Steveninck et al., 1994), but many open questions remain.

In this issue of *Neuron*, Brenner et al. (Brenner et al., 2000) go a step further and demonstrate that H1 is optimal in a concrete way. They start by deriving a new analytical tool which builds on the more common approach of computing the average stimulus preceding a spike. Under some circumstances, this spike-triggered average stimulus can be thought of as the feature in the stimulus that drives the neuron to fire and can be a meaningful way to characterize a neuron's responses. However, by studying the full distribution of stimuli preceding a spike rather than just the average of this distribution, the authors show that quickly varying dynamic stimuli have a more subtle effect on H1, so that there are essentially two relevant functions of the stimulus (roughly, the velocity and acceleration of the motion signal) that affect the firing of the neuron. In this approach, the number of parameters, as well as their relation to the stimulus, are determined by the structure of the data. Having found this simplified parameterization, it is possible to fully characterize the nonlinear input/output relation of the neuron.

Next, Brenner et al. show that H1 adapts to the variance of the velocity distribution of the motion signal, as it must do when the fly switches from straight flight to chasing behavior, for example. It is important to remember that this is an adaptation to the statistics of an ensemble of stimuli rather than to a particular stimulus or stimulus feature. They emphasize that all measurable higher order statistics of the spike train adapt, not just the firing rate. Yet, they find that the adaptation can be fully described in terms of a single parameter, the "stretch factor," which determines how the neuron matches its limited dynamic range of spike rates to the dynamic range or variance of its inputs. By computing the information rate in a model neuron set to different values of the stretch factor for the same stimulus ensemble, they prove their main result: H1 adapts to changes in the dynamic range or variance of the motion signal so as to maximize the rate of information of its output. Once again, constructing the appropriate stimuli and introducing new methods of analysis reveal optimal design principles necessitated by evolutionary pressure.

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Attending to Contrast

Studies of the neural mechanisms underlying attention build on the foundation of classical studies of the primate visual system that have focused on understanding how visual images are transduced, encoded, and analyzed by the brain. In most of these classical studies, anesthetized animals were presented with visual stimuli while physiologists recorded the activity of neurons carrying information from the retina to the lateral geniculate nucleus of the thalamus and then on to the hierarchically organized visual cortices. As Hubel and Wiesel (1959) were among the first to demonstrate, the sensitivity of each neuron in the visual cortex to patterns of light and dark can be described by a *receptive field*, which is the pattern of light and dark that maximally excites the cell. In a typical cell in cortical area V1, for example, the receptive field might be described as two vertically oriented dark regions flanking a vertically oriented light region: a vertical band of light flanked by darkness falls on a particular retinal location and maximally activates the cell. Perhaps the most interesting property of such a cell is that uniform illumination of the receptive field gives rise to no neuronal activity; it is the strength of the contrast between the light and dark regions that the cell encodes. For this reason a horizontally, as opposed to vertically, aligned bar of light fails to activate this cell because it does not present a light/dark contrast along the vertical axis. Of course, the receptive fields of cells in visual cortical areas vary in their responsiveness to the orientation, width (the spatial frequency of the light and dark bands), wavelength, and even the speed and direction of stimuli, but nearly all cells share this fundamental sensitivity to contrast.

Psychological studies have demonstrated that attending to a location improves our ability to detect or discriminate visual stimuli at that location (Sperling and Dosher, 1986; Kinchla, 1992; Lu and Dosher, 1998; Carrasco et al., 2000), and it seems only natural to ask how the neural architecture described by classic studies might accomplish this improvement. This question became experimentally tractable in the 1970s when it became possible to study the activity of neurons in the visual cortices of awake animals trained to attend to particular locations. Over the past 15 years this area of research has made significant progress, and two competing hypotheses have evolved to explain the neural

basis of the psychological phenomena of visual attention. Desimone and colleagues have suggested that attention may increase the efficiency with which attended stimuli are encoded, while Maunsell and colleagues have argued that attention boosts the overall strength of neural signals without altering the efficiency with which neurons encode information.

Desimone's view emerged from a series of experiments that studied neurons in cortical area V4 while monkeys either *attended to* or *ignored* visual stimuli presented in the receptive field of the neuron under study (Moran and Desimone, 1985). He and his colleagues trained animals to perform a simple visual discrimination task: animals indicated whether a second stimulus was the same color or orientation as a previously presented stimulus. They found that paying attention to a particular stimulus location altered how neurons encoded visual information. When the difference between the second and first stimulus was small, the task was more difficult, and animals were more efficient at the discrimination; their sensitivity for discriminating the two stimuli improved presumably because they paid more attention. In parallel with this increase in perceptual efficiency, they found that neurons also responded more strongly to a given stimulus when the task was more difficult (Spitzer et al., 1988). Based on these experiments, Desimone and colleagues suggested that attention increased the perceptual efficiency of the visual system by increasing the efficiency of individual neurons, perhaps by making them more strongly responsive to an optimal color or orientation and more weakly responsive to a suboptimal color or orientation.

To support their alternative hypothesis, Maunsell and his colleagues performed a quantitative analysis of the responses of V4 neurons under attended and ignored conditions while bars of light were systematically presented within the receptive field at a range of different orientations (McAdams and Maunsell, 1999a, 1999b). In agreement with the work of Desimone and colleagues, they found that the strength of the neuronal signal was enhanced in the attended condition, relative to the ignored condition, even though the physical stimulus presented was identical in these two conditions. However, when they analyzed neuronal firing rates in detail, they did not find an increase in the relative strength of neuronal responses for optimally versus suboptimally oriented bars. Attention boosted, or multiplied, neuronal activity by a constant fraction across all the bar orientations they examined.

One experiment that may well reconcile these two opposing views appears in this issue of *Neuron*, where Reynolds and colleagues consider the following: given that nearly all neurons in the visual system are sensitive to contrast, could attention alter the efficiency with which a given contrast stimulus activates cortical neurons and thus boost neuronal activity across orientation, without in any other way altering how information about orientation is processed? Put another way, does paying attention selectively enhance the contrast of stimuli at attended locations? If that were true, these authors reasoned, such an attentional mechanism would be detectable since it should shift the minimum, or threshold, contrast to which each neuron responds to a lower level.

To test this hypothesis, Reynolds and colleagues trained monkeys to stare straight ahead while directing their attention to one of two locations, one inside and one outside of the receptive field of a V4 neuron under study. Stimuli consisted of patches of sinusoidal gratings (rows of alternating bright and dark bars), which were presented at various levels of contrast. With this experimental design, the authors could compare the firing rates of neurons across a range of contrasts, and thus compute the neuron's contrast–response function, as well as study modulations in neuronal firing rates to identical visual stimuli with and without attention. They found that when attention was directed toward the location of a stimulus within the receptive field, V4 neurons behaved exactly as if the contrast of the low-contrast visual stimulus had been increased by 51%. Thus, as they predicted, these data indicate that paying attention shifts the contrast–response function, effectively enhancing neuronal responsiveness for low-contrast, or hard-to-see, stimuli, irrespective of other stimulus properties like orientation. This result might even account for the observation of Maunsell and colleagues that V4 neurons respond more strongly for all orientations, because the effective contrast at each orientation, which was fixed in that experiment, could have been enhanced uniformly by attention.

These results are exciting because they suggest that contrast may be even more special than previously realized: attended stimuli may be more efficiently seen because they assume an effectively greater contrast at the level of visual cortical neurons. Of course, a number of important issues remain to be resolved, and this finding serves as an interesting starting point because it proposes a hypothesis relating visual attention to contrast–response functions. Future studies will have to determine how generalizable this result is to other stimulus parameters and other visual areas (for example, the results of Treue and Maunsell, 1996) and how the neuronal circuitry of the visual cortex accomplishes a shift in the contrast–response function toward a higher contrast sensitivity. Perhaps more importantly, future studies will need to determine the relationship between changes at the neuronal level, in this case resulting from attentional enhancement, and the resulting visual percept (Parker and Newsome, 1999). Nonetheless, the work of Reynolds and colleagues may represent a seminal step in integrating traditional theories of visual processing and neurophysiological theories of attention.

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