be drawn from the data: (i) long-range intrinsic connections within V4 have the greatest effect on both constancy and induction; (ii) long-range intrinsic connections within V1/V2 have a smaller but significant effect on constancy. Changes shown in Figure 8a are significant at \( P < 0.01 \) (\( n = 10 \)) in the Wilcoxon signed-rank test. The changes underlying the average effect shown in Figure 8b are significant at \( P < 0.01 \) (\( n = 50 \)) in the Wilcoxon signed-rank test. The V1/V2 intrinsic connections have an effect on induction that depends on the size of the stimulus surround. With small surrounds, the V1/V2 intrinsic connections can have as much effect on induction as the V4 intrinsic connections; and (iii) backward connections from V1/V2 do not affect constancy in a significant manner. These connections have a small but measurable effect on induction. This effect is also surround size dependent, although to a smaller degree than with V4 and V1/V2 intrinsic connections. The differences in the shape of the curves in Figure 9 can be related directly to the modeled anatomy and are discussed below.

These selective lesion experiments demonstrate that both color constancy and color induction are mediated by the system as a whole and not by one specific circuit. Constancy or induction cannot be removed by the lesioning of just one pathway. The differential contributions of V4 and V1/V2 intrinsic connections to constancy and induction can be explained by considering the relative spread of connections within V4 as compared to within V2 (8 mm compared with 5 mm; see Table 5) and the ~2:1 ratio of cortical magnification factors between V2 and V4 (Van Essen and Zeki, 1978;Gattass et al., 1988). V4 intrinsic connections cover almost four times the visual angle as do similar connections within V2 and so V4 intrinsic connections have more potential to affect contextual integration than V2 intrinsic connections. Similarly, the back connections from V4 to V1/V2 cover only a small visual angle within the V1/V2 topographic map and so have less potential to affect contextual integration than the V4 intrinsic connections. The color induction stimuli further demonstrate the causal role of this difference in visual angle coverage. The curves in Figure 9 can be viewed as illustrating the relative effectiveness on induction of the different pathways in the intact model. A low value indicates a large effectiveness. Consider the curves relating to the intrinsic connections within both V1/V2 and V4. Both curves show an initial increase of effectiveness as size of the inducing surround is increased. This increase is due to an increase in the number of connections within both regions being activated. Thus both pathways become more effective at producing induction. At a certain surround size, the relative effectiveness of the V1/V2 intrinsic connections starts to decrease, producing the U shaped curves shown. This reversal occurs because, at a certain size of inducing surround, all the intrinsic connections within V1/V2 are active. Increasing the size of the stimulus further activates more V4 connections but not more V1/V2 connections. Thus the relative effectiveness of the V1/V2 connections decreases. Eventually the effectiveness of
the V4 connections reaches an asymptote when the stimulus size is big enough to activate them all.

A similar effect is seen with the backward connections except no initial increase in effectiveness is seen. This is because, with the smallest stimulus used, all of the back connections afferent to V1/V2 units at positions in the retinotopic map corresponding to the position of the center stimulus are active. Thus, increasing the surround size does not recruit any more back connections and their relative effectiveness decreases.

Unlike the long-range intrinsic connections within V1/V2 and V4, the detailed functional connectivity of the backward connections is not constrained by available data, other than the fact that they are less specific in their terminations. If the modeled connectivity of the backward connections is an accurate reflection of the real anatomical arrangement then the results presented above suggest that their role in contextual integration is small but also not detrimental.

Discussion

The simulations described here are concerned with the effects of context on color perception, as revealed by a dynamic, neurally based model capturing known anatomical details of the primate visual system. Since the demonstrations of contextual aspects of color vision by Land (1964), the effects of context on color perception have been studied by a number of different authors from many different perspectives, including physiology and psychophysics (McCann et al., 1976; Zeki, 1983a, b; Arend and Reeves, 1986; Valberg and Lange-Malecki, 1990). What is lacking, however, are theories that incorporate the essential features for color perception of cortical anatomy, dynamics and physiology in accord with the reported data. To instantiate such a theory, we constructed a model based on known anatomical and physiological properties of the visual cortex, in particular areas V1, V2, V4 and IT, and analyzed its behavior with stimuli obtained from signals from a video camera. Tests of the model were based on stimuli used in psychophysical experiments designed to investigate color constancy and color induction.

In the remaining parts of this discussion, the salient results of the study and links to the known physiology are considered in greater detail. The proposed role of IT in color vision is also discussed in more detail. Finally, the relationships to previous models and theories of color vision are examined.

Contextual Effects

A major result of the tests of the model is that the reentrant interactions within and between V4 and V1/V2 can give rise to firing patterns compatible with the psychological phenomena of color constancy and color induction. Specifically, the model demonstrates that both phenomena can be mediated by the same anatomical arrangement and that the effects can be nonlocal, e.g. the dependence of induction on the distance to surround parameter. The long-range intrinsic connections within V1/V2 and V4 and the backward connections between V4 and V1/V2 serve to mediate reentrant interactions that can span non-contiguous regions of the visual field, thus producing these non-local effects.

A simulated selective lesion study of the model illustrated how the phenomena of color constancy and color induction are the result of system-wide interactions; neither phenomenon can be destroyed by the lesion of one circuit alone. In addition, the testing of the lesioned model with different stimuli illustrated how the role of specific pathways is dependent on the stimulus configuration used. For example, the backward connections made no significant contributions to color constancy but had an influence on color induction. This occurs because the contextual background in the color induction experiments consists of one hue, compared with a mixture of many hues in the color constancy experiments, and so only a subset of all the backward connections are active, producing a differential influence on units within V1/V2. The relative contribution to induction of all three sets of connections was shown to be dependent on the size of the inducing surround. This effect is a direct result of the relative spread of these connections over the cortical maps. The changes seen in the neural equivalent of the psychological phenomena of color induction are directly dependent on changes made to the underlying anatomy.

Role of IT in Color Vision

In this paper we suggest that a functional role of area IT in color vision may be to provide a spatially organized map which explicitly represents a given color. This was obtained by remapping the activity levels of four sets of cells within V4 onto neural space within IT. The remapping constitutes a change from an implicit representation of hue and saturation, where color is represented as the ratio between the firing levels of four populations of cells, to an explicit relationship, in which color is represented by specific firing patterns within one population of cells. Our proposal is consistent with evidence in the literature concerned with the role of IT in color vision. Lesion data (Heywood et al., 1995) comparing monkeys with lesions to V4 and lesions to IT suggest that IT but not V4 is necessary for color vision. The data reveal that the IT lesioned animals show performance degradation on color related tasks that is similar to that shown by humans with cerebral achromatopsia, suggesting that IT corresponds to a brain region that is needed for conscious experience of color. In addition to the lesion data, cooling experiments (Horel, 1994) have shown IT to be involved with color and anatomical studies have shown IT to be a major recipient of V4 projections (Felleman and Van Essen, 1991). Moreover, electrophysiological recordings have shown chromatic specificity of cells within IT (Komatsu et al., 1992).

In the model, the pattern of connections from V4 to IT produces a 'chromatopic' map within IT: units spatially close to each other respond to similar colors. Although this spatial mapping is not used in the results presented here, the existence of such a topography is an interesting possibility. Some evidence exits as to the existence of columns within IT (Fujita, 1993) in which neurons with similar response properties are grouped together. However, it is not known whether such columns are organized in any systematic manner, and the existence or absence of a chromatopic organization within IT remains a question open to experimentation.

Traditionally, IT has been associated with higher level aspects of vision (see e.g. Tanaka, 1992; Miyashita, 1993; Desimone and Duncan, 1995) such as size and spatial invariance, memory and attention. The proposed role of IT in color vision obviously does not exclude involvement of this area in other aspects of vision. Indeed, the response of IT can be viewed as producing a spatially invariant representation of the constructed color which is a direct parallel of a proposed role of IT in form vision (e.g. Lueschow et al., 1994; Ito et al., 1995).

Other Models of Color Vision

Computational approaches have been employed to characterize color vision and may be considered complementary to those used in the present work. In such a computational approach,
color constancy is expressed as the problem of discounting the illuminant or the recovery of reflectance (Hurlbert, 1986). These approaches, however, produce a system of under-determined equations and additional assumptions must be made about the properties of the visual scene, the illuminant or both (for a review see Lennie and D'Zmura, 1988).

In addition to purely computational approaches, a number of neural network-based methods have been utilized to study color constancy. Hurlbert and Poggio (1988) showed how multi-layer perceptrons and radial basis function networks could be trained to recover reflectance. Although this approach utilizes neural networks, it says little about the actual underlying neural mechanisms involved in color vision. Duport and Lumsden (1991) constructed a network model based on double-opponent cells that was able to show color constancy and color categorization behavior. However, the existence of double-opponent cells in the visual cortex has recently been questioned (Lennie and D'Zmura, 1988; Ts'o and Gilbert, 1988) and the model of Duport and Lumsden does not attempt to address the role of cortical circuitry in color vision.

In a recent simulation study (Courtney et al., 1995) the relative contribution of retinal and cortical mechanisms to color constancy was studied; a comparison between the two models is useful. Our goal in the present study was to construct a model based on the anatomical details of the visual cortex in order to investigate the cortical bases of color vision. As such, the model presented here differs in a number of ways from that of Courtney et al.: (i) our model simulates multiple cortical areas corresponding to V1/V2, V4 and IT; (ii) it has a large collection of both intra- and inter-areal reciprocal connections. The convergence-divergence of the forward connections and the lateral extent of the intra-areal and backward connections are constrained by quantitative neuroanatomical data; (iii) changes in the responses of our model are documented by observing the changes in firing patterns in a non-retinotopically mapped population of neuronal units; (iv) our model does not require the proposal of a cell type that has not been observed in V4 or of a very specific 'push-pull' circuitry to produce a response consistent with color constancy and color induction; and (v) the model of Courtney et al. had the virtue of showing how both retinal and cortical stages can play a role in color constancy and color induction. Our model does not simulate retinal adaptation and the contribution of this mechanism to color perception after incorporating it into the model has not yet been studied.

**Limitations and Experimental Tests**

The units in region V1/V2 of our model are chromatically tuned to respond maximally along the perceptual color axes, following the proposal of De Valois and De Valois (1993). Their model shows how, by combining the output of the different cell types in ratios of their relative abundance, the S+ and S- cells can be utilized to provide a rotation of the cardinal axes (seen at the LGN) to the perceptual axes. The areas of visual cortex involved in this rotation are not known but evidence suggests that cells in the CO-rich blobs of V1 (Livingstone and Hubel, 1984; Ts'o and Gilbert, 1988; Hubel and Livingstone, 1990) and thin stripes of V2 (DeYoe and Van Essen, 1985; Hubel and Livingstone, 1987; Levitt et al., 1994a) are tuned to the perceptual axes. Controversy still exists, however, as to the existence of such tuning (Lennie et al., 1990).

Within our model, V4 units were also tuned, locally, to the perceptual color axes. The study of Schein and Desimone (1990) shows three definite peaks in the relative abundance of V4 cells tuned to different wavelengths, with the peaks occurring at approximately the wavelengths of red, yellow and blue light. A fourth peak at green, while not as definite, does suggest itself in their data. The model presented here is dependent on the existence of such chromatic tuning at stages V1/V2 and V4. If this turns out not to occur in the primate visual system, the fundamental assumptions of the model will have to be altered.

The long-range intrinsic connections in both V1/V2 and V4 are defined according to the functional connectivity of V4 cells highlighted by the study of Schein and Desimone (1990). This assumption seems reasonable since analogous functional connectivity (Allman et al., 1985; Desimone et al., 1985; Knierim and Van Essen, 1992) is seen in other visual areas, suggesting the possibility that this functional connectivity is a fundamental property of visual cortical areas. If the actual functional connectivity in V1 or V2 is radically different from that in V4 then this aspect of the model will have to be changed.

Although there is considerable evidence for the separation of function within the visual cortex, a fact that allows us to consider the color stream in isolation, there is also evidence of interactions between visual submodalities. For example, recent psychophysical studies (Wesner and Shevell, 1992; Zaidi et al., 1992; Bäuml, 1994; Jenness and Shevell, 1995) have shown how color perception can be altered by the spatial organization of the visual scene. An extension of the current model to study the interactions of different anatomical pathways may shed light on how the perception of color is affected by shape or motion.

The present results concerning context dependent effects could be tested with a number of different neurophysiological experiments. The selective lesion experiments suggest that, with small stimuli, V2 may have as much influence on contextual integration as V4. This could be tested directly by recording from V2 while a monkey is viewing stimuli designed to test color constancy or color induction. With large stimuli, the expected result would be that the firing of V2 neurons would be correlated with the local wavelength distribution of light reflected from the stimulus, whereas with small stimuli, V2 neurons would have firing rate correlated more with the perceived color. Other experiments that suggest themselves, but are not yet technically feasible, involve the selective deactivation of one or more of the reentrant pathways modeled in this study. Such experiments would directly confirm or contradict the results of the selective lesion experiments presented here.

The proposal concerning the role of IT in color vision could be tested experimentally by recording the response of a population of IT neurons to chromatic stimuli. A population vector could then be constructed along the lines outlined in Materials and Methods. Comparison of such a vector with the actual object color would provide a test of this hypothesis.

**Analogous Effects in Other Submodalities**

Phenomena analogous to color induction exist in other visual submodalities, such as in motion and form vision. Within motion vision there exists an analog of brightness induction (very similar to color induction) in which the perceived velocity of moving dots is altered by the velocity of surrounding dots (Loomis and Nakayama, 1973). The induced motion is in the direction opposite to the inducing motion field. In the form domain the tilt illusion forms an analogous perceptual phenomenon to color induction. In this illusion the perceived angle of a bar can be made to change when a surround of angled bars is introduced. The shift in perception is away from the angle of the inducing bars. Neurophysiological studies of motion sensitive cells in MT...
(Allman et al., 1985), of form-sensitive cells in V4 (Desimone et al., 1985) and of cells in V1 (Knierim and Van Essen, 1992) have shown analogous results to the V4 chromatic study of Schein and Desimone (1990). The modeling study of Gilbert and Wiesel (1990) suggests that such long-range interactions could explain the tilt illusion. However, in area 17 of the cat, they found that the majority of cells did not possess appropriate receptive field properties. A similar study in monkey (Knierim and Van Essen, 1992) did, nevertheless, find cells with the appropriate response properties. These results suggest that mechanisms similar to those described in the present paper may apply more generally to other systems. The regular pattern of long-range patchy connections seen throughout the cortex may serve to integrate context into visual percepts for various submodalities. This generalization could be tested relatively easily by changing the modal properties of units within a model similar to the one we have presented here.

Conclusion
The major goal of this work was to construct an anatomically and physiologically based model of the color stream of the visual cortex in order to investigate the neural bases of color perception. The model investigates the role of several cortical areas in color vision. The main results illustrate how a system of lateral and backward connections within and between cortical regions can mediate the integration of contextual cues into the color percept. Selective lesion experiments demonstrate the dependence of color constancy and color induction on all three recrrent pathways. These experiments also indicate that the relative contribution of the different pathways to contextual integration can vary depending on the stimulus properties.

Appendix A: Model Specifics
The general architecture of the model and the observations forming the basis of its construction were described in the main text. This appendix describes each area in more detail, outlining all the parameters used. Although units in each modeled region had specific parameters, a number of model parameters apply to many or all areas and will be described first. Several of these parameters are generally not constrained by experimental data and values were chosen to ensure that the model operated within reasonable dynamic bounds (e.g. so that no units are continuously saturated).

All units within the model had the same persistence parameter \( \omega = 0.3 \), and at each time step units in LGN had noise added to their activation levels. This noise value was drawn from a Gaussian distribution with a mean of 0.01 and an SD of 0.005. All voltage-dependent connections had the same sigmoidal function defined by \( \xi = 0.38 \). All \( \xi \)'s, except those defining the receptive field properties of the LGN cells and those connections from V4 to IT, were random values drawn from a Gaussian distribution with a mean of 0.5 and an SD of 0.1. Specificities of connection strengths between different unit types were defined by the scale factor, \( \eta \) and these values are described later.

LGN
The receptive field properties of the LGN cells were constructed using the forward connections from the input image sampled from the camera. The scheme of De Valois and De Valois (1993) was used to construct the chromatic specificity of the LGN units and the V1/V2 units. Following the data of Derrington et al. (1984), the overall strengths of connections to the center and surround were equal. Table 2 lays out the specific parameters used in constructing the receptive field properties of these cells.

**V1/V2 and V4**
The scale factors used for the forward connections between the LGN and V1/V2 and between V1/V2 and V4 are given in Tables 3 and 4 respectively.

1. **Local excitatory**: Excitatory units within V1/V2 and V4 receive four voltage-dependent connections from units of the same chromatic specificity within a 2 x 2 area centered at each unit. Within both regions, the scale factor is \( g_r = 0.15 \). Inhibitory units within V1/V2 and V4 also receive four voltage-dependent connections from excitatory units of the same chromatic

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**Table 2** Specific parameters used to construct the receptive field properties of the LGN units

<table>
<thead>
<tr>
<th>Cell type</th>
<th>Source image</th>
<th>Strength</th>
<th>Strength (S)</th>
<th>Strength (M)</th>
<th>Strength (L)</th>
</tr>
</thead>
<tbody>
<tr>
<td>L+</td>
<td>L</td>
<td>0.43</td>
<td>-0.315</td>
<td>-1.576</td>
<td>-3.15</td>
</tr>
<tr>
<td>M+</td>
<td>M</td>
<td>0.43</td>
<td>-0.315</td>
<td>-1.576</td>
<td>-3.15</td>
</tr>
<tr>
<td>S+</td>
<td>S</td>
<td>0.864</td>
<td>-0.083</td>
<td>-0.315</td>
<td>-0.63</td>
</tr>
<tr>
<td>L-</td>
<td>L</td>
<td>-0.432</td>
<td>0.315</td>
<td>1.576</td>
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</tr>
<tr>
<td>M-</td>
<td>M</td>
<td>-0.432</td>
<td>0.315</td>
<td>1.576</td>
<td>3.15</td>
</tr>
<tr>
<td>S-</td>
<td>S</td>
<td>-0.864</td>
<td>0.063</td>
<td>0.315</td>
<td>0.63</td>
</tr>
</tbody>
</table>

In all units the size of the center is one pixel and the surround is 3 x 3 pixels with no connection to the center pixel (i.e. a total of eight connections from each input image defines the surround). Note that the connections to the S+ and S- units are scaled down by a factor of \( S \). This is to ensure a reasonable dynamic operating range for these cells; this scale factor is corrected for in the subsequent forward connections from LGN to V1/V2.

**Table 3** Values of the scale factor \( \eta \) for the connections from LGN to V1/V2

<table>
<thead>
<tr>
<th>R</th>
<th>Ri</th>
<th>Y</th>
<th>Yi</th>
<th>G</th>
<th>Gi</th>
<th>B</th>
<th>Bi</th>
</tr>
</thead>
<tbody>
<tr>
<td>L+</td>
<td>1.2</td>
<td>0.27</td>
<td>1.2</td>
<td>0.27</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>M+</td>
<td>-</td>
<td>-</td>
<td>0.6</td>
<td>0.135</td>
<td>0.6</td>
<td>0.126</td>
<td>-</td>
</tr>
<tr>
<td>S+</td>
<td>1.2</td>
<td>0.27</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.2</td>
<td>0.27</td>
</tr>
<tr>
<td>L-</td>
<td>-</td>
<td>-</td>
<td>1.2</td>
<td>0.27</td>
<td>1.2</td>
<td>0.27</td>
<td>-</td>
</tr>
<tr>
<td>M-</td>
<td>0.6</td>
<td>0.135</td>
<td>0.6</td>
<td>0.135</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>S-</td>
<td>-</td>
<td>-</td>
<td>1.2</td>
<td>0.27</td>
<td>1.2</td>
<td>0.27</td>
<td>-</td>
</tr>
</tbody>
</table>

R refers to an excitatory unit tuned to red and Ri to an inhibitory unit tuned to red. The notation extends to Y and B for yellow, green and blue tuning. The relative strengths of these connections scale factors are in accordance with the model of De Valois and De Valois (1993), which specifies a ratio of connection strengths of LMS:10:5:2.

**Table 4** Values of the scale factor \( g_r \) for connections from V1/V2 to V4

<table>
<thead>
<tr>
<th>V4 R</th>
<th>V4 Ri</th>
<th>V4 Y</th>
<th>V4 Yi</th>
<th>V4 G</th>
<th>V4 Gi</th>
<th>V4 B</th>
<th>V4 Bi</th>
</tr>
</thead>
<tbody>
<tr>
<td>V4/V2 R</td>
<td>0.15</td>
<td>0.05</td>
<td>0.035</td>
<td>0.035</td>
<td>0.0115</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>V4/V2 Y</td>
<td>0.035</td>
<td>0.0115</td>
<td>0.15</td>
<td>0.05</td>
<td>0.035</td>
<td>0.0115</td>
<td>-</td>
</tr>
<tr>
<td>V4/V2 G</td>
<td>-</td>
<td>-</td>
<td>0.035</td>
<td>0.0115</td>
<td>0.15</td>
<td>0.05</td>
<td>0.035</td>
</tr>
<tr>
<td>V4/V2 B</td>
<td>0.035</td>
<td>0.0115</td>
<td>-</td>
<td>-</td>
<td>0.035</td>
<td>0.0115</td>
<td>0.15</td>
</tr>
</tbody>
</table>

Note that all units receive 10 connections from a 4 x 4 area on each V1/V2 map that projects to that particular unit type.

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specificity. Again the connections are from a 2 \times 2 area centered on the topographic position of the receiving cell and with \( g_i = 0.035 \).

2. **Local inhibitory**: Excitatory units within V1/V2 and V4 receive three sets of connections from inhibitory units tuned to the same chromatic region and the two neighboring regions (e.g., a yellow unit receives connections from yellow, red and green inhibitory units). Each set of projections consists of four connections from a 2 \times 2 region centered on the topographic position of the receiving unit. The scale factors for connections within V1/V2 were \( g_i = 0.34 \) from units tuned to the same chromatic region and \( g_i = 0.1 \) from cells tuned to the neighboring region. Within V4, the scale factors were \( g_i = 0.27 \) and \( g_i = 0.05 \). Inhibitory units received four connections from inhibitory units of the same chromatic specificity, again in a topographic manner, with \( g_i = 0.023 \) in both V1/V2 and V4.

3. **Long range excitatory**: Both excitatory and inhibitory units received long-range voltage-dependent, excitatory connections. These connections were arranged so that the probability for any unit to receive a connection from another unit \( \text{p} \text{(connect)} \) fell off exponentially with distance between the cells. This fall-off was approximated by a square wave starting value of \( \text{p} \text{(connect)} = 0.7 \) at a distance defined by an area of 3 \times 3 units centered on the topographic location of the receiving unit and falling to a value of \( \text{p} \text{(connect)} = 0.1 \) at a distance defined by the maximum spread of intrinsic connections. Each step width was two units wide in each direction. Within V1/V2, the area covered by the connections was 17 \times 17 units and the scale factor was \( g_i = 0.005 \). Within V4, the area covered by the connections was 27 \times 27 units and \( g_i = 0.002 \). In both areas the chromatic specificity was such that excitatory units received connections from units of the opposite chromatic tuning and inhibitory units from units of the same chromatic tuning.

4. **Backward excitatory**: Units in V1/V2, both excitatory and inhibitory, received excitatory voltage-dependent connections from V4. Each unit received three sets of 21 connections each from a 7 \times 7 area arranged topographically. The chromatic specificity was such that a V1/V2 unit received connections from units of the same chromatic specificity within V4 to which it projects with a scale factor of \( g_i = 0.005 \). The strength of the long-range excitatory connections in both V1/V2 and V4 and the backward excitatory connections were adjusted so that all connection types had an equal average effect on the post-synaptic unit.

To model the anatomy of visual cortex accurately up to V4, an attempt was made to quantify as much of the connectivity as possible. As a basis for the quantification, it was decided that four modeled units should correspond to an area of one experimentally observed patch of axonal arbors, ~340 \( \mu \)m in diameter in both V2 and V4 (Lund et al., 1993). In both of these areas the average observed inter-patch interval was ~650 m. In addition, anatomical data from V2 was used to define the connectivity to, within and from V1/V2. These assumptions allowed V1/V2 to be modeled as an array of 64 \times 64 units and V4 as an array of size 32 \times 32, which, from empirical observation, provided enough spatial resolution for the model's purpose. The 2:1 reduction in size between V1/V2 and V4 corresponds to the approximate 2:1 reduction in cortical magnification factor between V2 and V4 (Van Essen and Zeki, 1978;Gattass et al., 1988). Using these assumptions as a basis, various anatomical measurements can be translated into model parameters and these are summarized in Table 5.

### Table 5

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Anatomical data</th>
<th>References</th>
<th>Model specifics</th>
</tr>
</thead>
<tbody>
<tr>
<td>V1/V2 \rightarrow V4</td>
<td>a cell in V2 projects, on average, to 2.5 patches in V4 spaced 1-2 ( \text{in} ) inter-patch distances apart</td>
<td>Rockland (1992)</td>
<td>on average, a V1/V2 unit projects to 2.5 V4 units over an area of 2 x 2 inter-patch intervals. This is implemented by having each V4 unit receive 10 connections from a 4 x 4 grid of V1/V2 units.</td>
</tr>
<tr>
<td>Extent of V1/V2 intrinsic upper bound =5 mm patchy connections</td>
<td>Lund et al. (1993); Levit et al. (1994b)</td>
<td>-5 mm is equivalent to 7.7 inter-patch intervals and so to -17 V1/V2 units</td>
<td></td>
</tr>
<tr>
<td>Extent of V4 intrinsic upper bound =8 mm patchy connections</td>
<td>Yoshikita et al. (1992); Lund et al. (1993)</td>
<td>8 mm is equivalent to 12.3 inter-patch intervals and so to -27 V4 units</td>
<td></td>
</tr>
<tr>
<td>V4 \rightarrow V1/V2 convergence and divergence 1 V4 cell projects over 3-5 mm of V2</td>
<td>Rockland et al. (1994)</td>
<td>4 mm is equivalent to 6.2 inter-patch intervals and so to 14 V1/V2 units. Since V4 is half the size of V1/V2, one V1/V2 cell receives from a 7 x 7 V4 grid</td>
<td></td>
</tr>
</tbody>
</table>

### IT

The chromatic tuning of units in IT was constructed to reflect those actually observed in IT: a population of cells with broad chromatic tuning, a non-null response to white stimuli and a uniform distribution of preferred hues (Komatsu et al., 1992). In all experiments conducted with the model, the stimulus, as opposed to the contextual surround, was in the center of the visual field. Thus to ensure that the firing patterns within IT depended on the constructed color of the stimulus, the activity levels of the central 4 \times 4 units of V4 were remapped onto space in IT. This produced activity patterns within IT that depend on the relationship between the activity of the different units within V4. Each IT unit received 16 connections from each of the four V4 unit types. The strength of all connections \( \text{c}_{ij} \) was random and was drawn from a Gaussian distribution with an SD of 0.15. The mean of the distribution was determined by a gradient defined by the position of the receiving unit in IT. The gradients were defined to ensure an approximately even distribution of preferred directions (hue that excites a unit maximally) around the color circle. Mathematically the gradient used was defined by:

\[
c_m = c_{xy}(1-x)(1-y)+c_{10}x(1-y)+c_{01}(1-x)+c_{11}xy
\]

where \( x \) and \( y \) are the relative positions in the half of IT being considered. The \( c_{xy} \) values define the corner points of the gradient and are given by 0.5 for the maximum, 0.25 at the top left and right, -0.2 at the bottom center and -0.1 at the bottom left and right. The distribution of preferred directions is obtained by having the maximum strength connections at different positions in IT depending upon the chromatic specificity of the V4 units sending the projections. For example, for V4 red units the maximum point was at the bottom, for green units it was at the top, for yellow units on the right and for V4 blue units it was on the left.
Appendix B: Calculation of IT Preferred Directions

In order to calculate the preferred directions of units within IT, we presented the model with 10 different square stimuli on black backgrounds under white light. The stimuli were defined in terms of their Munsell notation and were chosen to cover the entire color circle at approximately equal intervals. Figure 4 gives the full Munsell notation of the stimuli used. For each stimulus, the activity of each unit in IT was recorded for a total of 40 simulation cycles, and the average activity level, over the last 10 cycles, scaled by the total mean activity of IT over the same cycles, was calculated for each unit. Using these 10 average values, a sinusoidal regression curve of the form,

\[ a(\theta) = b_0 + b_1 \cos(\theta) + b_2 \sin(\theta) \]

was calculated for each unit using least-squares regression. The maximum of the sinusoid was then obtained. This maximum was then taken as the preferred direction of that particular unit. If the \( r^2 \) statistic for a particular regression curve was <0.85 (i.e. the regression explained <85% of the data being fitted) then that unit was not used in subsequent calculations of population vectors (this means, in effect, that the particular unit in question was not tuned to a particular hue). No transformation exists between the Munsell color space (in which our stimuli are defined) and perceptual space, and so the formula given by De Valois and De Valois (1993) for the response of the perceptual axis in terms of the response of the three cones was used to define the axes. These are given by

\[ YB = 130L - 95M - 35S \]

\[ GR = -90L + 115M - 25S \]

where \( L, M \) and \( S \) are the response of the longwave, mediumwave and shortwave cones respectively. Practically, the average pixel value of each of the three gray images obtained when viewing a square of a particular stimulus color under white light was obtained and then used to calculate the positions in perceptual color space. Using these 10 basic stimuli, the preferred directions of the units in IT were calculated as described above.

Notes

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References


