How do attention and adaptation affect contrast sensitivity?

Franco Pestilli   Department of Psychology, New York University, New York, NY, USA

Gerardo Viera   Department of Psychology, New York University, New York, NY, USA

Marisa Carrasco   Department of Psychology and Center for Neural Science, New York University, New York, NY, USA

Attention and adaptation are both mechanisms that optimize visual performance. Attention optimizes performance by increasing contrast sensitivity for and neural response to attended stimuli while decreasing them for unattended stimuli; adaptation optimizes performance by increasing contrast sensitivity for and neural response to changing stimuli while decreasing them for unchanging stimuli. We investigated whether and how the adaptation state and the attentional effect on contrast sensitivity interact. We measured contrast sensitivity with an orientation-discrimination task, in two adaptation conditions—adapt to 0% or 100% contrast—in focused, distributed, and withdrawn attentional conditions. We used threshold and asymptotic performance to index the magnitude of the attentional effect—enhancement or impairment in contrast sensitivity—before and after adapting to high-contrast stimuli. The results show that attention and adaptation affect the contrast psychometric function in a similar but opposite way: Attention increases stimulus salience, whereas adaptation reduces stimulus salience. An interesting finding is that the adaptation state does not modulate the magnitude of the attentional effect. This suggests that attention affects the normalized signal once the effect of contrast adaptation has taken place and that these two mechanisms act separately to change contrast sensitivity. Attention can overcome adaptation to restore contrast sensitivity.

Introduction

The visual environment is rich in information. Despite the fact that the brain uses almost a quarter of the body's metabolic resources, the energy available at each instant is insufficient to process all incoming sensory information (Lennie, 2003). The brain has to maximize performance while maintaining energy expenditures within its metabolic limits to attain our astonishing perceptual abilities. Several mechanisms allocate perceptual resources to optimize our sensitivity to match salient parts of visual scenes. Spatial attention and contrast adaptation are two such managing mechanisms. In this study, we investigated whether and how the adaptation state and the attentional effects on contrast sensitivity interact. In particular, we explored whether attention can overcome adaptation and restore contrast sensitivity.

Visual attention

Visual attention is a key mechanism that enables the brain to optimize performance within its metabolic limits.

Attention can be allocated covertly, without eye movements (Posner, 1980). Covert attention allows us to prioritize the processing of some locations of the visual scene at the expense of others via a "push–pull" mechanism (Desimone & Duncan, 1995). Both temporal (Carrasco, Giordano, & McElree, 2006; Carrasco & McElree, 2001) and spatial (Cameron, Tai, & Carrasco, 2002; Carrasco, Ling, & Read, 2004; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Carrasco, Williams, & Yeshurun, 2002; Lu & Dosher, 1998; Yeshurun & Carrasco, 1998, 1999, 2000) aspects of visual information processing are enhanced by directing attention to a location in the visual field. Such enhancements at the attended location happen early in the visual stream (Gandhi, Heeger, & Boynton, 1999; Huk & Heeger, 2000; McAdams & Reid, 2005; Watanabe et al., 1998) and are accompanied by concurrent impairments at unattended locations (Desimone, 1998; Geng et al., 2006; Reynolds, Chelazzi, & Desimone, 1999; Vanduffel, Tootell, & Orban, 2000). The pervasiveness of this push–pull mechanism is evidenced by the finding that contrast sensitivity is increased at attended locations but is decreased at unattended locations even with very sparse displays (Pestilli & Carrasco, 2005).

Psychophysical studies have revealed two subsystems of covert attention. Sustained or endogenous attention is

voluntary, and it allocates perceptual resources according to task demands. Exogenous or transient attention is involuntary, and it allocates resources to the location where a sudden change in stimulation occurs, for example, luminance, contrast, or color. These two subsystems are mediated by partially segregated networks of brain areas (Corbetta & Shulman, 2002; Kastner & Ungerleider, 2000).

The black curve in Figure 1 shows a hypothetical contrast response function. The neural response to contrast is, at least in the first stages of the visual system, monotonic across the full contrast range (Albrecht & Hamilton, 1982; Anzai, Bearse, Freeman, & Cai, 1995; Avidan et al., 2002; Boynton, Demb, & Heeger, 1996; Dean, 1981; Tolhurst, Movshon, & Thompson, 1981). The red curve shows that with attention, less contrast is necessary to attain the same response level (Points 1 and 4; Carrasco et al., 2000; Reynolds, Pasternak, & Desimone, 2000), and stimulus contrast appears more intense (Points 2 and 4; Carrasco et al., 2004). Single-cell recording studies of sustained attention have found attention to both shift the contrast response function toward lower contrast (contrast-gain mechanism; Martinez-Trujillo & Treue, 2002; Reynolds et al., 2000) and to scale it proportionally (response-gain mechanism; Williford & Maunsell, 2006). To date, there is no single-cell recording study regarding the effects of transient attention on contrast sensitivity. A psychophysical study using a cueing paradigm shows that whereas transient attention acts via both contrast- and response-gain mechanisms, sustained attention acts via contrast gain (Ling & Carrasco, 2006a). Other studies in which sustained attention is manipulated via dual tasks have yielded mixed results; they support either a response-gain mechanism (Morrone, Denti, & Spinelli, 2004) or both contrast gain and response gain (Huang & Dobkins, 2005).

Contrast adaptation

The visibility of every image can be directly related to its contrast, which delineates what is visible to us and is the basis of all subsequent analyses performed on the visual input. Therefore, maintaining the best sensitivity to contrast in the environment is a primary task for the visual system. The sensitivity of individual neurons is restricted to a short contrast range, with neurons responding weakly at low contrast levels, and their response increases monotonically across a limited range of contrast values before saturating (Albrecht & Hamilton, 1982).

Contrast adaptation enables us to act in environments containing extremely wide contrast ranges, despite the fact that neurons have a limited dynamic range to contrast. It reduces the visual system's response to static, unchanging stimuli, while optimizing sensitivity to the most informative scene characteristics—differences around the time-averaged contrast level. Looking at a stimulus for an extended time reduces our sensitivity to that stimulus and
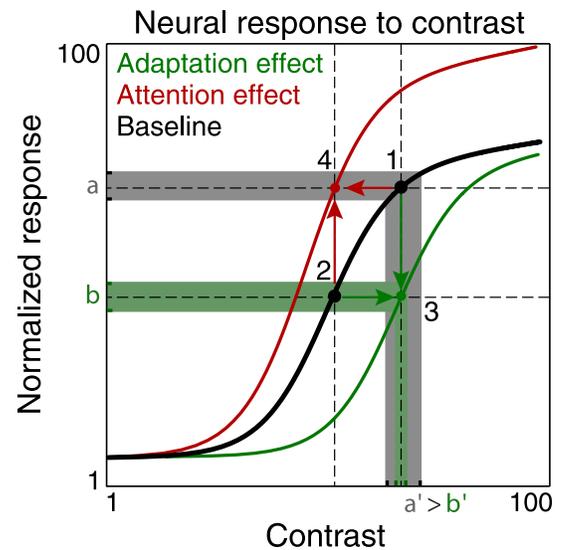

Figure 1. *Contrast response function: effects of adaptation and attention.* The neural response to contrast increases over a limited range then saturates (black curve). *Effect of attention*: The red curve shows the effect of attention on the contrast response function of a hypothetical neuron: Less contrast is needed to attain the same response level (Points 1 to 4), and the same contrast elicits a higher response (Points 2 to 4). *Effect of contrast adaptation*: (1) The contrast response function of a neuron is shifted to the right toward the adapter contrast (green curve, Point 2 to Point 3). As a result, the neural response to the same contrast is reduced after adaptation (Points 1 to 3). (2) Neurons' ability and, hence, our ability to discriminate contrast differences around the average contrast in the environment are effectively increased. We assume that there is minimum response difference needed to discriminate two contrasts (Nachmias, 1967). For example, shaded areas a (gray) and b (green) on the ordinate (response) are the same, but the just-noticeable contrast difference (the projection to the abscissa of the minimum response difference as returned by the neural response function) is larger before than after adaptation; a' (gray) is wider than b' (green) on the contrast axis.

similar stimuli as a result of a decreased neuronal response. Adapted neurons shift their contrast response function horizontally on the contrast axis, recentering it to the contrast of the adapting stimulus (green line in Figure 1; Bonds, 1991; Ohzawa, Sclar, & Freeman, 1982, 1985).

Theoretically, adaptation has a dual effect (Figure 1): (a) The neural response to the average contrast in the environment is reduced after adaptation (Points 1 and 3), and more contrast is needed to achieve the same response level (Points 2 and 3). (b) Neurons' ability to discriminate contrast differences around the average contrast in the environment is effectively increased. Assuming that a fixed minimum response difference is needed to discriminate two contrasts (Nachmias & Sansbury, 1974), the just-noticeable contrast difference is larger before than after adaptation. Note that the minimum response difference, defined with the same width on the ordinate for shaded areas a and b (in gray and

green, respectively), results in a smaller minimum contrast difference for the adapted than for the unadapted curves, areas a′ and b′ on the abscissa.

Studies on the cellular mechanisms associated with adaptation support the idea that adaptation is a significant active regulatory process rather than a mere fatigue process (Carandini & Ferster, 1997; Sanchez-Vives, Nowak, & McCormick, 2000a, 2000b). The same adaptation mechanisms found in cat and macaque cortex are also present in the neural response to contrast in humans, as measured by blood-oxygenation-level-dependent signals. This sigmoidal function also shifts and recenters around the adapter contrast, suggesting that both individual neurons and populations of neurons recalibrate sensitivity around the current environment contrast (Gardner et al., 2005).

Attention and adaptation

Given that both attention and adaptation serve to optimize performance but have opposite effects on the contrast response function, here we explored the way attention and adaptation interact. Were attention to modulate contrast sensitivity after adaptation to high contrast, it would effectively increase stimulus' apparent contrast (as is the case for the unadapted state; Carrasco et al., 2004), but it would also shift the contrast response function away from the adapted state. Furthermore, were adaptation and attention implemented by the same neural mechanisms but with opposite effects on the contrast response function, the effect of attention on contrast sensitivity would be expected to depend on the adaptation state.

Studies manipulating the attentional state during the adapting phase have shown attentional modulation of several perceptual aftereffects, such as tilt and motion aftereffects (Alais & Blake, 1999; Chaudhuri, 1990; McGraw, Whitaker, Skillen, & Chung, 2002; Montaser-Kouhsari & Rajimehr, 2004; Rezec, Krekelberg, & Dobkins, 2004), as well as contrast adaptation (Ling & Carrasco, 2006b). Instead, in this study, we explored whether contrast adaptation modulates the effect of transient attention. To investigate whether and how adaptation and attention interact on contrast sensitivity, we measured contrast sensitivity in two adaptation conditions—adapt to 0% or 100% contrast—when attention is focused, distributed, or withdrawn and compared the magnitude of the attentional effect (enhancement or impairment in contrast sensitivity) before and after adapting to high contrast.

Methods

Three observers performed a two-alternative forced-choice (2AFC) orientation-discrimination task on Gabor

patches located to the left and to the right of fixation (Figure 2). To assess contrast sensitivity, we measured orientation-discrimination performance as a function of stimulus contrast (Cameron et al., 2002; Carrasco et al., 2000; Nachmias, 1967). Observers performed the task in three attentional conditions under two levels of contrast adaptation. Before each test trial, observers adapted for 70 s
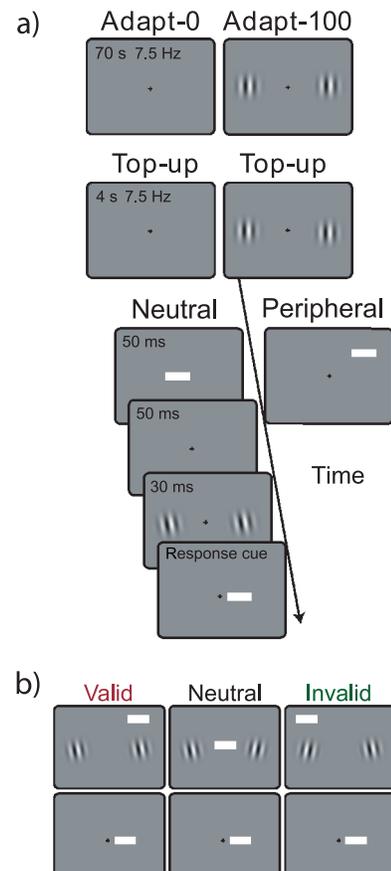

Figure 2. *Trial sequence and cueing conditions*. (a) At the beginning of each block of 20 test trials, observers adapted for 70 s to either a blank screen or two 100% contrast counterphase flickering Gabor patches. After this initial adaptation phase, there were 20 test trials preceded by a 4-s-long top–up phase. On each test trial, a peripheral cue could appear with 33% probability above the left stimulus, above the right stimulus, or at fixation. Two randomly tilted (±2.5°) Gabor patches followed the peripheral cue display and were presented at the location of the adapters. The stimuli had the same contrast randomly chosen from the full range (0–100%). Observers had to discriminate the orientation of the stimulus indicated by a response cue presented after stimulus offset. (b) There were three attentional conditions: In valid-cue trials (focused attention condition), the response cue indicated the stimulus preceded by the peripheral cue; in neutral-cue trials (distributed attention condition), the response cue had equal probability to indicate either stimulus; in invalid-cue trials (withdrawn attention condition), the response cue indicated the location of the stimulus that was not preceded by the peripheral cue.

either to a 100% contrast grating at the location of the test stimulus or to the same mean luminance blank screen (0% contrast). On each test trial, the stimulus was preceded by a peripheral cue that could appear at the target location (valid-cue, focused attention), at the distracter location (invalid-cue, withdrawn attention), or at fixation (neutral-cue, distributed attention), corresponding to focused, withdrawn, or distributed attention conditions.

Observers

Three trained psychophysical observers with normal or corrected-to-normal vision participated in this experiment. Observer J.F. was naive to the purpose of the experiment.

Apparatus

Stimuli were presented binocularly on a gamma-corrected P260 IBM 21-in. Multiscan color monitor in a dark environment. A video attenuator drove the green gun of the monitor to increase rendering precision at low contrast levels from 8 to 12 bits (Pelli & Zhang, 1991). The background luminance was set to the middle of the monitor range, 18 cd/m^2.

Stimuli

The stimuli were generated and presented on a G4 Macintosh computer using MATLAB 5.2.1 (Mathworks, Massachusetts) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). A small, dark circle was used as a fixation point (0.1° of visual angle). Stimuli were 5-c/deg Gabor patches subtending 4° of visual angle in diameter (σ of 1.5°) presented at 5° eccentricity to the left and to the right of fixation. The adapter was vertical, whereas the test was tilted ±2.5° from vertical. A peripheral cue, a 1° × 0.4° white horizontal rectangle, appeared with equal probability either at 3° above the center of one of the Gabor patches (peripheral cue) or at both sides of fixation (neutral cue). The response cue, a 1° × 0.4° white horizontal rectangle, was equally likely to appear to the left or to the right of fixation, indicating the Gabor patch that should be discriminated.

Procedure and design

Observers fixated at the center of the screen throughout the entire block while performing a 2AFC orientation-discrimination task on the peripheral stimuli. We assessed contrast sensitivity via the method of constant stimuli (observers F.P. and G.V.: 1, 2.5, 5, 10, 20, 40, 80, and 100%; observer J.F.: 1, 2.5, 5, 10, 15, 20, 40, and 80%). Observers were trained on the task for about 2 hr to make sure that they had obtained stable performance.

Each observer participated for 30 hr to complete about 12,500 trials in the experiment, half in each adaptation condition.

Adaptation procedure

There were two adaptation conditions: adapt-0, observers were adapted to the average background luminance, and adapt-100, observers were adapted to a 100% contrast stimulus.

Adapt-100

At the beginning of each block, observers were stimulated with adaptation stimuli; for 70 s, two counter-phase flickering (7 Hz) Gabor patches (4° of visual angle in diameter and σ of 1.5°) were presented to the left and to the right of fixation (5° eccentricity). Before each test trial, the same adaptation stimulation was repeated for 4 s to maintain a constant adaptation state (top–up).

Adapt-0

At the beginning of each block, observers adapted for 20 s to mean background luminance. There was a 2-s delay between each trial. The test stimulus consisted of Gabor patches randomly tilted ±2.5° from vertical.

Attentional manipulation procedure

Attention was manipulated during the test trials. In every test trial, a 60-ms cue was displayed either above a Gabor patch or at fixation. After a 40-ms ISI, the two tilted test Gabor patches were simultaneously presented to the left and to the right of fixation for 30 ms given the fact that goal-directed saccades require approximately 250 ms (Leigh & Zee, 1991; Mayfrank, Mobashery, Kimmig, & Fischer, 1986); no eye movements could occur between cue onset and stimulus offset. After 200 ms, a 100-ms response cue was presented at fixation, indicating the stimulus to be discriminated (either the one to the left or the one to the right).

There were three attentional conditions, each making up 33% of the trials: (a) In the valid-cue condition, observers were to report the tilt of the Gabor patch preceded by the peripheral cue; that is, the cue and the response cue indicated the same location. (b) In the invalid-cue condition, the observer was to report the tilt of the Gabor patch not preceded by a peripheral cue; that is, the peripheral cue and the response cue indicated the opposite locations. (c) In the neutral-cue condition, neither of the two stimulus locations were indicated by the peripheral cue, and the observer was to discriminate the tilt of the Gabor patch indicated by the response cue. In both valid-cue and invalid-cue conditions, the peripheral cue preceded one of the two Gabor patches, but its presence did not provide information regarding either target orientation or location. The validity of the peripheral cue was determined on each trial by the response cue: For the valid-cue condition, the location of the peripheral cue and the response cue matched; for the invalid-cue condition, they mismatched.

Responses were made by pressing the "1" key to indicate a discrimination of tilted left ($-2.5°$) and pressing the "2" key to indicate a discrimination of tilted right ($+2.5°$). One of three distinct feedback tones sounded after the discrimination was made; one for a correct response, one for an incorrect response, and a third for responses that were too slow (response times of more than 800 ms after response-cue offset). This third time-dependent tone was used to maintain regularly spaced trials and maintain a constant level of adaptation. After initial learning, trials in which observers took more than 800 ms to respond were rare (about 1% of the total trials).

Results

Psychometric functions for orientation discrimination in each attentional and adaptation condition were obtained for each observer by fitting Weibull functions (Weibull, 1951) to the data via maximum likelihood estimation (Figure 3). Each observer yielded six psychometric functions: one for each attention condition (valid, red; neutral, black; invalid, green) and adaptation condition (adapt-0, top row on white background; adapt-100, bottom row on shaded background).

For each observer, we estimated contrast thresholds at a fixed performance level of 70% (vertical thin lines, one per function in Figures 3 and 4). We fit a Weibull function to each of the 10,000 bootstrapped samples of the data and then limited each distribution of parameter estimates to the interval (2.5%, 97.5%), to obtain the 95% confidence intervals (horizontal lines around the threshold value in Figures 3 and 4). Asymptotic performance on the task was estimated by using the asymptote parameter of the Weibull function (top-right corner of each graph with their 95% confidence intervals obtained by bootstrap method [Efron & Tibshirani, 1993] in Figures 3 and 4).[1]

The pattern of results is consistent across observers. In the adapt-0 condition (vertical thin lines in the top row of
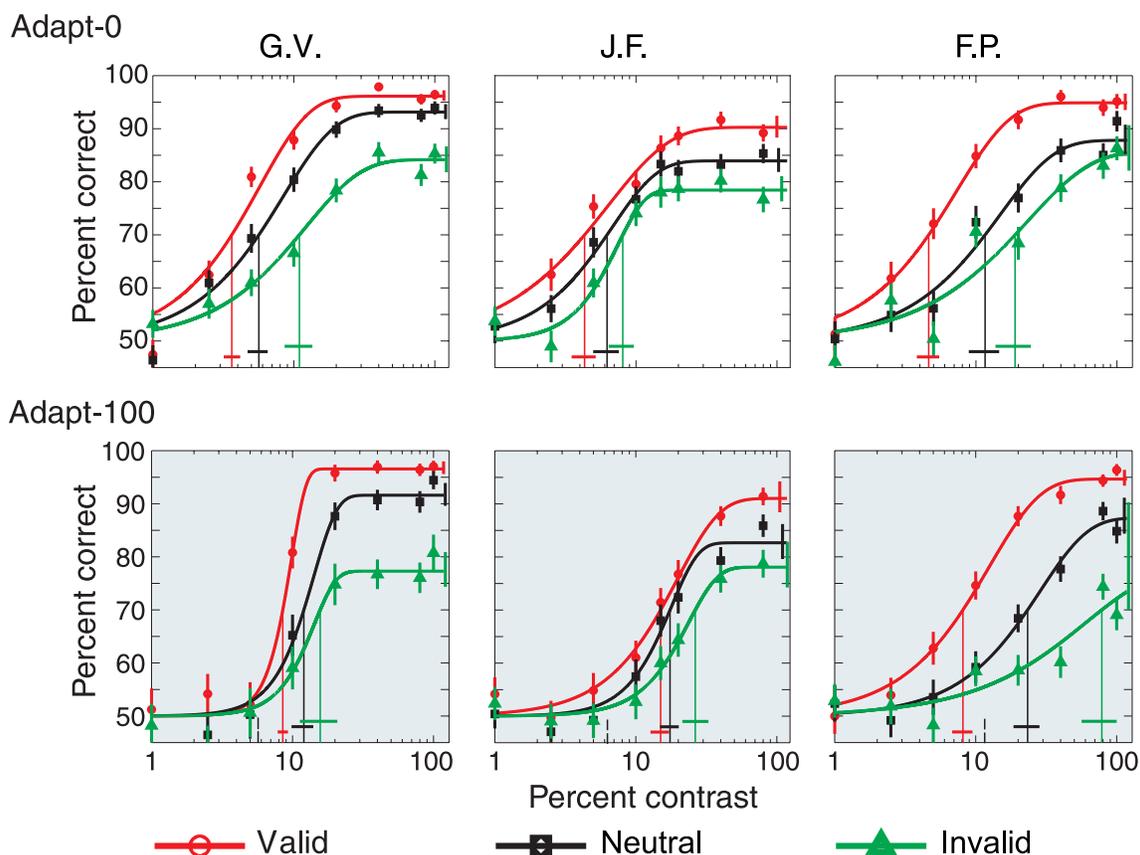

Figure 3. *Effects of attention*. Psychometric functions for orientation discrimination, estimated by maximum likelihood. Each column reports data from one observer (G.V., J.F., or F.P.). Top row (white background) reports the data from the adapt-0 condition; bottom row (shaded background) reports the data from the adapt-100 condition. Circles, squares, and triangles represent the data for valid-cue, neutral-cue, and invalid-cue conditions. The reported error bars on each data point are ± 1 *SD* of the mean of 10,000 samples obtained via the bootstrap method (Efron & Tibshirani, 1993). The thin vertical lines report the estimated threshold values at a fixed performance level of 70%. Error bars on thresholds and asymptote estimates are 95% confidence intervals obtained via the bootstrap method. The dashed lines on the abscissa of the adapt-100 condition (shaded) mark the threshold value in the adapt-0 neutral condition.
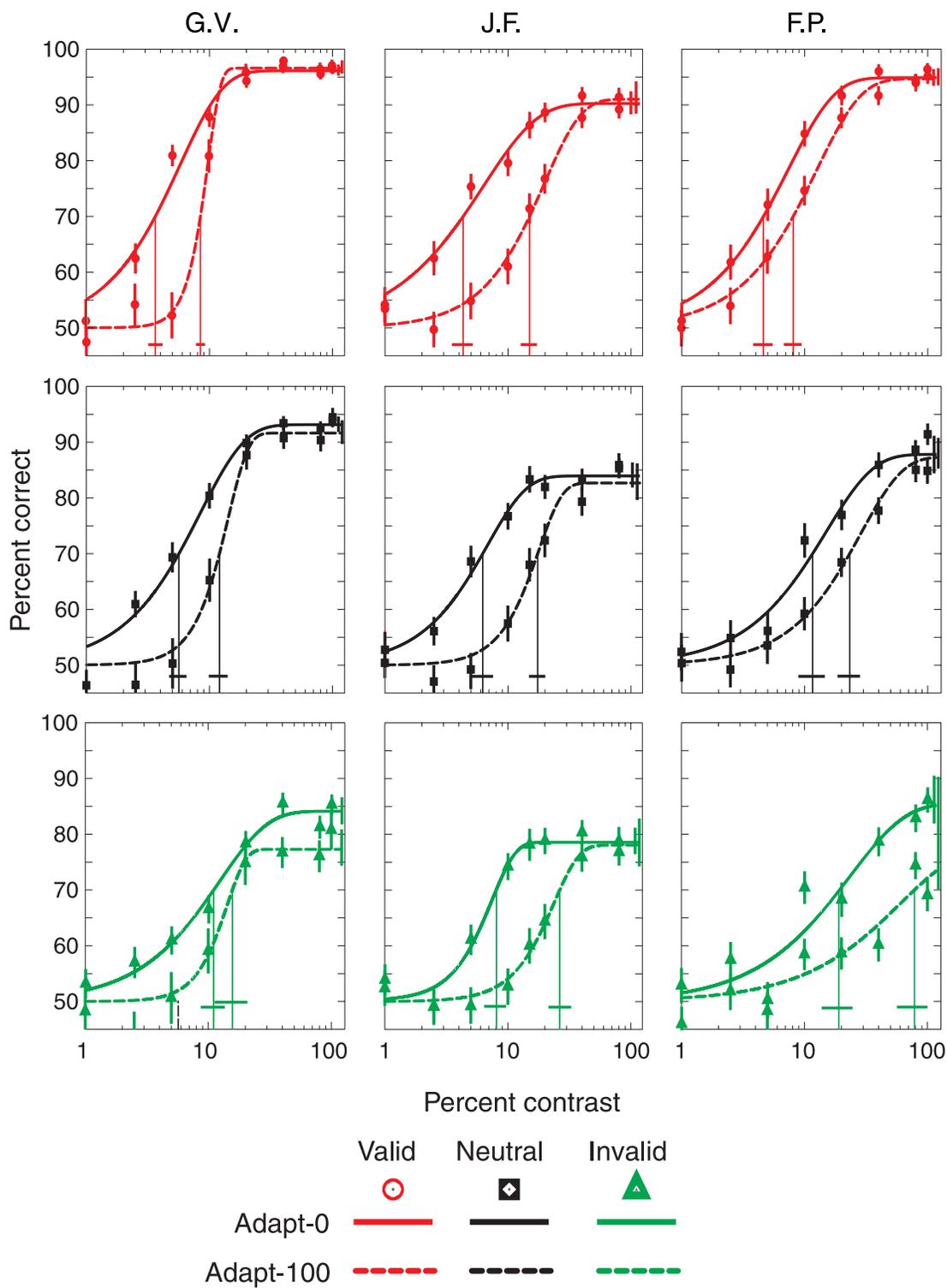
Figure 4. *Effect of contrast adaptation.* Each column reports data from one observer. Top row compares psychometric functions for orientation discrimination in the valid-cue condition (attended): adapt-0 (continuous) and adapt-100 (dashed). Middle row compares psychometric functions in the neutral-cue condition (distributed attention). Bottom row compares psychometric functions in the invalid-cue condition (unattended). Except for G.V.'s invalid-cue condition, the effect of contrast adaptation is to increase threshold without affecting asymptote.

Figure 3), contrast thresholds are lower in the valid-cue condition and higher in the invalid-cue condition as compared to the neutral-cue condition. The results are in agreement with Pestilli and Carrasco (2005), who obtained thresholds for these three attention conditions, and with Ling and Carrasco (2006a), who obtained psychometric functions for the neutral and valid conditions. In the adapt-100 condition (bottom row of Figure 3), contrast thresholds also increase from valid-cue to neutral-cue to invalid-cue conditions. The magnitude of the threshold shifts is comparable in the two adaptation conditions.

Figure 4 plots the psychometric functions from the same data set organized by cue condition to show the effect of contrast adaptation on the contrast thresholds and on the asymptote. Each column reports data from one observer. The top row shows psychometric functions for the valid-cue condition before (continuous line) and after (dashed line) adapting to 100% contrast. The middle row shows data for the neutral-cue condition, and the bottom row shows data for the invalid-cue condition. For all observers and conditions, adaptation increases thresholds but does not affect asymptote (except for G.V.'s invalid-cue condition). For each attentional condition, thresholds are lower in the adapt-0 than in the adapt-100 conditions. The results lend support to the hypothesis that adaptation acts via a contrast-gain mechanism.

Figure 5 summarizes the results of Figures 3 and 4 by plotting the average (across observers) of the asymptote (top panel) and threshold (bottom panel) values. Data from the adapt-0 condition are on the left panel with white background; data from the adapt-100 condition are on the right panel with the shaded background.

Attention affects the thresholds and asymptotes; adaptation only affects the thresholds. A within-subjects two-way analysis of variance (ANOVA; attentional condition: valid vs. neutral vs. invalid; adaptation condition: adapt-0 vs. adapt-100) on the log-transformed contrast thresholds confirms that both main effects of attention ($p < .005$) and adaptation ($p < .005$) are significant but that there is no interaction between these conditions ($p > .1$). As expected, attention and adaptation had a significant effect on threshold, reducing and increasing contrast threshold, respectively. Only attention affected the asymptote for the psychometric function, adaptation did not change the asymptote, and there was no interaction between attention and adaptation. A within-subjects two-way ANOVA on the asymptote values shows that the main effect of attention is significant ($p < .05$) but that neither the main effect of adaptation ($p > .1$) nor the interaction between attention and adaptation ($p > .1$) is significant.

Although comparing psychophysical performance with single-cell recording data is not a straightforward process and should be done with caution, it is important to try to relate results from the two levels of analysis. To establish a link between the psychometric function for orientation discrimination and the neural contrast response function, we need to ensure that the effects of attention and
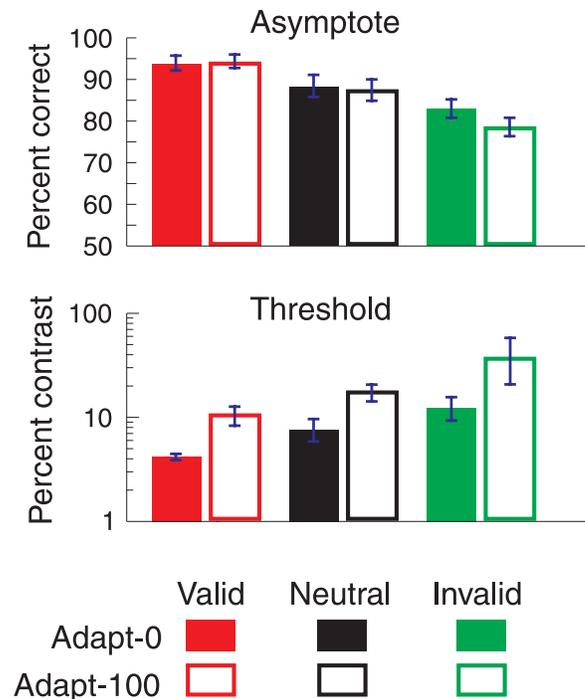

Figure 5. *Average parameter estimates.* Top graph represents the average of the asymptote parameters across the three observers. Bottom graph represents the average of the threshold parameters across the three observers. Data from the adapt-0 condition have filled bars; data from the adapt-100 condition have outlined bars. Error bars are ±1 *SEM.* *Effect of attention*: Asymptotes increase as a function of attentional allocation (valid > neutral > invalid) in both adaptation conditions by the same amount. Thresholds decrease (valid < neutral < invalid) in both adaptation conditions by the same amount. *Effect of adaptation*: Asymptotes in the adapt-0 condition (outlined bars) and the adapt-100 condition (filled bars) do not change; compare the same-color bars in the top graph. Thresholds increase between the adapt-0 condition (filled bars) and the adapt-100 condition (outlined bars); compare the same-color bars in the bottom graph.

adaptation on the contrast response function are not confounded by their effects on orientation discrimination. To that end, the parameters for our experiment are within ranges for which attention and adaptation have negligible effects on orientation tuning; for example, contrast adaptation does not change orientation discrimination within 10° from the adapter's orientation (Regan & Beverley, 1985), as is the case in our experiment. We note that the effect of attention in the orientation-discrimination task is similar with different orientation discriminations, ranging from ±2.5° to ±45° (Cameron et al., 2002; Carrasco et al., 2000; Ling & Carrasco, 2006a; Pestilli & Carrasco, 2005), which indicates that attention affects the contrast mechanisms independently of the orientation discrimination being performed. Moreover, whereas attention affects the contrast sensitivity of single neurons (Martinez-Trujillo &

Treue, 2002; Reynolds et al., 2000), it does not affect their orientation tuning (McAdams & Maunsell, 1999; Motter, 1993).

In sum, (a) adaptation decreases contrast sensitivity via a contrast-gain mechanism, and (b) transient attention affects sensitivity in a quantitatively similar way before and after adapting to high contrast. Attention increases contrast sensitivity at the attended location while decreasing it at the unattended location (for both threshold and asymptotic performance). This is consistent with attention acting via a mixture of contrast-gain and response-gain mechanisms.

Discussion

Both attention and adaptation influence contrast sensitivity. We find threshold and asymptote effects for the attention manipulation and only threshold effects for the adaptation manipulation. These findings are consistent with models of attention that posit a contrast gain (Martinez-Trujillo & Treue, 2002; Reynolds et al., 2000) and a multiplicative response gain (McAdams & Maunsell, 1999; Williford & Maunsell, 2006) and with models of adaptation that posit that the contrast response function shifts toward the adapter contrast (Bonds, 1991; Gardner et al., 2005; Ohzawa et al., 1982, 1985).

How do attention and adaptation interact? This study is the first to investigate whether and how the adaptation state modulates the effect of attention on contrast sensitivity. Specifically, it explores whether the extent of contrast sensitivity enhancement at the attended location and impairment at the unattended location differs before and after contrast adaptation. We obtained psychometric functions by measuring orientation-discrimination performance as a function of contrast (Nachmias, 1967). The adapt-0 condition showed that exogenous attention has an effect across the whole contrast range; it changed threshold and asymptotic performance. Thresholds at attended locations (i.e., valid cue) were lower than those obtained when attention was distributed across the two locations (i.e., in neutral cue), which were, in turn, lower than those obtained when attention was withdrawn from the target (i.e., invalid cue). These effects on threshold are consistent with those obtained through a similar orientation-discrimination paradigm and an adaptive staircase procedure (Pestilli & Carrasco, 2005). Consistent with a recent study (Ling & Carrasco, 2006a), exogenous attention also increased the asymptote of the psychometric function (valid-cue trials as compared to the neutral condition). Furthermore, the asymptotes of the psychometric functions were reduced in invalid-cue trials as compared to the neutral condition. An interesting finding was that transient attention changed sensitivity in a quantitatively similar way before and after adapting to high contrast. When transient attention was directed to a stimulus location, the sensitivity lost during adaptation was recovered; that is, attention can overcome adaptation to restore contrast sensitivity. This effect is consistent with the idea that exogenous attention enhances the salience of possibly important signals and, paradoxically, shows that attention seems to reduce the beneficial effect of contrast adaptation by shifting the adapted contrast psychometric function to lower contrasts.

Attention

Sustained attention affects the contrast response function of neurons. Single-cell recording studies support both a reduction in threshold of the neural contrast response function—contrast gain (Martinez-Trujillo & Treue, 2002; Reynolds et al., 2000)—and an effect of attention that increases with contrast—response gain (McAdams & Maunsell, 1999; Williford & Maunsell, 2006). Differences in the contrast-dependent mechanism mediating the effect of sustained and transient attention have been reported using a similar cueing paradigm to the one used here; the former is mediated via contrast gain, whereas the latter is mediated via both contrast gain and response gain (Ling & Carrasco, 2006a). The present results are consistent with transient attention acting via both contrast-gain and response-gain mechanisms: The enhancement in sensitivity and the increase in asymptotic performance at attended locations are accompanied by opposite impairments of sensitivity and reductions of performance at unattended locations, consistent with a reduction in both contrast gain and response gain.

Adaptation

Single-cell recording studies in the visual system of cats (Ohzawa et al., 1982, 1985; Sclar, Ohzawa, & Freeman, 1985) and macaques (Sclar, Lennie, & DePriest, 1989), as well as human neuroimaging studies (Gardner et al., 2005), have consistently shown that adaptation acts via a contrast-gain mechanism. Two predictions of such a contrast-gain model of adaptation are that contrast discrimination should be improved for contrasts around the adapter contrast and that there should be no effect of adaptation at high contrast levels. However, there is no consensus regarding altered contrast discrimination after adaptation (Abbonizio, Langley, & Clifford, 2002; Greenlee & Heitger, 1988; Maattanen & Koenderink, 1991; Ross, Speed, & Morgan, 1993). The present study supports the contrast-gain model of adaptation because the psychometric function shifted toward the adapter contrast, displacing its dynamic range toward higher contrast, and because there was no effect of adaptation at high contrast levels (Figure 4). A recent psychophysical study using an external noise paradigm has also supported such a model (Dao, Lu, & Dosher, 2006).

Interaction of attention and adaptation

We sought to evaluate the interaction of attention and contrast adaptation by pitting them against each other. Both attention and adaptation act on the contrast-processing neural mechanisms by modulating visual sensitivity in similar but opposite ways (Gardner et al., 2005; Martinez-Trujillo & Treue, 2002; Ohzawa et al., 1982, 1985; Reynolds et al., 2000; Sclar et al., 1985, 1989; Treue, 2004; Williford & Maunsell, 2006). The present study was motivated by the idea that these two different perceptual phenomena share the common goal of optimizing visual performance to match salient parts of visual scenes. The present findings have several implications.

Loss of beneficial effect of contrast adaptation: Not mere neural fatigue

One counterintuitive implication of the quick gain control mechanism of transient attention is that it beneficially increases visibility of salient stimuli, but at the same time, it alters the system's response that had been optimized by adaptation. Transient attention takes the adapted contrast response function away from its optimized state. The fact that the adaptation state can be quickly changed supports the idea that adaptation cannot be merely due to neuronal fatigue or saturation (Carandini & Ferster, 1997; Sanchez-Vives et al., 2000a, 2000b). This is evident in our results; the peripheral cue modifies the adapted signal response, resulting in higher sensitivity at attended locations than at unattended locations. The finding that attention can restore sensitivity indicates that response in the adapted state is not saturated.

Implications for mechanisms of attention and adaptation

A mixture model of contrast gain and response gain best characterized the way in which attention affected performance for both adaptation states. Were attention reflecting a fixed multiplicative factor on the contrast response function, the attentional effect would have been higher for the adapted condition, which is displaced toward higher contrasts (Figure 3). This similar effect of attention under different adaptation states suggests that the effect of contrast adaptation precedes transient attention; attention may act on a normalized response (i.e., divided by the maximum response). Attention seems to multiply the response to each contrast relative to the contrast response function's maximum response.

At the cellular level, the finding that the magnitude of the attentional effect does not depend on the adaptation state suggests that the attention effect is independent of the polarized/depolarized state of membrane involved in contrast adaptation. Were the effects of attention dependent on the membrane's polarization state, the magnitude of the attentional effect in the two adaptation conditions would have differed. This was not the case for our data.

Adaptation does not modulate attention. It is known that sustained attention affects the magnitude of contrast adaptation; it strengthens adaptation at the attended location and decreases it at the unattended location (Ling & Carrasco, 2006b). Based on these results, one could have hypothesized that the adaptation state would modify the attention effect. However, that was not the case. The magnitude of the attentional enhancement at attended locations and impairment at unattended locations was comparable in both adaptation conditions. This discrepancy can be due to a difference between the mechanisms by which transient and sustained attention act on contrast sensitivity—sustained attention acts via contrast gain only; transient attention acts via a mixture of contrast and response gain (Ling & Carrasco, 2006b)—or to the fact that adaptation and transient attention act via independent mechanisms, with attention being able to affect adaptation but not vice versa.

Conclusions

We investigated how the adaptation state modulates the magnitude of the attentional effects on contrast sensitivity. We considered attention and adaptation within a common framework of performance optimization. Although both attention and adaptation change the contrast response function, their effects do not interact: The effect of attention is independent of the adaptation state of the system. The fact that contrast adaptation does not modulate the effect of transient attention suggests that attention affects the normalized signal once the effect of contrast adaptation has taken place and implies that these two mechanisms act separately but concurrently to change contrast sensitivity. Adaptation is not merely neural fatigue: Sensitivity is promptly restored by attention.

Acknowledgments

Commercial relationships: none.
Corresponding author: Marisa Carrasco.
Email: marisa.carrasco@nyu.edu.
Address: 6 Washington Place Room 970, New York, NY 10003, USA.

Footnote

[1]The estimated variability for the asymptote parameter for observer F.P. in the invalid-cue condition for the adapt-100 condition is large because the strong adaptation effect in this observer did not allow the function to asymptote within the contrast range.

References

Abbonizio, G., Langley, K., & Clifford, C. W. (2002). Contrast adaptation may enhance contrast discrimination. *Spatial Vision, 16,* 45–58. [PubMed]

Alais, D., & Blake, R. (1999). Neural strength of visual attention gauged by motion adaptation. *Nature Neuroscience, 2,* 1015–1018. [PubMed] [Article]

Albrecht, D. G., & Hamilton, D. B. (1982). Striate cortex of monkey and cat: Contrast response function. *Journal of Neurophysiology, 48,* 217–237. [PubMed]

Anzai, A., Bearse, M. A., Freeman, R. D., & Cai, D. (1995). Contrast coding by cells in the cat's striate cortex: Monocular vs. binocular detection. *Visual Neuroscience, 12,* 77–93. [PubMed]

Avidan, G., Harel, M., Hendler, T., Ben-Bashat, D., Zohary, E., & Malach, R. (2002). Contrast sensitivity in human visual areas and its relationship to object recognition. *Journal of Neurophysiology, 87,* 3102–3116. [PubMed] [Article]

Bonds, A. B. (1991). Temporal dynamics of contrast gain in single cells of the cat striate cortex. *Visual Neuroscience, 6,* 239–255. [PubMed]

Boynton, G. M., Demb, J. B., Glover, G. H., & Heeger, D. J. (1999). Neuronal basis of contrast discrimination. *Vision Research, 39,* 257–269. [PubMed]

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10,* 433–436. [PubMed]

Cameron, E. L., Tai, J. C., & Carrasco, M. (2002). Covert attention affects the psychometric function of contrast sensitivity. *Vision Research, 42,* 949–967. [PubMed]

Carandini, M., & Ferster, D. (1997). A tonic hyperpolarization underlying contrast adaptation in cat visual cortex. *Science, 276,* 949–952. [PubMed]

Carrasco, M., Giordano, A. M., & McElree, B. (2006). Attention speeds processing across eccentricity: Feature and conjunction searches. *Vision Research, 46,* 2028–2040. [PubMed]

Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nature Neuroscience, 7,* 308–313. [PubMed]

Carrasco, M., & McElree, B. (2001). Covert attention accelerates the rate of visual information processing. *Proceedings of the National Academy of Sciences of the United States of America, 98,* 5363–5367. [PubMed] [Article]

Carrasco, M., Penpeci-Talgar, C., & Eckstein, M. (2000). Spatial covert attention increases contrast sensitivity across the CSF: Support for signal enhancement. *Vision Research, 40,* 1203–1215. [PubMed]

Carrasco, M., Williams, P. E., & Yeshurun, Y. (2002). Covert attention increases spatial resolution with or without masks: Support for signal enhancement. *Journal of Vision, 2*(6):4, 467–479, http://journalofvision.org/2/6/4/, doi:10.1167/2.6.4. [PubMed] [Article]

Chaudhuri, A. (1990). Modulation of the motion aftereffect by selective attention. *Nature, 344,* 60–62. [PubMed]

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience, 3,* 201–215. [PubMed]

Dao, D. Y., Lu, Z. L., & Dosher, B. A. (2006). Adaptation to sine-wave gratings selectively reduces the contrast gain of the adapted stimuli. *Journal of Vision, 6*(7):6, 739–759, http://journalofvision.org/6/7/6/, doi:10.1167/6.7.6. [PubMed] [Article]

Dean, A. F. (1981). The relationship between response amplitude and contrast for cat striate cortical-neurones. *The Journal of Physiology, 318,* 413–427. [PubMed] [Article]

Desimone, R. (1998). Visual attention mediated by biased competition in extrastriate visual cortex. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences, 353,* 1245–1255. [PubMed] [Article]

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual-attention. *Annual Review of Neuroscience, 18,* 193–222. [PubMed]

Efron, B., & Tibshirani, R. J. (1993). *An introduction to bootstrap.* New York: Chapman and Hall.

Gandhi, S. P., Heeger, D. J., & Boynton, G. M. (1999). Spatial attention affects brain activity in human primary visual cortex. *Proceedings of the National Academy of Sciences of the United States of America, 96,* 3314–3319. [PubMed] [Article]

Gardner, J. L., Sun, P., Waggoner, R. A., Ueno, K., Tanaka, K., & Cheng, K. (2005). Contrast adaptation and representation in human early visual cortex. *Neuron, 47,* 607–620. [PubMed] [Article]

Geng, J. J., Eger, E., Ruff, C. C., Kristjansson, A., Rotshtein, P., & Driver, J. (2006). On-line attentional selection from competing stimuli in opposite visual

fields: Effects on human visual cortex and control processes. *Journal of Neurophysiology, 96,* 2601–2612. [PubMed]

Greenlee, M. W., & Heitger, F. (1988). The functional role of contrast adaptation. *Vision Research, 28,* 791–797. [PubMed]

Huang, L., & Dobkins, K. R. (2005). Attentional effects on contrast discrimination in humans: Evidence for both contrast gain and response gain. *Vision Research, 45,* 1201–1212. [PubMed]

Huk, A. C., & Heeger, D. J. (2000). Task-related modulation of visual cortex. *Journal of Neurophysiology, 83,* 3525–3536. [PubMed] [Article]

Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience, 23,* 315–341. [PubMed]

Leigh, R. J., & Zee, D. S. (1991). *The neurology of eye movements.* Philadelphia, PA: F. A. Davis.

Lennie, P. (2003). The cost of cortical computation. *Current Biology, 13,* 493–497. [PubMed] [Article]

Ling, S., & Carrasco, M. (2006a). Sustained and transient covert attention enhance the signal via different contrast response functions. *Vision Research, 46,* 1210–1220. [PubMed] [Article]

Ling, S., & Carrasco, M. (2006b). When sustained attention impairs perception. *Nature Neuroscience, 9,* 1243–1245. [PubMed]

Lu, Z. L., & Dosher, B. A. (1998). External noise distinguishes attention mechanisms. *Vision Research, 38,* 1183–1198. [PubMed]

Maattanen, L. M., & Koenderink, J. J. (1991). Contrast adaptation and contrast gain control. *Experimental Brain Research, 87,* 205–212. [PubMed]

Martinez-Trujillo, J., & Treue, S. (2002). Attentional modulation strength in cortical area MT depends on stimulus contrast. *Neuron, 35,* 365–370. [PubMed] [Article]

Mayfrank, L., Mobashery, M., Kimmig, H., & Fischer, B. (1986). The role of fixation and visual attention in the occurrence of express saccades in man. *European Archives of Psychiatry and Neurological Sciences, 235,* 269–275. [PubMed]

McAdams, C. J. & Maunsell, J. H. (1999). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. *Journal of Neuroscience, 19,* 431–441. [PubMed] [Article]

McAdams, C. J., & Reid, R. C. (2005). Attention modulates the responses of simple cells in monkey primary visual cortex. *Journal of Neuroscience, 25,* 11023–11033. [PubMed] [Article]

McGraw, P. V., Whitaker, D., Skillen, J., & Chung, S. T. (2002). Motion adaptation distorts perceived visual position. *Current Biology, 12,* 2042–2047. [PubMed] [Article]

Montaser-Kouhsari, L., & Rajimehr, R. (2004). Attentional modulation of adaptation to illusory lines. *Journal of Vision, 4*(6):3, 434–444, http://journalofvision.org/4/6/3/, doi:10.1167/4.6.3. [PubMed] [Article]

Morrone, M. C., Denti, V., & Spinelli, D. (2004). Different attentional resources modulate the gain mechanisms for color and luminance contrast. *Vision Research, 44,* 1389–1401. [PubMed]

Motter, B. C. (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *Journal of Neurophysiology, 70,* 909–919. [PubMed]

Nachmias, J. (1967). Effect of exposure duration on visual contrast sensitivity with square-wave gratings. *Journal of the Optical Society of America, 57,* 421.

Nachmias, J., & Sansbury, R. V. (1974). Letter: Grating contrast: Discrimination may be better than detection. *Vision Research, 14,* 1039–1042. [PubMed]

Ohzawa, I., Sclar, G., & Freeman, R. D. (1982). Contrast gain control in the cat visual cortex. *Nature, 298,* 266–268. [PubMed]

Ohzawa, I., Sclar, G., & Freeman, R. D. (1985). Contrast gain control in the cat's visual system. *Journal of Neurophysiology, 54,* 651–667. [PubMed]

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10,* 437–442. [PubMed]

Pelli, D. G., & Zhang, L. (1991). Accurate control of contrast on microcomputer displays. *Vision Research, 31,* 1337–1350. [PubMed]

Pestilli, F., & Carrasco, M. (2005). Attention enhances contrast sensitivity at cued and impairs it at uncued locations. *Vision Research, 45,* 1867–1875. [PubMed]

Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology, 32,* 3–25. [PubMed]

Regan, D., & Beverley, K. I. (1985). Postadaptation orientation discrimination. *Journal of the Optical Society of America A, Optics and image science, 2,* 147–155. [PubMed]

Reynolds, J. H., Chelazzi, L., & Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *Journal of Neuroscience, 19,* 1736–1753. [PubMed] [Article]

Reynolds, J. H., Pasternak, T., & Desimone, R. (2000). Attention increases sensitivity of V4 neurons. *Neuron, 26,* 703–714. [PubMed] [Article]

Rezec, A., Krekelberg, B., & Dobkins, K. R. (2004). Attention enhances adaptability: Evidence from motion adaptation experiments. *Vision Research, 44,* 3035–3044. [PubMed]

Ross, J., Speed, H. D., & Morgan, M. J. (1993). The effects of adaptation and masking on incremental thresholds for contrast. *Vision Research, 33,* 2051–2056. [PubMed]

Sanchez-Vives, M. V., Nowak, L. G., & McCormick, D. A. (2000a). Cellular mechanisms of long-lasting adaptation in visual cortical neurons in vitro. *Journal of Neuroscience, 20,* 4286–4299. [PubMed] [Article]

Sanchez-Vives, M. V., Nowak, L. G., & McCormick, D. A. (2000b). Membrane mechanisms underlying contrast adaptation in cat area 17 in vivo. *Journal of Neuroscience, 20,* 4267–4285. [PubMed] [Article]

Sclar, G., Lennie, P., & DePriest, D. D. (1989). Contrast adaptation in striate cortex of macaque. *Vision Research, 29,* 747–755. [PubMed]

Sclar, G., Ohzawa, I., & Freeman, R. D. (1985). Contrast gain control in the kitten's visual system. *Journal of Neurophysiology, 54,* 668–675. [PubMed]

Tolhurst, D. J., Movshon, J. A., & Thompson, I. D. (1981). The dependence of response amplitude and variance of cat visual cortical neurones on stimulus contrast. *Experimental Brain Research, 41,* 414–419. [PubMed]

Treue, S. (2004). Perceptual enhancement of contrast by attention. *Trends in Cognitive Sciences, 8,* 435–437. [PubMed]

Vanduffel, W., Tootell, R. B., & Orban, G. A. (2000). Attention-dependent suppression of metabolic activity in the early stages of the macaque visual system. *Cerebral Cortex, 10,* 109–126. [PubMed] [Article]

Watanabe, T., Sasaki, Y., Miyauchi, S., Putz, B., Fujimaki, N., Nielsen, M., et al. (1998). Attention-regulated activity in human primary visual cortex. *Journal of Neurophysiology, 79,* 2218–2221. [PubMed] [Article]

Weibull, W. (1951). A statistical distribution function of wide applicability. *Journal of Applied Mechanics, 18,* 292–297.

Williford, T., & Maunsell, J. H. R. (2006). Effects of spatial attention on contrast response functions in macaque area V4. *Journal of Neurophysiology, 96,* 40–54. [PubMed]

Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs visual performance by enhancing spatial resolution. *Nature, 396,* 72–75. [PubMed]

Yeshurun, Y., & Carrasco, M. (1999). Spatial attention improves performance in spatial resolution tasks. *Vision Research, 39,* 293–306. [PubMed]

Yeshurun, Y., & Carrasco, M. (2000). The locus of attentional effects in texture segmentation. *Nature Neuroscience, 3,* 622–627. [PubMed] [Article]