

Available online at www.sciencedirect.com



Vision Research 45 (2005) 2397-2416

Vision Research

www.elsevier.com/locate/visres

# Components of bottom-up gaze allocation in natural images

Robert J. Peters <sup>a,b,\*</sup>, Asha Iyer <sup>a</sup>, Laurent Itti <sup>b</sup>, Christof Koch <sup>a</sup>

<sup>a</sup> Computation and Neural Systems, California Institute of Technology, Mail code 139-74, Caltech, Pasadena, CA 91125, USA <sup>b</sup> Computer Science and Neuroscience, University of Southern California, Los Angeles, CA 90089, USA

Received 4 September 2004; received in revised form 15 March 2005

#### Abstract

Recent research [Parkhurst, D., Law, K., & Niebur, E., 2002. Modeling the role of salience in the allocation of overt visual attention. *Vision Research 42* (1) (2002) 107–123] showed that a model of bottom-up visual attention can account in part for the spatial locations fixated by humans while free-viewing complex natural and artificial scenes. That study used a definition of salience based on local detectors with coarse global surround inhibition. Here, we use a similar framework to investigate the roles of several types of non-linear interactions known to exist in visual cortex, and of eccentricity-dependent processing. For each of these, we added a component to the salience model, including richer interactions among orientation-tuned units, both at spatial short range (for clutter reduction) and long range (for contour facilitation), and a detailed model of eccentricity-dependent changes in visual processing. Subjects free-viewed naturalistic and artificial images while their eye movements were recorded, and the resulting fixation locations were compared with the models' predicted salience maps. We found that the proposed interactions indeed play a significant role in the spatiotemporal deployment of attention in natural scenes; about half of the observed inter-subject variance can be explained by these different models. This suggests that attentional guidance does not depend solely on local visual features, but must also include the effects of interactions among features. As models of these interactions become more accurate in predicting behaviorally-relevant salient locations, they become useful to a range of applications in computer vision and human-machine interface design. © 2005 Published by Elsevier Ltd.

Keywords: Salience; Attention; Eye movements; Contours

## 1. Introduction

Selective attention is the ubiquitous mechanism that regulates the bottleneck between the massively-parallel world of sensation and the serial world of cognition (James, 1890). This is particularly true in the visual system of primates, where 50% of the primary visual cortex is devoted to processing input from the central 2% (10°) of the visual field (Wandell, 1995). In order to benefit from this non-uniform allocation of processing resources, the visual system relies on a combination of covert and overt attentional shifting mechanisms to efficiently bring behaviorally relevant stimuli under the processing capabilities of central vision (Treue, 2003).

We used eye movements as an overt measure of where observers were directing their covert attention. This method is based on the pre-motor theory of attention (Rizzolatti, Riggio, Dascola, & Umilta, 1987), which suggests eye movements and attention shifts are driven by the same internal mechanisms. Links between eye movements and attention have been demonstrated by behavioral (Hafed & Clark, 2002; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; Sheliga, Riggio, & Rizzolatti, 1994, 1995) as well as physiological (Kustov & Robinson, 1996; Moore & Fallah, 2001, 2004; Moore, Armstrong, & Fallah, 2003)

<sup>&</sup>lt;sup>\*</sup> Corresponding author. Present address: Department of Computer Science, Hedco Neuroscience Building, 3641 Watt Way, University of Southern California, Los Angeles, CA 91125, USA. Tel.: +1 213 740 9223; fax: +1 626 737 0463.

E-mail address: rjpeters@usc.edu (R.J. Peters).

<sup>0042-6989/\$ -</sup> see front matter @ 2005 Published by Elsevier Ltd. doi:10.1016/j.visres.2005.03.019

and brain imaging (Nobre, Gitelman, Dias, & Mesulam, 2000; Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001) studies. A number of studies have taken information-theoretical or statistical approaches to eye movements, asking how fixated regions differ from non-fixated regions (Krieger, Rentschler, Hauske, Schill, & Zetzsche, 2000; Privitera & Stark, 2000; Reinagel & Zador, 1999). These studies have shown that fixated regions have high contrast and high variance (low correlation) (Reinagel & Zador, 1999), distinctive higher-order statistics (Krieger et al., 2000), and high local symmetry (Privitera & Stark, 2000). Yet while such results help characterize expected fixation locations, they do not explicitly include a mechanism by which biological vision might extract the relevant features from the input.

In the present study we use biologically plausible quantitative models to test hypotheses regarding the links between brain and behavior. Each model variant operates in the basic framework of a model of bottomup saliency-driven attention (Itti & Koch, 2001; Itti, Koch, & Niebur, 1998)-which we refer to here as the baseline salience model. This model comprises a number of parallel channels for processing different feature types, such as luminance, orientation, and color, and the outputs from each of the channels are combined to produce a single, feature-independent salience map. This salience map signals salient, i.e., conspicuous or interesting, locations in the visual scene. It has been shown that such salience maps can predict locations likely to be fixated by human observers with significantly betterthan-chance accuracy (Parkhurst, Law, & Niebur, 2002). Despite these results, covert and overt attentional fixation locations may sometimes be distinct (Posner & Cohen, 1984); nevertheless it is likely that overt and covert shifts of attention are closely related except in the presence of considerable effort to meet explicit instructions to the contrary (e.g., "don't look at the stimulus, but keep on fixating").

We asked whether, and to what extent, human fixation behavior is influenced by three putative physiological mechanisms. First, we considered short-range interactions among orientation-tuned units found in early visual cortical areas with retinotopically-overlapping receptive fields. This effect, known as cross-orientation suppression (Deangelis, Robson, Ohzawa, & Freeman, 1992; Morrone, Burr, & Maffei, 1982), has traditionally been assumed to arise from local lateral connections within cortex (Crook, Kisvarday, & Eysel, 1997; Deangelis et al., 1992; Worgotter & Koch, 1991; Somers, Nelson, & Sur, 1995), although it has also been proposed that thalamocortical inhibition could produce a functionally similar result (Carandini, Heeger, & Senn, 2002; Freeman, Durand, Kiper, & Carandini, 2002). Regardless of the specific neuronal implementation, such divisive inhibition leads to contrast-enhancement and a sharpening of orientation tuning-similar to a center-surround operation, but operating in the orientation and frequency domains rather than in the spatial domain. Furthermore, divisive inhibition provides the gain control needed to work within the limited dynamic range of neurons (Heeger, 1992). A number of computational models for cross-orientation suppression have been proposed (Kolesnik & Barlit, 2003; Lauritzen, Krukowski, & Miller, 2001); in particular, one of these (Lee, Itti, Koch, & Braun, 1999) was shown to succinctly account for detection and discrimination thresholds in a range of psychophysical tasks involving isolated Gaborlike grating stimuli on a blank background. In the present study, we adapted this model to test the extent to which such local interactions may actually influence scanpaths over natural scenes.

Second, we considered long-range interactions among orientation-tuned units with non-overlapping receptive fields, which are thought to contribute to the visual system's exquisite sensitivity to contours. The presence of such lateral interactions has been inferred from neuroanatomy and electrophysiology (Blasdel, 1992; Das & Gilbert, 1999; Pettet & Gilbert, 1992; Stettler, Das, Bennett, & Gilbert, 2002) and from psychophysical studies demonstrating increased or decreased contrast detection thresholds at a central location depending on the presence and orientation of surround elements (Polat & Sagi, 1993, 1994a; Zenger & Sagi, 1996; Zenger, Braun, & Koch, 2000). An appropriate arrangement of connection strengths (Braun, 1999a; Polat & Sagi, 1994b; Li, 1998; Li & Gilbert, 2002), involving facilitation between nearly collinear edge segments and inhibition between non-collinear parallel and orthogonal segments, has the effect of enhancing the activity of units that respond to the segments comprising an elongated contour such as the Gabor "snakes" described in Section 2.2. A number of such models exist (e.g. Braun, 1999a; Li, 1998; Tang, Medioni, & Lee, 2001); here, we adapted the model of Mundhenk and Itti (2002) to test whether contour-facilitation plays a significant role in determining fixation locations in complex images, and furthermore how that role depends on the relevance of contours to the behavioral task.

Third and last, we considered the cumulative effects of eccentricity-dependent processing through the early stages of vision. Anatomically, these effects begin in the retina with a strongly peaked distribution of cone photoreceptors and retinal ganglion cells near the fovea, along with correspondingly smaller receptive field sizes, and continue with a further expansion of foveal representation in primary visual cortex. One psychophysical manifestation is the influence of eccentricity on the relationship between contrast detection thresholds and spatial frequency; a similar relation exists for orientation discrimination thresholds (Virsu & Rovamo, 1979). There are essentially two effects when moving from the fovea to the periphery: discrimination thresholds become generally higher (reflecting overall poorer visual sensitivity), and the optimal spatial frequency becomes lower (reflecting larger receptive fields). Parkhurst et al. (2002) found that observers' fixation locations followed a non-uniform spatial distribution favoring the center of stimulus images, while the baseline salience model predicted a uniform distribution of fixation locations. We designed a simple but efficient model of eccentricity-dependent effects in which the salience model's intermediate feature maps are attenuated according to spatial frequency and eccentricity, in a manner quantitatively consistent with previously published contrast-detection and orientation-discrimination thresholds (Virsu & Rovamo, 1979). Using the distribution of fixation locations generated by observers, we compared the detailed model of eccentricity-dependent effects with simpler approximations (such as used by Parkhurst et al., 2002).

In each of these three cases, we find that the physiological mechanisms have a significant influence on the selection of fixation locations, at least to the extent that our coarse models capture the essence of these mechanisms. Importantly, we find this effect in tasks involving free viewing of crowded naturalistic scenes, including grayscale outdoor scenes (van Hateren & van der Schaaf, 1998), grayscale satellite imagery, and full-color fractals. Our aim was to cover a range of natural image types with a small number of categories. Although topdown factors based on emotional reaction or explicit memory can certainly play a significant role in determining fixation locations (Yarbus, 1967), we deliberately avoided images that would strongly trigger such factors (such as close-up images of faces, familiar people, or well-known locations) since we assume them to be partly outside the scope of the bottom-up physiological mechanisms under consideration. With that constraint, we selected outdoor scenes with elements whose general types would be familiar (trees, grassy fields, streets and sidewalks, campus buildings) but whose particular identities would be unknown to most observers. We also selected overhead satellite imagery, involving scenes that are still interpretable (roads, mountains, fields are easily identifiable), but which, in contrast to outdoor scenes, are visually unfamiliar to most observers, due to the unusual overhead and wide-angle perspective. Fractal images contain spatial frequency spectra similar to natural images, but contain no familiar elements. Finally we used a set of images containing random arrangements of Gabor patches; these served to specifically highlight the role of non-local interactions.

The success of these models helps to support a quantitative link between observers' unconstrained overt behavior and the detailed functional properties of individual neurons as inferred from single-unit recordings and psychophysics experiments with constrained stimuli and task conditions. This detailed computational model of bottom-up, salience-based attention is useful for a range of applications from neuroscience to engineering. Machine vision systems face the same difficulties as do biological vision systems, and so a quantitative implementation of attentional selection can lead to similar improvements for machine vision systems. Indeed, models of bottom-up attention have been shown to improve the performance of traditional computer vision object recognition systems, both in the visual learning phase as well as in the subsequent recognition phase (Miau & Itti, 2001; Walther, Itti, Riesenhuber, Poggio, & Koch, 2002; Rutishauser, Walther, Koch, & Perona, 2004). Accurate models of behavior also serve a very practical goal in human-machine interface: particularly for visual attention, there are many attention-demanding contexts (e.g., driving, flying, surveillance, image analysis) in which even a trained expert could occasionally benefit from an assistant system that was trained to match the expert's optimal behavior. None of this denies the crucial roles of top-down, task-dependent attention in conscious vision (James, 1890; Koch, 2004), yet in the absence of detailed quantitative models, we have concentrated here on the contribution of bottom-up, salience-driven cues to fixation.

# 2. Methods

#### 2.1. Subjects

Psychophysics subjects (ages 18-25) from the Caltech community participated as paid volunteers as follows. Four of these ("group A") participated in the first set of free-viewing experiments involving outdoor photos, overhead satellite imagery, and fractals. Another four ("group B") participated in a second free-viewing experiment involving Gabor snakes and Gabor arrays. Finally, seven subjects ("group C") participated in a third experiment involving a comparison between the freeviewing and contour-detection tasks. Three of the subjects participated in more than one experiment, so the total number of individuals involved was 12. Tables 2 and 4 give results from groups A (columns 1-3) and B (columns 4–5), while Table 3 gives results from group C. Informed consent was obtained from all subjects, and experimental procedures were approved by the California Institute of Technology's Committee for the Protection of Human Subjects.

# 2.2. Stimuli

We used four classes of images (Fig. 1), ranging in size from  $1000 \times 1000$  to  $1536 \times 1024$  pixels, subtending a visual angle of roughly  $15.8^{\circ} \times 15.8^{\circ}$  to  $16.2^{\circ} \times 25^{\circ}$ . The experiments reported here typically included about 100 images from each image class: grayscale 10-meter



Fig. 1. Samples from each of the image databases used in psychophysics and modeling experiments. All of the databases contained only grayscale images, except for the fractals which contained exclusively full-color images. The four exemplar images in the left column (one from each category) are used in subsequent figures to illustrate the output of each model component. (a) Overhead satellite imagery. The inset provides a zoomed view of the boxed region. (b) Outdoor photographs. (c) Computer-generated fractals. (d) Gabor "snakes" and Gabor arrays—arrays of randomly spaced and oriented Gabor elements, some containing "snakes," or chains of elements aligned so as to form a strong percept of a contour. The inset shows the boxed area at higher resolution. Although the "snakes" are not highly visible at the scale shown here, these contours are strongly salient when viewed at the scale used in our psychophysics experiments. See Section 2.2 for details.

resolution "digital orthorectified" (DOI10m) overhead satellite imagery;<sup>1</sup> grayscale outdoor photographs<sup>2</sup> (van Hateren & van der Schaaf, 1998); color fractals generated with gnofract4d software<sup>3</sup> and from the Spanky Fractal Database;<sup>4</sup> grayscale Gabor "snakes" and Gabor arrays containing arrays of randomly spaced and oriented Gabor elements generated with a previously-described algorithm (Braun, 1999a, 1999b). The Gabor "snake" images included chains of Gabor elements that were properly aligned so as to induce a strong percept of

a contour, even though element spacing and Gabor phase were otherwise random.

## 2.3. Free-viewing task

Images were presented to subjects in a free-viewing task (Fig. 2a). Each trial began with a 1000 ms fixation cross at the center of a blank screen, which subjects were instructed to fixate. This imposed some consistency on the initial conditions of the subsequent scanpaths, across different images and observers. Following the fixation cross, a target image was shown for 3000 ms. Subjects were instructed to "look around the image" with no restrictions except the knowledge that they would have to provide a response, as follows. Immediately after the target image disappeared, a single line was presented

<sup>&</sup>lt;sup>1</sup> From the National Geospatial-Intelligence Agency (NGA) (http://geoengine.nga.mil/).

<sup>&</sup>lt;sup>2</sup> http://hlab.phys.rug.nl/imlib/.

<sup>&</sup>lt;sup>3</sup> http://gnofract4d.sourceforge.net/.

<sup>&</sup>lt;sup>4</sup> http://spanky.triumf.ca/.



Fig. 2. The two tasks performed by subjects while their eye movements were recorded. In the free-viewing task (a), each trial began with a fixation cross (1000 ms), followed by a stimulus image (3000 ms) drawn from one of the image categories shown in Fig. 1. Subjects were asked to freely inspect the image. After the image disappeared, subjects were presented with a single line bisecting the screen into two regions, and were asked to make a two-alternative forced choice (2-AFC) as to whether they thought "the most interesting point or area" in the just-seen image fell in region 1 or region 2. The orientation of the line varied randomly from trial to trial; since subjects could not predict the orientation, they were forced to consider the entire stimulus image, without being encouraged to focus on any particular aspect of the image. In the contour-detection task (b), each trial began with a fixation cross followed by a stimulus image as before. However, when the image disappeared it was replaced by a full-screen uniform white mask. This was followed by a new response screen containing a single schematic contour, and subjects made a 2-AFC as to whether there had been a matching contour at the same location in the just-seen image. On 50% of trials, there was in fact such a match, while on the other 50% of trials, a non-matching contour was selected from among the contours that matched other images in the same category.

at an arbitrary orientation bisecting the screen into two regions of equal size. The two regions were labeled as "1" and "2," and subjects were required to make a button press indicating which region contained the location that they had found "most interesting" in the previous image. Our motivations for requiring this response were twofold: (1) to encourage subjects to be vigilant in their task and engage in active eve movements (without a minimal task to motivate them, subjects might "efficiently" choose to make no eye movements at all); and (2) to avoid imposing any particular top-down bias on the task (such as would occur if subjects were asked to search for horizontal lines, or to judge the brightness of the image, or to name objects in the image), allowing direct comparisons with a model of bottom-up attention. Although no time limit was imposed on the responses, subjects were encouraged prior to the experiment not to dwell on the choice for too long, but rather to make their best guess if they felt unsure.

# 2.4. Contour-detection task

We used a second task to investigate the influence of contours on fixation locations (Fig. 2b). The overall format of the task was similar to the free-viewing task, except (1) the image presentation time was shortened from 3000 ms to 2500 ms, (2) a full-screen uniform white mask was presented for 500 ms immediately after each

image to prevent subjects from relying on retinal afterimages to perform the task, and (3) a different response was required, as explained next. After the image and the mask, subjects were presented with a single schematic line-drawn contour, and responded with a key press to indicate whether that contour matched a contour that was present at the same location in the image they had just seen. On half of the trials, the contour was in fact a match to the preceding image, and on the other half, the contour was a non-match (selected from a pool of contours that matched other images in the experiment). The schematic contours were Bezier curves that closely approximated the shapes of hand-picked salient contours in the target images.

#### 2.5. Eye tracking

Subjects were seated 75 cm from a CRT used for stimulus display, which subtended  $26^{\circ} \times 19^{\circ}$  of visual angle, and used a chinrest to minimize eye-tracking errors due to head movements. We used an infrared (IR) eye tracking system (ISCAN, Inc.) to sample and record subjects' eye position at 120 Hz. An illuminator and camera were placed ~65 cm from the subject, and his or her right eye was illuminated with a beam of low-intensity (~1 mW/cm<sup>2</sup>) invisible IR light (~850 nm). The camera recorded a close-up image of the eye, which was processed in real-time to extract the positions of two features: (1) p, the IR-dark spot at the center of the pupil, and (2) c, the IR-bright spot where the IR beam produces a specularity on the cornea. The vector difference v' = p - c of these two positions gives a measure of eye position that is independent of head position. An empirical correspondence between v' (in camera coordinates) and the subject's real-world point-of-regard v (in stimulus display coordinates) was established by a set of calibration trials in which the subject fixated a series of crosses shown at 25 different locations on an invisible  $5 \times 5$  grid in the stimulus display. These v - v' pairings could then be used to interpolate the subject's pointof-regard throughout the remainder of the session. Following each session, each lasting about 12 min, we re-recorded subjects' eye positions at the 25 calibration locations in order to assess how much drift had occurred during the recording session. Across all eye-tracking sessions, the overall error was  $0.54^{\circ} \pm 0.44^{\circ}$  (mean  $\pm$  s.d.) degrees of visual angle per calibration point.<sup>5</sup>

## 2.6. Salience model

All of the models described here<sup>6</sup> are based on the computational architecture of a salience model of bottom-up visual attention first proposed by Koch and Ullman (1985) and developed in detail by Itti et al. (1998) (see Fig. 3). Each input image is processed in parallel through a number of feature channels (e.g., one each for color, luminance, orientation), and the outputs of these channels are ultimately combined to form a single salience map. This map ascribes a scalar value to each point in the input image, indicating how salient or "interesting" that location is, regardless of which features contributed to the salience.

The individual channels share a common architecture. In general, the input image is first passed through a series of linear filters at nine spatial scales to form a dyadic pyramid. These filter outputs are then subject to spatial competition via a center-surround operation, implemented as a difference between fine and coarse scales in the pyramid. Typically there are six *feature maps* generated by this center-surround operation, using center scales  $c \in \{2,3,4\}$  and surround scales at  $s = c + \delta$ , with  $\delta \in \{3,4\}$ . The feature maps are summed across scales and passed through a non-linear normalization operation designed to reduce or eliminate numerous weak local maxima in favor of a small number of stronger near-global maxima. This produces a single *conspicuity map* representing the output of the channel; these conspicuity maps are eventually summed across channels and renormalized to produce the final salience map.

The standard channels for static images include a luminance channel that responds to luminance contrast, an orientation channel (including filter outputs from multiple scales and orientations) that responds to orientation contrast, and a color channel that responds to opponent-color contrast. These reflect many of the fundamental computational operations thought to be performed in the early stages of the visual system (Marr, 1982; Wandell, 1995). Nevertheless, the modular architecture of the salience model allows other new channels to be included in parallel to the standard channels, or even to replace one or more of them. This is the approach we used in testing more detailed models of interactions among orientation-tuned units, as described next.

#### 2.7. Short-range orientation interactions

We adapted a model of interactions among overlapping orientation-tuned units (Itti, Koch, & Braun, 2000; Lee et al., 1999) (see Fig. 4) that could be substituted for the standard orientation channel in the salience model. In this enhanced orientation channel, orientation-sensitive units tuned to overlapping spatial locations, but to different orientations  $\theta$  and spatial frequencies  $\omega$ , form an inhibitory pool. In the two-stage model, the feedforward first-stage response  $E_{\theta,\omega}$  is subject to self-excitation and suppression from the inhibitory pool. The result of these interactions is the non-linear second-stage response  $R_{\theta,\omega}$ , given by

$$R_{ heta,\omega} = rac{(E_{ heta,\omega})^{\gamma}}{S^{\delta} + \sum\limits_{ heta',\omega'} W_{ heta heta',\omega \omega'} (E_{ heta',\omega'})^{\delta}}$$

with  $\delta$ ,  $\gamma$ : power-law exponents; *S*: semi-saturation constant;  $W_{\theta\theta',\omega\omega'} = e^{-\frac{(\theta-\theta')^2}{2\Sigma_{\theta}^2}} e^{-\frac{(\omega-\sigma')^2}{2\Sigma_{\omega}^2}}$ ;  $\Sigma_{\theta}$ ,  $\Sigma_{\omega}$ : widths of inhibitory pool. It should be noted that in the original model, the feedforward responses  $E_{\theta,\omega}$  were calculated using ideal filters tuned for a given  $\theta$  and  $\omega$ :

$$E_{\theta,\omega} = Ac_{\rm s} {\rm e}^{-\frac{(\theta_{\rm s}-\theta)^2}{2\sigma_{\theta}^2}} {\rm e}^{-\frac{(\omega_{\rm s}-\omega)^2}{2\sigma_{\omega}^2}} + B$$

with  $c_s$ : stimulus contrast;  $\theta_s$ : stimulus orientation;  $\omega_s$ : stimulus spatial frequency;  $\sigma_{\theta}$ : sharpness of orientation tuning;  $\sigma_{\omega}$ : sharpness of spatial frequency tuning; *A*: contrast gain; *B*: background activity level.

In contrast, for the modified version that was incorporated into the salience model,  $E_{\theta,\omega}$  is given by the values already computed in the dyadic orientation-tuned pyramids. Lee et al. (1999) performed an extensive series of psychophysical experiments including detection and

<sup>&</sup>lt;sup>5</sup> Although observers' wearing of contact lenses or eyeglasses has been reported to lead to lower eye-tracking accuracy, we found no difference in the drift error between observers with corrected (n = 6) and uncorrected (n = 9) vision within our subject pool.

<sup>&</sup>lt;sup>6</sup> Source code for the iLab Neuromorphic Vision Toolkit (iNVT), including the salience model and each of the extensions described below, is freely available under the GNU General Public License (GPL) at http://ilab.usc.edu/toolkit/.



Fig. 3. Schematic diagram of the salience model (top) and salience maps (bottom row) corresponding to the four exemplar images in the left column of Fig. 1. In the salience model, an input image is processed in parallel through multiple channels. In each channel (here for luminance, orientation, and color), the image is filtered at nine spatial scales, and the resulting feature maps pass through a center-surround operation to accentuate contrast (e.g., the map at scale 7 is subtracted from the map at scale 4). The center-surround maps are combined across spatial scales leading to one conspicuity map per channel; finally these conspicuity maps are combined across features to produce a single feature-independent salience map. Additional channels may be included in parallel to the three channels shown here; in our experiments, we tested a modified orientation channel that included short-range orientation interactions (Fig. 4), a contour-facilitation channel based on long-range orientation interactions (Fig. 5), and a model of eccentricity-dependent effects in which the luminance and orientation feature maps were attenuated as a function of eccentricity and spatial scale (Table 1).

discrimination tasks for contrast, spatial-frequency and orientation, and used the results to calibrate the interactions in this model; we used these same calibrated values in our version of the model.

# 2.8. Long-range orientation interactions

We adapted a model of long-range orientation interactions from Mundhenk and Itti (2002) and Braun (1999a) (Fig. 5) that was included as a new channel in the salience model. Briefly, this model relies on a set of weight matrices that determine how one orientationtuned unit is influenced by other such units at different distances and orientations (Fig. 6), in a manner reflecting the long-range axonal connections thought to be present in primary visual cortex (Blasdel, 1992). These matrices are sometimes described by their shape which resembles a "butterfly" or "bow-tie," with wedges of excitatory connections leading from the central unit to other units that are similarly tuned and nearly collinear.



Fig. 4. At top is a schematic diagram of the short-range orientation interactions model (figure adapted from Lee et al., 1999). In this model, an input image is passed through a set of linear filters tuned to different orientations and spatial frequencies. The linear outputs feedforward into a second stage, in which the set of filter outputs corresponding to a given spatial location form a pool that divisively inhibits each unit's response at that location. As a result of this recurrent processing, the second stage output exhibits gain control and contrast enhancement relative to the first stage. We tested a modified version of the salience model from Fig. 3 in which the standard orientation channel is replaced by one including short-range orientation interactions; the bottom row of images here shows the salience maps produced by such a modified model for the four exemplar images from the left column of Fig. 1.

Outside these wedge-shaped regions, there are inhibitory connections from the central unit leading to other similarly tuned units that are nearly parallel but not collinear. Our model did not include interactions among orthogonal or nearly orthogonal units. A formal mathematical description is given in Appendix A.1.

#### 2.9. Eccentricity-dependent filtering

It has been reported that saccade targets tend to cluster around the current fixation location, rather than being uniformly distributed throughout the visual scene. That is, nearby targets are preferred over faraway ones. Although this effect has been fitted empirically with a Gaussian-decaying mask applied to the final salience map (Parkhurst et al., 2002), we asked whether a detailed model of eccentricity-dependent orientation-discrimination and contrast-detection thresholds would explain the behavior as well or better. We developed a model based on previously published psychophysical thresholds (Virsu & Rovamo, 1979) representing orientation discriminability and contrast detectability each as functions of both eccentricity and spatial frequency. These formed a convenient match to the internal structure of the orientation and luminance channels, each of which contains a set of feature maps for different spatial frequencies (see Fig. 3).<sup>7</sup> To apply the psychophysical thresholds to these internal feature maps, the value of each unit was attenuated according to two factors: (1) x, its eccentricity relative to the current fixation location, and (2)  $\omega$ , the spatial frequency to which it responds. The attenuation coefficient m is given by  $m = c_{\omega}e^{-k_{\omega}x}$ , where  $c_{\omega}$  and  $k_{\omega}$  are empirically-determined parameters depending on the spatial frequency  $\omega$ ; values for  $c_{\omega}$  and  $k_{\omega}$  are given in Table 1. This attenuation process is computationally efficient, since the attenuation values can be precomputed and stored as one "mask" for each spatial frequency; applying the masks when an input image is received requires just

<sup>&</sup>lt;sup>7</sup> Although interactions between color vision and eccentricity are widely reported (Anstis, 2002; Hibino, 1992; Imhoff, Volbrecht, & Nerger, 2004; Lu, Lesmes, & Sperling, 1999; Mullen & Losada, 1999), we did not include a model of such interactions in our study. This was partly because the complex interactions between hue perception, isoluminance, ambient illumination, and eccentricity do not map well onto the rough model of color processing contained in the baseline salience model's color channel, and partly because we found that a simple approximation to eccentricity effects, applied to the salience map as a whole, could already account well for observers' fixation locations.



Fig. 5. At top is a schematic diagram of the long-range orientation interactions (contour-facilitation) model. A formal description is given in Appendix A.1. In this model, an input image is passed through a series of filters tuned to 12 orientations (only 4 are depicted in this figure), all tuned to the same spatial scale. The output from these first-stage filters feeds into second-stage activation maps via a set of kernels that specify connection strengths as a function of relative spatial position and relative orientation tuning (see Fig. 6). These connections are arranged so as to selectively enhance locations that form part of an elongated contour. The activation maps are summed across orientations and passed through a sigmoid non-linearity to yield the final output map. The model output evolves iteratively (three iterations were used in the present study); the second-stage maps recurrently excite their first-stage counterparts, and the output map recurrently modulates the strength of inhibition within the connection kernels to limit the dynamic range of the output. In practice, the model was instantiated at three spatial scales, but there were no interactions between scales at the intermediate stages; the outputs from each of the spatial scales were summed at the final stage to produce an overall output. The bottom row of images shows the salience maps produced by a modified salience model including a separate contour-facilitation channel in addition to the standard orientation channel (Fig. 3), for the four exemplar images from the left column of Fig. 1.

one array shift and multiplication per spatial frequency, rather than a convolution or Fourier transform. Once the attenuation masks were applied to the internal feature maps in the luminance and orientation channels, the remainder of the salience algorithm proceeded as usual.

We also tested several approximations to this full model of eccentricity-dependent filtering, in which only the final salience map was multiplied by a spatial mask. These masks decayed with eccentricity x either as  $ce^{-kx}$ or  $ce^{-kx^2}$ , with varying values of the constants k and c.

Finally, in all of the eccentricity-dependent filtering computations, the model's "fixation location" (used as the center of the various spatial masks) was always yoked to the observer's actual fixation location. Thus, the eccentricity-dependent filtering models were run once for each observer against which they were to be compared. This reflects that our models do not specify a mechanism for generating *sequences* of eye movements, but instead merely identify likely locations for an upcoming fixation, given the current fixation location.

#### 2.10. Normalized scanpath salience (NSS)

Our analyses rest on the degree of correspondence between human fixation locations and model salience maps, taking into account the high inter-subject variability of eye movements. The most straightforward approach was as follows (Fig. 7). Each salience map was linearly normalized to have zero mean and unit standard deviation. Next, the normalized salience values were extracted from each point corresponding to the fixation locations along a subject's scanpath, and the mean of these values, or normalized scanpath salience (NSS), was taken as a measure of the correspondence between the salience map and scanpath. Due to the pre-normalization of the salience map, normalized scanpath salience values greater than zero suggest a greater correspondence than would be expected by chance between fixation locations and the salient points predicted by the model; a value of zero indicates no such correspondence, while values less than zero indicate an anti-correspondence between fixation locations and



Fig. 6. Illustration of the weight matrices that connect neighboring units at different orientations in the contour model of Fig. 5. See Appendix A.1 for details. (a) Each grid entry is a spatial array depicting the connection strengths between a central unit (unit 1) tuned to the orientation given by the column label, and a neighboring unit (unit 2) tuned to the orientation given by the row label. Within each grid entry, the spatial separation between unit 1 and unit 2 is represented by the *x*- and *y*-axes, and connection strength is represented by gray level: lighter pixels reflect regions of excitation, darker pixels reflect regions of inhibition, and gray pixels reflect the absence of any connection. The "butterfly" shape of the kernels reflects the symmetric cones of excitation connecting a central unit with neighbors whose position and orientation is such that the two units are "nearly collinear," as well as the symmetric flanks of inhibition between units representing contour elements that are nearly parallel but non-collinear. (b) An enlargement of the 90°/90° kernel. Here, connection strength is represented by *z*-axis height as well as gray level, with values above and below 0.0 representing excitation and inhibition, respectively. (c) The orientation-independent component  $\rho$  is a function of the distance between the receptive field centers of units 1 and 2. (d) The orientation-dependent component  $\psi$  is a function of the angular difference between the mean orientation ( $\alpha$ ) of units 1 and 2 and the orientation ( $\phi$ ) of the line segment connecting the two units. The connection kernels are formed by the sum of an inhibitory component that depends only on distance (via  $\rho$ ), and an excitatory component that depends on both distance ( $\rho$ ) and orientation ( $\psi$ ).

Table 1	
/alues used to construct the spatial-frequency-dependent masks for the eccentricity-dependent filtering model	

Spatial frequency ( <i>w</i> , cycles per degree)	Luminance channe	1	Orientation channel		
	$c_{\omega}$	$k_{\omega}$	$c_{\omega}$	$k_{\omega}$	
16.0	60.01	0.40	44.97	0.36	
9.0	180.00	0.35	130.08	0.26	
4.5	210.61	0.17	210.64	0.15	
2.3	236.45	0.13	286.12	0.12	
1.0	190.71	0.10	186.79	0.09	
0.7	166.29	0.09	162.38	0.08	
0.4	130.40	0.13	87.92	0.06	

For each unit in the internal feature maps of the luminance and orientation channels, its response value was attenuated by a factor  $m = c_{\omega}e^{-k_{\omega}x}$ , a function of the retinal eccentricity x (degrees of visual angle) and the spatial frequency  $\omega$  (cycles per degree), where  $c_{\omega}$  (unit-less) and  $k_{\omega}$  (degrees<sup>-1</sup>) are frequency-dependent constants fitted to empirical data from Virsu and Rovamo (1979). In this way, at each spatial location, the maximum possible salience was decreased by an factor that grew larger with increasing distance from the current center of fixation.



Fig. 7. Illustration of the method used to compare fixation locations obtained from eye tracking with salience maps obtained from various computational models. (a) A sample image is shown to both the human observer and the model. (b) The model generates a salience map (grayscale image), which is normalized to have zero-mean and unit standard deviation (see scalebar). A series of fixation locations is generated by the observer (connected dots), and the normalized salience value is extracted for each location (values are shown here next to the corresponding fixation locations). (c) The average normalized salience value across all fixation locations is taken as the *normalized scanpath salience* (NSS), and compared against the distribution of salience values across the entire salience map (gray histogram). For the scanpath shown here, the normalized scanpath salience indicates that, on average, the model-predicted salience at fixated locations was 1.304 standard deviations above chance level. Since the NSS is scale-free, it can be used to compare the degree of correspondence between observed and predicted behavior for different observers and images.

model-predicted salient points. Another benefit of the pre-normalization is that these measures could be compared across different subjects, image classes, and model variants; with such a data pool, statistical tests indicated whether the distribution of NSS values was different from the zero-mean distribution expected by chance.

This approach is similar to the one taken by Parkhurst et al. (2002) in that both rely on a linear transformation of salience values; however, our approach uses a variable dynamic range based on the variance of the salience values, while the alternate approach uses a fixed dynamic range based on the difference between the minimum and maximum values (which were rescaled to 0 and 100, respectively, in Parkhurst et al., 2002). In addition, our approach compares salience values at fixated locations to chance distributions unique to each image: the alternate approach compares salience values to a single chance distribution based on all images in a given image category. Our method was intended to accommodate the wide variety of salience distributions observed for different input images (for example, consider how a salience map with 100 points, 90 with value 1.0 and 10 with value 0.0, would be handled relative to a second salience map with 100 values spaced evenly between 0.0 and 1.0).

# 3. Results

A summary of all of the comparisons between models and human behavior in the free-viewing task is given in Tables 2 and 4. Each number gives the average NSS across all observers and images in that image class. In general, our data agree with previous results (Parkhurst et al., 2002) showing that the baseline salience model was significantly above chance ( $p < 10^{-23}$ ) at predicting locations likely to be fixated by observers in a free-viewing task. As expected, this result was largely independent of image category for naturalistic images such as overhead imagery, outdoor photos, and fractals, but did not hold for more artificial images such as the Gabor arrays, for which the baseline salience model was virtually at chance in predicting fixation locations. Indeed, we chose to use the Gabor arrays for exactly this reason: nothing in the baseline model can "see" the contours, yet they are perceptually salient to human observers.

We used two pseudo-models as controls to estimate the theoretical minimum and maximum NSS values that could be expected of the salience models. First, the theoretical range of NSS values is bounded from below by the behavior of a random model, in which the "salience maps" simply contain noise drawn from a normal distribution.<sup>8</sup> The very nature of our analysis method requires that this random model should produce NSS values of 0, and indeed we found values that were nearly 0 (BSM in Table 2; slight differences from 0 are due to the finite size of our data set).

Second, the theoretical range of NSS values is bounded from above by the behavior of an inter-observer model in which the "salience maps" are generated by the pooled fixation locations from all observers. For this, we constructed a spatial array containing a delta function peak at each fixation location from all observers, and blurred this array by convolving with a two-dimensional Gaussian, with half-width at half-height of  $\approx 1^{\circ}$  (see Fig. 8). The blurring was intended to allow for variability in different observers' fixation locations for the same target, and for spatial uncertainty from

<sup>&</sup>lt;sup>8</sup> We obtained nearly identical results (NSS values close to 0) with another pseudo-model whose salience maps were obtained by a random spatial scrambling of the values in the actual salience map.

Table 2			
Results of comparing each model	with scanpaths recorded	during the free-viewing	task (Fig. 2a)

	Outdoor	Fractal	Satellite	Gabor snake	Gabor array
NSS, mean $\pm$ s.e.m.					
Random model	$-0.01\pm0.01$	$-0.02\pm0.01$	$0.02\pm0.01$	$-0.01\pm0.01$	$0.02\pm0.02$
Baseline salience model (BSM)	$0.69\pm0.03$	$0.44\pm0.03$	$0.62\pm0.03$	$0.10\pm0.03$	$0.14\pm0.02$
BSM + Short-range interactions (SRI)	$0.75^*\pm0.03$	$0.56^*\pm0.03$	$0.71^*\pm0.03$	$0.11\pm0.02$	$0.14\pm0.02$
BSM + Contour-facilitation (CF)	$0.72\pm0.03$	$0.60^*\pm0.03$	$0.81^*\pm0.03$	$0.41^*\pm0.03$	$0.52^*\pm0.02$
BSM + SRI + CF	$0.74\pm0.03$	$0.66^*\pm0.03$	$0.85^*\pm0.03$	$0.40^*\pm0.03$	$0.50^*\pm0.02$
Inter-observer	$1.30^*\pm0.04$	$1.13^*\pm0.04$	$1.10^*\pm0.04$	$1.15^*\pm0.06$	$0.91^*\pm0.05$
NSS, % of Inter-observer NSS					
Random model	-0%	-2%	2%	-1%	2%
Baseline salience model (BSM)	53%	39%	57%	9%	15%
BSM + Short-range interactions (SRI)	57%	50%	65%	10%	15%
BSM + Contour-facilitation (CF)	55%	53%	74%	36%	58%
BSM + SRI + CF	57%	59%	77%	35%	55%
Inter-observer	100%	100%	100%	100%	100%

Each number represents the average normalized scanpath salience (NSS) value, for a given model, across all of the fixation locations recorded while observers freely viewed images for 3000 ms each. The normalized scanpath salience values were obtained by the method illustrated in Fig. 7, in which salience maps were first normalized to have zero mean and unit standard deviation, and then for each scanpath the average normalized salience was computed for the fixation locations along the scanpath. Thus for the data shown here, a value of zero would indicate the absence of a correspondence between model predictions and observed fixation locations; a value of one would indicate that, on average, the model-predicted salience was one standard deviation above chance at each fixation location for all observers and all images in the given image category. The upper rows show these correspondences for salience maps predicted by (1) a random "model", (2) the baseline salience model (BSM; see Fig. 3), (3) a modified model including short-range orientation interactions (BSM + SRI; see Fig. 4), (4) a second modified model including contour-facilitation (BSM + CF; see Fig. 5), (5) a combined model including both short-range interactions and contour facilitation (BSM + SRI + CF), and (6) the control condition in which the "salience map" is derived from all observers; as such, it provides a theoretical upper limit for the performance of the models, since the models are not designed to account for inter-observer variability. Thus, the lower rows express the performance of each model as a percentage of the corresponding upper limit. Numbers with a \* indicate models whose fit was significantly better than the corresponding baseline salience model (p < 0.05, paired *t*-test).

the eye tracking method. In practice, this process was slightly modified so that when predicting the fixation locations of observer A, the inter-observer model was based on data from all observers *except* A (i.e., a "leave-one-out" analysis). We found that this inter-observer model gave NSS values between 0.9 and 1.3, depending on the image type (Table 2).

One way to describe the performance of the salience model is to consider its performance as a percentage of the difference between the NSS scores of the random and inter-observer models. These values are shown in the bottom half of Table 2, and range from 39% to 57% for the natural image classes and from 9% to 15% for the Gabor arrays. Fig. 9 gives a graphical depiction of these results.

Although the primary goal of the forced-choice task ("which of two regions was more interesting") in the free-viewing experiment was to encourage observers to actively inspect the image without placing any particular top-down bias on their eye movements, observers' responses to this task also offer an opportunity to compare an implicit measure of salience (i.e., observers' fixation locations) with an explicit measure (i.e., their responses to the forced-choice task). Note that although during the free-viewing experiment (Fig. 2a) observers did not know the orientation with which the response screen would be bisected until after they had viewed the image, we can retrospectively divide observers' eye movements, as well as the models' salience maps, according to this bisecting line for the purpose of subsequent analysis. We found no significant difference between the amount of time observers spent viewing the subsequently selected (mean  $\pm$  s.e.m.: 1.42  $\pm$  0.02 s) and unselected  $(1.40 \pm 0.02 \text{ s})$  regions. There was also no significant difference between the average normalized salience in the subsequently selected  $(0 \pm 0.006)$  and unselected ( $0 \pm 0.006$ ) regions. However, there was a significant tendency (p < 0.05, paired *t*-test) for the portion of the observers' scanpath inside the selected region to have a higher NSS  $(0.52 \pm 0.02)$  than the portion that fell inside the unselected region  $(0.47 \pm 0.02)$ . That is, observers tended to view more salient locations within the subsequently-selected region than in the unselected region, even though they spent equal amounts of time viewing both regions, and both regions had the same average salience.

#### 3.1. Short-range orientation interactions

When the model of short-range orientation interactions was substituted for the standard orientation channel in the salience model, we observed a statistically



Fig. 8. Illustration of the inter-observer model, a control used to establish an upper bound on how well a model of bottom-up attention could be expected to predict observers' eye movements. For each input image (left), observers' scanpaths were recorded (center left column); each point in the scanpath represents a single sample from the 120 Hz eye-tracking trace. From each scanpath, a heatmap was constructed (center right) by placing a Gaussian "blob" (half-width at half-height  $\approx 1^{\circ}$ ) at the location of each sample from the eye movement trace. These blobs were summed across observers to produce a map (right) whose values represent how often observers were fixating in the vicinity of each location. As before, the bottom row of images corresponds to the four exemplar images from the left column of Fig. 1.

significant 10–20% improvement (p < 0.05, paired *t*-test) in the NSS scores across all of the image classes, except for the Gabor snake and Gabor array images in which there was no effect of the short-range orientation interactions. Average NSS values, as percentages of the inter-observer NSS values, ranged from 50% to 65% for the natural image classes, and from 10% to 15% for the Gabor arrays (BSM + SRI in Table 2).

## 3.2. Long-range orientation interactions

We added to the salience model a new channel for contour facilitation via long-range orientation interactions (BSM + CF in Table 2). This led to improved NSS scores over the baseline salience model by 19– 36% for the three image classes, and by  $\approx 300\%$  for the Gabor arrays. Notably, only with long-range orientation interactions did the model's performance rise above chance levels for the Gabor arrays. In addition, for all image classes except the outdoor photos, the baseline model with contour facilitation had significantly higher NSS scores than did the baseline model with short-range orientation interactions. We also tested a model that included both short-range and long-range orientation interactions (BSM + SRI + CF in Table 2). This combined model bettered the individual models in just those cases where the individual models each led to a statistically significant improvement over the baseline model. Finally, turning again to the theoretical upper limit on model performance attained by the NSS attained by the inter-observer model, we found that the modified salience model including a contour-facilitation channel reached 36-74% of this maximum across the different image classes (Table 2).



Fig. 9. Graphical presentation of the data from the bottom half of Table 2, illustrating the degree of correspondence (normalized scanpath salience, NSS) between observers' fixation locations and the various models, as a percentage of the theoretical maximum NSS given by the inter-observer model.

We used a second experiment to specifically address the role of elongated contours in selecting fixation locations, by asking subjects to view the same images under two different task conditions: first, the standard freeviewing task, and subsequently, a contour-detection task. Table 3 shows the results of comparing models with behavior in these two tasks. The baseline model performance was worse in predicting fixation locations in the contour-detection task than in the free-viewing task; this is likely because performing the contour-detection task involves a greater top-down component, whereas the model mimics only bottom-up components. Nevertheless, there was an interaction between task and model (Table 3, bottom half): the relative improvement due to the contour-facilitation model over the baseline model was greater for the contour-detection task than for the free-viewing task, significantly so for the Gabor snake and Gabor array images. That is, the contour-facilitation model was better suited to the contour-detection task.

# 3.3. Eccentricity-dependent filtering

Including eccentricity-dependent filtering in the salience model produced a large improvement in the ability to predict fixation locations. With the full implementa-

Table 3 Results of comparing each model with eye-tracking data from the two different tasks(Fig. 2)

	Outdoor	oor Satellite			Gabor snake		Gabor array	
	fv	cd	fv	cd	fv	cd	fv	cd
NSS, mean								
Baseline salience model (BSM)	0.45	0.51	0.43	0.27	0.13	0.12	0.13	0.12
BSM + Short-range interactions	$0.54^{*}$	$0.60^{*}$	$0.59^{*}$	$0.44^{*}$	0.14	0.13	0.12	0.13
BSM + Contour-facilitation	0.52	0.59	$0.66^*$	$0.49^{*}$	$0.51^{*}$	$0.54^*$	$0.49^{*}$	$0.55^{*}$
Difference, NSS – Baseline salience I	VSS							
Baseline salience model (BSM)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BSM + Short-range interactions	0.09	0.09	0.16	0.17	0.01	0.01	-0.01	0.01‡
BSM + Contour-facilitation	0.07	0.08	0.23	0.23	0.38	$0.42^{\ddagger}$	0.36	$0.44^{\ddagger}$

In the free-viewing task (*fv*), subjects passively observed images, while in the contour-detection task (*cd*), subjects were presented with a schematic contour following each image and were required to indicate whether that contour matched one that was present in the just-seen image. The top half shows the normalized scanpath salience (NSS) metric described in Fig. 7 and Table 2. (As in Table 2, all s.e.m. values were between 0.01 and 0.03, so for brevity these values have been omitted here.) Numbers marked with \* indicate models whose NSS was significantly greater than the NSS of the baseline salience model. The bottom half shows the increment of each model's NSS above the NSS of the baseline salience model. Numbers marked with  $\ddagger$  indicate models for which this increment was significantly greater (paired *t*-test, *p* < 0.05) in the contour-detection task than in the the free-viewing task. The only model to significantly improve upon the baseline model (\*) and to perform significantly better in the contour-detection task ( $\ddagger$ ) was the contour-facilitation model during the Gabor array and Gabor snake images.

tion (in which internal feature maps were modulated according to eccentricity and spatial frequency) the average normalized scanpath salience values were: for outdoor images, 1.02 (versus 0.69 for the baseline model); for fractal images, 1.07 (versus 0.44); for satellite photos, 1.10 (versus 0.62). These represent ratios of 1.48, 2.43, and 1.77 for the three image classes, respectively, relative to the baseline model performance. In addition, the exponential approximation (in which only the final salience map was modulated by an exponential  $e^{-x}$  decay with eccentricity x) produced results very similar to the full implementation (Table 4). Indeed, the normalized scanpath salience scores were 6% higher for the exponential approximation than for the full implementation. For comparison, we also implemented a Gaussian approximation in which the final salience map was modulated by an  $e^{-x^2}$  decay with eccentricity, using the same specifications as in the modified model of Parkhurst et al. (2002). We found that although this Gaussian approximation gave an improvement over the baseline model, the improvement was 35% smaller than with the exponential approximation (and 31%smaller than with the full implementation).

Since the exponential approximation worked at least as well as the full implementation, and required an order of magnitude less CPU time for image processing, we used only the exponential approximation in subsequent analyses. These involved combining eccentricity-dependent filtering with the short-range and long-range interaction models (BSM + SRI + EDF, BSM + CF + EDF in Table 4). In general, we found that if there was a significant improvement due to short-range or long-range interactions over the baseline model in the absence of eccentricity-dependent filtering, then this improvement also persisted in the presence of eccentricity-dependent filtering. This was true of all comparisons except for the short-range interactions with Gabor snake and Gabor array images; in that case, there was no significant difference relative to the baseline model in either the absence or presence of eccentricity-dependent filtering, although there was a non-significant downward trend in the latter case. Thus it appears that the various mechanisms produce independent and separable effects on observers' behavior.

## 4. Discussion

Our experiments were designed to explore the bottom-up physiological mechanisms that influence human behavior in an image-viewing task; we have disregarded important top-down contributions from attentional state, past experience, and other observer-specific factors, in order to assess how much can be attributed to bottom-up, stimulus-driven influences alone. In this respect, our method follows that of Parkhurst et al. (2002), and our results with the baseline salience model are in agreement with theirs: we found highly significant correspondences between model predictions and human fixation locations. However, the main focus of the present study was to extend this method to test, via more specific models, whether certain early vision mechanisms play a significant role in determining subjects' fixation locations.

We rely on an assumption of a substantial overlap between the biological mechanisms responsible for covert attention shifts and overt eye movements; on this "pre-motor theory of attention" (Rizzolatti et al., 1987), pure attention shifts during fixation are essentially planned saccades whose motor execution is inhibited. This is supported by behavioral evidence showing that, despite motor inhibition, the spatial locus of attention

Table 4

Results of comparing each model with the fixation locations recorded during the free-viewing task, identical to Table 2, except that each model now includes eccentricity-dependent filtering (EDF) in which salience values are increasingly attenuated at larger eccentricities (for eccentricity *x*, the attenuation is proportional to  $e^{-x}$ )

	Outdoor	Fractal	Satellite	Gabor snake	Gabor array
NSS, mean $\pm$ s.e.m.					
Random model + EDF	$-0.01\pm0.01$	$-0.01\pm0.01$	$0.02\pm0.01$	$0.00\pm0.01$	$-0.01\pm0.02$
Baseline salience model $(BSM) + EDF$	$1.19\pm0.03$	$1.01\pm0.03$	$1.12\pm0.03$	$1.15\pm0.03$	$1.08\pm0.03$
BSM + Short-range interactions $(SRI) + EDF$	$1.25^*\pm0.03$	$1.10^*\pm0.03$	$1.20^*\pm0.03$	$1.10\pm0.03$	$1.03\pm0.03$
BSM + Contour-facilitation (CF) + EDF	$1.21^*\pm0.03$	$1.10^*\pm0.03$	$1.23^*\pm0.03$	$1.28^*\pm0.03$	$1.22^*\pm0.04$
BSM + SRI + CF + EDF	$1.24^*\pm0.03$	$1.14^*\pm0.03$	$1.25^*\pm0.03$	$1.26^*\pm0.03$	$1.20^*\pm0.04$
Inter-observer + EDF	$1.44^*\pm0.04$	$1.28^*\pm0.04$	$1.24^*\pm0.04$	$1.42^{\ast}\pm0.06$	$1.17^*\pm0.05$
NSS, % of Inter-observer NSS					
Random model + EDF	-1%	-1%	1%	0%	-1%
Baseline salience model $(BSM) + EDF$	83%	79%	90%	81%	92%
BSM + Short-range interactions (SRI) + EDF	87%	86%	96%	77%	88%
BSM + Contour-facilitation (CF) + EDF	84%	86%	99%	91%	104%
BSM + SRI + CF + EDF	86%	89%	101%	89%	103%
Inter-observer + EDF	100%	100%	100%	100%	100%

Numbers with a \* indicate models whose fit was significantly better than the corresponding baseline salience model (p < 0.05, paired *t*-test).

exerts a small but detectable influence on the trajectories of subsequent saccades (Kustov & Robinson, 1996; Sheliga et al., 1994, Sheliga, Riggio, & Rizzolatti, 1995) or on the distribution of microsaccades during fixation (Hafed & Clark, 2002). These results suggest that computational models of attention and saccadic eye movements should be similar until the execution stage, where the dynamics would be expected to change due to the motor inertia of eye movements or the differing strengths of inhibition-of-return. Indeed, it is plausible that other modes of behavioral output, such as verbal report or finger-pointing, could be driven by the same core mechanisms. In ongoing work, we are using such approaches to further explore which computational elements are intrinsic to spatial attention, and which are specific to particular output modalities (Astafiev et al., 2003; Briand, Larrison, & Sereno, 2000).

We found that a large overall fraction of the observed eye movement behavior could be attributed to the basic elements of early vision (luminance, orientation, color), according to the strong correspondence between the observed fixation locations and the predictions of the baseline salience model. Allowing that this general model of vision is not intended to account for inter-observer differences, an absolute upper limit on the performance of such models is given by the ability to predict one subjects' behavior from the average behavior of the remaining subjects. The models we tested reached roughly 50%of this theoretical limit (Table 2, lower half); performance increased to 80-100% when eccentricity-dependent effects were accounted for (Table 4, lower half); as a crude measure, this suggests that the models could account for at least half of the variance in spatial positions of fixated locations, outside of inter-observer differences.

We tested three specific putative physiological mechanisms for their role in determining fixation locations. The first such mechanism that we tested was short-range inhibitory orientation interactions, also known as crossorientation suppression. These interactions were modeled on the lateral inhibition that takes place within a hypercolumn in early visual cortical areas, which in turn is an abstraction of the concept that for a given receptive field in visual space, there is a confined population of cells in visual cortex that are tuned to all possible spatial scales and orientations. Lateral inhibition is a ubiquitous feature of sensory processing along spatial, temporal, and higher-order feature dimensions, as it decorrelates the input and maximizes information density (Simoncelli & Olshausen, 2001). Ultimately, this allows behaviorally relevant input to be represented in a more explicit and compact manner. Lee et al. (1999) used psychophysical experiments to validate a hypercolumn model, showing that changes in attentional state could be explained by changing the relative contributions of feedforward excitatory and feedback inhibitory

connections. These connections determine, among other things, how easily an observer is able to identify a lowcontrast grating in the presence of an overlapping grating of a different orientation. When we included these connections in our salience model, we found that the model's salience maps predicted observers' fixation locations significantly better. Thus, these connections, previously modeled with well-controlled minimalistic laboratory stimuli, also appear behaviorally relevant under less restrictive task conditions involving free-viewing natural scenes.

The second mechanism that we tested was long-range connections between different hypercolumns. Computationally, such connections or their equivalent have been introduced to explain the subjective salience of implicit contours like Gabor "snakes" that would otherwise be invisible to purely local processing (Braun, 1999a; Li, 1998). Indeed, without long-range connections, the salience model performed very poorly in predicting observers' fixation locations in the Gabor arrays, since each individual Gabor element appears equally salient to a purely local mechanism. As we expected, the model performance increased dramatically (more than threefold) when the long-range connections were included. However, somewhat unexpected was the fact that these connections lead to more modest improvements in predicting fixation locations in the natural image categories. This could be explained in one of two ways: either the model was not accurately identifying what observers' considered to be "contours," or the observers were giving relatively little weight to the contours that were present. To distinguish between these possibilities, we conducted a second psychophysics experiment in which observers viewed images under two different task conditions, one requiring them to specifically attend to contours, and one requiring only free viewing. If our model of contour facilitation based on long-range connections was simply inaccurate, then it should not have shown any additional benefit in predicting observers' contour-detection behavior over their free-viewing behavior. Instead, we found that the improvement in model fit due to contour facilitation was greater when subjects performed the contour-detection task than when they performed the free-viewing task. Thus one possible conclusion is that, although our contour-facilitation model was accurately highlighting what would qualitatively be identified as "contours," observers' fixation locations were only weakly influenced by the presence of elongated contours in natural images where other salient image features were also present.

The third biological vision mechanism that we tested was the decay of sensitivity in peripheral relative to foveal vision. Anatomically, this decay is found throughout the visual system, including the decreasing density of photoreceptors and retinal ganglion cells away from the fovea, and "cortical magnification"—the over-representation in cortical surface area of central vision throughout visual cortex. This anatomical organization manifests itself behaviorally in increased contrast detection and orientation discrimination thresholds in the periphery, and in a non-uniform distribution of saccade targets with a disproportionate tendency toward the image center (Parkhurst et al., 2002). We used published reports of contrast-detection and orientation-discrimination thresholds (Virsu & Rovamo, 1979) to construct a detailed functional model of eccentricity-dependent effects, and asked whether this model could explain observers' non-uniform distribution of saccade targets within the context of the salience model. Indeed, we observed a strong increase in the model's predictive ability when it included eccentricity-dependent filtering, in agreement with Parkhurst et al. (2002). Furthermore, we found that the behavior of the full eccenmodel was matched tricity-dependent by an approximation in which a single exponentially-decaying mask, centered at the current fixation location, is applied to the salience map. Such an exponentially-decaying mask gave a better fit to behavior than did a Gaussian-decaying mask as used in Parkhurst et al. (2002). It should be noted that since our experiments did not separately control covert attention shifts and overt eye movements, we cannot distinguish between mechanisms that might separately favor eye movements near the center of attention and the center of fixation. Along this line, future studies should explore how the functionally-defined shape of "central vision" might change with behavioral modalities such as covert attention, eye movements, finger-pointing, or verbal report.

In addition to building our understanding of biological vision, we have aimed to develop computational algorithms that are efficient enough to be useful in real-world machine vision applications. The models of short-range orientation interactions and eccentricity-dependent filtering described here have efficient implementations that do not significantly impact the execution time of the salience model, yet have significant effects on the model's ability to match human behavior. In contrast, the model of contour facilitation requires roughly an order of magnitude more processing time and is weakly relevant to behavior in some task conditions, but is also critically important in predicting behavior under other conditions such as the Gabor snakes that we tested, and also potentially in real-world tasks like road-finding in overhead imagery. Taken together, this suggests that a machine vision implementation might best compute an initial salience map based on local features alone, and secondarily perform more computationally intensive tasks like contour facilitation or object recognition within a restricted window selected by the first stage. Such systems will ultimately be useful both as stand-alone applications and as semi-automated assistants in tasks that rely on a human executor. The

interface between biology and engineering is rich in research directions that will lead us closer not only toward understanding the inner workings of vision, but also toward building machines that assist, interact, collaborate, and synergize with real human visual systems.

## Acknowledgments

This work was supported by the National Geospatial-Intelligence Agency (NGA, formerly known as the National Imagery and Mapping Agency, NIMA), the Sandia National Laboratories, the Engineering Research Centers (ERC) Program of the National Science Foundation under Award Number EEC-9402726, the Keck Foundation, and by a Predoctoral Fellowship from the Howard Hughes Medical Institute to R.J. Peters. The authors affirm that the views expressed herein are solely their own, and do not represent the views of the United States government or any agency thereof. The authors would like to thank Nathan Mundhenk for a reference implementation of the contour-facilitation model.

## Appendix A

#### A.1. Contour-facilitation model

The weights in the connection matrix (shown in Fig. 6), following the model of Braun (1999a), are composed of two factors: (1) an orientation-independent factor,  $\rho$ , depending on the spatial positions  $(x_a, y_a)$  and  $(x_b, y_b)$  of the receptive field centers of two units, and (2) an orientation-dependent factor,  $\psi$ , depending on the units' preferred orientations,  $\theta_a$  and  $\theta_b$ , and on the orientation of the line segment connecting the receptive field centers,  $\phi_{ab}$ . Four external parameters control this matrix:  $d_{\text{max}}$ ,  $k_{\text{exc}}$ ,  $k_{\text{inh}}$ , and  $\beta$ . The orientation-independent factor is a function of the Euclidean distance between the two positions:

$$d_{ab} = \frac{((x_a - x_b)^2 + (y_a - y_b)^2)^{1/2}}{d_{\max}}$$
$$\rho_{ab} = (d_{ab} \cdot \exp(1 - d_{ab}))^2.$$

The orientation-dependent factor relies on the following definitions. For a given angle  $\theta$ , we define  $\tilde{\theta}$  such that  $\theta = \tilde{\theta} + n\pi$  with *n* being the integer for which  $0 \le \tilde{\theta} < \pi$ . Then the canonical difference  $\delta$  between two angles is defined as

$$\delta(\theta_a, \theta_b) = \frac{\pi}{2} - \left| \left| \tilde{\theta}_a - \tilde{\theta}_b \right| - \frac{\pi}{2} \right|$$

or, equivalently:

$$\delta(\theta_a, \theta_b) = \begin{cases} |\tilde{\theta}_a - \tilde{\theta}_b| & \text{if } |\tilde{\theta}_a - \tilde{\theta}_b| < \pi/2, \\ \pi - |\tilde{\theta}_a - \tilde{\theta}_b| & \text{otherwise.} \end{cases}$$

Three angles are significant; these are the two units' preferred orientations  $\theta_a$  and  $\theta_b$  (as well as the average  $\alpha_{ab} = (\theta_a + \theta_b)/2)$ , and the orientation of the line segment connecting the units' receptive field centers:

$$\phi_{ab} = \tan^{-1} \left( \frac{y_b - y_a}{x_b - x_a} \right).$$

From these angles, the orientation-dependent factor  $\psi_{ab}$  is given as

$$\psi_{ab} = \begin{cases} \exp(-\beta \cdot \delta(\alpha_{ab}, \phi_{ab})) \\ \text{if units } a \text{ and } b \text{ are nearly collinear,} \\ 0 \text{ otherwise.} \end{cases}$$

Two units are considered to be "nearly collinear" if the following conditions all hold:

$$\delta( heta_a, heta_b) < \pi/4 \ \delta( heta_a, \phi_{ab}) < \pi/4 \ \delta( heta_b, \phi_{ab}) < \pi/4.$$

Thus,  $\psi$  will be large if the average of the two units' preferred orientations is similar to the orientation of the line segment connecting the two units, which is precisely the condition satisfied by a smooth contour.

Finally, the connection strength  $w_{ab}$  between units a and b is given by a weighted sum of an excitatory part and an inhibitory part:

$$w_{ab} = w_{ab}^{
m exc} + w_{ab}^{
m inh},$$
  
with  
 $w_{ab}^{
m exc} = k_{
m exc} \cdot \rho_{ab} \cdot \psi_{ab}$ 

$$w_{ab}^{\text{inh}} = k_{\text{inh}} \cdot \rho_{ab}$$

Note that the inhibitory nature of  $w_{ab}^{inh}$  is conferred by choosing a negative value for  $k_{inh}$ , so overall excitatory or inhibitory connections are denoted by positive or negative values of  $w_{ab}$ , respectively. The contour-facilitation algorithm can be pruned for CPU efficiency by setting  $k_{inh} = 0$  when  $\delta(\theta_a, \theta_b) > \pi/4$ , so that  $w_{ab} =$  $w_{ab}^{\text{exc}} = w_{ab}^{\text{inh}} = 0$  under those conditions; this significantly reduces the number of computations that must be performed by the algorithm, at the price of a reduced ability to reject orthogonal line segments as unlikely contours. In order to allow algorithm parameters to be unit-less, the connection strength matrix is normalized by the maximum connection strength, so that after normalization the new maximum connection strength is 1. Sample wab matrices are illustrated in Fig. 5 ("connection kernel") and Fig. 6.

The iterative algorithm for contour-facilitation proceeds independently in three scale bands whose outputs are summed at the end of the process. Each scale band involves a network of several layers of units; some of these layers are triply indexed by x and y spatial positions as well as orientation  $\theta$ , while others are doubly indexed by the spatial positions only, and finally the dynamic activity in several of the layers is tracked by a time-step counter *t*:

- $\mathscr{I}(x, y, \theta)$ : input given by oriented filtering of the original input image;
- $\mathcal{N}^{t}(x, y, \theta)$ : activation levels from interactions among units in  $\mathcal{I}$ ;
- $\mathscr{G}^{t}(x, y)$ : group-inhibition weights depending on time derivative of  $\mathscr{E}$ ;
- $\mathscr{S}^{t}(x,y)$ : leaky orientation-independent units driven by  $\mathcal{N}$ :
- $\mathscr{E}^{t}(x,y)$ : output energy given by sigmoidal transformation of  $\mathscr{G}$ .

Note that in the following description, symbols of the form  $k_*$  are external free parameters of the model. The immediate input to the contour-facilitation algorithm,  $\mathcal{I}(x, y, \theta)$  (labeled as "filter output" in Fig. 5), is given by applying the baseline salience model's dyadic orientation-tuned pyramids (Itti et al., 1998) to the input image. The *i*th entry in the activation matrix,  $\mathcal{N}^{i}(x_{i}, y_{i}, \theta_{i})$  (labeled as "activation maps" in Fig. 5), is given by the transformation of the input  $\mathscr{I}$  via the connection weights  $w_{ab}$ :

$$\mathcal{N}^{t}(x_{i}, y_{i}, \theta_{i}) = \left[\sum_{j} w_{ij} \cdot f(\mathcal{N}^{t-1}(x_{j}, y_{j}, \theta_{j})) \cdot g_{ij}^{t-1} \cdot \mathscr{I}(x_{i}, y_{i}, \theta_{i}) \cdot \mathscr{I}(x_{j}, y_{j}, \theta_{j})\right],$$

where  $|\cdot|$  represents rectification,  $f(\mathcal{N}^{t-1}(x_i, y_i, \theta_i))$  is a fast plasticity term that amplifies outgoing connections from units whose activity in the previous time step was high (labeled as "recurrent excitation" in Fig. 5):

$$f(\mathcal{N}^{t-1}(x_j, y_j, \theta_j)) = \begin{cases} 1 & \text{if } k_{\text{fast}} \cdot \mathcal{N}^{t-1}(x_j, y_j, \theta_j) < 1, \\ 5 & \text{if } k_{\text{fast}} \cdot \mathcal{N}^{t-1}(x_j, y_j, \theta_j) > 5, \\ k_{\text{fast}} \cdot \mathcal{N}^{t-1}(x_j, y_j, \theta_j) & \text{otherwise,} \end{cases}$$

and  $g_{ii}^{t-1}$  is a group-inhibition term that selectively modulates inhibitory connections (indicated by "modulation of inhibition" in Fig. 5):

$$g_{ij}^{t-1} = \begin{cases} 1 & \text{if } w_{ij} >= 0, \\ \mathscr{G}^{t-1}(x_j, y_j) & \text{otherwise.} \end{cases}$$

Т

Then  $\mathscr{G}^{t}(x, y)$  (indicated by the box containing a " $\Sigma$ " in Fig. 5) is given by

$$\mathscr{S}^{t}(x_{i}, y_{i}) = \left[ \mathscr{S}^{t-1}(x_{i}, y_{i}) - k_{\text{leak}} + \sum_{\theta} \mathscr{N}^{t}(x_{i}, y_{i}, \theta_{i}) \right]$$

and  $\mathscr{E}^{t}(x, y)$  (labeled as "output" in Fig. 5) is given by a sigmoidal transformation of  $\mathcal{G}^{t}(x, y)$ :

$$\mathscr{E}^{t}(x,y) = \left(1 + \exp\left(2 - 4 \cdot \frac{\mathscr{S}^{t}(x,y)}{k_{\text{sigthresh}}}\right)\right)^{-1}.$$

Finally, the group-inhibition weights are updated based on a lowpass-filtered version of the change in output energy between time steps t - 1 and t:

$$\begin{split} \Delta^{t}(x,y) &= \text{lowpass}(\mathscr{E}^{t}(x,y) - \mathscr{E}^{t-1}(x,y)), \\ \mathscr{G}^{t}(x,y) &= \mathscr{G}^{t-1}(x,y) + k_{\text{gadd}} \cdot \lfloor \Delta^{t}x, y - k_{\text{gtop}} \rfloor \\ &- k_{\text{gsub}} \cdot \lfloor k_{\text{bottom}} - \Delta^{t}x, y \rfloor, \end{split}$$

with initial group-inhibition values at time t = 0 of  $\mathscr{G}^0(x, y) = 1$ . So, local inhibitory strength increases if the output energy is increasing at a rate faster than  $k_{\text{gtop}}$ , and decreases if the output energy is increasing at a rate slower than  $k_{\text{bottom}}$ .

#### References

- Anstis, S. (2002). The purkinje rod-cone shift as a function of luminance and retinal eccentricity. *Vision Research*, 42(22), 2485–2491.
- Astafiev, S., Shulman, G., Stanley, C., Snyder, A., Van Essen, D., & Corbetta, M. (2003). Functional organization of human intraparietal and frontal cortex for attending, looking, and pointing. *Journal of Neuroscience*, 23(11), 4689–4699.
- Beauchamp, M., Petit, L., Ellmore, T., Ingeholm, J., & Haxby, J. (2001). A parametric fMRI study of overt and covert shifts of visuospatial attention. *Neuroimage*, 14(2), 310–321.
- Blasdel, G. (1992). Orientation selectivity, preference, and continuity in monkey striate cortex. *Journal of Neuroscience*, 12(8), 3139–3161.
- Braun, J. (1999a). Contour salience and striate cortex: A new model matches human sensitivity. *Investigative Ophthalmology & Visual Science*, 40(4), S780–S780.
- Braun, J. (1999b). On the detection of salient contours. *Spatial Vision*, *12*(2), 211–225.
- Briand, K., Larrison, A., & Sereno, A. (2000). Inhibition of return in manual and saccadic response systems. *Perception & Psychophysics*, 62(8), 1512–1524.
- Carandini, M., Heeger, D., & Senn, W. (2002). A synaptic explanation of suppression in visual cortex. *Journal of Neuroscience*, 22(22), 10053–10065.
- Crook, J., Kisvarday, Z., & Eysel, U. (1997). GABA-induced inactivation of functionally characterized sites in cat striate cortex: Effects on orientation tuning and direction selectivity. *Visual Neuroscience*, 14(1), 141–158.
- Das, A., & Gilbert, C. (1999). Topography of contextual modulations mediated by short-range interactions in primary visual cortex. *Nature*, 399(6737), 655–661.
- Deangelis, G., Robson, J., Ohzawa, I., & Freeman, R. (1992). Organization of suppression in receptive-fields of neurons in cat visual-cortex. *Journal of Neurophysiology*, 68(1), 144–163.
- Freeman, T., Durand, S., Kiper, D., & Carandini, M. (2002). Suppression without inhibition in visual cortex. *Neuron*, 35(4), 759–771.
- Hafed, Z., & Clark, J. (2002). Microsaccades as an overt measure of covert attention shifts. *Vision Research*, 42(22), 2533–2545.
- Heeger, D. (1992). Normalization of cell responses in cat striate cortex. Visual Neuroscience, 9(2), 181–197.
- Hibino, H. (1992). Red-green and yellow-blue opponent-color responses as a function of retinal eccentricity. *Vision Research*, 32(10), 1955–1964.
- Hoffman, J., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception & Psychophysics*, 57(6), 787–795.
- Imhoff, S., Volbrecht, V., & Nerger, J. (2004). A new look at the bezold-micke hue shift in the peripheral retina. *Vision Research*, 44(16), 1891–1906.
- Itti, L., & Koch, C. (2001). Computational modeling of visual attention. Nature Reviews Neuroscience, 2(3), 194–203.

- Itti, L., Koch, C., & Braun, J. (2000). Revisiting spatial vision: Towards a unifying model. *Journal of the Optical Society of America, JOSA-A, 17*(11), 1899–1917.
- Itti, L., Koch, C., & Niebur, E. (1998). A model of saliency-based visual attention for rapid scene analysis. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 20(11), 1254– 1259.
- James, W. (1890). The principles of psychology. Cambridge, Massachusetts: Harvard University Press.
- Koch, C. (2004). The quest for consciousness: A neurobiological approach. Denver, Colorado: Roberts & Company.
- Koch, C., & Ullman, S. (1985). Shifts in selective visual-attention towards the underlying neural circuitry. *Human Neurobiology*, 4(4), 219–227.
- Kolesnik, M., & Barlit, A., 2003. Iterative orientation tuning in v1: A simple cell circuit with cross-orientation suppression. In: *Image Analysis, Proceedings; Lecture Notes in Computer Science*. Vol. 2749, pp. 232–238..
- Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research*, 35(13), 1897–1916.
- Krieger, G., Rentschler, I., Hauske, G., Schill, K., & Zetzsche, C. (2000). Object and scene analysis by saccadic eye-movements: An investigation with higher-order statistics. *Spatial Vision*, 13(2-3), 201–214.
- Kustov, A., & Robinson, D. (1996). Shared neural control of attentional shifts and eye movements. *Nature*, 384(6604), 74–77.
- Lauritzen, T., Krukowski, A., & Miller, K. (2001). A model of crossorientation inhibition in cat primary visual cortex. *Neurocomputing*, 38, 757–762.
- Lee, D., Itti, L., Koch, C., & Braun, J. (1999). Attention activates winner-take-all competition among visual filters. *Nature Neurosci*ence, 2(4), 375–381.
- Li, W., & Gilbert, C. (2002). Global contour saliency and local colinear interactions. *Journal of Neurophysiology*, 88(5), 2846–2856.
- Li, Z. (1998). A neural model of contour integration in the primary visual cortex. *Neural Computation*, 10(4), 903–940.
- Lu, Z., Lesmes, L., & Sperling, G. (1999). Perceptual motion standstill in rapidly moving chromatic displays. *Proceedings of the National Academy of Sciences of the United States of America*, 96(26), 15374–15379.
- Marr, D. (1982). Vision: A computational investigation into the human representation and processing of visual information. San Francisco, California: W.H. Freeman & Company.
- Miau, F., & Itti, L., 2001. A neural model combining attentional orienting to object recognition: Preliminary explorations on the interplay between where and what. *Proc. IEEE Engineering in Medicine and Biology Society* (EMBS), Istanbul, Turkey..
- Moore, T., Armstrong, K., & Fallah, M. (2003). Visuomotor origins of covert spatial attention. *Neuron*, 40(4), 671–683.
- Moore, T., & Fallah, M. (2001). Control of eye movements and spatial attention. Proceedings of The National Academy of Sciences of the United States of America, 98(3), 1273–1276.
- Moore, T., & Fallah, M. (2004). Microstimulation of the frontal eye field and its effects on covert spatial attention. *Journal of Neurophysiology*, 91(1), 152–162.
- Morrone, M., Burr, D., & Maffei, L., 1982. Functional implications of cross-orientation inhibition of cortical visual cells. 1. Neurophysiological evidence. In: *Proceedings of the Royal Society of London Series B—Biological Sciences*. Vol. 216. pp. 335–354..
- Mullen, K., & Losada, M. (1999). The spatial tuning of color and luminance peripheral vision measured with notch filtered noise masking. *Vision Research*, 39(4), 721–731.
- Mundhenk, T., & Itti, L. (2002). A model of contour integration in early visual cortex. *Biologically Motivated Computer Vision, Pro*ceedings, 2525, 80–89.

- Nobre, A., Gitelman, D., Dias, E., & Mesulam, M. (2000). Covert visual spatial orienting and saccades: Overlapping neural systems. *Neuroimage*, 11(3), 210–216.
- Parkhurst, D., Law, K., & Niebur, E. (2002). Modeling the role of salience in the allocation of overt visual attention. *Vision Research*, 42(1), 107–123.
- Pettet, M., & Gilbert, C. (1992). Dynamic changes in receptive-field size in cat primary visual-cortex. *Proceedings of The National Academy of Sciences of the United States of America*, 89(17), 8366–8370.
- Polat, U., & Sagi, D. (1993). Lateral interactions between spatial channels—suppression and facilitation revealed by lateral masking experiments. *Vision Research*, 33(7), 993–999.
- Polat, U., & Sagi, D. (1994a). The architecture of perceptual spatial interactions. *Vision Research*, 34(1), 73–78.
- Polat, U., & Sagi, D. (1994b). Spatial interactions in human vision from near to far via experience-dependent cascades of connections. *Proceedings of The National Academy of Sciences of the United States of America*, 91(4), 1206–1209.
- Posner, M., & Cohen, Y. (1984). Components of performance. In H. Bouma & D. Bowhuis (Eds.), *Attention and performance X* (pp. 531–556). Hillsdale, NJ: Erlbaum.
- Privitera, C., & Stark, L. (2000). Algorithms for defining visual regions-of-interest: Comparison with eye fixations. *IEEE Trans*actions on Pattern Analysis and Machine Intelligence, 22(9), 970–982.
- Reinagel, P., & Zador, A. (1999). Natural scene statistics at the centre of gaze. *Network-Computation in Neural Systems*, 10(4), 341–350.
- Rizzolatti, G., Riggio, L., Dascola, I., & Umilta, C. (1987). Reorienting attention across the horizontal and vertical meridians evidence in favor of a premotor theory of attention. *Neuropsychologia*, 25(1A), 31–40.
- Rutishauser, U., Walther, D., Koch, C., & Perona, P., 2004. Is attention useful for object recognition? *IEEE International Conference on Computer Vision and Pattern Recognition*.
- Sheliga, B., Riggio, L., & Rizzolatti, G. (1994). Orienting of attention and eye movements. *Experimental Brain Research*, 98(3), 507–522.
- Sheliga, B., Riggio, L., & Rizzolatti, G. (1995). Spatial attention and eye movements. *Experimental Brain Research*, 105(2), 261–275.

- Simoncelli, E., & Olshausen, B. (2001). Natural image statistics and neural representation. *Annual Review of Neuroscience*, 24, 1193–1216.
- Somers, D., Nelson, S., & Sur, M. (1995). An emergent model of orientation selectivity in cat visual cortical simple cells. *Journal of Neuroscience*, 15(8), 5448–5465.
- Stettler, D., Das, A., Bennett, J., & Gilbert, C. (2002). Lateral connectivity and contextual interactions in macaque primary visual cortex. *Neuron*, 36(4), 739–750.
- Tang, C., Medioni, G., & Lee, M. (2001). N-dimensional tensor voting and application to epipolar geometry estimation. *IEEE Transac*tions On Pattern Analysis And Machine Intelligence, 23(8), 829–844.
- Treue, S. (2003). Visual attention: The where, what, how and why of saliency. *Current Opinion in Neurobiology*, 13(4), 428–432.
- van Hateren, J., & van der Schaaf, A. (1998). Independent component filters of natural images compared with simple cells in primary visual cortex. *Proceedings of The Royal Society of London B*, 265, 359–366.
- Virsu, V., & Rovamo, J. (1979). Visual resolution, contrast sensitivity, and the cortical magnification factor. *Experimental Brain Research*, 37(3), 475–494.
- Walther, D., Itti, L., Riesenhuber, M., Poggio, T., & Koch, C. (2002). Attentional selection for object recognition—a gentle way. *Biologically Motivated Computer Vision—Lecture Notes in Computer Science*, 2525, 472–479.
- Wandell, B. (1995). Foundations of vision. Sunderland, Massachusetts: Sinauer Associates.
- Worgotter, F., & Koch, C. (1991). A detailed model of the primary visual pathway in the cat—comparison of afferent excitatory and intracortical inhibitory connection schemes for orientation selectivity. *Journal of Neuroscience*, 11(7), 1959–1979.
- Yarbus, A. (1967). Eye movements during perception of complex objects. In L. Riggs (Ed.), *Eye Movements and Vision*. New York, NY: Plenum Press.
- Zenger, B., Braun, J., & Koch, C. (2000). Attentional effects on contrast detection in the presence of surround masks. *Vision Research*, 40(27), 3717–3724.
- Zenger, B., & Sagi, D. (1996). Isolating excitatory and inhibitory nonlinear spatial interactions involved in contrast detection. *Vision Research*, 36(16), 2497–2513.