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A feedforward model of spatial lightness computation by the human visual system

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Abstract

A model of lightness computation by the human visual system is proposed. The model is consistent with known properties of retinal and cortical visual pathways and it makes exact quantitative predictions regarding lightness (perceived reflectance) matches made in psychophysical experiments. The model's behavior is computer-simulated to demonstrate that it can account, specifically, for Munsell matches made to grayscale surfaces in an experiments based on a Staircase Gelb display (grayscale papers arranged in order from darkest to lightest) and two related experiments in which the location of the paper with the highest physical reflectance is repositioned to neighbor the paper with the lowest physical reflectance either on the left or on the right.

Model Description

Random Walk Model of Fixational Eye Movements

Under natural viewing conditions, our eyes are always in motion. This is true even when we have the subjective impression that we are gazing steadily at an object. In the latter case, our eyes undergo a constant random jitter known as *fixational eye movements* [1,2]. Rather than degrading our visual perception of the world, fixational eye movements are instead a necessary component of natural vision. If fixational eye movements are artificially blocked, the visual world fades perceptually within a few seconds [3,4].

In previous work, fixational eye movements have been modeled as a 2D random walk [5,6]. In the simulations presented here, they were modeled in the following way. On each discrete time step on the simulation, it was assumed that the a photoreceptor array translated to a new position relative to the input image. The translation was modeled as a lateral shift either to the left, right, up, or down, each with a ¼ probability. The direction of the shifts occurred independently in successive time steps.

Photodetection of Luminance Increments and Decrements

At every location in the retinal array, a photodetector having the spatial profile of a 2D gaussian with equal standard deviations along the x- and y-axes was assumed to exist. The response of the photodetector on time step t depended on the *difference* in log units of the input image luminance spatially filtered by the photodetector's spatial profile on time step t and the luminance the input image filtered by the detector's spatial profile on time step t-1 (in other words, the spatially-weighted luminance in log units that photodetector saw before the eye movement). A neural gain factor was applied to this difference signal that depended on whether the photodetector response increased or decreased on time step t relative to is on time step t-1. The neural gain applied to luminance increments was 0.27, and the neural gain applied to luminance decrements was 1.0 (see [7] for a motivation of these neural gain parameters).

Combining Eye Movement Direction with Incremental or Decremental Luminance Change

At a subsequent level of processing within the visual pathways (probably located in visual cortex), a neural signal is created that is specific to *both* eye movement direction and the polarity of temporal luminance change within the spatial integration window of a given photoreceptor. At each spatial location, a neuron at this cortical processing level is activated *if and only if* the eye movement that produces an incremental or decremental photoreceptor response corresponds to a particular eye movement direction (either left, right, up, or down—that is, the direction corresponding to the eye movement that produced the photoreceptor response change) and a given polarity of the photoreceptor response change. In the simulations presented here, this resulted in eight different cortical activation maps corresponding to the eight different possible combinations of eye movement direction and luminance change polarity: L+, R+, U+, D+, L-, R-, U-, and D-. Each of these maps contained neural activations at all spatial locations for which an eye movement in a particular direction resulted in an incremental or decremental response at time t relative to the photoreceptor's response at time t-1.

ON and OFF Networks

At a yet higher stage of cortical lightness computation, two separate layers of ON and OFF cells having large receptive fields spatially sum the outputs of the + and – neurons, respectively in the first cortical map. ON cells sum the outputs of the L+, R+, U+, and D+ neurons, and OFF cells sum the outputs of the L-, R-, U-, and D- neurons. The amount of activation in any particular ON or OFF unit depends on both the distance between the location of ON or OFF cell within the higher-level cortical network (where all cortical maps are defined in retinal coordinates) and the location of the + or - neuron whose response is summed, and also on the angle of a vector drawn from the location of the + or - neuron in the first cortical map to the location of the ON or OFF cell that performs the summing in the second cortical map.

In the simulations presented below, it was assume, specifically, that: 1) that the amount of activation falls off exponentially with distance according to an exponential function having a space constant of 1.8 deg; and 2) that the amount of activation falls of as a halfwave rectified cosine function of the angle between a vector normal to the eye movement direction that generated the + or - cell activation in the first cortical map and a vector drawn from the position of the + or - neuron in the first cortical map to the position of the ON or OFF cell doing the summing in the second cortical map being. The justification of the halfwave rectification is that the cosine function must be positive so that ON and OFF cells are only activated in a direction that correlates positively with the eye movement direction that activated the + or - neuron response whose response is being summed by the ON or OFF cell.

Lightness Map

At the *final* stage of the model, the OFF network activity at each spatial location is added to the ON network activity at the same spatial location to produce a map of perceived reflectance, or achromatic colors, corresponding to each location in the input image. By convention, increments in photoreceptor activations, activations in the first cortical map generated by increments in photoreceptor activations, and ON network activations, are here coded as positive quantities; while decrements in photoreceptor activations, activations in the first cortical map generated by decrements in photoreceptor activations, and OFF network activations, are coded as negative quantities. In cortical neurophysiology, values are typically encoded by neural spike rates, which are invariably positive. So it remains an open question how the processing stages of the computational model as described here are represented by spike rates in human visual neurophysiology.

Temporal Averaging

Since luminance increments and decrements are at least potentially detected by the model on each successive time step, and all neuronal activations prior to the final "lightness map" stage are also computed independently on each time step, the lightness map would change abruptly and randomly on each time step if no temporal summation was assumed to occur anywhere in the visual pathway modeled. Furthermore, the directions of the ON and OFF network activations would also vary randomly as a function of eye movement direction on each time step. Therefore, the ON and OFF network activations must be summed or averaged over the various random directions of lightness and darkness induction in order to produce a stable percept of achromatic color or lightness.

In the model simulations, reported here temporal summation was assumed to take place at the level of the lightness map only. The lightness map was temporally integrated over successive time steps with an exponential filter having a characteristic time of 99 time steps when eye movements occurred, and a relaxation time of 142 time steps after the fixational eye movements were halted. These particular values were chosen somewhat arbitrarily and could be easily adjusted to fit behavioral or neural data. The distinction between the temporal summation time during a period of active stimulation of the lightness map and the corresponding relaxation time during the decay phase was introduced in order to simulate the fact that perceptual integration time after stimulus onset is generally much faster than the few seconds fading time that applies to artificially stabilized images. In a more realistic model of the visual nervous system, both time courses might be instantiated through the introduction of a single non-linear temporal filter. However in a more complete realistic physiological model, temporal filtering would also be expected to occur at various levels of the visual hierarchy. These problems are left for future modeling.

Lightness Anchoring

The time-averaged values in the lightness map were further adjusted according to a lightness anchoring rule such the highest value in the lightness map always matched the lightness of a 9.5 Munsell standard (which is always perceived as white). This was accomplished by adding or subtracting a constant value from all activation values in the lightness map. Thus, not only was the highest value in the lightness map adjusted to correspond to white, but all other values in the lightness map were also adjusted by the same additive constant. The rationale for including this lightness anchoring step in the model was that a large body of psychophysical data suggests that the highest lightness is a visual scene always appears white [8-11]. Accordingly, the time-averaged and anchored lightness map formed the model output which modeled the conscious percept of the visual input.

Application of the Model to Explaining Perceptual Data

Dynamic Range Compression in the Staircase Gelb Illusion

Gelb [8] reported that if a single homogeneous grayscale surface is viewed in a spotlight, the surface always appeared white regardless of its actual physical reflectance (grayscale value). In an important extension of Gelb's result, Cataliotti and Gilchrist [12] asked their subjects to judge the lightness (perceived reflectance) of five grayscale papers arranged in spatial order from lowest to highest reflectance and viewed in a spotlight. Lightness judgments were carried out by means of a Munsell match. In addition to replicating Gelb's finding that the highest reflectance paper always appeared white (i.e., matched a Munsell 9.5 standard), Cataliotti and Gilchrist also discovered a new effect: namely, that the range of perceived paper reflectances was highly compressed relative to the range of physical paper reflectances. When the perceived reflectances measured by Cataliotti and Gilchrist are plotted versus physical reflectance on a log-log plot, they are well-described by a straight line with a slope of about 1/3, indicating an approximate cube-root relationship between perceived reflectance and physical reflectance [7,13]. By comparison, a slope of 1.0 would be expected if the lightness matches conformed to veridical reflectance ratio matches (ground truth) [7]. In what follows, I will refer to the finding that the highest in the display always appeared white, combined with dynamic range compression observed by Cataliotti and Gilchrist with the Staircase Gelb display, as the *Staircase Gelb Illusion*.

In an important follow-up study [14], Zavagno, Annan, and Caputo replicated Cataliotti's and Gilchrist's experiment (ZAC's Figure 1, Series A) and added two new conditions in which the paper with the highest reflectance was placed to the immediate left of the paper with the lowest reflectance (their Series C), or to its immediate right, between the lowest reflectance and second-to-lowest reflectance paper (their Series B). Importantly, they found that the spatial arrangement of the papers influenced the lightness judgements in a manner that can be summarized as indicating that local contrast exerts an influence on lightness above and beyond the factors responsible for the basic Staircase Gelb Illusion.

In the following sections, I will apply the neural lightness computation model described in previous sections to the explanation of the results from Zavagno et al.'s Series A, B, and C. I will simulate the model and show that it can account for the lightness matches made in these experiments to within 5% error. In addition to accounting for Zavagno et al.'s results, applying the model to these data will serve to illustrate the computations performed by the model at its various processing stages.

Luminance Increment and Decrement Detections Sorted by Eye Movement Direction

On each time step of the simulation, the photoreceptor array translates either left, right, up, or down with respect to the input image (or, equivalently, the image translates down, right, down, or up relative to the photoreceptor array). This simulates fixational eye movements that occur randomly on each time step. A fixation eye movement may or may not result in an increase or decrease on time step t of the activity of a given photoreceptor with respect to its activity on time step t-1. Photoreceptors are modeled as gaussian spatial filters of the input. For the Staircase Gelb and related displays modeled here, a photoreceptor will increase its activation level if and only if the center of its gaussian filter kernel crosses a paper edge from the dark side to the light side from time step t-1 to time step t. Similarly, a photoreceptor will *decrease* its activation if and only if the center of its gaussian filter kernel crosses an edge from the light side to the dark side from time step t-1 to time step t. The sizes of simulated eye movements were constrained so that two edges were never both crossed within a single eye movement.

A key assumption of the model is that the neural gain applied to an incremental or decremental photoreceptor responses differs for luminance increments and decrements. In the case of increments, the gain is assumed to be 0.27; whereas in the case of decrements the gain is assumed to be 1.0. The photoreceptor response immediately following an eye movement is described by the following equation:

$$g[s(x,y,t)logI(x,y) - s(x,y,t-1)logI(x,y)] \,, \qquad (1)$$

Where: g is the photoreceptor gain (which equals 0.27 if the quantity in brackets is positive and 1.0 is the quantity in brackets is negative); s(x,y,t) is the gaussian spatial profile of the photoreceptor integration area on time step t; and log(I(x,y)) is the spatial luminance profile of the input (e.g., the Staircase Gelb display) in log units.

Physiological evidence from macaque monkey [7,15,16], whose early visual pathways are thought to closely correspond to those of humans, suggests that Eq. (1) results from a logarithmic transformation at the cortical level [20] of an earlier physiological response in the retina or LGN that has a power law dependence on local image intensity, as in

$$R(I) = kI^g(x,y) \,, \qquad (2)$$

where k is a constant. This further suggests the representation of the photoreceptor output models the photoreceptor output *as seen at the cortical level* and not the retinal photoreceptor output *per se*. At the retinal level, prior to the presumed logarithmic transformation of the photoreceptor output, the photoreceptor response probably depends on the *ratio* of the amount of its light stimulation immediately before and after an eye movement. When the photoreceptor activation increases after an eye movement, $g = 0.27$, and when it decreases, $g = 1.0$. These aspects of the model will be further developed in a subsequent paper.

A sorting of photoreceptor responses into those that signal luminance increments or decrements when an eye movement occurs in either the left, right, up, or down direction results in eight spatial maps that exist at the cortical level. Two of these maps indicate post eye movement coordinates of luminance increments and two indicate post eye movement coordinates of luminance decrements. As an example of one of these eight maps, Figure 1(a) illustrates the locations of increments in photoreceptor activations that occurred when the eye moved to the right and the input was a Staircase Gelb display. Figure 1(b) similarly illustrates the locations of decrements in photoreceptor activations that occurred when the eye moved to the right and the input was a Staircase Gelb display. In general, the eight such maps which make up the entire set may all potentially contribute to lightness computation, though in practice only some of them may include activations that contribute to lightness in a particular situation. In the case of the Staircase Gelb display, incremental photoreceptor responses that are generated when upward eye movements cross the bottom edges of the Gelb papers from below, and incremental photoreceptor responses that are generated when downward eye movements cross the upper edges of the Gelb papers from above will also contribute to the lightness of the individual Gelb papers, as will incremental photoreceptor responses that are generated when leftward eye movements cross the far right edges of the highest reflectance from the right side.

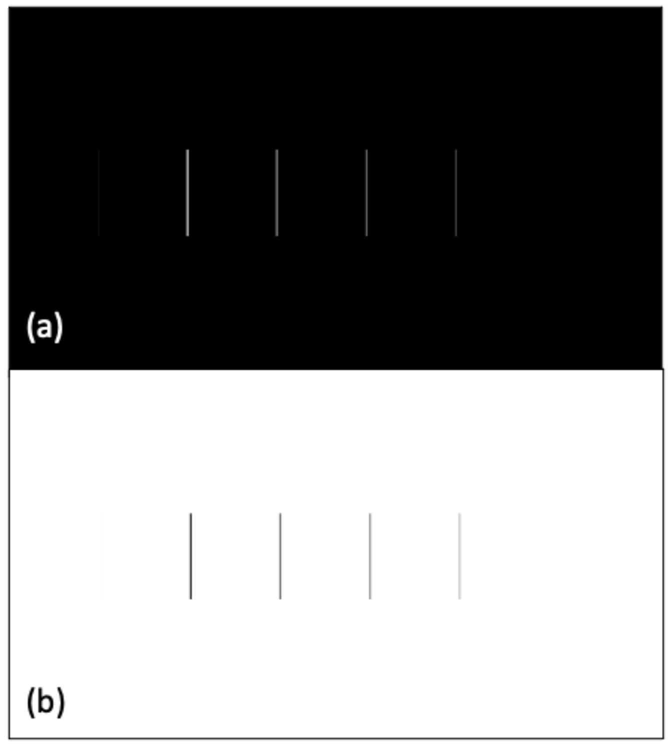

Figure 1. *(a) Spatial map of incremental photoreceptor activations produced when the eye moves to the right. (b) Decremental photoreceptor activations produced when the eye moves to the left. In both cases, the input was a Staircase Gelb display.*

Long-range Spatial Integration of Motion Direction-Specific Increment and Decrement Signals

At the next stage of visual processing, cortical neurons with large receptive fields spatially integrate the outputs of the eight types of directionally-specific neural luminance increment and decrement detectors. This process takes place independently in separate ON and OFF networks. High-level neurons in the ON network sum the responses of the four types of luminance increment signals—left, right, up, and down; and high-level neurons in the OFF network sum the responses of the four types of luminance decrement signals—also left, right, up, and down.

For individual cells in both the ON and OFF networks, the input summation depends both on the distance in the spatial map of the receptive field center of the high-level cell doing the summing from the location of the low-level incremental or decremental activation being summed, and the angle of a vector drawn from the location of the activation in the low-level map to the receptive field center of the high-level summing cell, measured with respect to a vector that points in the direction of the eye movement that generated the low-level activation. More specifically, the activation produced in a high-level cell whose receptive field center is located at spatial coordinate (x_0,y_0) by a low-level neural activation located at spatial coordinate (x,y) is given by the equation

$$A(x_0, y_0) = \Gamma e^{-\sqrt{(x-x_0)^2+(y-y_0)^2}/d}[cos^n\theta]^+ , \qquad (3)$$

Where: Γ is a constant of proportionality; d is the space constant of the exponential summation process (which is here assumed to equal 1.8 deg); the symbol $[\ \ ]^+$ denotes halfwave rectification; θ is the angle between a vector drawn from (x,y) to (x_0,y_0) and a vector pointing in the direction of the eye movement that produced the low-level incremental or decremental photoreceptor activation; and n is a free parameter of the model which determines the amount of directional specificity of lightness and darkness induction in the model. The parameter n was set to 1.0 in the present simulations. Note that the halfwave rectification guarantees that lightness or darkness signals will only be induced in the ON and OFF networks with a vector component in the direction of the eye movements that induced the activations. Also note that since the angle θ is defined relative to the vectorial direction of the eye movement that produced a low-level photoreceptor activation, it will have a different definition for each of the four eye movement directions: left, right, up, or down.

Figures 2(a) and (b) illustrate the patterns of activation in the ON and OFF networks, respectively, induced by rightward eye movements (a) and leftward eye movements (b). The total ON or OFF network activation on any time step will be generated by a random eye movement made to the left, right, up, or down. Thus, the illustrations shown in Figure 2 indicate 2 out of the 8 possible activations that might be generated in response to the Staircase Gelb display on any given time step.

Lightness Map

The output stage, which represents lightness (i.e., perceived reflectance), and models the observer's conscious percept, is computed by adding together the outputs of the ON and OFF networks, temporal integrating over several time steps with an exponential kernel, and anchoring the highest lightness in the lightness map to white (specifically, to match a Munsell 9.5 standard).

Figure 3 presents a spatial lightness map that was generated according to this algorithm using the Staircase Gelb display as the input image. To create this image, the stepwise lightness map was temporally integrated with an exponential filter having a characteristic time of time steps. In Figure 3, the area of the lightness map lying outside that of the Gelb papers has been masked off to make it easier to focus on the predicted lightness of the papers.

Chevreul Illusion

Although the papers in the Staircase Gelb display (i.e., the model input) are homogeneous in their reflectance, the model output (Figure 3) predicts that observers should perceive a scallop-like pattern of lightness when observing the display, with papers regions near a neighboring paper exhibiting a contrast effect that tends to dissipate with distance from the borders between the papers. This illusion is well known and is referred to in the lightness literature as the *Chevreul illusion*, after the 19th Century French scientist Michel Eugene Chevreul, who pioneered the study of color and lightness contrast [17]. Figure 4 demonstrates his illusion. Here, the vertical stripes actually are homogeneous in luminance but the viewer perceives them as a scalloped pattern of lightness.

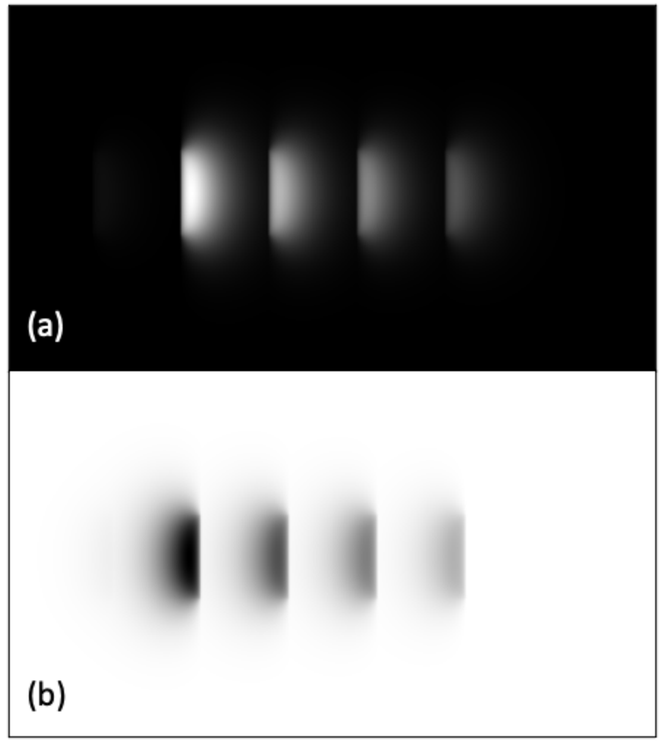

Figure 2. *(a) Rightward cortical spatial integration of the incremental photoreceptor activations shown in Figure 1(a). Leftward spatial integration of the decremental photoreceptor activations shown in Figure 1(b).*

Figure 3. *Lightness map generated by the model in response to a Staircase Gelb display.*

The Chevreul illusion is often ascribed to edge enhancement produced by center-surround receptive fields in the visual nervous system (lateral inhibition). However, the perceived scalloped patterns extend further from the paper borders than is predicted by such an explanation [18]. The model presented here instead explains the Chevreul illusion on the basis of the spatial summation performed by the high-level cortical ON and OFF cells, which integrate low-level increments and decrements in photoreceptor activities with an exponential spatial decay characterized by a space constant of about 1.8 deg.

Figure 4. *Chevreul illusion. The physical pattern consists of a series of increasing luminance steps along the x-axis. The perception is of a scalloped pattern of lightness change along that same axis.*

Lightness Matching Data of Zavagno et al. (2004)

To model the complete set of lightness matching data of Zavagno, Annan, and Caputo, I carried out three separate simulations in which the input stimulus was either the Staircase Gelb display (Zavagno et al.'s Series A), or one of two spatially reconfigured Staircase Gelb displays in which the highest reflectance paper in the series was placed to either the left (their Series C) or to the right (Series B) of the lowest reflectance paper. The log perceived reflectance of each paper was modelled as the value of the lightness map at the spatial location corresponding to the center of each paper after adjusting according to the lightness anchoring rule described above. Note that this method ignores the spatial inhomogeneity within the area of each paper that explains the Chevreul illusion.

Applying the lightness anchoring rule to the simulation output constrained the highest reflectance paper in each series to appear white (that is, to match a 9.5 Munsell standard). This was achieved by shifting the perceived reflectance of each paper computed by the model prior to anchoring vertically on the log-log plot of perceived versus physical reflectance by a different constant value for each series. It should be noted that shifting the simulation data in this manner did not affect the lightness *scaling* of the papers in any given series with respect to each another. This shifting procedure is required in order to accurately model the perceptual data. Furthermore, and more generally, considerable evidence exists to support the idea that the highest reflectance in a scene always appears white [7-10]. Highest reflectance anchoring is therefore *always* assumed to be an essential feature of the computational lightness model and does not only apply to this data set.

Figure 5 plots the log perceived reflectance computed using this procedure for the five papers in each of Zavagno et al.'s Series A, B, an C against the log of the physical reflectance of the papers. Also shown on the plot are the average matches made by the human observers in the original experiment. To evaluate the quality of the model fits, the percent error in the simulated matches were expressed as a percentage of the total variance in the original reflectance matches on the log-log scale. By this measure, the percent error was 5.3, indicating an excellent fit to the data.

Additional implications of the Model

Perceptual Fading of Stabilized Images

Fixational eye movements must occur in order for human vision to operate normally. If fixational eye movements are artificially prevented through a stabilized image technique, the visual world appears to fade within a few seconds [3,4]. The neural lightness model presented here also exhibits this behavior. In an additional simulated experiment with the Staircase Gelb display, fixational eye movements were allowed to undergo a random walk until the lightness map statistically. The eye movements then ceased on subsequent time steps of the simulation. After the eye movements were halted, a gradual fading of the lightness map occurred with an exponential time course. Figure 6 shows a snapshot of the lightness map after the fading was mostly complete.

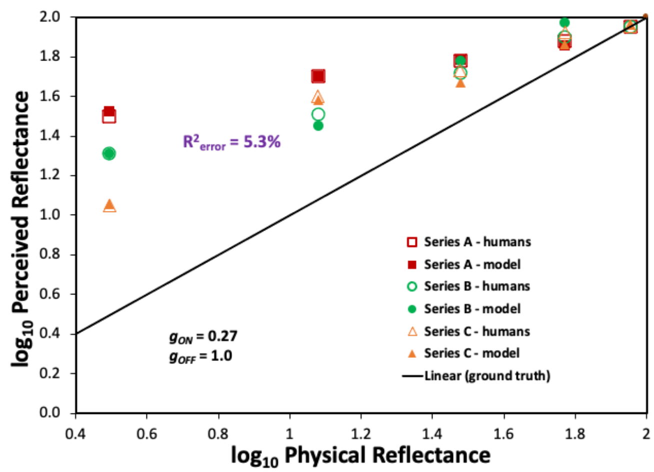

Figure 5. *Simulation of Zavagno et al.'s Series A, B, and C lightness matches.*

Figure 6. *The simulated lightness map fades to low contrast within a few seconds after eye movements are halted.*

An important outstanding problem for future development of the model is that perceptual fading occurs in reality more slowly than the rise time of the percept when eye movements are taking place. This effect was here simulated by assuming different time constants apply to the temporal integration of the lightness map in the presence and absence of eye movements (as was implemented here). But work will be required to instantiate those differences as an automatic property of the model and to establish experimentally that the assumed time constants accurately data on perceptual response time and fading. It is worth noting in this regard that an important implication of the model is that there should be a particular short-term visual memory associated with the temporal decay of the lightness map.

Model Extensions and Future Directions

ON-Center and OFF-Center Visual Neurons

In the computational model simulated here, photoreceptor responses to luminance increments and decrements were sorted based on the direction of the eye movement that elicited them. This raises the question of whether there actually are neurons in the early human visual system that respond selectively to luminance increments and decrements, since such "labelled line" detectors might be required as a basis for sorting neural responses at the cortical level. One possibility is that this is accomplished by post-photoreceptoral ON-center and OFF-center neurons, which are known to exist in the retina, lateral geniculate nucleus (LGN), and cortical visual area 1 (V1), rather than by the photoreceptors per se. ON-center neurons respond selectively to patterns of light consisting of positive photic stimulation surrounded by lesser or no stimulation; while OFF-center neurons respond selectively to rings of light surrounding a less-illuminated region. Might ON-center and OFF-center neurons instead comprise the labeled lines whose responses are combined with information about eye movement direction to sort luminance increments and decrements on the basis of the eye movement direction that produced them?

It is well known that ON-center cells respond to an luminance edges only near the edge and on the side of the edge with the higher luminance, and that OFF-center cells respond similarly to a luminance edge on the side of the edge with the lower luminance. This situation is illustrated in Figure 7, where the ON-center and OFF-center receptive fields are illustrated in red in order to help distinguish them from the achromatic regions representing the visual stimulus.

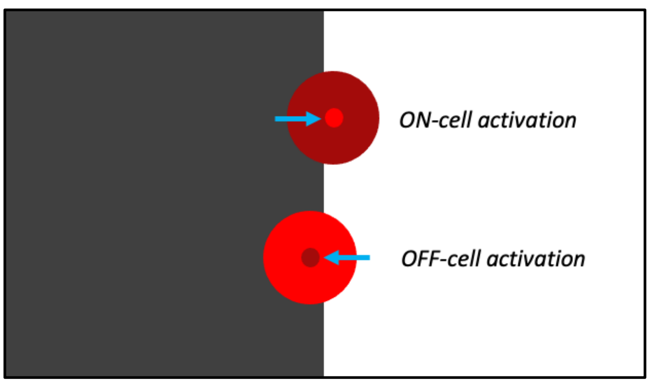

Figure 7. *An increase in ON-cell activation can occur when an ON-cell receptive field crosses over to the more luminant side of an edge as a result of a fixational eye movement, An increase in OFF-cell activation can similarly occur when an OFF-cell receptive field crosses over to the less luminant side of the edge.*

One indirect piece of evidence that supports the idea that ON-center and OFF-center cells might in fact function as the labelled lines that detect luminance increments and decrements is that the responses of ON-center cells in macaque LGN are described by a power law of luminance, with a power law exponent of 0.27, as in Eq. (2) [7,15,16]. As mentioned above, a logarithmic transformation of the neural response subsequent to the LGN would convert this exponent to a neural gain that would apply to luminance increments only. If OFF-center cell responses were characterized by a power law exponent of 1.0 (linear response to decremental luminance), then the quantitative properties of lightness perception would thus follow from the dual assumptions that ON-center and OFF-center cells form the labelled lines that detect luminance increments and decrements in the visual system and that the outputs of these cells are subject to a logarithmic transformation prior to spatial integration at the cortical level.

The situation is further complicated, though, by the fact that ON-center and OFF-center cells will be activated near an edge *regardless* of whether an eye movement that placed them in this position was one that actually crossed the edge or else moved the neural receptive field from a position in the surface interior to a position near the surface's edge. Specifically, this fact complicates the sorting of luminance increment and decrement signals on the basis of eye movement direction. The development of an eye movement-based lightness model founded on ON-center and OFF-center cell activations rather than directly on photoreceptor responses will therefore be deferred to a future paper.

Summary and Conclusions

This paper has introduced a novel computational model of lightness perception (perceived reflectance) inspired by primate physiology and visual psychophysics. In the model, fixational eye movements are modeled as a random walk in 2 dimensions. On any given time step of the model simulations, the eye moves either to the left, right, up, or down, with the result that the photoreceptor array translates across the input image.

When an eye movement occurs in the model, the activity level of any individual photoreceptor—modeled here as a gaussian spatial filter on the input log luminance—may or may not increase or decrease, depending on whether the regions of the image that the photoreceptor "looks at" before and after the eye movement increases in luminance, decreases in luminance, or does not change in luminance. The photoreceptor response is modeled by the *change* in loh luminance across the eye movement, with increases in log luminance characterized by a photoreceptor gain of 0.27 and decreases in log luminance characterized by a photoreceptor gain of 1.0.

At the cortical level, incremental and decremental photoreceptor responses are sorted, on the basis of the direction of the eye movement that caused them, to produce eight spatial maps that correspond to the two photoreceptor response polarities and four eye movement directions. The individual spatial maps contain the locations of increments or decrements in photoreceptor response for each potential eye movement direction.

At a subsequent stage of cortical processing, the activities in the eight are spatially integrated by neurons having large receptive fields that exist in in separate ON and OFF networks. Neurons in the ON network integrate responses from the four spatial maps corresponding to luminance increments, while neurons in the OFF network integrate responses from the four spatial maps corresponding to luminance decrements. The mathematical properties of the spatial integration performed by an ON and OFF cells depends on the spatial location the ON or OFF cell that performs the spatial integration and the spatial location of the neural unit in the lower level map whose activity is being summed. More specifically, the level of activation produced in an ON or OFF neuron falls off exponentially as a function of the distance between the ON or OFF cell receptive field center and the location of the unit in an increment or decrement map whose response is being integrated, with a spatial decay constant of 1.8 deg. The level of activation in the ON or OFF cell also falls off as a halfwave-rectified cosine function of the angle between a vector drawn from the location of the activating cell and the receptive field center of the activated cell and a vector oriented in the direction of the eye movement that produced the incremental or decremental activation in the lower-level map.

At the final (output) stage of the model, a map of log perceived reflectance, or lightness, is formed by summing the outputs of the ON and OFF network activations and temporally integrating that sum with an exponential temporal kernel. The time-integrated lightness map is subsequently renormalized (anchored) such that the activity of each neural unit within the computed lightness map is shifted to make the highest value within the map appear white (that is, to match a 9.5 Munsell paper). The time-integrated and renormalized lightness map models the observer's conscious visual percept.

The computational lightness model described here reproduces several key observations about visual perception. First, the lightness map that is computed in response to a Staircase Gelb display has a scalloped appearance in keeping with the well-known Chevreul illusion, whereby a series of vertical stripes of homogeneous luminance give rise to a percept in which regions of the stripes located near luminance borders are more highly influenced by border contrasts than are regions lying more some distance from the border. Second, when eye movements are artificially inhibited, the conscious percept gradually fades with a time constant of a few seconds. Third, quantitative lightness matches deduced from simulated behavior of the model closely approximate those of actual human observers for input stimulate consisting of a five-paper Staircase Gelb display and two altered versions the Staircase Gelb display in which the paper having the highest reflectance is relocated to a position just to the left or right of the paper with the lowest reflectance. Taken together, the quantitative "Gelb" simulation results account for the fact that the dynamic range of human lightness perception is highly compressed relative to the range of physical reflectances in the actual physical stimulus (ground truth). The model accounts for this compression, as well as for the various releases of compression produced by spatially reordering the papers, by assuming that lightness in neurally computed by spatially integrating directed steps in log luminance at borders, with steps in log luminance that increment in the direction of a region whose lightness is being computed with a lesser neural gain than that which is applied to steps in log luminance that decrement in the direction of the region whose lightness is being computed.

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