Attention and visual perception

Geoffrey M Boynton

Somewhere between the retina and our conscious visual experience, the majority of the information impinging on the eye is lost. We are typically aware of only either the most salient parts of a visual scene or the parts that we are actively paying attention to. Recent research on visual neurons in monkeys is beginning to show how the brain both selects and discards incoming visual information. For example, what happens to the responses of visual neurons when attention is directed to one element, such as an oriented colored bar, embedded among an array of other oriented bars? Some of this research shows that attention to the oriented bar restricts the receptive field of visual neurons down to this single element. However, other research shows that attention to this single element affects the responses of neurons with receptive fields throughout the visual field. In this review, these two seemingly contradictory results are shown to actually be mutually consistent. A simple computational model is described that explains these results, and also provides a framework for predicting a variety of additional neurophysiological, neuroimaging and behavioral studies of attention.

Addresses
The Salk Institute, Systems Neurobiology Laboratories -B, 10010 North Torrey Pines Road, La Jolla CA, 92037-1099, USA

Corresponding author: Boynton, Geoffrey M (boynton@salk.edu)

Current Opinion in Neurobiology 2005, **15**:465–469

This review comes from a themed issue on
Sensory systems
Edited by David Julius and Andrew King

Available online 14th July 2005

0959-4388/$ – see front matter

DOI 10.1016/j.conb.2005.06.009

Introduction

Much has been learnt in recent years about how attention influences the neuronal representation of visual stimuli. The majority of recent studies of attention can be categorized as studies of either spatial attention or feature-based attention. Cueing a monkey to shift spatial attention from outside to inside the receptive field (RF) of a neuron increases the responses of visual neurons, possibly by increasing the effective contrast of the stimulus [1,2]. Cueing a monkey's feature-based attention to one of two stimuli presented together within the RF of a neuron biases neuronal responses as though attended stimulus was presented alone [3,4]. This is conceptually similar to restricting the RF to the attended stimulus. This can be called 'local feature-based attention' because it describes feature-based attentional effects locally within the focus of spatial attention. Monkey electrophysiological [2,5•] and functional magnetic resonance imaging (fMRI) studies [6] show evidence of 'global feature-based attention', in which attention affects the response of neurons with RFs well outside the focus of spatial attention. This might seem contradictory because local feature-based attention restricts the RF and global feature-based attention affects neurons regardless of RF location. These effects of spatial in addition to local and global feature-based attention might seem complex. However, a simple model of attention presented in this review predicts a wide variety of experimental results.

The neuronal contrast–response function

A variety of stimulus-driven responses in the macaque visual cortex [7–9] can be described by a divisive contrast normalization process. Neurons have an inherent peak sensitivity for a specific feature of a stimulus, such as direction of motion, color or orientation. If stimuli are defined as consisting of multiple components presented within the RF of a neuron, each of which has its own feature, x_i, and contrast, c_i, then the response of a neuron to a stimulus can be described by equation (1).

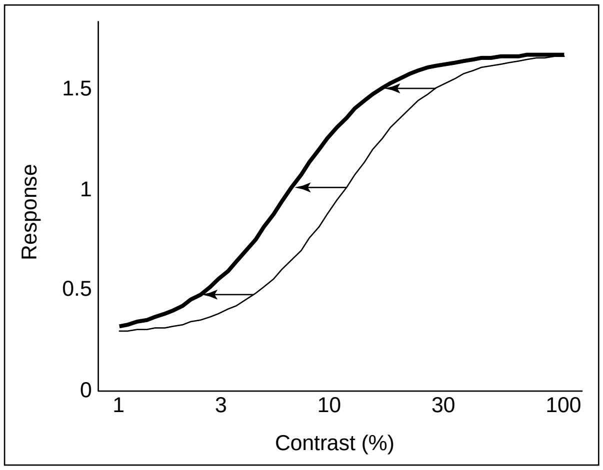
$$H(x_x, c_i) = \frac{\sum_i (c_i F(x_i))^2}{\sum_i c_i^2 + \sigma^2} \quad (1)$$

The total excitatory response in the numerator is the sum of squared linear responses to each stimulus component. The inhibitory response in the denominator is the sum of squared contrasts plus a semisaturation term, (σ). This term in the denominator corresponds to the contrast energy of the stimulus and represents a divisive input from a population of neurons selective across the spectrum of feature space [7]. This model predicts an S-shaped, or sigmoidal, contrast–response function that is suppressed divisively when non-preferred stimuli are added to the RF. The model correctly predicts that increasing stimulus contrast increases neuronal responses without altering the selectivity of a neuron for a given feature, such as orientation or spatial frequency [10–13].

Contrast-gain model of spatial attention

Recent electrophysiological studies of attention in monkeys suggest that spatial attention increases the effective contrast of a stimulus in color-selective area V4 [1] and motion-selective area MT [2]. This can be described either by multiplying all contrast components by a constant or, equivalently, by dividing the semisaturation

Figure 1



Contrast-gain model of spatial attention. Spatial attention directed from outside the RF (light curve) to inside the RF (dark curve) shifts the contrast response function of the model neuron leftward. Responses are in arbitrary units. Model parameters: semisaturation constant $\sigma = 10\%$, feature-based gain G = 1.4, spatial attention contrast gain factor: 1.75. Baseline response $\delta = 0.2$.

parameter, σ, by the same constant. Dividing the parameter σ by a constant $k>1$ increases the effective contrast of the stimulus by the same factor, shifting the contrast–response function leftward on a log–contrast axis. Figure 1 shows the effect of spatial attention on the contrast–response function of a model neuron. The light curve is the contrast–response function when attention is directed away from the stimulus, and the dark curve is the contrast-response function of the attended stimulus. Note that spatial attention should have its maximal influence for intermediate contrasts.

The feature similarity gain model of global feature-based attention

Treue and Martinez-Trujillo [5•] have shown that, for example, if a neuron in area MT of the macaque is selective to upward motion, then attention to upward motion will enhance the response of this neuron, whereas attention to downward motion will suppress the response. Interestingly, this modulation is found even when the spatial focus of attention is outside the RF of the cell. These authors suggest a 'feature-similarity gain model' of attention. In this model, attention directed to a particular feature modulates the firing rate by a gain factor that has a tuning function similar to the stimulus-driven tuning function of that neuron [2,5•,14].

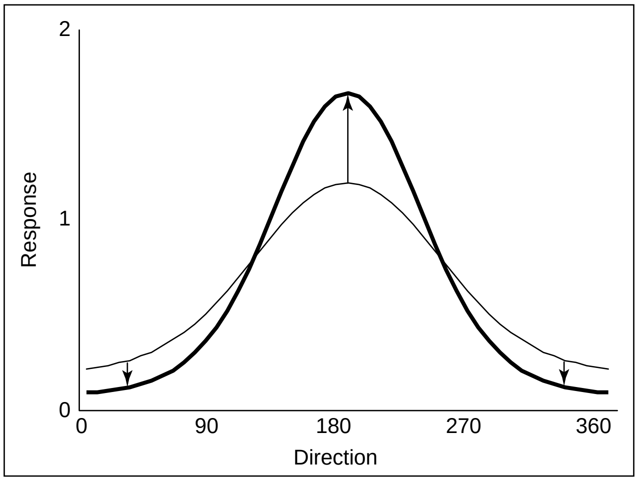
$$R(x_i, c_i, y) = G(y)[H(x_i, c_i) + \delta] \tag{2}$$

To quantify the feature similarity gain model, the response of a neuron from equation (1) is modulated by a gain factor, G, that depends on the attended feature *y* (Equation (2)).

Here, H is the response of the neuron from equation 1. The parameter δ is the inherent baseline-firing rate of the neuron. The gain factor $G(y)$ peaks at a value greater than one for the preferred feature of the neuron, and drops below one when attention is directed to features well outside the preferred feature. Importantly, the attended feature y does not need to be present in the stimulus used to map the RF and can, for example, be a feature present in a stimulus attended outside the RF of the neuron. That is, $G(y)$ is a purely feature-based effect, and is independent of the spatial focus of attention and the properties of the visual stimulus.

Figure 2 shows how feature-based attention affects the response of a model neuron under experimental conditions similar to those of Martinez-Trujillo and Treue [5•]. Both curves show responses to a stimulus when the monkey was focusing attention away from the stimulus. The light curve shows a direction-tuning curve for a hypothetical MT neuron when the monkey is performing a task unrelated to motion at the point of fixation. The dark curve shows the response to the same stimulus, but when attention was to another stimulus outside the RF and moving in the same direction as the stimulus inside the RF. Feature-based attention enhances the response when attention is directed towards the preferred direction

Figure 2



Feature-similarity gain. The light curve is the direction tuning curve for a model MT neuron (preferring 180 degree motion) with attention directed outside the RF towards fixation. The dark curve is attention directed to the same direction of motion, also outside the RF. Feature-based attention towards the preferred direction enhances the response, whereas attention towards the anti-preferred direction suppresses the response. Responses are in arbitrary units. Model parameters: same as for figure 1 except stimulus contrast: 100%, direction selectivity: F(x) = Gaussian with 1/e width of 90 degrees. Feature similarity gain, G(x) = 0.6 F(x) + 0.8.

of the neuron (G>1), but suppresses the response when attention is directed towards the non-preferred direction (G<1).

Biased competition model of local feature-based attention

In a classic study, Moran and Desimone [3] measured electrophysiological responses in the monkey from area V4 and from neurons in the inferotemporal cortex (IT) neurons when two stimuli were presented within the RF of a neuron. One stimulus was called the 'preferred' stimulus because, when presented alone, it produced a larger response than the 'non-preferred' stimulus. When attention was directed away towards a fixation task, the response to the pair of stimuli fell between that to the preferred and that to the anti-preferred stimuli when they had been presented in isolation. When attention was directed to the preferred stimulus, responses increased, and when attention was directed to the anti-preferred stimulus, responses decreased. Desimone described these results with a 'biased competition model' in which attention to one of two stimuli within the RF of the neuron biases the response of the neuron as if the attended stimulus was presented alone [15].

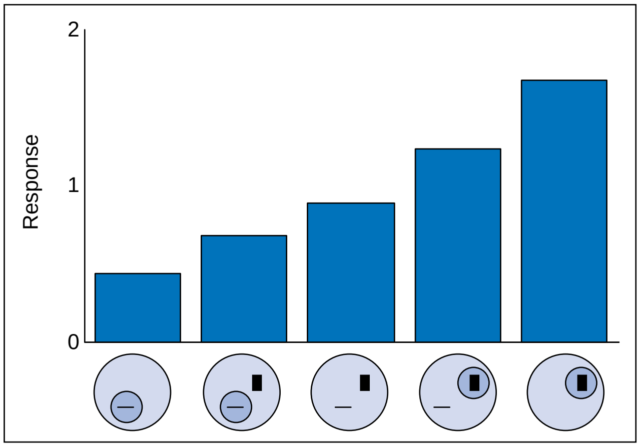
In a subsequent study, Reynolds, Chelazzi and Desimone [16] made similar measurements in areas V2 and V4 using oriented colored bars. A quantitative description of the biased competition model predicts their results, in which the response to the pair of stimuli is a weighted average of the response to each stimulus alone. Attention away from the pair results in an average response, or an equal weight for each stimulus. Attention to one of the pair shifts the weight towards the attended stimulus.

The feature similarity gain model predicts biased competition

The biased competition model is analogous to shrinking the effective size of the RF [4] but the feature-similarity gain model seems to achieve almost the opposite effect because it is a spread of attention to all neurons in the visual field [17]. However, the simple model described above can explain both effects by assuming that the same feature-based attention mechanism operates both within and outside the RF of a neuron.

Consider the case when attention is directed towards fixation when a pair of stimuli is placed in the RF. Here, we assume a neutral feature-based gain factor (G) of one. If the stimuli are at full contrast, then the semisaturation constant in the denominator of equations. 1 and 2 can be ignored (because $\sigma^2 \ll 1$). The model predicts that the response to each of the two stimuli, having features x_i, will be simply x_1^2, and that the response to the pair will be $(x_1^2 + x_2^2)/2$. That is, the response to the pair is correctly predicted to be the average of the response to each of the two stimuli alone.

Figure 3



Feature-similarity gain predicts biased competition. Model V4 neuron with vertical preferred orientation. Icons show the stimulus inside the RF (light circle), with the attended component inside the smaller circle (except for middle bar when attention is directed towards fixation). Attention to one of two stimuli inside the RF (second and fourth bars) biases the response away from the condition in which attention is directed towards fixation (middle bar) and towards the condition in which the attended stimulus is presented alone (first and fifth bars). Responses are in arbitrary units. Model parameters: same as figure 2 except with orientation replacing direction. Stimuli: 90 and 180 degree orientations for anti-preferred and preferred stimuli respectively.

Attention to stimulus component 1 in the RF invokes the feature-based gain factor $G(x_1)$. If, again, the effects of the semisaturation constant are ignored, the response to the pair will be $G(x_1)(x_1^2 + x_2^2)/2$. This is simply the average response multiplied by the feature-based gain factor. The gain factor will be greater than one if the attended stimulus is the preferred stimulus of the neuron, and less than one if the attended stimulus is anti-preferred. This is qualitatively consistent with the predictions from the biased competition model; instead of attention biasing the response towards the response to the attended stimulus, the model makes the equivalent prediction that attention biases the response away from the mean response.

Figure 3 shows predictions of the responses of a model neuron under conditions similar to those used by Reynolds *et al.* [16]. The response to the pair when attention is directed towards fixation is roughly halfway between the responses to each of the stimuli when presented alone. Attention directed from fixation to the preferred and anti-preferred stimulus increases and decreases the response, respectively.

Model predictions of other attention studies

Spatial attention

The model described above provides a framework for understanding a variety of studies on spatial and feature-based attention, and helps reconcile apparent discrepancies in their results. For example, McAdams and

Maunsell [18] measured the effects of attention on the orientation-selectivity of V1 and V4 neurons. Orientation tuning curves in both V1 and V4 were found to increase in a multiplicative fashion with spatial attention. This, at first, seems like a contradiction of the contrast-gain model of spatial attention described above. However, it is easy to show that if the effects of contrast and orientation are separable, a change in the semisaturation constant changes the tuning functions multiplicatively [19].

Human psychophysical studies are generally consistent with the contrast-gain model of spatial attention. A recent study used the motion aftereffect to assess the response to an attended and unattended stimulus and found that attention acted as a contrast gain [20]. Another psychophysical study measuring contrast discrimination thresholds is consistent with spatial attention acting both as a contrast gain and as a multiplicative gain [21].

In addition to a contrast gain change with spatial attention, there is some fMRI and macaque electrophysiology evidence suggesting that spatial attention might also increase the baseline response of neurons in the absence of visual stimulation [22–27]; for reviews see [28,29].

Local feature-based attention

Competitive interactions for multiple stimuli within the RF of a cell have also been found in area MT. Treue and Maunsell [17] trained monkeys to attend to one of two dots (that oscillated back and forth) within the RF of MT neurons. Firing rates increased when the attended dot moved in the preferred direction of the neuron. In a related study, Seidemann and Newsome [30] recorded from MT neurons in monkeys trained to attend to one of two fields of moving dots in the RF, one field moving in the preferred direction, one in an anti-preferred direction. Responses increased when attention was directed to the preferred motion compared with that to the anti-preferred motion. Just as for the competitive interaction results in V2 and V4, the feature-similarity gain model can predict these attentional effects in MT.

Seidemann and Newsome [30] measured attentional effects in two other conditions that can be predicted by the model. In one experiment, the anti-preferred dots were placed outside the RF. The modulation of response when attention was shifted between the preferred and the anti-preferred dots was nearly identical to that observed when both stimuli were presented inside the RF. Note that only spatial attention is different between the first and the second condition; feature-based attention is the same. The model predicts this result because the dots were of high contrast, so the additional effects of spatial attention should be negligible. Only spatial attention was varied in a third experiment, in which both the moving dot field inside the RF and the field outside the RF moved in the preferred direction. As expected, little attentional modulation was found when the monkey switched spatial attention between the two stimuli.

In a later study in macaque V4 by McAdams and Maunsell [31], when attention shifted between identical oriented grating stimuli inside and outside the RF, response modulation was less than when attention shifted between the grating stimulus inside the RF and a colored spot outside the RF. The first condition manipulated spatial attention alone, whereas both spatial- and feature- based attention varied in the second condition.

Global feature-based attention

An analogous fMRI study in the human visual system supports the feature similarity gain model [6]. The fMRI response to an unattended upward moving field of dots in one visual hemifield increased and decreased when subjects alternated attention to upward and downward motion, respectively, in the opposite visual hemifield. These effects were found throughout the early retinotopically organized visual areas (V1, V2, V3, V3A and MT+). The attentional effect was also found for color; for example, the fMRI response to an unattended red stimulus was found to increase and decrease when attention was alternated between a red and green stimulus, respectively, in the opposite visual hemifield. A related psychophysical study showed that it is easier to attend to two stimuli simultaneously if they share a common direction, motion or color [32].

A very recent study [33•] found evidence of feature-based attention for orientation in human V1 with fMRI. A pattern classifier algorithm was used to categorize distinctive patterns of fMRI responses in V1 associated with different stimulus orientations. Then, when subjects attended to one of two orientations on a plaid stimulus, the authors could predict which orientation the subject was attending to. Accurate prediction required incorporating the response over a large region in V1. It seems reasonable that this experiment worked only because global feature-based attention modified the responses of all V1 neurons, regardless of the location of spatial attention, so that the overall pattern of responses was sufficiently biased to resemble the pattern induced by the attended orientation alone.

Conclusions

The model in this review proposes a simple relationship among the effects of spatial, local and global feature-based attention on visual neuronal responses. Spatial attention acts as a contrast-gain mechanism. Local and global feature-based attention are mediated by the same mechanism, and operate separably with spatial attention. Although this model explains biased competition through global feature-based attention, a related model explains global feature-based attention through biased competition of neurons in area IT [34,35].

Some predictions of the model remain untested. For example, spatial and feature-based attention should operate separably, so that the effects of feature-based attention should have the same multiplicative gain whether attention is allocated inside or outside the RF of the neuron. Also, as suggested by fMRI studies [22,23,36], feature-based attention should affect baseline responses throughout the visual field, even without the presence of a stimulus. It is well known that attention changes the perceptual quality and behavioral performance on visual stimuli. It should be easy to modify models of the neurophysiological effects of attention, such as the one presented here, to predict the effects of attention on perception and behavioral performance. Hopefully, this will provide a framework for understanding the relationship between the effects of attention of the brain and its effects on behavior.

References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Reynolds JH, Pasternak T, Desimone R: **Attention increases sensitivity of V4 neurons**. *Neuron* 2000, **26**:703-714.
2. Treue S, Martinez Trujillo JC: **Feature-based attention influences motion processing gain in macaque visual cortex**. *Nature* 1999, **399**:575-579.
3. Moran J, Desimone R: **Selective attention gates visual processing in the extrastriate cortex**. *Science* 1985, **229**:782-784.
4. Desimone R, Duncan J: **Neural mechanisms of selective visual attention**. *Annu Rev Neurosci* 1995, **18**:193-222.
5. • Martinez-Trujillo JC, Treue S: **Feature-based attention increases the selectivity of population responses in primate visual cortex**. *Curr Biol* 2004, **14**:744-751.
A follow up study of Treue and Martinez-Trujillo [2] further quantifying the effects of global feature-based attention.
6. Saenz M, Buracas GT, Boynton GM: **Global effects of feature-based attention in human visual cortex**. *Nat Neurosci* 2002, **5**:631-632.
7. Heeger DJ: **Modeling simple-cell direction selectivity with normalized, half-squared, linear operators**. *J Neurophysiol* 1993, **70**:1885-1898.
8. Heeger DJ, Simoncelli EP, Movshon JA: **Computational models of cortical visual processing**. *Proc Natl Acad Sci USA* 1996, **93**:623-627.
9. Carandini M, Heeger DJ, Movshon JA: **Linearity and normalization in simple cells of the macaque primary visual cortex**. *J Neurosci* 1997, **17**:8621-8644.
10. Tolhurst D: **Separate channels for the analysis of the shape and the movement of a moving visual stimulus**. *J Physiol* 1973, **231**:385-402.
11. Dean AF: **The variability of discharge of simple cells in the cat striate cortex**. *Exp Brain Res* 1981, **44**:437-440.
12. Albrecht DG, Hamilton DB: **Striate cortex of monkey and cat: contrast response function**. *J Neurophysiol* 1982, **48**:217-237.
13. Sclar G, Freeman RD: **Orientation selectivity in the cat's striate cortex is invariant with stimulus contrast**. *Exp Brain Res* 1982, **46**:457-461.
14. Treue S: **Neural correlates of attention in primate visual cortex**. *Trends Neurosci* 2001, **24**:295-300.
15. Desimone R: **Visual attention mediated by biased competition in extrastriate visual cortex**. *Philos Trans R Soc Lond B Biol Sci* 1998, **353**:1245-1255.
16. Reynolds JH, Chelazzi L, Desimone R: **Competitive mechanisms subserve attention in macaque areas V2 and V4**. *J Neurosci* 1999, **19**:1736-1753.
17. Treue S, Maunsell JH: **Attentional modulation of visual motion processing in cortical areas MT and MST**. *Nature* 1996, **382**:539-541.
18. McAdams CJ, Maunsell JHR: **Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4**. *J Neurosci* 1999, **19**:431-441.
19. Reynolds JH, Chelazzi L: **Attentional modulation of visual processing**. *Annu Rev Neurosci* 2004, **27**:611-647.
20. Rezec A, Krekelberg B, Dobkins KR: **Attention enhances adaptability: evidence from motion adaptation experiments**. *Vision Res* 2004, **44**:3035-3044.
21. Huang L, Dobkins KR: **Attentional effects on contrast discrimination in humans: evidence for both contrast gain and response gain**. *Vision Res* 2005, **45**:1201-1212.
22. Kastner S, Pinsk MA, De Weerd P, Desimone R, Ungerleider LG: **Increased activity in human visual cortex during directed attention in the absence of visual stimulation**. *Neuron* 1999, **22**:751-761.
23. Ress D, Backus BT, Heeger DJ: **Activity in primary visual cortex predicts performance in a visual detection task**. *Nat Neurosci* 2000, **3**:940-945.
24. Ferrera VP, Rudolph KK, Maunsell JH: **Responses of neurons in the parietal and temporal visual pathways during a motion task**. *J Neurosci* 1994, **14**:6171-6186.
25. Luck SJ, Chelazzi L, Hillyard SA, Desimone R: **Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex**. *J Neurophysiol* 1997, **77**:24-42.
26. Chelazzi L, Miller EK, Duncan J, Desimone R: **A neural basis for visual search in inferior temporal cortex**. *Nature* 1993, **363**:345-347.
27. Bisley JW, Zaksas D, Droll JA, Pasternak T: **Activity of neurons in cortical area MT during a memory for motion task**. *J Neurophysiol* 2004, **91**:286-300.
28. Driver J, Frith C: **Shifting baselines in attention research**. *Nat Rev Neurosci* 2000, **1**:147-148.
29. Pasternak T, Greenlee MW: **Working memory in primate sensory systems**. *Nat Rev Neurosci* 2005, **6**:97-107.
30. Seidemann E, Newsome WT: **Effect of spatial attention on the responses of area MT neurons**. *J Neurophysiol* 1999, **81**:1783-1794.
31. McAdams CJ, Maunsell JH: **Attention to both space and feature modulates neuronal responses in macaque area V4**. *J Neurophysiol* 2000, **83**:1751-1755.
32. Saenz M, Buracas GT, Boynton GM: **Global feature-based attention for motion and color**. *Vision Res* 2003, **43**:629-637.
33. • Kamitani Y, Tong F: **Decoding the visual and subjective contents of the human brain**. *Nat Neurosci* 2005, **8**:679-685.
The use of clever fMRI analysis techniques enabled these authors to measure stimulus-driven and attention-driven responses to orientation in human V1.
34. Corchs S, Deco G: **Large-scale neural model for visual attention: integration of experimental single-cell and fMRI data**. *Cereb Cortex* 2002, **12**:339-348.
35. Corchs S, Deco G: **Feature-based attention in human visual cortex: simulation of fMRI data**. *Neuroimage* 2004, **21**:36-45.
36. Chawla D, Rees G, Friston KJ: **The physiological basis of attentional modulation in extrastriate visual areas**. *Nat Neurosci* 1999, **2**:671-676.