

Attention enhances contrast appearance via increased input baseline of neural responses

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Covert spatial attention increases the perceived contrast of stimuli at attended locations, presumably via enhancement of visual neural responses. However, the relation between perceived contrast and the underlying neural responses has not been characterized. In this study, we systematically varied stimulus contrast, using a two-alternative, forced-choice comparison task to probe the effect of attention on appearance across the contrast range. We modeled performance in the task as a function of underlying neural contrast-response functions. Fitting this model to the observed data revealed that an increased input baseline in the neural responses accounted for the enhancement of apparent contrast with spatial attention.

Introduction

Covert spatial attention allows the visual system to focus limited processing resources on different locations in the visual field without making eye movements. The influence of spatial attention on the accuracy of perceptual judgments, and the relation between these behavioral results and the underlying neural responses, has been systematically investigated (for reviews, see Anton-Erxleben & Carrasco, 2013; Carrasco, 2011). Performance enhancements at attended locations are observed at the expense of poorer performance at

unattended locations. This holds true in perceptual tasks designed to assess a variety of metrics, including contrast sensitivity (e.g., Cameron, Tai, & Carrasco, 2002; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Doshier & Lu, 1998; Herrmann, Montaser-Kouhsari, Carrasco, & Heeger, 2010; Lu & Doshier, 1999; Pestilli & Carrasco, 2005), spatial resolution (e.g., Montagna, Pestilli, & Carrasco, 2009; Yeshurun & Carrasco, 1998, 1999), and speed of processing (e.g., Carrasco, Giordano, & McElree, 2006; Giordano, McElree, & Carrasco, 2009). There are also notable cases in which attention hinders performance, for example, in texture-segmentation tasks with exogenous attention cues, when enhanced spatial resolution is detrimental to the task (e.g., Carrasco, Loula, & Ho, 2006; Yeshurun & Carrasco, 1998).

Covert attention also changes the perceptual appearance of visual stimuli. Attention enhances the perception of low-level visual features including contrast (e.g., Carrasco, Ling, & Read, 2004; Liu, Abrams, & Carrasco, 2009; Störmer, McDonald, & Hillyard, 2009), spatial frequency (Abrams, Barbot, & Carrasco, 2010; Gobell & Carrasco, 2005), brightness (Tse, 2005), speed (Anton-Erxleben, Herrmann, & Carrasco, 2013; Fuller, Park, & Carrasco, 2009; Turatto, Vescovi, & Valsecchi, 2007), flicker rate (Montagna & Carrasco, 2006), and color saturation (but not hue; Fuller & Carrasco, 2006). Higher order features such as object size (Anton-Erxleben, Henrich, & Treue, 2007), object shape (Fortenbaugh, Prinzmetal, & Robertson, 2011),

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and motion coherence (Liu, Fuller, & Carrasco, 2006) are also affected. It is hypothesized that these changes in stimulus appearance are due to attentional enhancement of visual neural responses (e.g., Carrasco, 2009a, 2011; Luck, 2004; Treue, 2004; Reynolds & Chelazzi, 2004). It has been argued that these results might be due to possible confounds (e.g., cue bias, response bias) rather than a change in appearance, but each of these possible confounds has been ruled out by a number of control experiments (see Discussion for details).

The specific way in which attention modulates contrast-dependent neural responses varies across experiments. Electrophysiology and fMRI studies show reliable attentional modulation of activity in the visual system beginning early in the processing stream; attention-related increases have been shown in V1 and extrastriate cortex (e.g., Gandhi, Heeger, & Boynton, 1999; Herrmann et al., 2010; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Liu, Pestilli, & Carrasco, 2005; Moran & Desimone, 1985; Offen, Schluppeck, & Heeger, 2009; Pestilli, Carrasco, Heeger, & Gardner, 2011; Ress, Backus, & Heeger, 2000; Reynolds, Pasternak, & Desimone, 2000; Silver, Ress, & Heeger, 2007) and as early as the lateral geniculate nucleus and superior colliculus (Schneider & Kastner, 2009; for reviews see Carrasco, 2011; Reynolds & Heeger, 2009). Two different multiplicative effects of attention have been characterized. First, some single-neuron recordings show that attention increases the response gain, i.e., neurons' firing rates are increased by a multiplicative scale factor (McAdams & Maunsell, 1999; Treue & Martinez-Trujillo, 1999). Second, other studies show that attention causes contrast gain increases, i.e., that attention increases the effective contrast of stimuli within the receptive field by a multiplicative scale factor (Li & Basso, 2008; Martinez-Trujillo & Treue, 2002; Reynolds et al., 2000). Two analogous additive effects of attention have also been hypothesized. The first, which we refer to as an output baseline increase, is a constant added to the output firing rates. The second, which we refer to as an input baseline increase, is a constant added to the input stimulus drive, increasing the effective stimulus contrast by an additive constant. There are numerous reports of baseline response increases in single-unit electrophysiology experiments (Chawla, Rees, & Friston, 1999; Haenny & Schiller, 1988; Luck, Chelazzi, Hillyard, & Desimone, 1997; Reynolds et al., 2000). Baseline increases independent of stimulus contrast are typically seen in contrast-response functions measured with functional magnetic resonance imaging (fMRI; Buracas & Boynton, 2007; Kastner et al., 1999; Murray, 2008; Offen et al., 2009; Pestilli et al., 2011; Ress et al., 2000; Silver et al., 2007; but see Lu, Li, Tjan, Doshier, & Chu, 2010, for

evidence of contrast gain change). Still others report that attention yields a mixture of different effects including additive and multiplicative increases in responses (Williford & Maunsell, 2006). A clear link has been established between various attention-enhanced neural responses and performance accuracy in contrast-dependent perceptual tasks (Anton-Erxleben & Carrasco, 2013; Herrmann et al., 2010; Herrmann, Heeger, & Carrasco, 2012; Liu, Pestilli, & Carrasco, 2005; Pestilli, Ling, & Carrasco, 2009; Pestilli et al., 2011; Ress et al., 2000).

This study is the first to characterize the relation between contrast-response functions and contrast appearance, as distinct from task performance (e.g., accuracy). There is evidence for a correlation between the magnitude of the attention-induced increase in ventral occipitotemporal responses and the associated increase in perceived contrast, suggesting that early visual areas are involved in contrast perception (Störmer et al., 2009). But the specific contrast-response functions underlying the phenomenon have not been investigated. We assumed a linking hypothesis that perceived contrast is monotonically related to the pooled activity of a large population of visual neurons, and we developed a model that predicts the shifts in perceived contrast by comparing simulated neural contrast-response functions for attended and unattended stimuli. The model includes parameters that control the contrast gain, response gain, and input baseline of the contrast-response functions. The model was fit to psychophysical data from a two-alternative forced-choice (2-AFC) task designed to assess the perceived contrast of a wide range of physical contrasts under different attention conditions. The best-fitting model revealed an input baseline increase in the underlying neural responses to the attended stimulus.

Methods

Observers

Five observers each participated in five psychophysical sessions: one 30-min practice session to measure individual 80% performance thresholds for orientation judgment, and four 60-min sessions for the main experiment. Three observers were experienced psychophysical observers and all five were naïve to the purpose of the experiment. All observers had normal or corrected-to-normal vision and all provided informed consent. The University Committee on Activities Involving Human Subjects at New York University approved the experimental procedures.

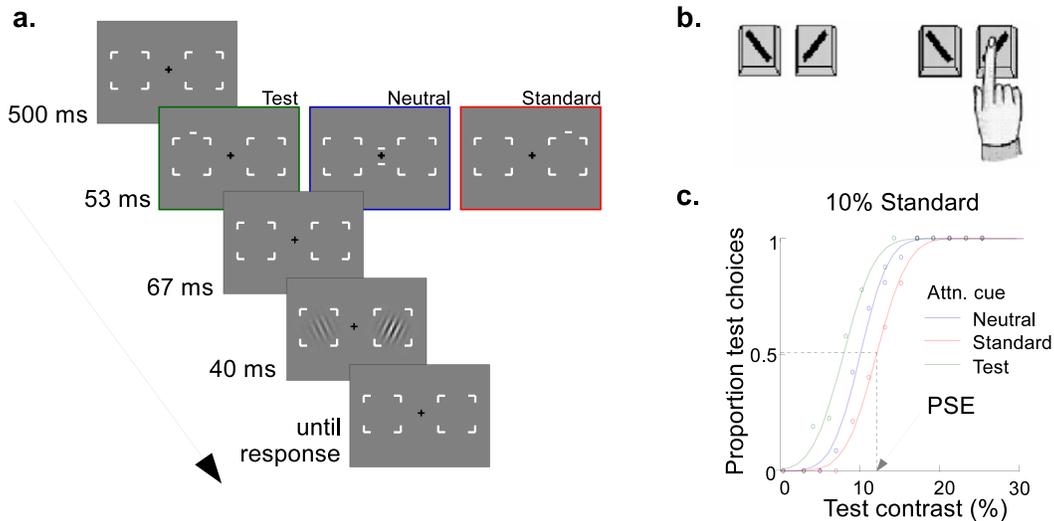


Figure 1. Trial sequence and data analysis. (a) Trial sequence. Colored borders around precue panels indicate attention conditions (red: standard; blue: neutral; green: test) and were not displayed to observers. (b) Response keys. With one button press observers indicated the orientation of the higher contrast stimulus. (c) Data analysis: Colors correspond to attention conditions in (a). Example shown is for one observer with 10% standard stimulus.

Stimuli

The stimuli were sinusoidal gratings within circular apertures (Figure 1). The apertures were tapered at the edges by a half cycle of a raised cosine. Two stimuli were presented on each trial: one chosen from a set of six standard stimuli, each of which had a fixed contrast level (5%, 10%, 20%, 40%, 60%, or 80%) and a corresponding test patch whose physical contrast varied from trial to trial. The stimuli were 6° in diameter and appeared on the horizontal meridian at 6° of eccentricity, with the location of the standard (left or right of fixation) chosen randomly on each trial. Each grating was rotated either clockwise or counter-clockwise from vertical. The amount of rotation was established, separately for each observer and separately for each standard contrast, to maintain performance in the orientation discrimination task at about 80% correct (see Orientation discrimination thresholds). Placeholders, denoting the stimulus locations, remained on the screen throughout the experiment. The placeholders were four right angles composed of two white lines (0.05° in length), forming the corners of an imaginary $6^\circ \times 6^\circ$ square surrounding the stimulus location in each hemifield. A central black fixation cross (0.4 degrees in length), remained on the screen throughout the experiment. Stimuli were displayed on a gamma-corrected monitor with a background luminance of 25 cd/m^2 , equal to the mean luminance of the gratings. We use *physical contrast* to denote the value defined by the difference in luminance values of the presented stimuli and *perceived contrast* to indicate the

perceptual value interpolated from the psychophysical data.

Task

Observers viewed two stimuli on each trial and were instructed to report the orientation of the stimulus of higher contrast (Figure 1). They responded with one of four buttons, two representing the possible orientations for each stimulus, thus providing both the contrast judgment—i.e., which stimulus appeared higher—and the orientation judgment with one key press. This psychophysical protocol was developed to assess the phenomenological correlate of exogenous attention and perceived contrast (Carrasco et al., 2004) and has been used to assess the effect of exogenous attention on several dimensions (for a review see Carrasco, 2009a). This protocol is considered an objective and rigorous way to study subjective experience (Treue, 2004; Luck 2004; see Discussion for additional references).

Each trial consisted of 500 ms of fixation, followed by a 67 ms attention cue, a 53 ms interstimulus interval (ISI), and a 40 ms stimulus presentation (Figure 1). The stimulus appearance, 120 ms after the onset of the exogenous attention cue (see Attention manipulation), was designed to coincide with the maximum effect of exogenous attention; the 160 ms interval between cue onset and stimulus offset was too brief for observers to make overt eye movements and ensured that they instead used covert attention. Following the observer's response, a 500 ms inter-trial interval (ITI) preceded the next trial.

Observers completed each experimental session on a different day. Each experimental session consisted of three 20-min blocks, for a total of 4,440 experimental trials. Standard contrast was blocked, subject to the constraint that each session consisted of one high (60% or 80%), one medium (20% or 40%), and one low-contrast (5% or 10%) block. There were thus two blocks of each standard contrast over the four days. The order of blocks was counterbalanced across observers and, for each observer, across days.

Attention manipulation

Exogenous attention cues (Figure 1) were either peripheral ($0.4^\circ \times 0.2^\circ$ white bar presented 1.5° above the top edge of one of the stimulus apertures) or central (two lines, each $0.4^\circ \times 0.1^\circ$, presented above and below fixation). This created three attention conditions, which we refer to as neutral (central cue), standard cued (peripheral cue above the standard stimulus aperture), and test cued (peripheral cue above the test stimulus aperture). Peripheral cues provided no information about the contrast and orientation tasks, and observers were explicitly informed of this. Attention cues were interleaved within blocks; within each block, all three attention conditions occurred with equal frequencies.

Psychophysical staircase procedure

The contrast of each test stimulus was systematically varied using a psychophysical staircase procedure. There were two interleaved one-up, one-down staircases for each of the 18 experimental conditions: 3 Attention (test cued, standard cued, neutral) \times 6 Standard Contrasts. One staircase was initialized at a much higher contrast than the standard and the other one at a much lower contrast.

Orientation discrimination thresholds

The amount of tilt was established during practice sessions, separately for each observer and separately for each standard contrast, to maintain performance in the orientation discrimination task at about 80% correct. During the practice sessions, the orientation of the stimuli was varied using a staircase procedure to determine orientation thresholds. Six staircases were run independently, one for each standard contrast, so as to equate the task difficulty across contrasts. Orientation tilts obtained during these practice sessions were used throughout the rest of the experiment, unless accuracy in any block dropped below 70% or exceeded 85%, averaged across all trials in that block, which

included all three attention conditions and the full range of contrasts. When performance accuracy deviated beyond this range, the tilt at that standard contrast was adjusted (on the order of 0.4°) by the experimenter before the next block in that condition was presented.

Data analysis

We measured the difference in perceived contrast between standard-cued and test-cued conditions. Our measure of perceived contrast was the point of subjective equality (PSE; Figure 1c), defined as the test contrast at which observers chose the test stimulus with a frequency of 50%. For each of the 18 conditions (6 Standards \times 3 Attention Cues), and for each test contrast, we calculated the proportion of trials on which the observer reported the test stimulus as having higher perceived contrast than the standard (test-choice trials). Psychometric functions (proportion test choice vs. test contrast) were fit based on simulated visual neural responses as described below in Model fitting, and the PSEs were interpolated. We took the difference in PSE between the standard-cued and test-cued conditions for each standard contrast as a measure of the attention-induced change in perceived contrast. The neutral condition was included as a control to evaluate whether attention both increased the perceived contrast of the standard when it was attended (standard-cued condition) and decreased its perceived contrast when the test stimulus was attended (test-cued condition).

To measure contrast discrimination performance—as distinct from contrast appearance—we calculated the just-noticeable differences (JNDs), separately for each experimental condition. JNDs were defined as the difference between the test contrasts at which observers chose the test stimulus with frequencies 50% and 75%. We used the 50% point, instead of the symmetrical 25% point, as the lower bound because contrast discrimination is typically measured using contrast increments, rather than decrements (e.g., Boynton et al., 1999; Pestilli et al., 2011). However, using the 25% point yielded similar results supporting the same conclusions.

As a measure of performance on the orientation discrimination task, we calculated inverse efficiency scores (IES), which is defined as the quotient of mean response time and accuracy, and thus has units of milliseconds/percent correct (e.g., Kimchi & Peterson, 2008). In this analysis we included only the subset of trials on which the standard stimulus was chosen; this allowed us to compare performance accuracy to the same physical stimulus in three attention conditions: test cued, standard cued, and neutral (Fuller, Rodriguez, & Carrasco, 2008; Liu, Abrams, & Carrasco, 2009; Liu, Fuller, & Carrasco, 2006). Performance

accuracy was averaged across standard contrast because the tilts were selected separately for each standard contrast to maintain performance in the orientation discrimination task at about 80% correct (see Orientation discrimination thresholds). To discount intersubject variability, we normalized IES scores by subtracting each observer's grand mean IES score, collapsed over all conditions, from their scores in each attention condition. The adjusted IES scores reported are the means of this measure, averaged across observers.

Model fitting

In addition to fitting standardized psychometric curves to the data (see below, cumulative normal fits), we implemented a model that predicted observers' behavior based on the contrast-dependent neural responses typically recorded in the visual system. For each pair of stimuli, the model generated a pair of values: one for the simulated neural response evoked by the test stimulus and one for the neural response evoked by the standard. A theoretical observer could then use the difference between the magnitudes of the two responses to inform the contrast judgments required for the psychophysical task. This value is equivalent to the observer's accuracy, d' , at discriminating the two contrasts, assuming additive, independent, and identically distributed noise and a maximum-likelihood decision rule. The model converted this d' value to percent test choice (Figure 2). Thus the behavior predicted by the model depended ultimately on the neural contrast-response functions; we parameterized those functions as described below and used maximum-likelihood optimization to find the best-fitting values for the parameters.

The model included two simulated neural contrast-response functions, for attended and unattended stimuli. These were approximated mathematically as modified Naka-Rushton functions (a standard shape for contrast-dependent responses, see Busse, Wade, & Carandini, 2009), using three attention-related parameters, two exponents, and one additional scale factor:

$$R = aN \frac{(c + b)^{(p+q)}}{\left((c + b)^q + \left(\frac{c}{s}\right)^q\right)}, \quad (1)$$

where c represents stimulus contrast and σ is the semi-saturation constant. Attention parameters included response gain, a , which controlled the asymptotic value of the function; contrast gain, s , which divisively modulated the semi-saturation point to shift the function left (for $s > 1$) or right ($s < 1$) on the log-contrast axis; and the input baseline, b , which allowed a shift in the input baseline. A change in output baseline

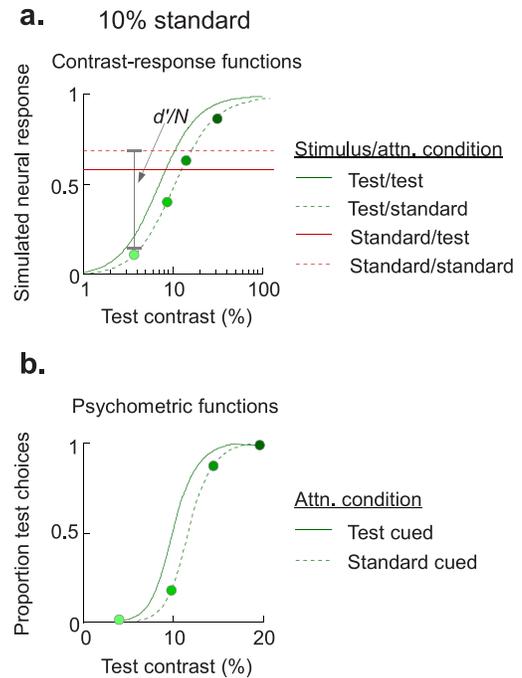


Figure 2. Psychometric functions from a model of underlying neural responses. (a) Simulated neural responses to test (green) and standard (red) stimuli in test-cued (solid) and standard-cued (dotted) attention conditions. Example shown is for 10% standard. Gray bar indicates accuracy for standard cued condition. (b) Discrimination accuracy is converted from d' to proportion test choices (see Methods).

could therefore be expressed in this model by an increase in b combined with an increase in a , so we did not include an additional parameter for output baseline. The exponents, p and q , and the scale factor, N , were included to improve the fits to the data and were held constant across all conditions. The values of a , s , and b were fixed ($a = 1$, $s = 1$, $b = 0$) to generate the contrast-response function for the unattended stimulus; these parameters were optimized for the responses to the attended stimulus to achieve the best fit to the data. The scale factor N and the exponents p and q were also free, but were constrained to be equal across attention conditions. The semi-saturation constant, σ , was fixed to 0.22 (typical of population responses, see Busse et al., 2009). There were thus six free parameters in the full model, constrained by the total number of test contrasts within the dynamic range of the psychometric functions ($n = 84\text{--}96$ per observer).

We fit several different versions of the model, including the full model, which allowed all three attention parameters to vary, and each single-parameter version, in which only one attention parameter was free and the others were set to one (a or s) or zero (b). We also considered the null hypothesis, that attention had no effect, by testing the model in which a and s were set to one and b to zero. Moreover, to check that

these models were good predictors of the data, we also considered the model in which separate cumulative normal psychometric functions were fit to each of the 90 Observer \times Attention \times Standard Contrast conditions, and compared the predictions with those of the full model.

Statistics

We used bootstrapping to obtain confidence intervals on the PSEs. For each of the 18 Attention \times Standard Conditions, a new data set was simulated for each observer by resampling (with replacement) from the raw data. At each test contrast, the simulated observer's response on a single trial was determined by randomly selecting one from the set of measured responses. We simulated the same number of trials as were acquired in the experiment (which was different for each test contrast due to the adaptive staircase procedure implemented in the experiment) and calculated the proportion of trials on which the simulated observer chose the test stimulus. We thus simulated the entire experiment, refit each psychometric function, and interpolated the PSEs. This was repeated 2,000 times to generate a distribution of PSEs for each condition, from which we defined the 68% confidence intervals.

A randomization test determined the statistical significance of the best-fit parameter values. This statistical test was based on obtaining null distributions for the relevant values. To generate null distributions, the attention condition labels for the entire set of trials were randomly permuted, separately for each standard contrast and separately for each observer, and the psychometric functions were refit. This was repeated 2,000 times, generating null distributions for each of the parameter values. The parameter values fit to the data with the correct condition labels were then compared with the null distributions. If any of the best-fit parameter values fell outside the 95% confidence intervals of the null distribution, it indicated that the best-fit model (with the correct condition labels) was significantly different from one that would fit if there were no effect of attention.

Models were compared pairwise using a cross-validation analysis. The raw data were partitioned into two sets by permuting a list of all trials and dividing it in half. Each model (the full model and each single-parameter version) was fit to one half of the data; we kept the resulting optimal parameter values and calculated the negative log-likelihood of these models with respect to the second half of the data. The data were repartitioned and this procedure was repeated 2,000 times, generating a distribution of error values for each model. (All analyses used maximum-likelihood

fitting to optimize the parameter fits; here we use “error” to refer to the negative log-likelihood value associated with a particular model, unless otherwise stated.) Statistical significance of any differences in the model fits was determined by comparing the distributions of these error values. For each pair, Model A and Model B, the difference in the distributions of error values ($\text{error}_A - \text{error}_B$) was used to determine a p value defined as the proportion of difference values that was greater than zero. A p value of less than 0.05, indicating that less than 5% of the distribution was greater than zero, meant that the error associated with Model B was significantly greater than that associated with Model A and thus that Model A was a better fit. Conversely, a p value larger than 0.95 indicated that over 95% of the distribution was greater than zero, and thus Model B was a better fit. Importantly, this analysis accounts for differences in the number of free parameters in different models. For each repartitioning of the data, models with more free parameters will tend to overfit first half of the raw data, reflecting noise in that half of the data set and resulting in more error with respect to the second half. Models were fit individually to each observer's data, and comparisons were done both within and across observers (by summing the error across subjects for each repartitioning of data).

Predicted results

Attention may effect a change in response gain, contrast gain, or input baseline; adjusting the corresponding model parameters for the attended stimulus changes the form of the contrast-response function in various ways. Combined with the linking hypothesis described above, this predicts different patterns of change in the perceived contrast (Figure 3).

Alternative model

We explored a variation on the model of the contrast-response function. In this alternative model, the contrasts of both stimuli are included in the denominator, accounting for possible cross-hemifield normalization in the responses (Equation 2; c_2 represents the contrast of the stimulus not in the relevant hemifield).

$$R = aN \frac{(c + b)^{(p+q)}}{\left((c + b)^q + (c_2)^q + \left(\frac{c}{s}\right)^q \right)}. \quad (2)$$

In some cases, normalization among widely separated stimuli has been shown to explain psychophysical performance (Ma, Navalpakkam, Beck, van den Berg, & Pouget, 2011). This model has been used also for

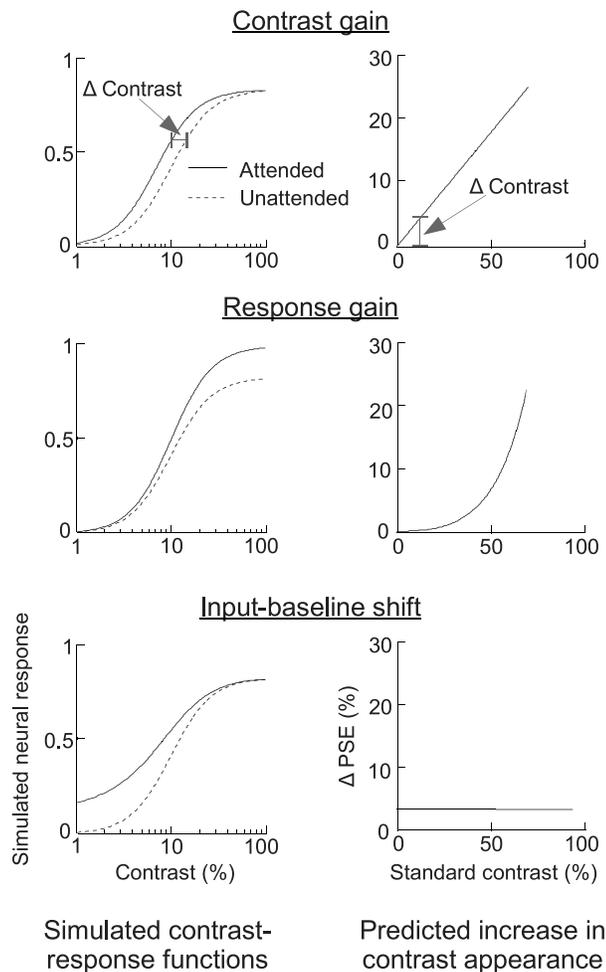


Figure 3. Model predictions for the effect of attention on perceived contrast. Left: contrast-response functions (dotted: unattended; solid: attended) plotted on a log scale; right: change in perceived contrast due to attention, plotted on a linear scale. Top row: contrast-gain increase; middle row: response-gain increase; bottom row: input baseline increase.

neural responses in extrastriate areas such as MT, where neural receptive fields are large (Lee & Maunsell, 2009; Martinez-Trujillo & Treue, 2002). For data sets that were significantly better fit by the alternative model than by the original model (both with all attention parameters free), we also explored the single parameter versions of the alternative model.

Results

Attention increased perceived contrast

Our measure of the increase in perceived contrast was the difference in PSEs between test-cued and standard-cued conditions, which was statistically sig-

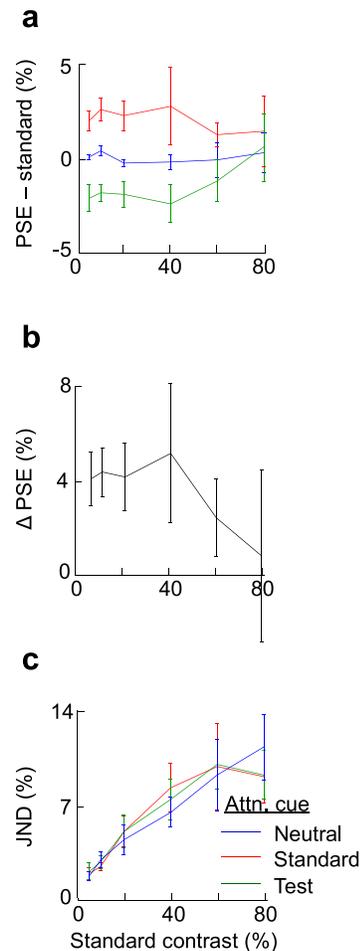


Figure 4. Attention increases perceived contrast. (a) PSE minus standard contrast. Blue, neutral condition. Green, test-cued condition. Red, standard cued. (b) Standard PSE minus test PSE (i.e., difference between red and green curves in Panel A). (c) Just-noticeable differences defined as the difference between the test contrasts at which observers chose the test stimulus with frequencies 50% and 75%. Colors consistent with Panel A. All panels show means across observers, taken from the cumulative normal model fits; error bars, \pm standard error of the mean (SEM).

nificant for all but the highest standard contrast (5%, 10%, 20%, 40%, $p < 0.0005$; 60%, $p < 0.01$; 80%, $p = 0.22$; p values based on bootstrapping tests, see Statistics section in Methods; Figure 4a, b). The larger error bars at high contrast reflect expected variability, given that contrast discrimination thresholds are higher at high contrast (Figure 4c). Mean PSEs were significantly greater for standard-cued than neutral-cued trials for all but the two highest standard contrasts (60% and 80%; Figure 4a). Likewise, PSEs were significantly lower for test-cued trials than for neutral-cued for all but the highest two standard contrasts (Figure 4a).

Orientation discrimination

There was no significant effect of attention on performance of the orientation discrimination task. Mean accuracy across observers was 76% correct. Inverse efficiency scores ($\pm SEM$) were -0.0012 ± 0.0163 ms, 0.0000 ± 0.0157 ms, and 0.0012 ± 0.0156 ms in standard-cued, neutral, and test-cued conditions, respectively.

Contrast discrimination

JNDs increased with standard contrast for all three attention conditions (Figure 4c).

As expected, there was no difference in the JND between peripheral and neutral cues. The cued stimulus was either higher or lower in contrast than the uncued stimulus, and these two situations occurred with equal frequency in both the test-cued and the standard-cued conditions.

Model fits

We used pairwise comparisons of the log-likelihoods of five different neural response models, in which a simulated neural response, given by Equation 1, generated predictions for behavioral performance. These included the full model, in which a , s , and b were all allowed to vary; the response gain model, in which a was free while s and b were set to one and zero, respectively; the contrast gain model, in which s was free while a and b were set to one and zero, respectively; the input-baseline model, in which b was free and a and s were both set to one; and the null model, in which a and s were set to one and b to zero. (The scale factor N and the exponents p and q were free in all five models.) We also compared these model fits to an alternative model based on neural responses given by Equation 2 (full version), wherein the simulated neural responses are normalized across the stimuli in both visual hemifields, and, for observers whose data were better fit by Equation 2, we also compared the full version of this model to each of its single-parameter versions. As a metric of goodness of fit, we compared the neural response models to the cumulative normal model, in which a separate psychometric function was fit to each of the 90 Observer \times Attention \times Standard Contrast conditions. We used this model as a benchmark; with 72 free parameters, it is the best-fitting reasonable model for the psychophysical data. Each neural response model was therefore compared with the cumulative normal model and defined as a good fit if the error (negative log-likelihood) was not significantly greater than that associated with the cumulative

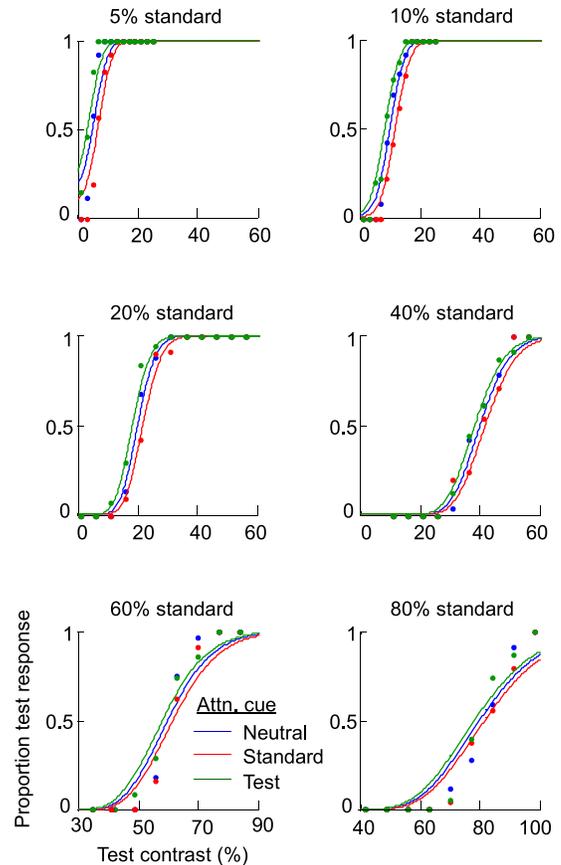


Figure 5. Psychometric curves. Data shown is from a representative observer. Blue, neutral condition. Green, test-cued condition. Red, standard-cued.

normal model. All model comparisons were done using cross-validation analysis, which takes into account the different numbers of free parameters in each model (see Statistics in Methods). All p values for model comparisons are derived from the same cross-validation analyses; for parameter fits, p values are derived from the bootstrapping analyses (see Statistics in Methods).

The full neural response model provided a good fit to the data, as shown by the cross-validation analyses comparing them to the cumulative normal model. There was no significant difference between the full model and cumulative normal model errors, neither for any individual observer ($p > 0.1$) nor across the group ($p > 0.05$). Although the cumulative normal functions provided a numerically better fit to the psychometric data, that model included 72 free parameters per observer (versus six in the full model). That the cross-validation analysis provided no evidence for a statistically significant difference between the cumulative normal and full model fits indicated that the cumulative normal model was overfitting the data.

The input baseline model predicted the observed increase in perceived contrast (Figure 5). For all five observers, as well as the across-observers analysis, the

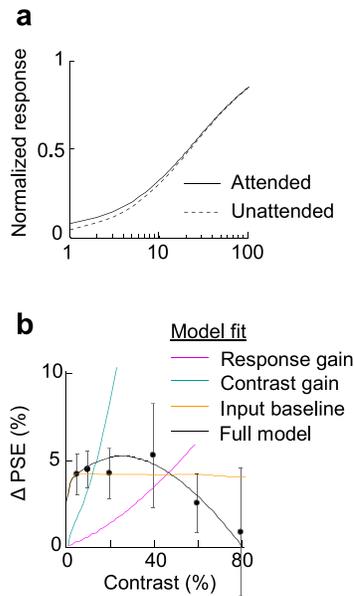


Figure 6. Model fits. (a) Contrast-response functions predicted by input baseline model. Solid, response to attended stimulus. Dotted, response to unattended stimulus. (b) PSE shifts predicted by the models. Magenta, best-fit response gain model; cyan, best-fit contrast gain model; orange, best-fit input baseline model; black, best-fit full model. Null model predicts no appearance change. Filled symbols, means across observers, taken from the cumulative normal model fits; error bars \pm standard error of the mean (SEM).

input baseline model (Figure 6) resulted in significantly better predictions of the data than either the contrast-gain or response-gain models ($p < 0.05$). The full model was numerically a better fit to the data. However, cross-validation showed no significant difference between the input baseline model fit and the full model fit neither for any of the five observers nor for the across-observers analysis ($p \geq 0.1$). Both the input baseline model and the full model fits were significantly better than the null model ($p < 0.05$) and the baseline parameter of the input baseline model was significantly greater than zero ($p < 0.05$, randomization test) for all observers and for the across-observers analysis. Best-fitting parameters for both models are shown in Tables 1 and 2.

Observer	N	a	s	$b (\times 10^{-2})$	p	q
1	13.5	0.986	1.13	3.15	0.0878	1.01
2	20.0	0.959	1.21	0.67	0.286	1.32
3	20.0	0.958	1.22	0.38	0.162	1.11
4	12.0	1.00	0.917	3.47	0.218	1.00
5	20.0	0.969	1.08	0.54	0.195	1.17
Mean	17.1	0.972	1.11	1.64	0.190	1.12

Table 1. Parameter fits, full model. N , scale factor; a , response gain increase with attention; s , contrast gain increase with attention; b , input baseline response increase with attention; p and q , exponents.

Alternative model

The alternative model (see Equation 2), with all attention parameters free, provided a statistically better fit than the original model for three observers. However, for all three of these individuals, the full alternative model was not significantly better than the input baseline version of the alternative model ($p > 0.1$). Thus, an increase in input baseline explained the observers' behavior, although the computation of perceived contrast may involve normalization across both hemifields for this appearance task, which entails a comparison between both stimuli.

Discussion

We found that attention increased perceived contrast across the contrast range, consistent with an attention-related increase in the input baseline of the underlying neural response. We measured observers' perception in a two-alternative forced-choice task designed to assess the effect of attention on perceived contrast (Carrasco et al., 2004). A model of the neural responses to attended and unattended stimuli was fit to the psychophysical data, assuming a monotonic relation between the response and the perceived contrast. Parameters controlling the contrast gain, response gain, and input baseline of the response to the attended stimulus were fit to the data. Allowing the input baseline to increase with attention was sufficient to explain the psychophysical results. We thus evince an increase in the input baseline as the process underlying the increase in perceived contrast.

Computational models of attention

Divisive normalization has been proposed as a key neural process that interacts with attention to allow for the observed modulations of neural contrast-response functions (Boynton, 2009; Lee & Maunsell, 2009; Reynolds & Heeger, 2009). In these models, the response of an individual neuron consists of an

Observer	N	$b (\times 10^{-2})$	p	q
1	14.0	4.08	0.0013	1.00
2	20.0	1.76	0.245	1.36
3	20.0	1.44	0.165	1.00
4	11.8	2.22	0.207	1.00
5	20.0	0.75	0.190	1.01
Mean	17.2	2.05	0.162	1.07

Table 2. Parameter fits, input baseline model. N , scale factor; b , input baseline response increase with attention; p and q , exponents.

excitatory component driven directly by the stimulus properties, which is divided by a suppressive component, computed as the summed activity of neighboring neurons. This computation explains several nonlinear properties of neural responses observed in the visual system and in other perceptual systems and has therefore been hypothesized to be a canonical computation, repeatedly co-opted for different purposes throughout the brain (for a review see Carandini & Heeger, 2012). Reynolds and Heeger (2009) proposed that attention modulates the excitatory input to a population of neurons before the responses are normalized, via a multiplicative gain and/or an additive increase. The Reynolds-Heeger model predicts that contrast-response functions may undergo variable amounts of contrast gain, response gain, and baseline increase depending on the size of the attention field, defined as the set of neurons affected by the attentional gain, with respect to the stimulus size. A multiplicative attention field causes contrast gain increase when the attention field is large (i.e., larger than the neuron's receptive field) and the stimulus is small. When the attention field is small and the stimulus is large, a multiplicative attention field causes a response-gain increase. The model also allows for an additive attention field, which adds a constant activity increase to the affected neurons, regardless of the stimulus contrast (Reynolds & Heeger, 2009).

In accordance with this model, spatial attention has been found to improve orientation-discrimination performance in a manner consistent with either contrast gain increase when the attention field was large and the stimulus small, or response gain increase when the stimulus was large and the attention field small (Herrmann et al., 2010). Feature-based attention, however, has been found to increase response gain, regardless of whether the range of attended feature values was large or small (Herrmann et al., 2012). This result is also consistent with the Reynolds-Heeger model, considering that tuning of excitation and suppression in the relevant feature domain (orientation) is broader than even the wider attention field manipulation (Herrmann et al., 2012). Both of these previous studies used orientation discrimination tasks,

and the results were modeled assuming an optimal read-out from the neural population (Herrmann et al., 2012; Herrmann et al., 2010).

Simulations suggest that a baseline increase is consistent with a different read-out of the Reynolds-Heeger model predictions. Pooling the mean stimulus-evoked responses of a large population of visual neurons, rather than using an optimal decision rule, produces an increase in output baseline activity to attended stimuli (Hara, Pestilli, & Gardner, 2014). Whereas neurons optimally tuned to the stimulus undergo contrast gain or response gain increases individually, many additional neurons in the population are driven less strongly by the stimulus and thus contribute to yield an increase in the output baseline of the pooled responses. Our result suggests that an increase in the input baseline underlies attention-related increases in perceived contrast. Given the feed-forward aspect of visual processing, one interpretation of our result is that attention additively increases the output baseline of early visual responses, consistent with Hara et al.'s (2014) simulations, but that contrast appearance is mediated by a successive stage of processing. The increase in output baseline in early visual areas becomes an input to the successive stage of processing, where normalization presumably also occurs. The responses from this successive stage of processing, consequently, would be best described by an increase in the input baseline, consistent with our psychophysical data. Increases in contrast appearance are correlated with activity in ventral occipitotemporal cortex (Störmer et al., 2009). Our conclusion is consistent with this finding although it is agnostic to which specific visual area or areas may support contrast appearance.

Attention and perceptual appearance

Vision comprises not only our performance accuracy in perceptual judgments but also our subjective experiences, and attention plays a crucial role in both. A quarter century of empirical research has shown the effects of attention on the accuracy and efficiency of visual tasks, but only the last decade has seen rigorous investigation of attention with respect to subjective perception. The debate over the role of attention in this aspect of perception dates back to the forefathers of experimental psychology and psychophysics. Helmholtz and James argued that attention intensified perceptions, while Fechner claimed attention did not affect stimulus appearance (Helmholtz, 1866; James, 1890). Recent research has conclusively supported the former: attention alters our subjective experiences of the visual world (for reviews see Anton-Erxleben & Carrasco, 2013; Carrasco, 2009a, 2009b, 2011).

It has been argued that the behavioral effects observed in 2-AFC experiments like the one reported here may not be due to attention but to other factors. For instance, it was hypothesized that the effects were due to sensory interactions, and that reversing the luminance polarity of the precue in the Carrasco et al. (2004) protocol should lead to differential cueing effects (Schneider, 2006). However, a black cue and a white cue had the same effect regrading perceived contrast, thus ruling out such alternative explanation (Ling & Carrasco, 2007). A cue-bias explanation for the Carrasco et al. (2004) results was proposed because for targets of low visibility, observers may bias their response toward the cued location (Prinzmetal, Long, & Leonhardt, 2008). Indeed, the cue-bias hypothesis is a plausible explanation for Prinzmetal et al.'s (2008) results, given the characteristics of their stimuli, but such an explanation has no bearing on studies with suprathreshold stimuli and a wide range of stimulus contrasts (Carrasco, Fuller, & Ling, 2008; Carrasco et al., 2004). Lastly, it was claimed that equality judgments are bias-free whereas comparative judgments are bias prone and an alternative interpretation of the previous findings based on a decision bias was proposed (Schneider & Komlos, 2008). In response to that claim, contrast appearance was measured using both a comparative and an equality judgment. Observers judged the contrasts of two simultaneously presented stimuli, while either the contrast of one stimulus was physically incremented or exogenous attention was drawn to it. The equality protocol was shown to be less sensitive and more bias-prone than the comparative judgment, but an effect of attention with both paradigms is consistent with an increase of apparent contrast by attention (Anton-Erxleben, Abrams, & Carrasco, 2010). Schneider (2011) suggested that bias in equality judgments may have been due to skewed response distributions. Further analysis by Anton-Erxleben, Abrams, and Carrasco (2011), however, showed no correlation between the amount of skew and the PSE across observers, and moreover, that even a model that incorporated skewed response distributions was consistent with an attention-related change in perceived contrast.

Several additional studies have also ruled out cue bias, response bias, and alternative interpretations of these perceptual appearance experiments (for reviews see Carrasco, 2009a, 2011). Control experiments have included: (a) Reversing the direction of the task question (e.g., instructing observers to choose the lower contrast stimulus instead of the higher contrast stimulus) to rule out a response bias (Anton-Erxleben et al., 2010; Anton-Erxleben et al., 2007; Anton-Erxleben et al., 2013; Carrasco et al., 2004; Fuller & Carrasco, 2006; Gobell & Carrasco, 2005, Ling &

Carrasco, 2007, Liu et al., 2009; Montagna & Carrasco, 2006; Turatto et al., 2007); (b) Lengthening the interval between the cue and target, to rule out a cue bias, such that exogenous attention would have been extinguished before the target stimuli were presented (Carrasco et al., 2004; Fuller et al., 2008; Hsieh, Caplovitz, & Tse, 2005; Ling & Carrasco, 2007; Liu et al., 2006; Turatto et al., 2007); (c) Using postcues instead of precues to rule out a cue bias, showing that the latter but not the former altered appearance, even though the spatial and temporal contiguity between cue and stimulus were the same (Anton-Erxleben et al., 2007; Carrasco et al., 2008; Fortenbaugh et al., 2011; Fuller & Carrasco, 2006; Fuller et al., 2009; Gobell & Carrasco, 2005; Turatto et al., 2007).

Here we present the first effort to fully characterize the effect of attention on perceived contrast, and probe the link between apparent contrast and neural activity. We fit a model of neural contrast responses to the psychophysical data and found that an input baseline increase in the neural response accounted for the observed increases in apparent contrast. This increase in the input baseline can be reconciled with mean population responses predicted by the Reynolds-Heeger normalization model of attention (Hara et al., 2014; Reynolds & Heeger, 2009), which has previously explained various physiological and psychophysical results within a common framework. Our findings shed light on the neural processing underlying contrast appearance and on the implications of normalization models for population responses.

Conclusion

We systematically investigated the effects of attention on perceived contrast and found that they can be modeled by a baseline shift in the neural responses. By characterizing this effect across the contrast range, we probed the source of contrast appearance and the population responses from which it arises. An attention-related increase in input baseline of the neural responses accounted for the behavioral data.

Keywords: covert attention, contrast appearance

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