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Attentional effects on contrast discrimination in humans: evidence for both contrast gain and response gain

Liqiang Huang, Karen R. Dobkins *

Department of Psychology, 0109, University of California, San Diego, La Jolla, CA 92093-0109, USA

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Abstract

In order to understand how attention affects visual processing, we investigated the degree to which attention effects can be accounted for by increases in the *contrast gain* of the contrast response function, CRF (represented by an increase in effective contrast) vs. increases in the *response gain* (represented by an overall amplification of response). To this end, we used a dual-task paradigm to compare psychophysical "threshold vs. pedestal contrast" (TvC) curves obtained under conditions of full- vs. poor-attention. The *attention effect*, defined as the ratio of thresholds for poor- vs. full-attention conditions, was roughly four-fold at a pedestal contrast of 0% (i.e., at detection threshold) and there was a significant decrease in attention effect with increasing pedestal contrast, from approximately ten-fold at the lowest non-zero pedestal contrast tested (0.25%) to three-fold at the highest pedestal contrast tested (64%). These findings are consistent with the existence of both contrast gain effects of attention (needed to account for the substantial attention effect at detection threshold and the decrease in attention effect with increasing pedestal contrast) as well as response gain effects of attention (needed to account for the fact that attention was beneficial across all pedestal contrasts—rather than harmful at some contrasts, as a pure contrast gain model would predict). The results of a model fitting Naka–Rushton CRF equations to the TvC data also support this conclusion. Here we found a two-fold increase in contrast gain and a five-fold increase in response gain in the CRF for the full-attention, as compared to the poor-attention, condition. Because pure contrast gain effects, on the order of two-fold, have been observed at early stages of visual processing (for example in areas V4 and MT), our psychophysical results suggest a hybrid model of attention; contrast gain control at an early stage of visual processing, followed by response gain control at a later stage.

Keywords: Attention; Thresholds; Contrast discrimination; Contrast gain; Response gain

1. Introduction

Previous psychophysical studies have demonstrated that, under many conditions, increasing the amount of attention allocated to a visual task can enhance performance on that task (e.g., Lee, Koch, & Braun, 1997; Sperling & Melchner, 1978). Given that increasing the *contrast* of a visual stimulus can also enhance task performance, the possibility has been raised that attention may benefit visual processing by increasing the "effective" contrast of a stimulus (see Reynolds, Pasternak, & Desimone, 2000). The effect of contrast on visual processing is typified by the "contrast response function" (CRF); neurons in the visual system exhibit a systematic non-linear increase in firing rate with increasing stimulus contrast (e.g., Albrecht & Hamilton, 1982). As exemplified in Fig. 1, CRFs exhibit an expansive non-linearity at low contrast, a relatively linear portion at intermediate contrasts, and a compressive (saturating) non-linearity

* Corresponding author. Tel.: +1 858 534 5434; fax: +1 858 534 7190.
E-mail address: kdobkins@ucsd.edu (K.R. Dobkins).

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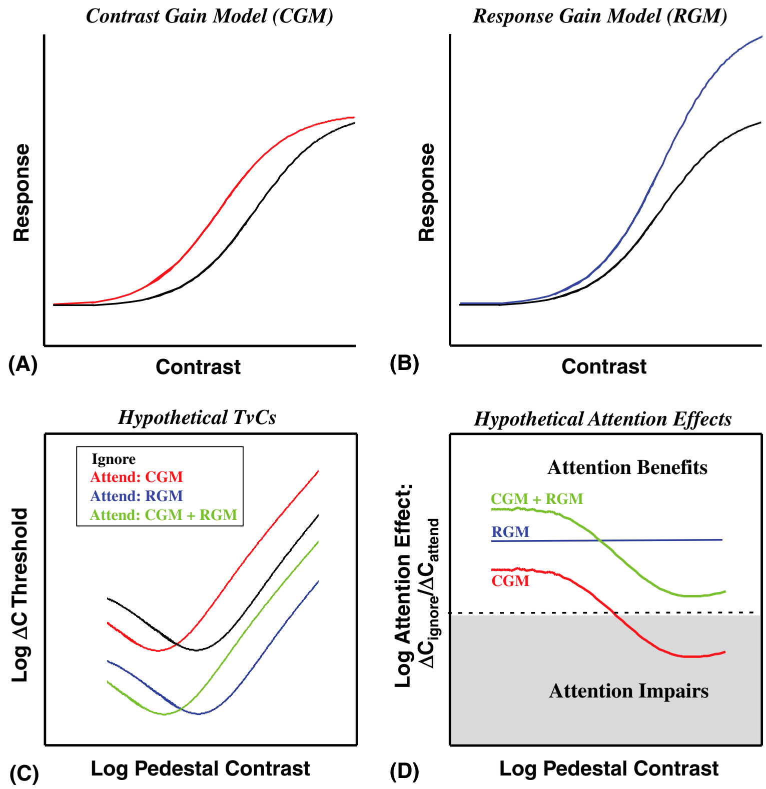

Fig. 1. Different models of attention. (A) Contrast gain model (CGM). The contrast response function (CRF) for an attended stimulus (red line) is shifted leftward from that of an ignored stimulus (black line), which reflects a decrease in the semi-saturation constant ($C50$). (B) Response gain model (RGM). The CRF for an attended stimulus (blue line) is shifted upward by a constant multiplicative factor from that of an ignored stimulus (black line), which reflects an increase in the response maximum (R_{max}). (C) Hypothetical TvC curves ($\log \Delta C$ threshold vs. log pedestal contrast) for an ignored stimulus (black line) and an attended stimulus, for three different models of attention: "attend: CGM" (red line), "attend: RGM" (blue line), and a hybrid model, "attend: CGM + RGM" (green line). (D) Predicted attention effects ($\Delta C_{Ignore}/\Delta C_{Attend}$) for the three models of attention: CMG (red line), RGM (blue line), CGM + RGM (green line). The dashed line represents an attention effect of 1.0 (i.e., no attention effect). Above this line attention benefits, below this line attention impairs, performance.

at high contrasts. If attention acts to increase the effective contrast of a stimulus, this would translate to a leftward shift in the CRF. This model of attention, referred to as the "contrast gain model" (CGM), supposes that attention and contrast interact, being interchangeable with one another (see Fig. 1A). An alternative model of attention, the "response gain model" (RGM), supposes that attention and contrast act independently on neural responses. In this scenario, attention is expected to shift the CRF upward by a constant multiplicative factor across all stimulus contrasts (see Fig. 1B).

Recently, Reynolds et al. (2000) investigated the interaction of attention and contrast in monkey area V4 neurons by comparing population CRFs (as well as Receiver Operator Characteristics, ROC, curves) obtained while the monkey performed a form task on a stimulus placed inside a neuron's receptive field (producing "attend" CRFs) vs. outside (producing "ignore" CRFs). The results of this study were consistent with the contrast gain model of attention, i.e., attention produced mainly a leftward shift of the CRF, reducing the $C50$ value by about two-fold (and see Martinez-Trujillo & Treue, 2002 for similar results obtained in visual motion area MT).

Both the contrast and response gain models make specific (and distinct) predictions regarding the effects of attention on visual psychophysical performance as a function of stimulus contrast. In a recent psychophysical study, Carrasco, Ling, and Read (2004) manipulated attention with a spatial pre-cue and reported that attention increases the perceived contrast of stimuli more so at lower than at higher contrasts, a result that is consistent with the existence of contrast gain effects of attention. In the current study, we investigated the effects of attention on *contrast discrimination thresholds* as a function of pedestal contrast, i.e., "threshold vs. contrast" (TvC) curves. This paradigm is particularly fitting since TvC curves can be used to model the shape of the underlying CRF, often referred to as the "transducer function" (e.g., Legge & Foley, 1980; Ross & Speed, 1991). This model assumes that the threshold change in contrast (ΔC) needed to make two contrasts discriminable from one another is that which produces a fixed change in the neural response (ΔR). Due to the non-linear shape of the CRF, discrimination thresholds are expected to vary with pedestal contrast, specifically, decreasing over the expansive non-linear portion of the CRF (producing the "dipper" function) and then increasing over the compressive (saturating) non-linear portion of the CRF.

To illustrate the effects different models of attention should have on the TvC curve, in Fig. 1C we present hypothetical TvC curves ($\log \Delta C$ threshold vs. log pedestal contrast) that might be generated for a stimulus that is ignored (black line) vs. those that would be generated assuming different models of attentional effects on the CRF. (Note that all TvC curves are of the prototypical shape based on the non-linearity of the CRF). The *contrast gain model* of attention predicts that the TvC curve for an attended stimulus (Fig. 1C, red line) should be shifted leftward from the ignore TvC curve. However, if the CRF actually saturates completely, the attend and ignore TvC curves are predicted to come back together at a sufficiently high contrast (not shown in figure). By comparison, the *response gain model* predicts that the TvC curve for an attended stimulus (Fig. 1C, blue line) should be shifted downward from the ignore TvC curve by a constant amount, although this amount will tend to be smaller at a pedestal contrast of 0%, i.e., at detection threshold (not shown in figure). A third possibility is that attention affects *both* the contrast gain and the response gain of the CRF. In this case, the TvC curve for the attended stimulus is predicted to be shifted both down and to the left of the ignore TvC curve (Fig. 1C, green line).

In Fig. 1D, the predicted "attention effect", defined as the threshold ratio between the ignored and attended conditions (i.e., $\Delta C_{\text{Ignore}}/\Delta C_{\text{Attend}}$), is plotted as a function of pedestal contrast for the different models of attention. For the *contrast gain model* (red line) the attention effect is above 1.0 (dashed line) at low pedestal contrasts, and then decreases below 1.0 once the pedestal contrast reaches some critical value. That is, the contrast gain model predicts that attention should benefit performance at low contrasts but actually impair it at high contrasts. For the *response gain model* (blue line) the attention effect is constant, and always greater than 1.0, as pedestal contrast is increased (although at 0% pedestal contrast, the attention effect should be somewhat reduced, *see above*). For the *contrast gain + response gain model* (green line), the attention effect decreases with increasing pedestal contrast, but given that the response gain component is sufficiently large, will remain greater than 1.0 at all pedestal contrasts.

In the current study, we tested these different models of attention by obtaining TvC curves under conditions of poor- vs. full-attention, and computing attention effects ($\Delta C_{\text{Poor}}/\Delta C_{\text{Full}}$) as a function of pedestal contrast. The results demonstrate a significant decrease in attention effect with increasing pedestal contrast, with the attention effect remaining greater than 1.0 across all pedestal contrasts. These findings are consistent with a hybrid model of attention; a contrast gain control at an early stage of visual processing (as has been shown in areas V4 and MT), followed by a response gain control at a later stage of processing.

2. Methods

2.1. Subjects

A total of eight subjects participated as either volunteers or as paid research subjects. All had normal or corrected-to-normal vision, and were naïve to the purpose of the experiment. Data were obtained from two different subject groups, both of which included four subjects.

2.2. Apparatus

Stimuli were generated by a Cambridge Research Systems (CRS) VSG 2/3 video board, residing in a Pentium-based PC. Stimuli were presented on a 50.8 cm color monitor (NANAO, 1600 × 1200 pixels, 100 Hz refresh rate).

2.3. Stimuli

Stimuli consisted of horizontally-oriented sinusoidal gratings (size: 7° × 7°, spatial frequency: 2 cycles/degree, mean luminance of gratings and background: 45 cd/m^2). In order to obtain contrast discrimination thresholds, on each trial two gratings were simultaneously presented (for 50 ms), centered 7° to the left and right side of a central fixation cross. One grating was presented at a baseline contrast (referred to as the "pedestal"), while the other grating (referred to as the "target") was greater than this amount. The left vs. right location of pedestal and target was randomized across trials. With the exception of one subject (the first one tested in subject group 1), the two gratings were each surrounded by a white square frame (inner edge = 7°, outer edge = 7.3°, 90 cd/m^2), presented simultaneously with the gratings (for 50 ms). The purpose of this square frame was two-fold. First, it provided spatial certainty as to the location of the gratings. Second, we reasoned that higher contrast gratings might grab subjects' attention more than lower contrast gratings. Because the square frame itself was quite salient, its presence was expected to *equalize*, across the different test contrasts, the amount of attention diverted to the location of the gratings. [1]

[1] This was particularly important to consider for the condition in which attention to the peripheral gratings was meant to be drastically reduced (because the subject was simultaneously conducting a central task, see "Paradigm", below). If the amount of attention grabbed by the peripheral gratings under these poor-attention conditions varied with contrast, this could contribute to differing magnitudes of attentional effects as a function of stimulus contrast.

For subject group 1, nine different pedestal contrasts were employed: 0.25%, 0.5%, 1%, 2%, 4%, 8%, 16%, 32%, 64%. For subject group 2, these same nine pedestal contrasts were employed plus one more, 0%. The thresholds obtained for this 0% pedestal contrast condition allowed us to look at the effects of attention at *detection threshold*. For subject group 1, the different pedestal contrasts were presented in either a *blocked* fashion (i.e., pedestal contrast remained constant across trials) or an *intermixed* fashion (i.e., pedestal contrast was randomized across trials). The purpose of these two conditions was to compare thresholds for the case where there was certainty (blocked design) vs. uncertainty (intermixed design) regarding the predominant contrast of the stimuli presented. Because we found negligible differences between the two conditions, for subject group 2, we employed only the intermixed pedestal contrast design.

Paradigm. All subjects were tested in a dark room and viewed the video display binocularly from a chin rest situated 57 cm away. They were instructed to maintain fixation on a small fixation cross, and provide perceptual reports via key-presses on a keyboard. For subject group 1, we presented a rapid serial visual presentation (RSVP) at the fixation cross in order to modulate the amount of attention paid to the peripheral contrast discrimination task. The RSVP stimulus consisted of nine 2° by 2° letters ($\approx$20 cd/m^2, which were 56% dimmer in luminance than the background), each lasting 50 ms with 0 ms blank in between, for a total duration of 450 ms. The color of the letters alternated between red and orange (with the initial color randomized across trials). A "target letter", which was the letter "T" (and was either red or orange), was always presented as the sixth, seventh, eighth or ninth letter, thus occurring 250, 300, 350 or 400 ms, respectively, after the onset of the RSVP. The two peripheral gratings were presented 250 ms after the onset of the RSVP, lasting 50 ms (and thus were synchronized with the presentation of the sixth letter in the RSVP).

In one condition, which we refer to as "*full-attention*", subjects performed a *single task*; on each trial they performed the contrast discrimination task, i.e., reporting which grating ("left-side" vs. "right-side", 2-AFC) was of higher contrast using two digits on their right hand, ignoring the (irrelevant) RSVP at the center of gaze. In the other condition, which we refer to as "*poor-attention*", subjects performed a *dual task* on each trial. Here, they were required to first, report whether the "T" in the RSVP was red or orange (using two digits on their left hand), and second, which of the two peripheral gratings was of higher contrast (using their right hand). Because the central RSVP task was extremely demanding, subjects paid substantially less attention to the peripheral gratings in this condition. Also, because the target letter "T" never appeared earlier than the grating stimuli (*see above*), this precluded the possibility that subjects could complete the RSVP task before the contrast discrimination task, thereby freeing up their attention for the latter. For both attention conditions, feedback (in the form of computer beeps) was provided at the end of each trial (for the poor-attention condition, feedback was first provided for the RSVP, and then for the grating task). The next trial began 200 ms after feedback was provided.

For subject group 2, we employed two different central tasks in the poor-attention condition (tested in different sessions). First, we employed the RSVP central task (like subject group 1). Second, we employed a "pop-out" task, which required reporting the location of a target amongst distractors. This pop-out task was employed because it was expected to be less attentionally-demanding than the RSVP task, thus allowing for the comparison of attention effects under conditions that usurped more attention (RSVP task) vs. less attention (pop-out task) from the contrast discrimination task. The pop-out stimulus consisted of nine dots (each 0.7° diameter) in a 3×3 array (center to center distance between dots = 1.75°) centered on the fixation cross. One dot (the target) was orange while the remaining eight were red (same red and orange colors used in the RSVP task), and the orange dot was situated in either the left or right column of the array (it never appeared in the central column). The pop-out central stimulus was presented simultaneously with the two peripheral gratings, 250 ms after the start of a trial, and lasted for 50 ms. (Note that the timing for the presentation of the peripheral gratings in the pop-out central task condition was identical to that employed in the RSVP central task condition, *see above*.) In the *full-attention* condition, subjects ignored this central pop-out stimulus, performing only the contrast discrimination on the peripheral gratings. In the *poor-attention* condition, subjects had to first report the location of the single orange dot (left or right), followed by their report on the peripheral gratings.

2.4. Obtaining contrast discrimination thresholds

For all conditions, thresholds were obtained using a staircase procedure, applied separately to each pedestal contrast condition. Two successive correct responses led to a 0.05 log unit decrease in contrast of the target grating, while one incorrect response led to a 0.05 log unit increase. (At the start of the staircase, where contrast differences were very large, we used a 0.2 log unit decrease until the first incorrect response was made.) Fifty total trials were presented per pedestal condition. Trials from the first five reversals were excluded, and the difference between the pedestal contrast and the mean target contrast of the remaining trials in the staircase was taken as the "contrast discrimination threshold", or ΔC (which reflects ≈71% correct performance).

For each subject, we obtained (and averaged) three discrimination thresholds for each pedestal contrast under four different conditions: For subject group 1, tested with only the RSVP central task, these four conditions were two *attention* conditions (full vs. poor) and two *certainty* conditions (blocked vs. intermixed pedestal contrasts). For subject group 2, tested with only the intermixed pedestal contrasts, these four conditions were two *attention* conditions (full vs. poor) and two *central task* conditions (RSVP vs. pop-out.) In total, 6000 trials were obtained from each subject, which required roughly nine hours of testing (6 sessions of 1.5 h each). Blocks of full- vs. poor-attention conditions were alternated within a testing session. Blocks of the other condition types (subject group 1: blocked vs. intermixed pedestal contrasts; subject group 2: RSVP vs. pop-out central task) were alternated across testing sessions. All analyses were performed on log contrast discrimination thresholds, and all group mean data are presented as log means.

3. Results

3.1. Group mean TvC data: subject group 1

Group mean contrast discrimination thresholds (ΔC) and standard errors are plotted as a function of pedestal contrast for subject group 1 in Fig. 2A, separately for full-attention (open circles) and poor-attention (filled circles) conditions. Data are shown for the condition where pedestal contrast was intermixed (left panel) vs. blocked (right panel). For subject group 1, the central attention-demanding task in the poor-attention condition was the RSVP task (see *Methods*). Group mean performance and standard errors on this RSVP task as a function of pedestal contrast are presented as insets. As expected, in all conditions, contrast discrimination thresholds increased with increasing pedestal contrast, yielding slope values (determined in a linear regression analysis) in log–log coordinates of 0.59 (full-attention, intermixed contrast), 0.40 (poor-attention, intermixed contrast), 0.65 (full-attention, blocked contrast) and 0.47 (poor-attention, blocked contrast). These values for the full-attention conditions are close to those reported in previous studies in which subjects paid attention to the stimulus (Greenlee & Heitger, 1988; Legge, 1981; Legge & Foley, 1980; Ross, Speed, & Morgan, 1993). For the poor-attention condition in our study, the slope values were substantially lower. Also, at all pedestal contrasts, attention lowered contrast discrimination thresholds, on average, by 5.5-fold.

By comparing data obtained under conditions of blocked vs. intermixed pedestal contrasts, we can examine whether thresholds are affected by *contrast* certainty, which can be considered one type of *featural* certainty. If subjects are able to selectively monitor different contrast levels, thresholds are expected to be lower for conditions of contrast certainty (i.e., in the blocked design). The results of a correlated t-test (data collapsed across pedestal contrast) supported this possibility for the poor-attention condition (although thresholds differed only slightly, by 1.14-fold, $p < 0.02$, 1-tailed t-test), but not the full-attention condition ($p = 0.72$). (Although some sort of contrast-specific adaptation in the blocked design condition could have, in theory, overridden the benefits of certainty, this is fairly unlikely given the brief presentation, i.e., 50 ms, of our stimuli.) In sum, these results reveal only small effects of contrast certainty on contrast discrimination thresholds, which is consistent with previous psychophysical findings (Davis, Kramer, & Graham, 1983; but see Pashler, Dobkins, & Huang, 2004), and also with the lack of evidence for the existence of neurons in the visual system tuned for contrast (but see Peng & Van Essen, in press for a report of luminance-tuned neurons in V1 and V2).

3.2. Group mean TvC data: subject group 2

Group mean TvC curves are plotted for subject group 2 in Fig. 2B, separately for full-attention (open circles) and poor-attention (filled circles) conditions. Because we found only small effects of contrast certainty for subject group 1, for subject group 2, all conditions were presented with pedestal contrast intermixed. Two things differed between subject groups 2 and 1. First, subject group 2 was tested at an additional pedestal contrast, 0%, which allowed us to investigate attention effects at *detection threshold*. Second, in the poor-attention condition, subject group 2 was tested with both an RSVP central task (like group 1) as well as a pop-out central task, the latter thought to be less attentionally-demanding. Group mean TvC data obtained using these two different central stimulus/task conditions are shown separately in the left panel (RSVP task) and right panel (pop-out task), and the group mean performance and standard errors on the central tasks are presented as insets. (Note, of course, that data for the full-attention condition, where there was no task performed on the central stimulus, should be nearly identical in the left and right panels, which they are.) As expected, thresholds increased with increasing pedestal contrast, yielding slope values (determined in a linear regression analysis) in log–log coordinates of 0.63 (full-attention, central task = RSVP), 0.38 (poor-attention, central task = RSVP), 0.63 (full-attention, central task = pop-out), and 0.60 (poor-attention, central task = pop-out).

There are several things to note about the results from subject group 2. First, they provide a replication of data obtained from subject group 1, showing that

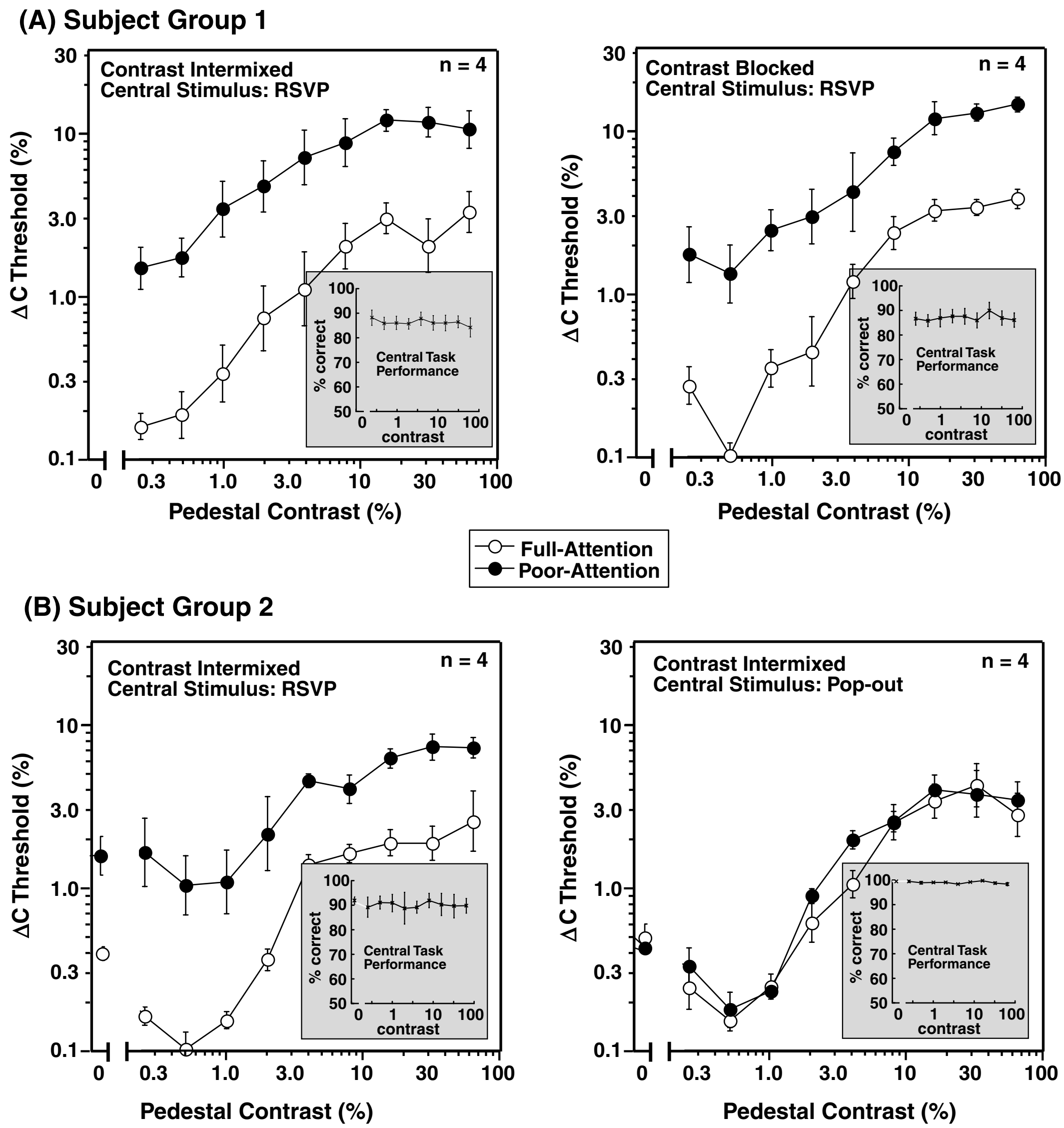

Fig. 2. Group mean contrast discrimination thresholds plotted as a function of pedestal contrast (TvC curves), separately for full-attention (open circles) and poor-attention (filled circles) conditions. Insets show group mean percent correct performance on the central task in the poor-attention condition. Error bars denote standard errors of the means. (A) Subject group 1 ($n = 4$) was tested with an RSVP central task in the poor-attention condition, and the pedestal contrast was either intermixed (left panel) or blocked (right panel). (B) Subject group 2 ($n = 4$) was tested with the intermixed pedestal contrast design, and the central task in the poor-attention condition was either an RSVP task (left panel) or a pop-out task (right panel).

attention substantially lowers discrimination thresholds across pedestal contrasts when the central task in the poor-attention condition is an RSVP task (compare 2A and 2B, left panels). This is true even at a pedestal contrast of 0%, demonstrating that attention decreases absolute detection threshold. Second, the effects of attention are much larger when the central task in the poor-attention condition is an RSVP task than when it is a pop-out task. In fact, there is no attention effect observed when the central task is a pop-out task (a finding that is addressed further in the *Discussion*). Finally, when the central task in the poor-attention condition is an RSVP task, the dipper effect appears less pronounced for poor- vs. full-attention. This effect has previously been observed in studies that manipulate attention with a dual-task paradigm, as in the current study (Lee, Itti, Koch, & Braun, 1999) or with a spatial cueing paradigm (Solomon, Lavie, & Morgan, 1997), and in these previous studies, the effect has been attributed to spatial uncertainty affecting responses at the decision level. However, in the current study, spatial uncertainty is unlikely to account for the effect since we controlled for this factor by having the peripheral grating stimuli always appear in the same location, and by adding a surrounding white frame to help define the stimulus location (see *Methods*). Rather, we believe that the different shapes of the TvC curves for full- vs. poor-attention reflect differences at a relatively low level of visual processing (described further below).

3.3. Group mean attention effects: subject groups 1 and 2

To more directly evaluate the effects of attention as a function of pedestal contrast, for each subject, we computed the ratio of contrast discrimination thresholds in the poor- vs. full-attention conditions ($\Delta C_{Poor}/\Delta C_{Full}$), separately for each pedestal contrast. Group mean attention effects and standard errors are plotted as a function of pedestal contrast in Fig. 3. With the data plotted in this format, we can address whether the effects of attention (1) are beneficial and roughly *constant* across pedestal contrast (in line with the "response gain model" of attention, Fig. 1D, blue line), (2) decrease with increasing pedestal contrast and actually *impair* performance at some level of contrast (in line with the "contrast gain model" of attention, Fig. 1D, red line), or (3) decrease with increasing contrast but remain beneficial at all contrast levels (in line with the "contrast gain+response gain model" of attention, Fig. 1D, green line).

For subject group 1 (Fig. 3A), there was a significant decline in the effect of attention with increasing pedestal contrast, in both the intermixed contrast (filled squares) and blocked contrast (open squares) conditions (linear regression, $p < 0.0005$), although the effect remained above 1.0 at all pedestal contrasts. Specifically, the effect went from roughly ten-fold at the lowest contrast (0.25%) to three-fold at the highest contrast (64%). Similarly, for subject group 2 tested with the central RSVP task (Fig. 3B), there was a significant decline in attention effect (linear regression, $p < 0.0005$). The magnitude of this decrease was nearly identical to that observed for subject group 1, although note that the attention effect at detection threshold (pedestal contrast = 0%) was substantially smaller (four-fold) than that observed just above detection threshold (i.e., ten-fold at 0.25% pedestal contrast). (Data are not shown for the pop-out central task condition since there was no effect of attention under this condition.) These effects of attention, observed in two different subject groups, are consistent with the existence of both *contrast gain* and *response gain* control mechanisms for attention (compare to Fig. 1D, green line).

It is important to point out that the decline in attention effect as a function of pedestal contrast is unlikely to be explained by an (inadvertent) contrast-related increase in the amount of attention placed on the peripheral grating task in the poor-attention condition, which could occur if higher contrast gratings grab attention away from the central RSVP task more than do lower contrast gratings. We infer that this was not the case since 1-factor ANOVAs showed that performance on the RSVP task did not vary across different pedestal contrasts, for subject group 1 (intermixed contrast: $p = 0.63$, blocked contrast, $p = 0.83$) or subject group 2 (intermixed contrast, $p = 0.86$). This performance invariance can be seen in the data insets of Fig. 2.

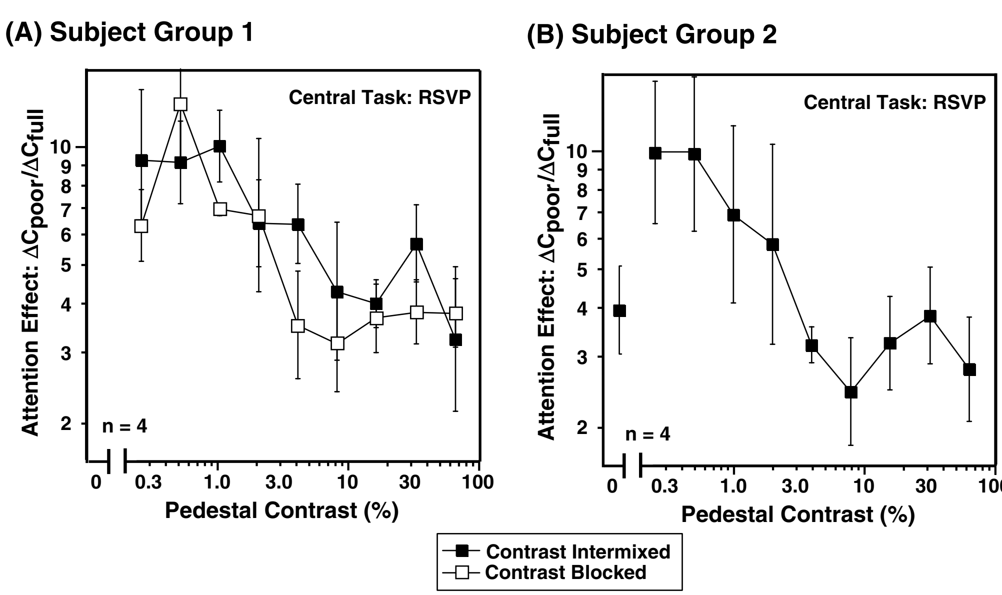

Fig. 3. Group mean effects of attention plotted as a function of pedestal contrast. Error bars denote standard errors of the means. (A) Subject group 1. Data are shown separately when pedestal contrast is intermixed (filled squares) vs. blocked (open squares). The central task in the poor-attention condition was an RSVP task. (B) Subject group 2. These subjects were tested only with intermixed pedestal contrasts. Data are shown for the case where the central task in the poor-attention condition was an RSVP task. For both subject groups 1 and 2, attention effects decrease significantly with increasing pedestal contrast (at least for contrasts greater than detection threshold) and remain above 1.0 at all contrasts. This result is consistent with the existence of combined effects of contrast gain and response gain (compare to Fig. 1D, green line).

It is also important to point out that the attention effect being greater than 1.0 across all pedestal contrasts (rather than decreasing to less than 1.0, as a pure contrast gain model would predict) cannot be explained by us not having tested at high enough pedestal contrasts (the current study tested up to 64% contrast), since extrapolation of the TvC curves to 100% contrast was not found to produce a crossover of the full- vs. poor-attention curves.

3.4. Probability of seeing curves

The effects of attention on contrast discrimination thresholds we observed in our dual-task paradigm employing a central RSVP task are much larger than others have reported employing other types of central tasks in a dual-task paradigm (Lee et al., 1999; Morrone, Denti, & Spinelli, 2004 and see *Discussion*). We entertained the possibility that the large attention effect we observed could be due to our RSVP task in the poor-attention condition being so difficult that, on some trials, subjects simply decided to disengage entirely from the peripheral contrast discrimination task. If this were the case, probability of seeing curves for the peripheral task in the poor-attention condition should asymptote at a value lower than, and should possess slopes that are shallower than, those obtained in the full-attention condition (i.e., when subjects perform only the peripheral task).

To address this possibility, we needed to average percent correct data across the different pedestal contrasts, because for any one pedestal contrast, there were not enough trials at each contrast difference to provide a reliable function (since we used a staircase design). To this end, for each pedestal contrast, we first normalized the contrast difference on a given trial with respect to the mean contrast difference presented in the staircase before averaging data across the different pedestal contrast conditions. Data were also averaged across the different subjects. This analysis was performed separately for the full- and poor-attention conditions. (Note that this was performed only for the RSVP central task condition, since there was no effect of attention for the pop-out central task condition.)

Normalized and averaged probability of seeing curves are presented in Fig. 4, for subject group 1 (Fig. 4A) and subject group 2 (Fig. 4B), with the data points fit with Weibull functions. As can be seen in these plots, the curves for full-attention (open circles) are very similar to those for poor-attention (filled circles), although the slopes are somewhat shallower in the poor-attention condition (subject group 1: full-attention = 1.0, poor-attention = 0.67; subject group 2: full-attention = 1.0, poor-attention = 0.80). The overall similarities between probability of seeing curves for full- vs. poor-attention conditions suggests that the significantly higher contrast discrimination thresholds in the poor-attention condition are unlikely to reflect subjects disengaging from the peripheral contrast discrimination task in the poor-attention condition.

In sum, the data from subject groups 1 and 2 demonstrate that attention effects decrease significantly with increasing pedestal contrast (at least for contrasts greater than detection threshold) and remain above 1.0 at all

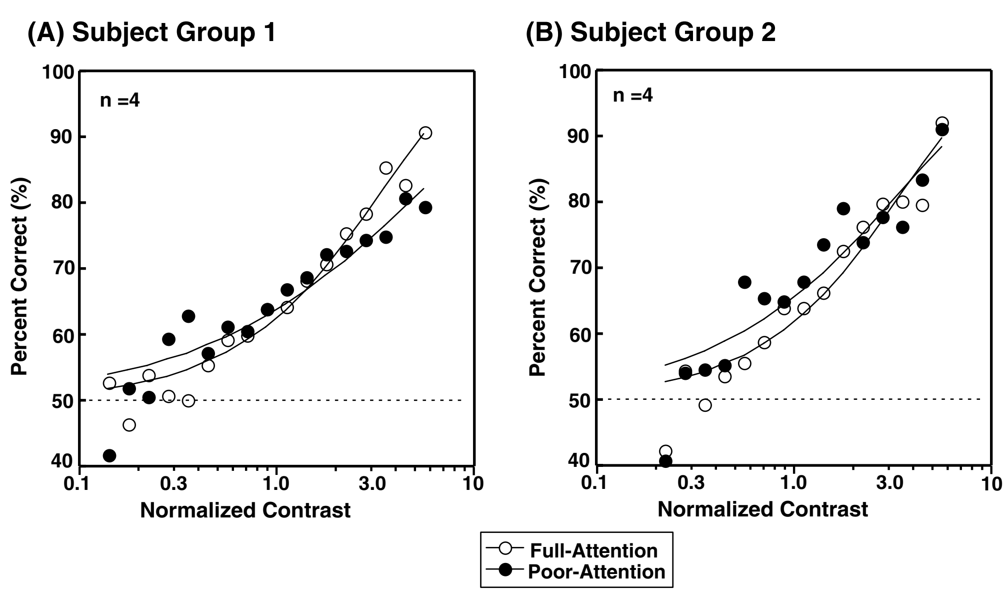

Fig. 4. Normalized and averaged probability of seeing data for full-attention (open circles) and poor-attention (filled circles) conditions, fitted with Weibull functions. (A) Subject group 1. Data are averaged across both the intermixed and blocked pedestal contrast conditions. The central task in the poor-attention condition was an RSVP task. (B) Subject group 2. These subjects were tested only with intermixed pedestal contrasts. Data are shown for the case where the central task in the poor-attention condition was an RSVP task (see text for details).

contrasts. This result is consistent with the existence of both *contrast gain* and *response gain* control mechanisms for attention. In order to quantify the contrast and response gain components underlying our results, we modeled the underlying contrast response functions (CRFs) in the full- vs. poor-attention conditions, as described in the next section.

3.5. Modeling underlying contrast response functions (CRFs)

The TvC curves for full- and poor-attention were fitted using the following Naka–Rushton equation for the CRF, described in Ross and Speed (1991):

$$R = R^{*}_{max}(C^\wedge(n+m)/(C^\wedge n + C50^\wedge n)) \quad (1)$$

where R is the neural response, R_{max} is the maximum response, C is stimulus contrast, $C50$ is the semi-saturation constant, n is the steepness of the function, and m is the steepness of the saturating portion of the function. A difference in the value of the $C50$ parameter between the full- and poor-attention CRFs can be taken as an indicator of *contrast gain*. A difference in the value of the R_{max} parameter can be taken an indicator of *response gain*.

For this analysis, we averaged data across subject groups 1 and 2 (8 total subjects) for the condition the two had in common (i.e., intermixed pedestal contrasts, central stimulus/task = RSVP, see Fig. 2A and B, left panels). This averaging was performed in order to reduce overall noise in the data. (Note that, because thresholds of subject group 1 were overall higher than those of subject group 2, on average by 0.19 log units, subject group 1 data were normalized by 0.19 log units before averaging with subject group 2.) Group mean TvC data from eight subjects are shown in Fig. 5A, separately for full-attention (open circles) and poor-attention (filled circles) conditions.

The fits were achieved using a simplex method to search for the optimal fit, i.e., that producing the smallest mean square error (MSE). The fits were attempted using several different starting parameter values in order to avoid local minima. Because we wished to focus on changes in $C50$ (reflecting contrast gain) and R_{max} (reflecting response gain), we forced the two other parameters (n and m) to be the same for full- and poor-attention CRFs (i.e., although the n and m parameters were both allowed to vary in the optimization method). The possibility that our results could instead be explained by differences in n and m between the full- and poor-attention conditions is addressed in the *Discussion*.

The model fits to group mean TvC data are shown in Fig. 5A (smooth lines). The MSE for these fits was low (0.019 log units), with the model capturing the data quite well except at the very highest pedestal contrasts (specifically, in the poor-attention condition). The model CRFs are shown in Fig. 5B. The n and m values (which were the same for the full- and poor-attention CRFs) were 1.26 and 0.46, respectively. The $C50$ values for the full- and poor-attention CRFs were 0.29 and 0.57. This two-fold decrease in $C50$ in the full- vs. poor-attention condition reflects a two-fold increase in contrast gain due to attention. The R_{max} values for the full- and poor-attention CRFs were 53 and 10, respectively, reflecting a roughly five-fold increase in response gain due to attention.

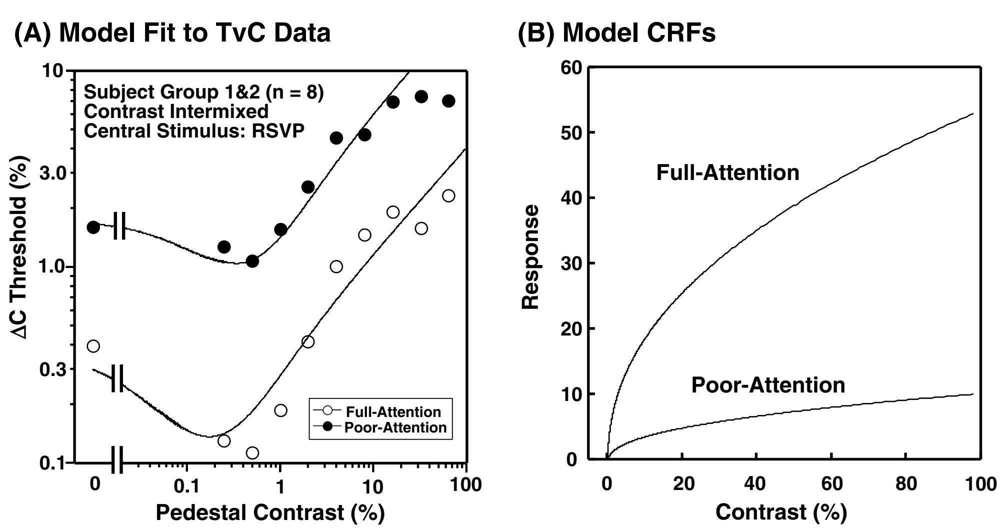

Fig. 5. Model results. (A) Group mean TvC curves from subject groups 1 and 2 (n = 8) for the full-attention (open circles) and poor-attention (filled circle) conditions fitted with the Naka–Rushton CRF equations (smooth lines). These data are for the case where the central task in the poor-attention condition was an RSVP task, and the pedestal contrasts were intermixed (Fig. 2A and B, left panels). (B) Model CRFs reveal a two-fold decrease in $C50$ (which reflects a two-fold increase in contrast gain) and a five-fold increase in R_{max} (which reflects a five-fold increase in response gain) in the full-attention, as compared to the poor-attention, condition (see text for actual parameter values).

4. Discussion

The results of these studies demonstrate that attention decreases contrast detection and discrimination thresholds (when the central task in the poor-attention condition is an RSVP task), and that the degree of this effect decreases significantly with increasing pedestal contrast. These findings are consistent with the existence of both *contrast gain* and *response gain* control mechanisms for attention. In the remainder of this *Discussion*, we first compare our results to those of previous studies investigating the effects of attention on contrast detection and discrimination thresholds, and address potential reasons for discrepancies across studies. Second, we discuss the possibility that our results might be accounted for by attention acting on aspects of contrast coding other than contrast and response gain. Third, we address possible neural substrates underlying our results.

Does attention affect contrast detection thresholds? Several previous studies, using a variety of different paradigms, have investigated whether attention alters *contrast detection thresholds*. For studies using a spatial cueing paradigm as a way of manipulating attention, the majority report that contrast detection thresholds for a cued stimulus are lower than those for an uncued stimulus (Carrasco, Penpeci-Talgar, & Eckstein, 2000; Davis et al., 1983; Foley & Schwarz, 1998; Lee et al., 1999; Lu & Dosher, 1998; but cf. Solomon et al., 1997). However, the results of these spatial cueing paradigms need to be interpreted with caution. Rather than providing evidence for attention modulating responses at an early stage of visual processing, these results are more likely accounted for by spatial uncertainty affecting responses at a late *decision* stage (see Davis et al., 1983 for discussion, but Carrasco et al., 2000 for an alternative view). Studies using the dual-task paradigm, which varies the amount of attention devoted to processing a stimulus rather than altering spatial certainty for that stimulus, are better equipped to address whether attention affects contrast detection threshold. Unfortunately, results from such studies are inconsistent. While the current study and at least one other study (Lee et al., 1999) report significant effects of attention on detection thresholds, others report no effect (Lee et al., 1997; Morrone, Denti, & Spinelli, 2002; Morrone et al., 2004 and see Di Russo, Spinelli, & Morrone, 2001 for similar results obtained with visually evoked potentials).

One obvious potential reason for different results across studies might be that studies finding no attention effect use a central task that is not attentionally-demanding enough to show an effect. However, what makes a central task more or less attentionally-demanding is not necessarily straight forward. Recently, Morrone et al. (2004) demonstrated that the difficulty of a central task, measured with percent correct, may not correlate with how attentionally-demanding that task is, measured by how much the central task affects peripheral thresholds (see Huang & Pashler, in press for similar conclusions). We propose that the attentional demands of the central task are likely tied to how *persistently* that task holds attention. Specifically, it is probable that an RSVP task keeps a tighter rein on attentional resources than does a static pop-out task. (In addition, if the pop-out stimulus is presented for a relatively long period of time, subjects could even have time to switch their attention efficiently between the central and peripheral tasks.) This could explain the significant effects of attention at detection threshold seen in the current study using the RSVP central task yet the lack of attention effects seen in the current and previous studies (Lee et al., 1997; Morrone et al., 2002, 2004) using a pop-out central task. There are also other reasons why central tasks may vary in the degree to which they affect peripheral thresholds, which is related to whether the central and peripheral tasks are mediated by the same or different featural mechanisms (e.g., color vs. luminance, as suggested by Morrone et al., 2002, 2004). We return to a discussion of this below, when addressing the effects of attention on the TvC curve.

How does attention affect TvC curves? In addition to addressing how attention affects detection thresholds, the question of how attention affects contrast discrimination thresholds above detection threshold has also been previously addressed. Here, we restrict our discussion to only those studies that have used the dual-task paradigm to measure TvC curves under conditions of both full- and poor-attention. (Note that, because these studies tested at a pedestal contrast of 0%, they are necessarily a subset of the studies described above that investigated attention effects at contrast detection threshold). In line with the current study, Lee et al. (1999) showed significant attention effects at contrast threshold, which decreased as pedestal contrast was increased (and attention effects always remained above 1.0). Such results are consistent with the existence of both contrast gain effects of attention (as demonstrated in early visual areas, like V4 and MT, Martinez-Trujillo & Treue, 2002; Reynolds et al., 2000) and response gain effects of attention. Unlike the current study, however, the Lee et al. study was not designed to specifically distinguish between contrast gain vs. response gain effects of attention, and therefore, these investigators only reported a gain effect in general. [2]

Contrary to the results of the current study, Morrone and colleagues (Morrone et al., 2002, 2004 and see

[2] In the Lee et al. (1999) paper, they refer to their effects as being due to "contrast gain", however, this term was used liberally (since the issue of contrast vs. response gain was yet to be distinguished in the literature). In fact, the effect they modeled was a "response gain" effect.

Di Russo et al., 2001 for similar results obtained with visually evoked potentials) found roughly constant effects of attention at pedestal contrasts above 0% and (as mentioned above) no effect of attention at detection threshold. These results are consistent with pure response gain effects of attention, with no need to consider additional effects on contrast gain. How might the discrepancy between our study and theirs be explained? One possible explanation for the difference is that Morrone et al. did not test contrasts as high as we did (they went up to 10%, or sometimes 30%, while we went up to 64%), and thus they might have missed the existence of decreasing attention effects at higher contrasts. This, of course, would still not explain the discrepancy between our study and theirs at a pedestal contrast of 0%.

A second possibility refers back to the idea that different central tasks may be more or less attentionally-demanding. What if it were the case that both response gain and contrast gain effects of attention require that the central task divert a certain amount of attention away from the peripheral task, but that this criterion amount is simply greater for contrast gain effects? According to this hypothesis, studies showing only response gain effects may have employed a central task that was not attentionally-demanding enough to produce contrast gain effects. And, by extension of this argument, the strongest contrast gain effects would be produced when a subject ignores the peripheral stimulus altogether, although, of course, these effects could not be measured psychophysically (a subject cannot respond to a completely ignored stimulus). In fact, the contrast gain effects seen in early visual areas (V4 and MT) are observed under conditions where the monkey completely ignores (i.e., does not respond to) the stimulus. To determine whether this very strong diversion of attention away from a stimulus is necessary for producing contrast gain effects, one would need to compare the degree of neural contrast gain under conditions where the monkey completely ignores a stimulus vs. is allowed to pay some attention to it.

There is another potential discrepancy between our study and the previous studies of Morrone et al. (2002, 2004). In their studies, they used two types of central tasks in the poor-attention condition (luminance or color pop-out, i.e., is an oddball present or absent?) and two types of peripheral tasks (luminance or color contrast discrimination). They found that only when the central and peripheral tasks were of the same domain (both luminance or both color) were there any attention effects (and that these attention effects only occurred above detection threshold). These results were interpreted as evidence for separate attentional resources devoted to color vs. luminance tasks. In our study, the two central tasks both involved color discrimination (and the peripheral task was always luminance contrast discrimination). In our RSVP task, subjects were required to report whether a T presented in a stream of letters was red or orange. In our pop-out task, subjects were required to report the location of an orange dot presented amongst red dots (in one static frame). The results of our pop-out condition mirrored those of Morrone et al., i.e., both laboratories found no effect of a central color pop-out task on luminance contrast discrimination thresholds (see Fig. 2B, right panel). However, we found significant effects of attention on luminance contrast discrimination thresholds when using a central RSVP task that required color discrimination. Although, at first glance, this finding appears contradictory to the notion of separate attentional resources for color and luminance, our RSVP findings can be reconciled with the results of Morrone et al. if we assume that the most important part of our RSVP task was finding a luminance-defined form (the letter "T") rather than reporting its (relatively high contrast) color.

Other potential factors underlying the decrease in attention effect with increasing pedestal contrast. Our finding of a decrease in attention effect with increasing pedestal contrast is consistent with the existence of a contrast gain effect (in addition to a response gain effect) of attention. This conclusion is also directly supported by our model, where we fit parameters to the underlying CRF for the full- and poor-attention TvC curves (see Fig. 5). Here, we found that when we force the parameters m and n to be the same for the poor- and full-attention conditions, there is a two-fold decrease in $C50$ (which reflects a two-fold increase in contrast gain) and a five-fold increase in R_{max} (which reflects a five-fold increase in response gain) in the full-attention, as compared to the poor-attention, CRF. However, this result should be viewed with some caution. In another analysis, we found that the model fit was almost as good if we forced the $C50$ to be the same for the two attention conditions than if we allowed the $C50$ to differ (as the current model did). In other words, there is not enough power in our data to demonstrate that the difference in $C50$ between the poor- and full-attention CRF is statistically significant.

For this reason, we must entertain the possibility that the decrease in attention effect with increasing pedestal contrast reflects other changes in the CRF, specifically, either the m or n parameters. To address this, we also conducted our model fits allowing all parameters to differ between full- vs. poor-attention conditions. Here, we found that the value for m (the steepness for the saturating portion of the CRF) was 1.5-fold larger for the poor-attention condition (the n value was nearly identical for the two attention conditions). Like the case for $C50$ described above, however, the model for forcing m to be the same, vs. allowing it to differ, between attention conditions produces statistically indistinguishable fits.

In sum, our model fits are not strong enough to resolve which change ($C50$ vs. m) best accounts for our results, although changes in *C*50 are consistent with neurophysiological data (see below). Nonetheless, the fact that we observed a significant decrease in attention effect with increasing pedestal contrast (that was replicated three times, see Fig. 3) allows us to say with certainty that attention does not simply amplify the responses of the CRF by a constant multiplicative factor (consistent with a pure response gain), but rather, deforms it in some way.

Potential neural substrates. Given that our results reflect attentional effects on the *C*50 and R_{max} of the CRF, we address potential neural substrates for these effects. Early visual areas like V4 and MT are likely to mediate the contrast gain effect, since neurons in these areas have been shown to undergo changes in contrast gain under manipulations of attention (e.g., Martinez-Trujillo & Treue, 2002; Reynolds et al., 2000). In fact, the magnitude of the decrease in *C*50 in our model due to attention (two-fold) nicely matches that observed in V4 neurons. The origin of the response gain effect is far less certain, however. One possibility is that it is a result of the heavier memory and motor load in the poor-attention task (which required subjects to remember and input two, rather than a single, responses). However, we think this possibility unlikely since we (and others) found no attention effect at all when the central task in the poor-attention condition was a pop-out task (despite the fact that this pop-out task carried the same motor, and presumably the same memory, load as the RSVP task). Instead, we suggest that the response gain reflects additional stages of processing within other visual on non-visual areas, presumably past the level of V4 and MT. In sum, we propose that the effect of attention on visual processing (as revealed through contrast discrimination thresholds) may be mediated by a hybrid mechanism; contrast gain control at an early stage of visual processing, followed by response gain control at a later stage.

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References

Albrecht, D. G., & Hamilton, D. B. (1982). Striate cortex of monkey and cat: contrast response function. *Journal of Neurophysiology, 48*(1), 217–237.

Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *National Neuroscience, 7*(3), 308–313.

Carrasco, M., Penpeci-Talgar, C., & Eckstein, M. (2000). Spatial covert attention increases contrast sensitivity across the CSF: support for signal enhancement. *Vision Research, 40*, 1203–1216.

Davis, E. T., Kramer, P., & Graham, N. (1983). Uncertainty about spatial frequency, spatial position, or contrast of visual patterns. *Perception and Psychophysics, 33*(1), 20–28.

Di Russo, F., Spinelli, D., & Morrone, M. C. (2001). Automatic gain control contrast mechanisms are modulated by attention in humans: evidence from visual evoked potentials. *Vision Research, 41*(19), 2435–2447.

Foley, J. M., & Schwarz, W. (1998). Spatial attention: effect of position uncertainty and number of distractor patterns on the threshold-versus-contrast function for contrast discrimination. *Journal of the Optical Society of America A, 15*(5), 1036–1047.

Greenlee, M. W., & Heitger, F. (1988). The functional role of contrast adaptation. *Vision Research, 28*(7), 791–797.

Huang, L., & Pashler, H. (in press). Attention capacity and task difficulty in visual search. *Cognition.*

Lee, D. K., Itti, L., Koch, C., & Braun, J. (1999). Attention activates winner-take-all competition among visual filters. *National Neuroscience, 2*(4), 375–381.

Lee, D. K., Koch, C., & Braun, J. (1997). Spatial vision thresholds in the near absence of attention. *Vision Research, 37*(17), 2409–2418.

Legge, G. E. (1981). A power law for contrast discrimination. *Vision Research, 21*(4), 457–467.

Legge, G. E., & Foley, J. M. (1980). Contrast masking in human vision. *Journal of the Optical Society of America, 70*(12), 1458–1471.

Lu, Z.-L., & Dosher, B. A. (1998). External noise distinguishes attention mechanisms. *Vision Research, 38*(9), 1183–1198.

Martinez-Trujillo, J., & Treue, S. (2002). Attentional modulation strength in cortical area MT depends on stimulus contrast. *Neuron, 35*(2), 365–370.

Morrone, M. C., Denti, V., & Spinelli, D. (2002). Color and luminance contrasts attract independent attention. *Current Biology, 12*(13), 1134–1137.

Morrone, M. C., Denti, V., & Spinelli, D. (2004). Different attentional resources modulate the gain mechanisms for color and luminance contrast. *Vision Research, 44*(12), 1389–1401.

Pashler, H., Dobkins, K., & Huang, L. (2004). Is contrast just another feature for visual selective attention? *Vision Research, 44*(12), 1403–1410.

Peng, X., & Van Essen, D. C. (in press). Peaked encoding of relative luminance in macaque areas V1 and V2. *Journal of Neurophysiology*, http://jn.physiology.org/cgi/reprint/00793.2004v1.

Reynolds, J. H., Pasternak, T., & Desimone, R. (2000). Attention increases sensitivity of V4 neurons [see comments]. *Neuron, 26*(3), 703–714.

Ross, J., & Speed, H. D. (1991). Contrast adaptation and contrast masking in human vision. *Proceedings of Royal Society of London B: Biological Science, 246*(1315), 61–69.

Ross, J., Speed, H. D., & Morgan, M. J. (1993). The effects of adaptation and masking on incremental thresholds for contrast. *Vision Research, 33*(15), 2051–2056.

Solomon, J. A., Lavie, N., & Morgan, M. J. (1997). Contrast discrimination function: Spatial cuing effects. *Journal of the Optical Society of America, 14*(9), 2443–2448.

Sperling, G., & Melchner, M. J. (1978). The attention operating characteristic: examples from visual search. *Science, 202*(4365), 315–318.