Stimulus visibility and uncertainty mediate the influence of attention on response bias and visual contrast appearance

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Although attention is known to improve the efficacy of sensory processing, the impact of attention on subjective visual appearance is still a matter of debate. Although recent studies suggest that attention can alter the appearance of stimulus contrast, others argue that these changes reflect response bias induced by attention cues. Here, we provide evidence that attention has effects on both appearance and response bias. In a comparative judgment task in which subjects reported whether the attended or unattended visual stimulus had a higher perceived contrast, attention induced substantial baseline-offset response bias as well as small but significant changes in subjective contrast appearance when subjects viewed near-threshold stimuli. However, when subjects viewed suprathreshold stimuli, baseline-offset response bias decreased and attention primarily changed contrast appearance. To address the possibility that these changes in appearance might be influenced by uncertainty due to the attended and unattended stimuli having similar physical contrasts, subjects performed an equality judgment task in which they reported if the contrast of the two stimuli was the same or different. We found that, although there were still attention-induced changes in contrast appearance at lower contrasts, the robust changes in contrast appearance at higher contrasts observed in the comparative judgment task were diminished in the equality judgment task. Together, these results suggest that attention can impact both response bias and appearance, and these two types of attention effects are differentially mediated by stimulus visibility and uncertainty. Collectively, these findings help constrain arguments about the cognitive penetrability of perception.

Introduction

There is a wealth of studies showing that attention facilitates behavioral performance by enhancing the efficiency of sensory information processing (Anton-Erxleben & Carrasco, 2013; Carrasco, 2011; Desimone & Duncan, 1995; Itthipuripat & Serences, 2016; Serences & Kastner, 2014; Sprague, Saproo, & Serences, 2015). However, there is a long-standing debate about whether attention can actually alter subjective perceptual experience (Anton-Erxleben, Abrams, & Carrasco, 2010, 2011; Beck & Schneider, 2016; Block, 2007, 2010; Carrasco & Barbot, 2019; Fodor, 1984; Helmholtz, 1866; James, 1890; Ling & Carrasco, 2007; Prinzmetal et al., 1996; Pylyshyn, 1999; Raftopoulos, 2001; Schneider, 2011; Schneider & Komlos, 2008; Tse, 2005). Recently, Carrasco, Ling, and Read (2004) introduced a psychophysical attention-cueing paradigm that measures the perceived contrast of attended and unattended visual stimuli (see Figure 1a, left). They presented human subjects with two visual stimuli on the left and right of the fixation point following an exogenous spatial attention cue above one of the two visual stimuli and asked subjects to rate whether the cued or the uncued stimulus was rendered at a higher contrast (i.e., comparative judgment). Using variants of this method, they and others have demonstrated that an attended stimulus appears to have a higher contrast than an unattended stimulus (Anton-Erxleben et al., 2010, 2011; Carrasco, Fuller, & Ling, 2008; Carrasco et al., 2004; Cutrone, Heeger, & Carrasco, 2014; Firestone & Scholl, 2014b, 2014a, 2015; Fuller, Park, & Carrasco, 2009; Fuller, Rodriguez, & Carrasco, 2008; Ling & Carrasco, 2007; Prinzmetal, Long, & Leonhardt, 2008; Störmer, McDonald, & Hillyard, 2009).

However, another set of studies argues that the changes in appearance revealed by the comparative judgment task were instead related to response bias induced by spatial attention cues (Beck & Schneider, 2016; Prinzmetal et al., 2008; Schneider, 2006, 2011; Schneider & Komlos, 2008). Collectively, these studies suggest that there are at least two sources that may influence response bias: stimulus visibility and uncertainty. In support of the response bias account, Prinzmetal et al. (2008) found that, in a visual attention task in which subjects were asked to detect visual stimuli rendered at low contrasts (i.e., near threshold), spatial attention cues induced response bias but did not change contrast sensitivity. Moreover, they observed that, when there was no stimulus presented (i.e., "blank" trials), spatial attention cues still made subjects more likely to believe that there was a stimulus present compared to the blank stimulus on the uncued side (Prinzmetal et al., 2008). Together, these results suggest that spatial attention cues may impact subjects'

guessing (termed here as baseline-offset response bias) rather than their perceptual experience. In reply, Carrasco et al. (2008) argued that the cue-bias hypothesis might only apply to stimuli with low visibility.

In addition to stimulus visibility, Schneider and colleagues argued that stimulus uncertainty also induces response bias (Beck & Schneider, 2016; Schneider, 2006, 2011; Schneider & Komlos, 2008). In particular, when the cued and uncued stimuli are rendered at similar contrasts and subjects cannot tell them apart, subjects may be inclined to report the cued stimulus as higher in contrast even though their perception is unaltered (Beck & Schneider, 2016; Schneider, 2006, 2011; Schneider & Komlos, 2008). To test this idea, they introduced a different psychophysical method in which subjects were asked to rate whether the two stimuli had the same or different contrast (termed here as an equality judgment; see Figure 1a, right). Using this procedure, they found no evidence for attention changing visual contrast appearance (Schneider, 2006, 2011; Schneider & Komlos, 2008). As a response, Carrasco and colleagues later conducted a study using both comparative and equality judgment tasks and found that both measurements showed attention could alter the perceived contrast appearance of visual stimuli and argued that the previously reported null finding was due to discrepancies in data fitting procedures across different studies (Anton-Erxleben et al., 2010, 2011).

Based on these studies, we hypothesized that the effects of attention on contrast appearance and response bias might coexist and might be differentially expressed at different levels of stimulus visibility and uncertainty. Although a few recent studies have begun to study the effect of attention on visual appearance across a full range of stimulus contrast levels, none of them have concurrently examined attention effects on response bias that may depend on stimulus visibility and uncertainty (Cutrone et al., 2014; Zhou, Buetti, Lu, & Cai, 2018). Therefore, we adopted an experimental approach in which comparative and equality contrast judgments were performed between attended and unattended stimuli while stimulus contrast was varied independently across a full range of values ranging from near threshold to highly visible (Figure 1a and b; Materials and methods; also see Cutrone et al., 2014; Zhou et al., 2018). Unlike past studies, we also introduced a fitting procedure that allowed us to concurrently measure changes in contrast appearance and baseline-offset response bias we predicted to be mediated by stimulus visibility (see Figure 2a through c). Moreover, changes in psychophysical measurements thought to index contrast appearance in the comparative judgment task were compared with those observed in the equality judgment task to account for the
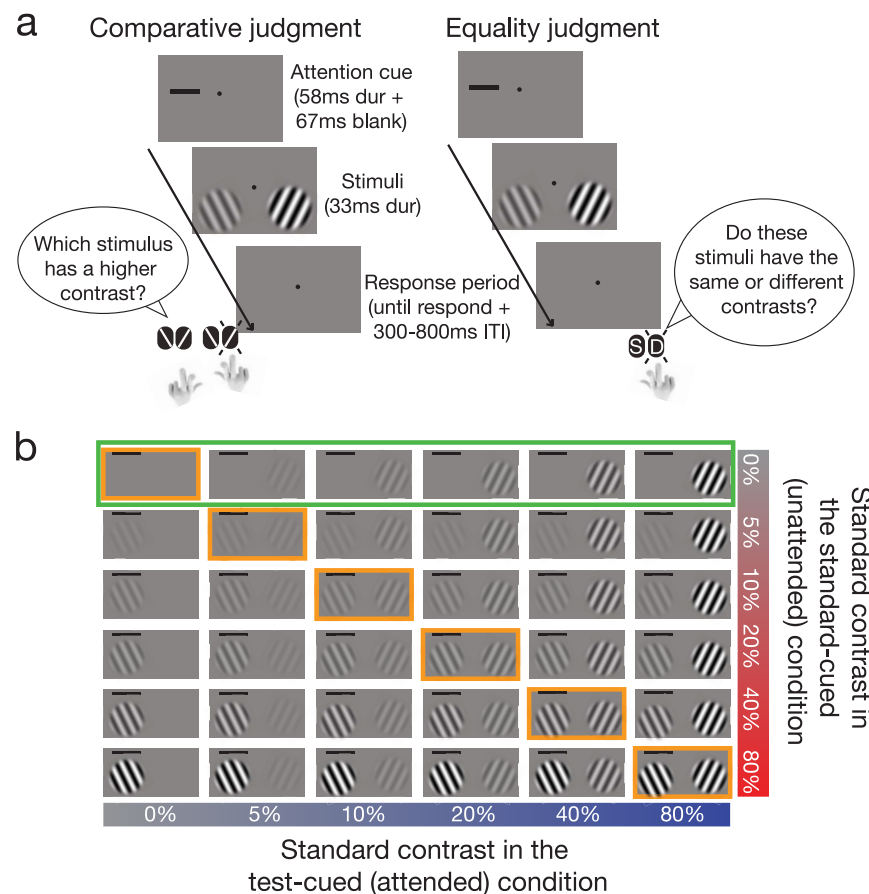
Figure 1. Behavioral paradigms. (a) The comparative and equality contrast judgment tasks (left and right, respectively). For both tasks, each trial started with an exogenous attention cue, followed by a set of two Gabor stimuli of which contrast values were manipulated independently from 0% to 80%. In the comparative judgment task, subjects reported the orientation of the stimulus (CW or CCW) that was perceived with higher contrast with the hand corresponding to the spatial location of the selected stimulus. In the equality judgment task, another group of subjects reported if the two stimuli appeared at the same (S) or different (D) contrasts. (b) All experimental conditions showing that the contrast values of cued and uncued stimuli were manipulated independently. A large green box marks trials in which the attention cue was expected to have the most influence on guessing or baseline-offset response bias because the cued stimulus was not visible (0% contrast). Orange boxes mark trials in which the cued and uncued stimuli were rendered at the same physical contrast values and the attention cue was, thus, expected to have the most influence on response bias induced by stimulus uncertainty. We also expected that the effect of stimulus uncertainty on response bias should also increase as a function of stimulus visibility.

effect of response bias driven by stimulus uncertainty (see Figure 2d and e).

As predicted, in the comparative judgment task, we found that when subjects viewed low-to-medium contrast stimuli, attention induced a substantial amount of baseline-offset response bias as well as small but significant changes in perceived contrast. However, when subjects viewed higher contrast stimuli, response bias decreased, and attention primarily changed the psychophysical measurements that indexed contrast appearance. On the other hand, in the equality judgment task, there were still changes in contrast appearance with stimuli rendered at low contrast, but the robust changes in contrast appearance at high contrasts observed in the comparative task were diminished. Collectively, these results suggest that attention can impact both response bias and appearance, and these two types of attention effects are differentially mediated by stimulus visibility and uncertainty.

Materials and methods

Participants

Eighteen neurologically healthy human observers with normal or corrected-to-normal vision were recruited from the University of California, San Diego (UCSD). All participants provided written informed
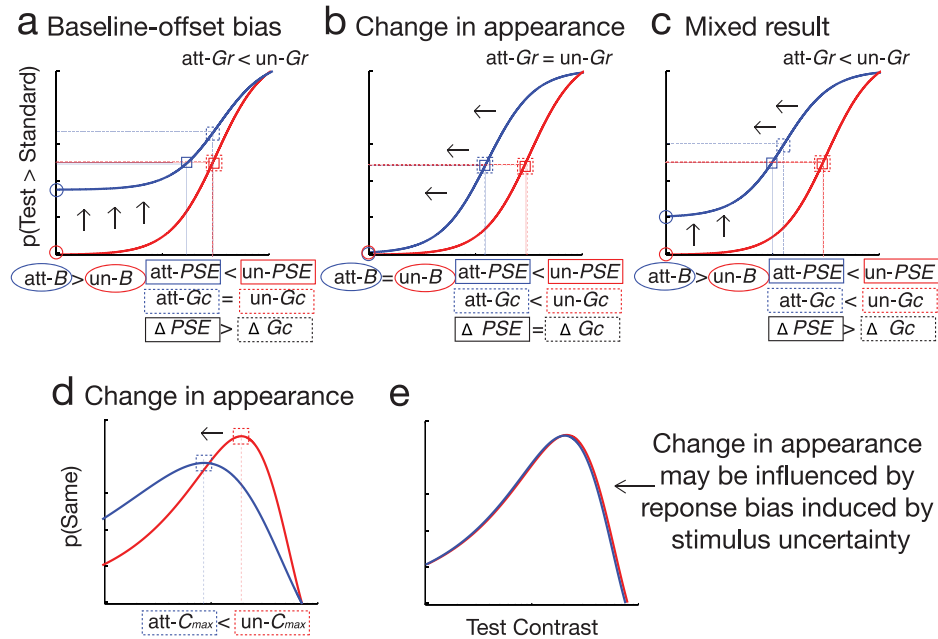
Figure 2. Predictions. (a–c) Possible patterns of the psychophysical data obtained from the comparative judgment task. (a) Attention induces baseline-offset response bias (B; additive upward shift) without changing contrast sensitivity (G_c; horizontal shift). In this scenario, even though there is no change in G_c, changes in the PSE (the point at which the probability value reaches 50%) are observed, which is simply due to changes in B. This indicates that PSE is not an accurate measure of contrast sensitivity when taking possible changes in B into account. Changes in B are assumed to be driven by increasing guessing or subjects following the cue stimulus even when it was not visible (0% contrast; see an orange box in Figure 1b). (b) Attention alters perceived contrast of visual stimuli. In this scenario, attention should only decrease G_c, but it should not change B. When there is no change in B, the PSE changes in a similar degree as G_c. (c) Attention could induce both changes in subjective appearance indexed by G_c and response bias as indexed by B. In this scenario, PSE also overestimates changes in contrast sensitivity due to changes in B. Because the probability value cannot exceed one, the response gain parameter (G_r; the slope of the psychometric function) decreases if B increases (a and c). (d and e) Possible patterns of the psychophysical data obtained from the equality judgment task. (d) If the comparative data is truly driven by changes in appearance, we should observe a horizontal shift in the contrast value where the equality function peaks (C_{max}). (e) If there is no change in C_{max}, changes in PSE and G_c in the comparative data may be partly influenced by response bias induced by stimulus uncertainty (e.g., when the cued and uncued stimuli were rendered at similar contrast values; see orange boxes in Figure 1b).

consent as required by the local institutional review board at UCSD. Subjects were compensated at a rate of $10/hr. Of these 18 subjects, 10 of them participated in the comparative judgment task (the main experiment), and the other eight participated in the equality judgment task (see details related to task design in the next section). The data from one subject were excluded from the comparative judgment task because orientation discrimination performance was below chance, leaving data from nine subjects in the final analysis (seven female, 20–24 years old, one left-handed). One of the eight subjects in the equality judgment task did not complete the task, leaving data from seven subjects in the final analysis of this task (five female, 18–26 years old, all right-handed). The comparative judgment task included four experimental sessions, spread out on four different days. There was one session of the equality judgment task. Each testing session contained 1,296 trials and lasted approximately 1.5 hr. Note that we ran

the equality judgment task as a follow-up study, and we acquired the equality data for one session because the comparative judgment data were consistent across four days. The sample sizes are within the typical range used in these types of studies in which attentional modulations are measured across different contrast levels across multiple experimental sessions (Anton-Erxleben et al., 2010; Anton-Erxleben, Henrich, & Treue, 2007; Cutrone et al., 2014; Itthipuripat, Cha, Byers, & Serences, 2017; Itthipuripat, Garcia, Rungratsameetaweemana, Sprague, & Serences, 2014; Itthipuripat, Sprague, & Serences, 2019; Ling & Carrasco, 2007; Pestilli, Carrasco, Heeger, & Gardner, 2011).

Stimuli and task

Stimuli were presented on a PC running Windows XP using MATLAB (MathWorks, Natick, MA) and

the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Participants were seated 60 cm from the CRT monitor (which had a gray background of 34.51 cd/m^2, 120 Hz refresh rate) in a sound-attenuated and dark room.

Two different groups of subjects performed the comparative and equality contrast judgment tasks (Figure 1a and b). They were presented with two Gabor stimuli, one on the right and one on the left. The subjects were asked to report whether the Gabor that was higher contrast was tilted clockwise (CW) or counterclockwise (CCW) from vertical (spatial frequency = 3 c/°, standard deviation of the Gaussian envelop = 2.18°, stimulus radius = 6.53°, eccentricity = 13.74°). In the comparative judgment task, the participants were instructed to fixate at the fixation point and to report if the stimulus on the left or the right of the fixation point had a higher contrast. If the stimulus on the left had a higher contrast, they reported the orientation of the left stimulus (CW or CCW) by pressing one of the two buttons using their left hand. If the stimulus on the right had a higher contrast, they reported the orientation of the right stimulus (CW or CCW) by pressing one of the other two buttons using their right hand. The stimulus properties and experimental conditions in the equality judgment task were identical to those in the comparative judgment task except that in the equality judgment task subjects were asked to report if the two visual stimuli appeared at the same or different contrasts with their right index and middle fingers, respectively. There was no response deadline, and the duration of the intertrial interval was pseudo-randomly drawn from the uniform distribution of 300–800 ms.

To examine the impact of covert spatial attention on subjects' report about stimulus contrast, we presented an exogenous cue (0.36° × 3.63° length × thickness) for 58 ms (either to the left or right of fixation 8.57° above the stimulus center) 133 ms before the onset of the two Gabor stimuli (1:1 left-cued:right-cued). The contrast values of the two stimuli were independently manipulated and drawn from six contrast levels (0%, 5%, 10%, 20%, 40%, and 80% Michelson contrasts). In the comparative judgment task, we directly assayed response bias by including trials with 0% contrast stimuli (i.e., stimulus-absent trials) as we reasoned that any behavioral responses in favor of a cued 0% contrast stimulus (Figure 1c and e) must be driven by cue-induced response bias and could not be driven by an interaction between cue-driven attention signals and the response evoked by the (absent) stimulus (c.f. Prinzmetal et al., 2008). Unlike some previous studies in which standard contrasts were manipulated on a block-by-block basis and task difficulty was titrated for each standard contrast (thus, stimulus orientation offsets were varied across different standard contrasts;

Anton-Erxleben et al., 2010; Cutrone et al., 2014; Zhou et al., 2018), we intermixed trials of different standard and test contrasts within the same blocks (Schneider & Komlos, 2008). We chose this particular design for two reasons. First, we wanted the levels of standard contrasts to be unpredictable across trials so that subjects were not adapted to a certain standard contrast level. Second, we wanted to ensure that the distributions of stimulus orientation offsets were the same across standard contrast levels. By doing this, task difficulty would be varied across different standard contrasts, and this could influence the pattern of attentional modulations. Thus, we added in a manipulation of stimulus orientation offsets (0°, 10°, and 15° offsets with equal trial proportions for all experimental conditions) to address the possible influence of task difficulty on attentional modulations. Finally, trial orders were pseudo-randomized.

Analysis

Comparative judgment task

On each trial, two stimuli were presented, and we evaluated the probability that each was selected based on its contrast and the cued location. We, thus, operationalized one stimulus as the "standard" stimulus and the other as the "test" stimulus and then computed the probability of selecting each based on contrast and the locus of attention. Then the identity of the standard and the test were switched, and the analysis was repeated. As a result, both stimuli served as standards and tests on each trial. For the standard stimulus of a given contrast (i.e., the stimulus of interest), we calculated the probability that subjects reported the test stimulus (i.e., the stimulus that was paired with the standard stimulus, which could be rendered at 0%–80% contrast) as higher in contrast, termed here as p(test > standard). We did this step separately for when the test and standard stimuli were cued as well as for all trials and correct-only trials. In the all-trial analysis (Figures 3 through 5), to compute p(test > standard), we used the number of all trials in which the tested stimulus was chosen as a higher contrast as a numerator regardless of the accuracy of orientation discrimination, and we used the number of all trials as a denominator. For the correct-only analysis (Figures 3, 4, and 6), we instead used the number of trials in which the reported orientation of the stimulus of interest was correct as a numerator while keeping the denominator the same as the all-trial analysis. Note that we could not use the correct-only trials as the denominator because in some bins there would be no correct trials and, thus, the denominator would be zero.

Because there was no stimulus presented in the 0% contrast stimulus condition, we randomly labeled the
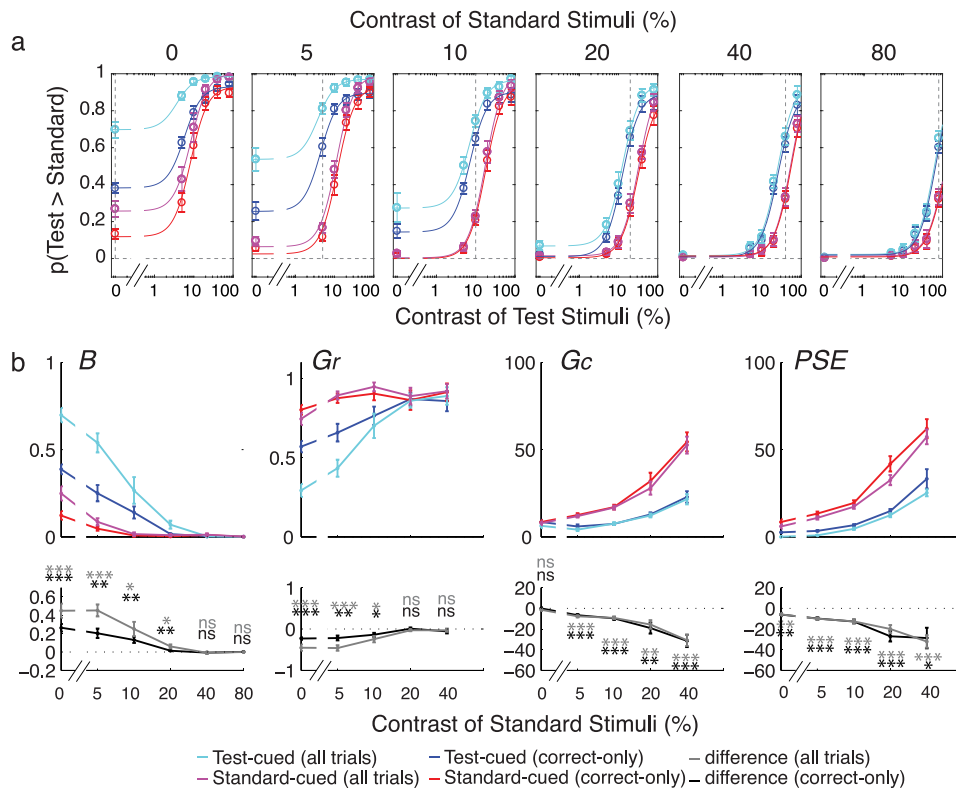
Figure 3. The data from the comparative judgment task. (a) The probability of subjects reporting the test stimulus as higher in contrast than the standard stimulus, plotted as a function of the contrast of the standard (0%–80%). This probability is plotted separately for trials in which the test stimulus was cued (cyan and blue for all trials and correct-only trials, respectively) and for trials in which the standard stimulus was cued (magenta and red for all trials and correct-only trials, separately). (b) Corresponding best-fit parameters of the psychometric functions are shown in panel a. Overall, attention-induced response bias was prominent when stimuli were rendered at low contrasts, and this response bias decreased as the standard contrast increased. This results in the increase in the baseline-offset parameter (*B*) and the corresponding reduction in the response gain parameter (*G_r*). In contrast, the degree of attention-induced changes in perceived contrast increased as measured by the contrast gain parameter (*G_c*) and perceived *PSE* increased as a function of the standard contrast. *, **, and *** indicate differences in fitting parameters compared to zero with *ps* < 0.05, 0.01, and 0.001, FDR-corrected, respectively (gray and black for all trials and correct-only trials). Error bars represent between-subjects ±1 *SEM*. Note that we did not include the *G_c*, *PSE*, and *G_r* parameters when the standard stimulus had a contrast of 80% because we could not obtain the entire psychometric function in this condition.

direction of the orientation offset (CW or CCW) before subjects performed the experiment and "correct" responses in this condition were determined based on a match to these randomly assigned labels. The difference between the probability of choosing a cued versus an uncued test stimulus on these 0% contrast trials was used to estimate the influence of exogenous cues on subjects' guessing or baseline-offset response bias (Figure 2a).

Next, we fit individual subject data with a Naka–Rushton equation using a maximum likelihood estimation method:

$$P(c) = G_r \frac{c^q}{c^q + G_c{}^q} + B, \quad (1)$$

where $P(c)$ is $p(\text{test} > \text{standard})$ a given contrast value, B is the baseline offset (indexing response bias), G_c is a contrast gain factor that controls the horizontal shift of the curve (indexing perceived appearance), G_r is a multiplicative response gain factor that controls the vertical shift of the psychometric curve, and q is the exponent fixed at 2 (Carandini & Heeger, 2012). The fit was constrained so that $0 \geq G_r \leq 1$, $0 > G_c < 100$, $P(100) \leq 1$, and $P(0) \geq 0$. This fitting method was done separately for each standard contrast, attention condition, and orientation offset. We also used another version of the Naka–Rushton function (adapted from Cutrone et al., 2014), termed a baseline-input model:

$$P(c) = G_r \frac{c + B_{input}{}^q}{(c + B_{input})^q + G_c{}^q}. \quad (2)$$

In this version, an increase in B_{input} will only lead to an increase in the baseline offset of the probability function (or raising the probability value at low
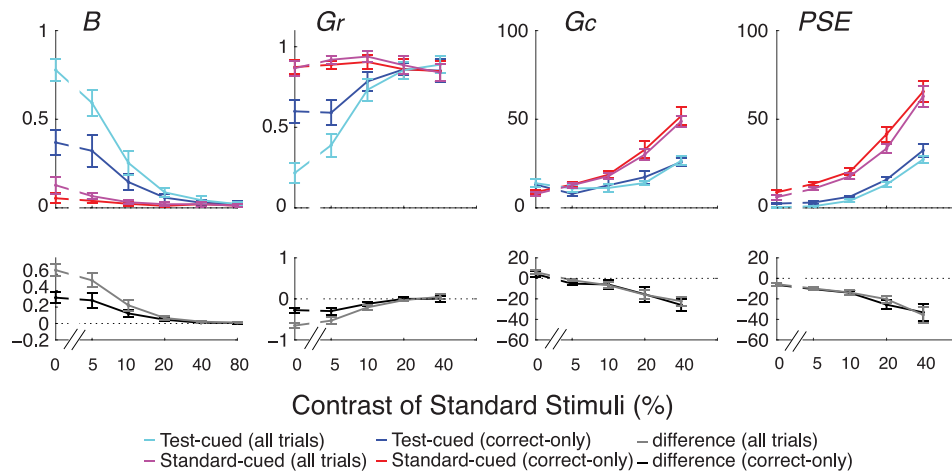
Figure 4. Corresponding best-fit parameters of the psychometric functions shown in Figure 3a. These parameters were obtained from the fitting protocol that excluded trials in which the test stimuli had 0% contrast. This fitting protocol produced data consistent with those from the main analysis (Figure 3b). Error bars represent between-subjects ±1 *SEM*.
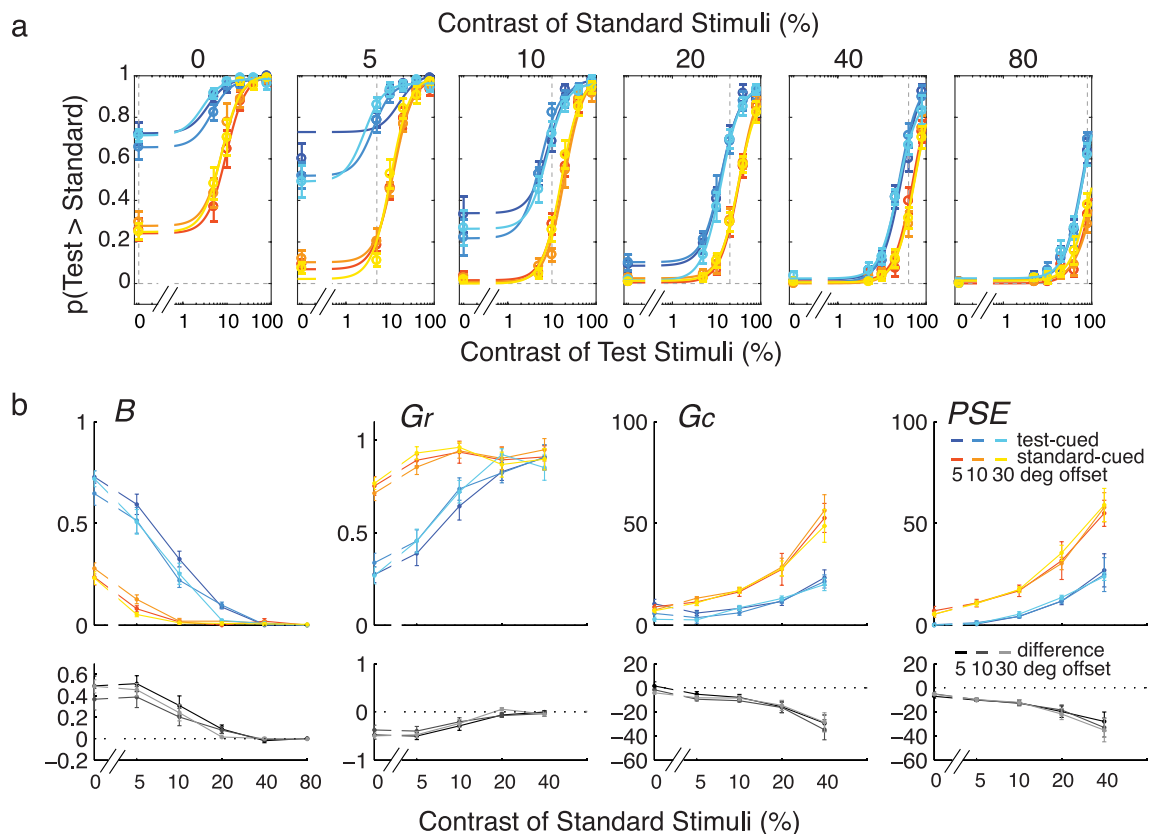

Figure 5. (a) The probability of subjects reporting the test stimulus as higher in contrast than the standard stimulus, plotted as a function of the contrast of the standard (0%–80%) across different difficulty levels (or orientation offsets). This probability was computed based on data from all trials and plotted separately for trials in which the test stimulus was cued (cold colors), for trials in which the standard stimulus was cued (hot colors), and for trials with stimuli of different orientation offsets. (b) Corresponding best-fit parameters of the psychometric functions shown in panel a. Consistent results can be seen across different difficulty levels. Error bars represent between-subjects ±1 *SEM*.
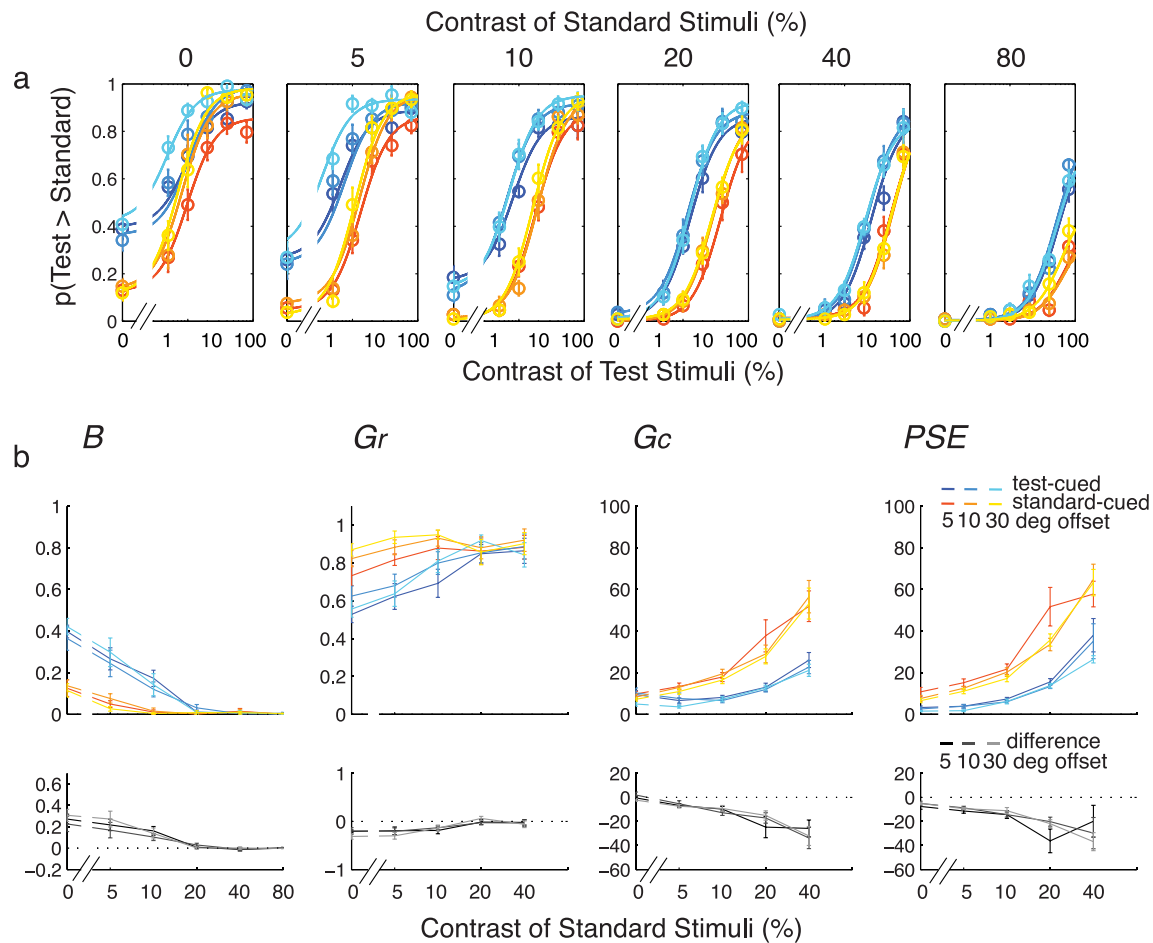
Figure 6. (a) The probability of subjects reporting the test stimulus as higher in contrast than the standard stimulus, plotted as a function of the contrast of the standard (0%–80%) across different difficulty levels (or orientation offsets). The probability was computed based only on correct trials and plotted separately for trials in which the test stimulus was cued (cold colors), for trials in which the standard stimulus was cued (hot colors), and for trials with stimuli of different orientation offsets. (b) Corresponding best-fit parameters of the psychometric functions shown in panel a. There was an increase in the number of correct trials when the task was easier, leading to increased G_r, decreased G_c, and decreased *PSE*. That said, task difficulty did not change the degree to which attention modulated any of the fit parameters as there was no interaction between attention and task difficulty. Error bars represent between-subjects ± 1 *SEM*.

contrasts) without changing the value of the function at high contrasts (see Figure 7c, left). That said, we chose Equation 1 instead of Equation 2 to the fit the psychometric functions in the comparative judgment task because Equation 1 yielded better fits in all subjects in the all-trial analysis and in a majority of subjects in the correct-only analysis (seven out of nine subjects). Moreover, Equation 1 yielded *B* values that fall into a realistic range ($0 \leq B \leq 1$), whereas in our data the baseline-input formula yielded *B* values that were $\gg 1$. Although we chose Equation 1 over Equation 2 for fitting the behavioral data, we used both equations to test different competing neural mechanisms that may influence attentional modulations of these psychometric functions, particularly the models that assume additive baseline shifts and baseline input changes indexed by changes in *B* and B_{input} in

Equations 1 and 2, respectively (see details in the next section).

Note that changes in subjective appearance have been traditionally indexed by changes in the point of subjective equality (*PSE*, the point at which the probability value reaches 50%; e.g., Anton-Erxleben et al., 2010, 2011; Carrasco et al., 2008; Carrasco et al., 2004; Cutrone et al., 2014; Fuller et al., 2009; Fuller et al., 2008; Ling & Carrasco, 2007; Prinzmetal et al., 2008; Störmer et al., 2009). However, only computing the *PSE* does not allow an assessment of possible changes in the baseline offset of the probability functions that are indicative of baseline-offset response bias. Thus, we focused our primary analysis of subjective appearance on the G_c parameter because it provides a suitable contrast sensitivity measure in the context of a model that also simultaneously estimates
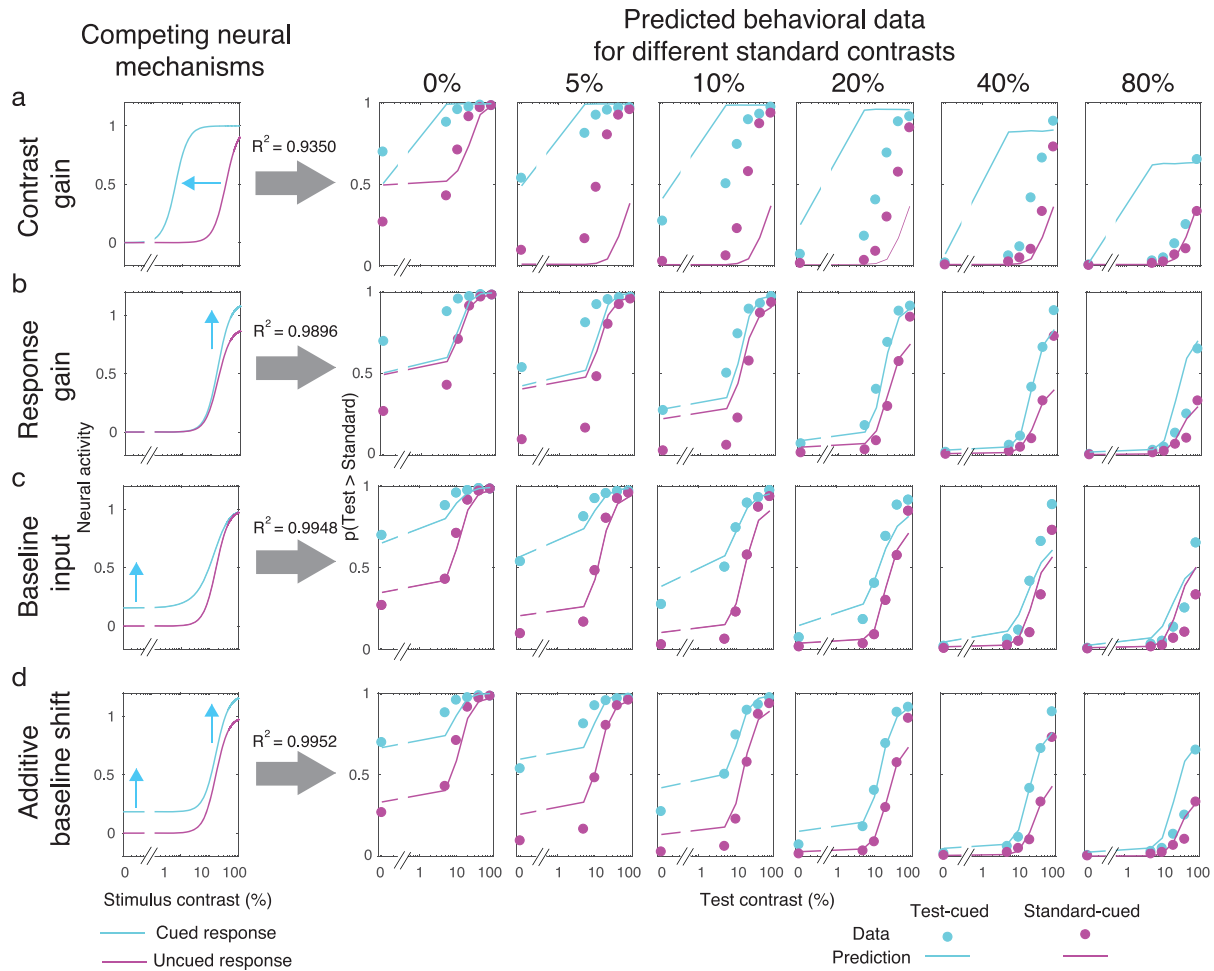
Figure 7. Predicting behavioral data based on different attentional mechanisms using SDT, plotted as a function of standard contrast. The leftmost panels show different neural mechanisms that may support attentional modulations of sensory responses. The data in each of these panels are estimated neural CRFs that yielded the best behavioral predictions for each model with the goodness of fit above each of the gray arrows. We also show the corresponding goodness of fit for each level of standard contrasts in Table 1. (a) Across all different models, the contrast gain model (i.e., attention shifting contrast sensitivity or the neural CRF horizontally to the left) was the worst at predicting the behavioral data). (b) The response gain model (i.e., attention multiplicatively enhances the neural CRF) performed better because it could capture attentional modulations of the psychometric functions at higher standard contrasts. However, gain alone could not capture cue-induced changes in the baseline-offset response bias at lower contrasts. (c) The baseline-input model (i.e., attention increasing the neural response at lower contrasts and even when the stimulus is absent) performed better than the response gain model with respect to predicting changes in the baseline-offset response bias at low standard contrasts. However, it performed worse than the response gain model at predicting attentional modulations at higher contrasts. (d) Overall, the additive baseline shift model (attentional shifting of the neural CRF up additively) performed the best among all models. Additive changes across all contrast levels can be used to predict the baseline-off response bias at lower contrasts and attentional gain at higher contrasts.

B. That said, we also report all data analyzed using the traditional *PSE* results for comparison.

After fitting Equation 1, we used three-way, repeated-measures ANOVAs to test the main effects of attention conditions (test cued/standard cued), contrast values of standard stimuli, and orientation offsets or difficulty (easy/medium/hard), and interactions between these factors on fitting parameters including B, G_r, G_c, and *PSE*. Note that we did not include the fitting data, specifically the G_r, G_c, and *PSE* parame-

ters, for the standard stimulus of 80% contrast because there were no test stimuli that were rendered higher than 80% contrast; hence, we could not obtain good estimates of these parameters. For all fitting parameters (B, G_r, G_c, and *PSE*), post hoc t tests were used to examine differences between attention conditions (test cued/standard cued) for each standard contrast (two-tailed). The false discovery rate (FDR) method was used to correct for multiple comparisons (Benjamini & Hochberg, 1995). Note that the same fitting procedures

and statistical analyses were performed separately for the data in which the probability values were computed from all trials and from trials in which correct stimulus orientations were reported (i.e., correct-only trials).

Modeling behavioral data

There are several types of neural mechanisms that are known to support attentional modulations of sensory responses (Cutrone et al., 2014; Herrmann, Montaser-Kouhsari, Carrasco, & Heeger, 2010; Itthipuripat, Garcia, et al., 2014; Itthipuripat & Serences, 2016; Kim, Grabowecky, Paller, Muthu, & Suzuki, 2007; Lee & Maunsell, 2009; Reynolds & Heeger, 2009; Zhang, Japee, Safiullah, Mlynaryk, & Ungerleider, 2016). These include contrast gain, response gain, baseline input, and additive baseline shift mechanisms. The contrast gain model posits that attention horizontally shifts neural responses measured as a function of stimulus contrast—referred to as the neural contrast response function (CRF). This leads to an increase in contrast sensitivity (Figure 7a, left). Alternatively, the response gain model predicts that attention amplifies the magnitude of the neural CRF multiplicatively, leading to an upward shift of the CRF that is prominent only at high stimulus contrasts (Figure 7b, left). The baseline input model posits that attention primarily leads to increases in the baseline input response, increasing neural activity at low but not at high contrasts (Figure 7c, left). Finally, the additive baseline shift model predicts that attention increases neural CRFs additively such that response amplitude increases by an equal amount across all stimulus contrast levels (Figure 7d, left).

To examine which of these competing models best describes the behavioral data, we adopted a quantitative modeling method based on signal detection theory (SDT; see a similar method in Cutrone et al., 2014). Here, we estimated $p(\text{test} > \text{standard})$ based on the amplitude difference between neural responses evoked by test and standard stimuli that can be drawn from the hypothetical neural CRFs given a certain level of hypothetical neuronal noise (or trial-by-trial variability). For each standard and test pair, we simulated 10,000 trials in which responses to the standard and test stimulus were randomly drawn from a normal distribution with means obtained from the hypothetical neural CRFs. Neuronal noise, or the standard deviation of the normal distribution, was assumed to be the same across all standard and test contrast levels as well as across the different attention conditions. Assuming a maximum likelihood decision rule, $p(\text{test} > \text{standard})$ was estimated based on the probability at which the test stimulus–related response was higher than the standard stimulus–related response in the 10,000 stimulated trials. For all different models, we first used a Naka–

Rushton function (Equation 1) to determine the hypothetical neural CRFs for the cued and uncued stimuli with the exponent (q) fixed at 2, the baseline offset parameter (B) fixed at 0, and the response gain parameter (G_r) fixed at 1 for both cued and uncued conditions. Next, we exhaustively searched for the noise and contrast gain (G_c) values shared across the cued and uncued conditions that yielded the best fit to the comparative task data in the all-trial analysis averaged across subjects by finding the noise and G_c values that yielded the maximum log-likelihood (noise was varied from 0.02 to 0.4 in 0.001 incremental steps, and G_c was varied from 0.02 to 100 in 0.01 incremental steps). After this step, we found that the best noise and G_c values were 0.292 and 16.39%, respectively.

For the contrast gain model (Figure 7a, left), we then varied the G_c parameter across the cued and uncued conditions by subtracting/adding 0.05 from/to the best common G_c value obtained from the previous step and exhaustively repeated this step until G_c in the cued condition reached 0%. Here, all the other parameters, including q, B, G_r, and noise, were fixed and were shared across attention conditions. For the response gain model (Figure 7b, left), we varied the G_r parameters across the cued and uncued conditions by adding/subtracting 0.0025 to/from 1 exhaustively until the G_r value in the uncued condition reached 0. Here, q, B, G_c, and noise were shared across attention conditions. For the baseline input model (Figure 7c, left), we optimized the B_{input} values across the cued and uncued conditions using Equation 2. Here, B_{input} in the uncued condition was fixed at 0, and B_{input} in the cued condition was varied from 0 to 15 in 0.03 incremental steps while fixing q, B, G_c, and G_r across attention conditions. For the additive baseline shift model (Figure 7d, left), we instead optimized the B values using Equation 1. Here, B in the uncued condition was fixed at 0, and B in the cued location was varied from 0 to 0.5 in 0.001 incremental steps while fixing q, B, G_c, and G_r across attention conditions. Note that the range of B was much narrower than the range of B_{input} because a much larger change in B_{input} was required to yield the same degree of baseline offset changes of the hypothetical neural CRFs. For each model, we selected the parameter that yielded the maximum log-likelihood. Then, we compared the predictability of different models by their goodness of fit (R^2) given that individual models had the same number of free parameters.

Equality judgment task

The equality data sorting method was similar to the comparative judgment analysis except that the dependent variable was now the probability of subjects reporting the cued and uncued stimuli having the same

contrast, termed here as p(same). We also collapsed the data across different orientation offsets because p(same) does not rely on response accuracy. Next, we fit individual subject data with a scaled and skewed normal function (after Azzalini, 1985; Schneider, 2011; Schneider & Komlos, 2008) using a maximum likelihood estimation method:

$$P(\Delta c) = 2h\sqrt{2\pi}\varphi\left(\frac{\Delta c - \alpha}{\sigma}\right)\Phi\left(\gamma\frac{\Delta c - \alpha}{\sigma}\right), \quad (3)$$

where $P(\Delta c)$ is p(same) as a function of the difference between the physical contrasts between the two visual stimuli (Δc). $\Phi(x) \equiv \int_{-\infty}^{x} \varphi(u)\mathrm{d}u$ and $\varphi(x) = \frac{1}{\sqrt{2\pi}}e^{-x^2/2}$. h is a scaling factor, γ is a skew parameter, α is the hypothesized attentional modulation in the perceived contrast of the cued stimulus, and σ is the standard deviation of the skewed normal function that describes the perceived contrast difference. The fit was constrained so that $0 \leq h \leq 1, \gamma \leq 5$, and $0 < \sigma \leq 100$. Next, we obtained the contrast values for which individual fit functions reached the maximum probability values (C_{max}) for each experimental condition and used a two-way, repeated-measures ANOVA to test the main effect of attention condition (test cued/ standard cued) and the contrast value of standard stimuli as well as their interaction on C_{max}. Because we found a significant interaction, we next performed post hoc t tests to examine differences between attention conditions (test cued/standard cued) for each standard contrast. We used one-tailed tests under the assumption that attention should increase the perceived contrast, and this was suggested by the reduction in G_c and PSE with attention observed in the comparative judgment task. The FDR method was used to correct for multiple comparisons (Benjamini & Hochberg, 1995).

Results

Comparative judgment task

Attention induces baseline-offset response bias for low-to-medium stimulus contrasts

Figure 3a shows the probability of subjects reporting the test stimulus as higher in contrast than a standard stimulus rendered at each individual contrast level (left to right columns). The cyan/blue and magenta/red data correspond to the test-cued (attended) and standard-cued (unattended) conditions, respectively. The corresponding baseline fit parameters (B) are shown in Figure 3b. We observed that B increased as the standard contrast decreased: main effect of contrast, $F(5, 40)$s = 113.92 and 69.78, both ps < 0.0001 for all trials and correct-only trials, respectively. This finding indicates that, when the standard stimulus was lower

contrast and less visible, subjects were more likely to report the 0% contrast test stimulus as having a higher contrast than the standard stimulus. We next compared data across attention conditions. We observed that attended stimuli were associated with a higher B compared to unattended stimuli: main effect of attention, $F(1, 8)$s = 26.58 and 23.77, ps = 0.0009 and 0.0012 for all trials and correct-only trials, respectively. However, the magnitude of attention effects on B decreased as the contrast of the standard increased: interaction between attention and contrast, $F(5, 40)$s = 29.62 and 21.45, both ps < 0.0001 for all trials and correct-only trials, respectively. Post hoc t tests revealed that attention increased B only when the standard stimuli had low-to-medium contrasts: all trials, 0%, 5%, 10%, and 20% with $t(8)$s = 5.7275, 6.9585, 3.2395, and 2.8071 and ps = 0.0004, 0.0001, 0.0119 and 0.0229, respectively, and an FDR-corrected threshold of 0.0229; correct-only trials, 0%, 5%, 10%, and 20% with $t(8)$s = 6.3024, 3.9091, 3.8276, and 4.1283 and ps = 0.0002, 0.0045, 0.0050, and 0.0033, respectively, and an FDR-corrected threshold of 0.0050. However, attention did not change B at higher contrast values: all trials, 40% and 80% with $t(8)$s = −0.9875 and −0.9319 and ps = 0.3523 and 0.3786, respectively; correct trials, all trials, 40% and 80% with $t(8)$s = −0.9149 and 0.5695, ps = 0.3870 and 0.5846, respectively. Collectively, these results suggest that attention induces response bias when the contrast of the standard is low to medium but not when the contrast of the standard is higher (Figure 1c and d).

Because there was no stimulus physically presented when the stimulus was in the 0% contrast condition, task accuracy in this stimulus condition was coded by comparing whether the orientation label (CW or CCW), which was randomly assigned for each 0% contrast trial, matched the subject's response. This stimulus-response coding should not affect attention-induced changes in the baseline parameter (B) as we showed consistent patterns of cueing effects on B regardless of response accuracy. Also note that the reduction of the proportion of p(test > standard) in the correct-only analysis (compared to the all-trial analysis) was more robust in the test-cued compared to the standard-cued conditions. This is not just a side effect of how stimuli and responses were coded. Instead, this observation can be explained by a more robust effect of response bias when the tested stimuli were cued compared to when they were uncued. Note that the proportion of p(test > standard) in the correct-only analysis relied mainly on the accuracy of orientation responses to the test stimuli, not the standard stimuli. Thus, when the test stimuli were cued, response bias should lead to more incorrect responses to the test stimuli and, hence, a lower proportion of p(test > standard) in the correct-only compared to the all-trial

analyses. That said, to ensure that the results were not simply an artifact of this arbitrary stimulus-response coding, we performed an auxiliary analysis in which we excluded trials in which the test stimuli were rendered at 0% contrast from the fitting protocol. As shown in Figure 4, we observed data patterns that were qualitatively consistent with those obtained from the main analysis (compared to Figure 3b).

Changes in the baseline parameter (B) necessarily impact G_r because the value of p(test > standard) cannot exceed one. Thus, as B increases, G_r decreases, providing a complementary measure of response bias. Overall, we observed a significant main effect of standard contrast, $F(4, 32)s = 30.35$ and 11.09, both $ps < 0.0001$ for all trials and correct-only trials, and attention on G_r, $F(1, 8)s = 27.22$ and 18.19, $ps = 0.0008$ and 0.0027 for all trials and correct-only trials, respectively, as well as a significant interaction between these two factors, $F(4, 32)s = 22.98$ and 6.90, both $ps < 0.0001$ and $= 0.0004$ for all trials and correct-only trials, respectively. Post hoc t tests revealed that this interaction was driven by an attention-related decrease in Gr at the lowest three contrast levels: all trials, 0%, 5%, and 10% with $t(8)s = -5.8182, -6.9721$, and -3.1432 and $ps = 0.0004, 0.0001$, and 0.0137, respectively, with an FDR-corrected threshold of 0.0137; correct-only trials, 0%, 5%, and 10% with $t(8)s = -6.9678, -3.5792$, and -2.9189 and $ps = 0.0001, 0.0072$, and 0.0193, respectively, with an FDR-corrected threshold of 0.0193. In contrast, the effects of attention on G_r were negligible at higher contrast values: all trials, 20% and 40% contrast with $t(8)s = -1.0872$ and -0.7514 and $ps = 0.3086$ and 0.4739, respectively; correct-only trials, 20% and 40% contrast with $t(8)s = 0.2238$ and -1.1051 and $ps = 0.8285$ and 0.3012, respectively. This overall pattern is consistent with the observation that attention increased bias when the standard stimuli had low contrasts and had little impact on bias when the standard stimuli had higher contrasts.

Attention induces subjective contrast appearance for higher stimulus contrasts

We found that the contrast gain parameter (G_c), which indexes changes in perceived contrast, increased as the contrast of the standard increased: main effect of standard contrast, $F(4, 32)s = 77.67$ and 70.20, both $ps <0.0001$ for all trials and correct-only trials, respectively. This G_c shift demonstrates that, when the standards became more visible, subjects were less likely to report test stimuli as having a higher contrast. On the other hand, attention cues had the opposite effect and led to decreases in G_c and to a corresponding shift of the psychometric curves to the left: main effect of attention, $F(1, 8)s = 32.17$ and 29.12, $ps = 0.0005$ and

0.0006 for all trials and correct-only trials, respectively. This leftward shift indicates that attended stimuli were more likely to be reported as higher contrast compared to unattended stimuli. Moreover, the magnitude of these attention-induced changes in G_c increased as a function of the contrast of the standard: interaction between attention and standard contrast, $F(4, 32)s = 20.37$ and 15.99, both $ps < 0.0001$ for all trials and correct-only trials, respectively. Post hoc t tests reveal that attention did not induce any change in G_c when the standard stimulus was rendered at 0% contrast, $t(8)s = -1.2900$ and 0.0213, $ps = 0.2331$ and 0.9835 for all trials and correct-only trials, respectively, but that G_c did change at all the other contrast levels: all trials, 5%, 10%, 20%, and 40% with $t(8)s = -7.8231, -7.6038, -3.7137$, and -5.6944 and $ps = 0.0001, 0.0001, 0.0059$, and 0.0005, respectively, with an FDR-corrected threshold of 0.0059; correct-only trials, 5%, 10%, 20%, and 40% with $t(8)s = -6.8541, -6.4164, -3.5470$, and -5.3112 and $ps = 0.0001, 0.0002, 0.0075$, and 0.0007, respectively, with an FDR-corrected threshold of 0.0075. Together, these results demonstrate that attention has a larger impact on perceived contrast as stimulus visibility increases. In addition, the observation that attention cues did not impact G_c when the standard stimulus was rendered at 0% contrast rules out the unlikely possibility that the presentation of a cue induced a false perception of an actual stimulus. If this had occurred, G_c should have shifted even when the standard was absent.

PSE overestimates changes in subjective appearance at lower contrasts

We found that *PSE* values also increased as the contrast of the standard increased: main effect of standard contrast, $F(4, 32)s = 440.64$ and 163.86, both $ps < 0.0001$ for all trials and correct-only trials, respectively, and decreased with attention: main effect of attention, $F(1, 8)s = 38.64$ and 23.48, $ps < 0.0001$ and $= 0.0013$ for all trials and correct-only trials, respectively. The magnitude of attention-induced *PSE* changes also increased as a function of standard contrast, leading to an interaction between attention and standard contrast: $F(4, 32)s = 18.14$ and 5.78, $ps = 0.0001$ and 0.0013 for all trials and correct-only trials, respectively. However, in contrast to the G_c results, attention had a significant impact on the *PSE* even when the standard stimulus was absent: $t(8)s = -4.2091$ and -3.5734, $ps = 0.0030$ and 0.0073 for all trials and correct-only trials, respectively, in addition to all the other contrast levels: all trials: 5%, 10%, 20%, and 40% with $t(8)s = -9.1597, -4.74790, -5.2329$, and -5.3155 and all $ps < 0.0001, = 0.0001, = 0.0008$, and $= 0.0007$ and an FDR-corrected threshold of 0.0030; correct-only trials, 5%, 10%, 20%, and 40% with $t(8)s =$

Model	R^2 for different standard contrasts (model ranking: first to fourth from best to worst)						
	0%	5%	10%	20%	40%	80%	All
Contrast gain (G_c-free)	0.9878 (third)	0.8331 (fourth)	0.9038 (fourth)	0.9468 (fourth)	0.9673 (fourth)	0.9902 (fourth)	0.9350 (fourth)
Response gain (G_r-free)	0.9804 (fourth)	0.9727 (third)	0.9861 (third)	0.9962 (second)	0.9936 (first)	0.9970 (first)	0.9896 (third)
Baseline input (B_{input}-free)	0.9974 (first)	0.9968 (first)	0.9968 (first)	0.9955 (third)	0.9905 (third)	0.9958 (third)	0.9948 (second)
Additive baseline shift (B-free)	0.9953 (second)	0.9939 (second)	0.9956 (second)	0.9976 (first)	0.9936 (first)	0.9969 (second)	0.9952 (first)

Table 1. Corresponding goodness of fit from different neural mechanisms at predicting behavioral data in Figure 7.

-7.9482, -6.8165, -5.2278, and -2.8713 and $ps <$ 0.0001, $= 0.0001$, $= 0.0008$, and $= 0.0208$, respectively, and an FDR-corrected threshold of 0.0073. Moreover, we found that the attention-induced changes in PSE were larger than G_c changes for low standard contrasts: all trials, 0%, 5%, and 10% with $t(8)s = -2.6394$, -2.6889, and -3.5714 and $ps = 0.0297$, 0.0275, and 0.0073, respectively, and an FDR-corrected threshold of 0.0297; correct-only trials, 0%, 5%, and 10% with $t(8)s = -3.4931$, -2.3009, and -3.1335 and $ps = 0.0082$, 0.0504, and 0.0139, respectively, and an FDR-corrected threshold of 0.0139. However, for higher contrasts, the attentional modulations of PSE and G_c were comparable: all trials: 20% and 40% with $t(8)s = -2.0493$ and -0.2831, $ps = 0.0746$ and 0.7843, respectively; correct-only trials, 20% and 40% with $t(8)s = -1.6658$ and 0.2720, $ps = 0.1343$ and 0.7925, respectively. These results suggest that with lower stimulus contrasts, PSE overestimated changes in perceived contrast compared to the contrast gain parameter (G_c).

No effect of task difficulty on attention-induced changes in response bias or subjective appearance

Note that Figures 3 and 4 shows the data collapsed across all difficulty levels (i.e., orientation offsets). Here, we also present data for different difficulty levels for the data computed across all trials and correct-only trials in Figures 5 and 6, respectively. For the all-trial data, we observed comparable patterns of results across difficulty levels. Statistically, there was no main effect of difficulty on any fit parameter, $F(2, 16)s = 3.13$, 1.54, 0.94, and 0.25 and $ps = 0.0714$, 0.2450, 0.4128, and 0.7791 for B, G_r, G_c, and PSE, respectively. For the correct-only data, we found no main effect of difficulty on B as expected given that response bias should not change with task difficulty, $F(2, 16) = 0.12$, $p = 0.8866$. However, there was an increase in the number of correct trials when the task was easier, which led to increased G_r, decreased G_c, and decreased PSE, $F(2, 16)s = 10.18$, 3.95, and 9.66 and $ps = 0.0014$, 0.0405, and 0.0081 for G_r, G_c, and PSE, respectively. That said, task

difficulty did not change the degree to which attention modulated any of the fit parameters as there was no interaction between attention and task difficulty $F(2, 16)s = 1.49$, 1.54, 0.27, and 0.69 and $ps = 0.2556$, 0.5036, 0.7666, and 0.5163 for B, G_r, G_c, and PSE, respectively.

Modeling suggests that different neural mechanisms explain attention-cueing effects in the behavioral data at low and high contrasts

Here, we compared several models of potential neural mechanisms that might cause the attentional modulations observed in the behavioral data measured across different levels of standard contrast. As shown in Figure 7 (left panels), these mechanisms include contrast gain (attention shifts the neural CRF horizontally), response gain (attention increases the neural CRF multiplicatively), baseline input (attention increases the baseline input of the neural CRF without changing responses at high contrasts), and additive baseline shift mechanisms (attention scales neural responses up equally across all contrast levels).

We found that the contrast gain model performed the worst among all the models (Figure 7a and Table 1). In particular, the contrast gain model overestimated the degree of attentional modulations across all standard contrast levels (except 0% contrast) while trying to account for large changes in the baseline-offset response bias at low standard contrasts. On the other hand, the response gain model performed better than the contrast gain model (Figure 7b and Table 1). Importantly, the response gain model was best at predicting attentional modulations of the psychophysical data at the two highest contrasts (40% and 80%). However, the model could not account for changes in baseline-offset response bias at lower contrasts. Conversely, the baseline input model could best describe baseline-offset response bias at lower standard contrasts even when there was no stimulus presented (0%–10%; Figure 7c and Table 1). However, the model was worse than the response gain model at capturing attentional gain modulations in higher standard

contrasts. The different patterns produced by the response gain and the baseline input models suggest that attentional modulations at the baseline of the hypothetical neural CRFs and those at higher contrasts differentially contribute to baseline-offset response bias and attention-induced changes in contrast appearance occurring at low and high standard contrasts, respectively. Consistent with this idea, the additive baseline shift model, which assumes an equal amount of neuronal changes at low and high stimulus contrasts, could capture both baseline-offset response bias at low contrasts as well as attentional gain modulations of the comparative data at high contrasts, making it the best model for predicting behavior across the full range of standard contrasts (Figure 7d and Table 1).

Equality judgment task

For the comparative judgment task, we found a large baseline-offset response bias (changes in B) at 0% and other lower contrast levels. Importantly, this baseline-offset response bias decreased as a function of the standard contrast, and this was accompanied by increased perceived contrast as measured by changes in G_c and PSE. That said, a lack of attentional modulation of the baseline-offset parameter at higher contrasts in the comparative judgment task does not necessarily account for other types of response bias. For example, response bias was driven by stimulus uncertainty when the cued and uncued stimuli were both rendered at similar suprathreshold contrasts, and the subject could not readily determine which stimulus had a higher contrast. Thus, the observed changes in G_c and PSE could be a result of response bias driven by stimulus uncertainty, especially when visual stimuli were rendered at high contrasts because the effect of stimulus uncertainty on response bias should increase as a function stimulus visibility. Thus, we ran a follow-up study in which another group of subjects performed the equality judgment task, which is thought to be less prone to this type of response bias (Beck & Schneider, 2016; Schneider, 2006, 2011; Schneider & Komlos, 2008).

Figure 8a shows the probability of subjects reporting the test and standard stimuli appearing at the same contrast at each individual standard contrast level (left to right columns). The cyan and magenta data correspond to the test-cued (attended) and standard-cued (unattended) conditions, respectively. As expected, although the comparative data had the largest differences when the attended and unattended stimuli were rendered at similar physical contrasts (Figure 3a, data points near/at the vertical dotted lines), the data from the equality task reveal negligible differences (Figure 8a). This indicates that the equality judgment

task may be less prone to response bias induced by stimulus uncertainty as suggested by previous studies (Beck & Schneider, 2016; Schneider, 2006, 2011; Schneider & Komlos, 2008). The height of the probability function also increased as a function of standard contrast, consistent with the assumption that the subjects' perceptual reports should be more precise as they were able to more clearly discriminate the contrast of the two stimuli. To examine changes in perceived contrast in the equality data, we compared the contrast values at which the probability functions reached their maximum value (C_{max}; see similar methods in Anton-Erxleben et al., 2011; Schneider, 2011). As predicted, we found a significant main effect of standard contrast on C_{max}, demonstrating that the probability functions peaked near the points at which the two stimuli were rendered at similar contrasts, $F(5, 30) = 224.09$, $p = 0$. Importantly, we found a significant interaction between attention and the magnitude of the standard contrast, $F(5, 30) = 6.00$, $p = 0.0006$. This interaction was driven by attentional modulations found to be prominent at 5% and 10% standard contrast levels, $t(6)s = -2.2467$ and -3.8203, $ps = 0.0329$ and 0.0044, respectively, with no significant attentional modulations at other standard contrast levels, $t(6)s = -1$ to 0.1432, $ps = 0.1780$ to 0.4454 with the FDR-corrected threshold of 0.0044. Overall, the absence of attentional modulations in C_{max} at high standard contrasts suggest that robust changes in G_c and PSE found at these contrast levels in the comparative task data might be driven in part by response bias induced by stimulus uncertainty.

Discussion

There has been a long-standing debate about the impact of cognitive factors such as attention on subjective perceptual experience (Anton-Erxleben et al., 2010, 2011; Carrasco et al., 2008; Carrasco et al., 2004; Cutrone et al., 2014; Firestone & Scholl, 2014b, 2014a, 2015; Fuller et al., 2009; Fuller et al., 2008; Ling & Carrasco, 2007; Prinzmetal et al., 2008; Störmer et al., 2009). Here, we show that the effects of spatial attention on visual appearance and on response bias can coexist and that the balance between these two types of modulation depends upon stimulus visibility and uncertainty. First, we found that, in the comparative judgment task when the standard was near threshold, exogenous attention cues induced a large baseline-offset response bias that led to an increase in the probability that subjects would choose the cued stimulus compared to the uncued stimulus. This bias was observed even when there was no stimulus present at the cued location (as reflected by changes in the
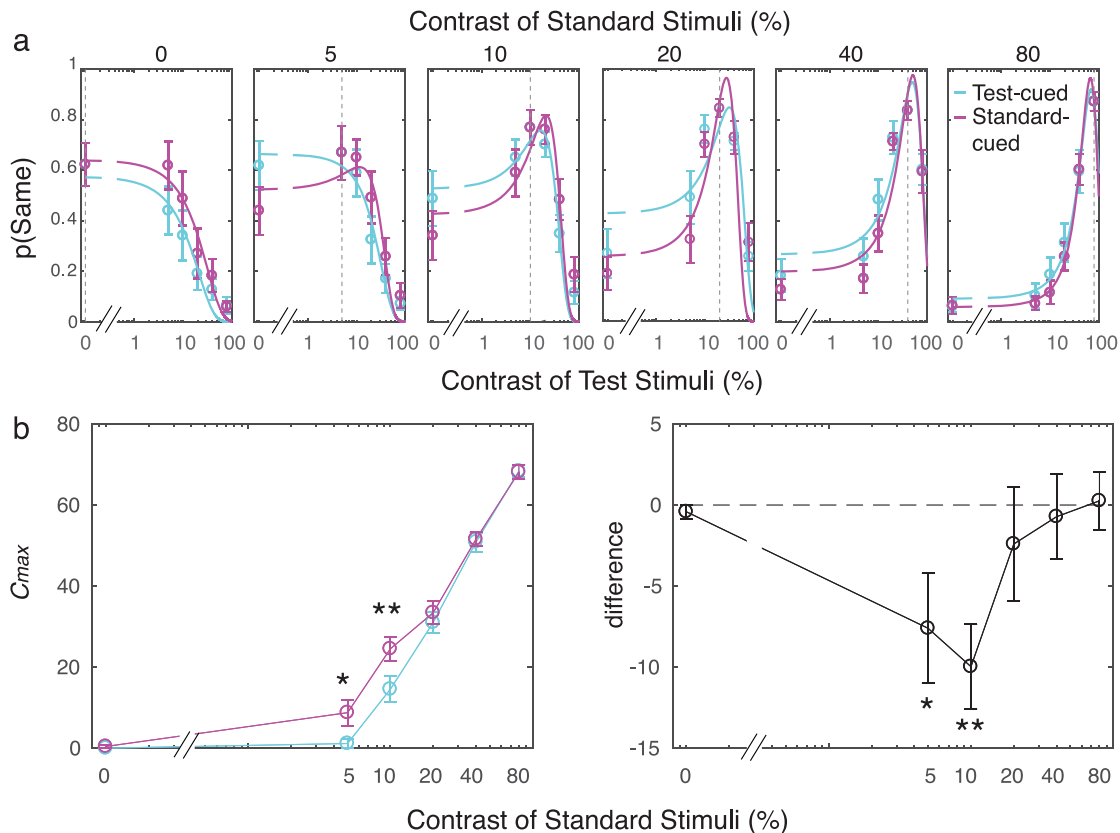
Figure 8. Data from the equality judgment task. (a) The probability of subjects reporting the test and standard stimuli having the same contrast, plotted as a function of the contrast of the standard stimulus (0%–80%). (b) Corresponding averaged C_{max} values obtained from fitting the data shown in (a) with a scaled skewed normal function across test- and standard-cued conditions. There was a significant interaction between attention (i.e., cueing condition) and standard contrast ($p = 0.0006$), which was driven by attention-induced changes in C_{max} at low contrast levels (5%–10%). * and ** indicate significant differences in C_{max} compared to zero with $p < 0.05$ (noncorrected) and $p < 0.01$ (passing the FDR-corrected threshold of 0.0044). Error bars represent between-subjects ± 1 *SEM*.

baseline offset or B). However, there were still small but significant changes in perceived contrast as indexed by changes in G_c and *PSE*. On the other hand, when the contrast of the standard was high, spatial attention primarily changed perceived contrast appearance. In the equality judgment task, we also found significant attentional modulations in the parameter that indexed changes in contrast appearance (C_{max}) for near-threshold visual stimuli. However, the robust changes in contrast appearance of suprathreshold stimuli observed in the comparative judgment task were diminished in the equality judgment task. This suggests that robust changes in G_c and *PSE* at high contrasts in the comparative judgment task may be driven by another type of response bias induced by stimulus uncertainty (i.e., when the cued and uncued stimuli were rendered at similar suprathreshold contrasts, subjects may be forced to select the cued stimulus without any change in appearance). Overall, the present findings help reconcile the long-standing debate about the effects of attention on perceptual experience and response bias and suggest that stimulus visibility and

uncertainty differentially mediate the balance between the effects of attention on contrast appearance and response bias.

Some previous studies have examined attention effects on the perceived contrast of test stimuli relative to standard stimuli across different contrast levels: 16%–36% contrast (Anton-Erxleben et al., 2011), 8% and 22% contrast (Carrasco et al., 2004), 5%–80% contrast (Cutrone et al., 2014), and 15%–60% (Zhou et al., 2018). However, these studies used the *PSE* metric to index changes in perceived contrast and did not examine the possibility that the baseline parameters of the probability functions increased due to cue-related baseline-offset response bias. Thus, relying solely on changes in *PSE* to index changes in contrast appearance may not capture all the nuances in the data, especially when the standard stimuli are low contrast. For instance, we showed that, when the standard stimulus had 0% contrast (i.e., the stimulus was absent), attention induced a substantial baseline-offset response bias as reflected by a large increase in the baseline parameter (B). Importantly, this occurred even

though the perceptual sensitivity did not change as reflected in the contrast gain parameter (G_c). However, although no change in the G_c parameter was observed, we found a significant shift the PSE value with attention even though there was no stimulus to compare. This result suggests that, in conditions in which there are changes in response bias that induce changes in the baseline parameter (i.e., low-to-medium standard contrast), changes in the PSE parameter may not accurately index changes in contrast appearance.

Attention has been shown to change the neural CRFs measured in visual cortex in many different ways (Figure 7, left panels). These include (a) contrast gain by which attention shifts the horizontal position of neural CRFs, (b) response gain by which attention scales neural activity multiplicatively, (c) baseline input increases by which attention predominantly enhances the baseline input of the neural CRFs without mediating neural responses at high contrasts, and (d) additive baseline shifts by which attention increases the magnitude of sensory signals equally across all contrast levels (Buracas & Boynton, 2007; Di Russo, Spinelli, & Morrone, 2001; Hara & Gardner, 2014; Itthipuripat et al., 2017; Itthipuripat, Cha, Deering, Salazar, & Serences, 2018; Itthipuripat, Ester, Deering, & Serences, 2014; Itthipuripat, Garcia, et al., 2014; Itthipuripat et al., 2019; Kim et al., 2007; Lee & Maunsell, 2009; Li, Lu, Tjan, Dosher, & Chu, 2008; Murray, 2008; Pestilli et al., 2011; Pooresmaeili, Poort, Thiele, & Roelfsema, 2010; Reynolds & Heeger, 2009; Reynolds, Pasternak, & Desimone, 2000; Sprague, Itthipuripat, Vo, & Serences, 2018; Sundberg, Mitchell, & Reynolds, 2009; Treue & Martinez-Trujillo, 1999; Wang & Wade, 2011; Williford & Maunsell, 2006).

Interestingly, results from psychophysical studies suggest that different types of attentional modulations can best account for attention-induced changes in contrast appearance. The original attention-alters-appearance study reported by Carrasco et al. (2004) found that the magnitude of attention-induced changes in contrast appearance increased approximately two-fold as the standard contrast increased from 8% to 22%, consistent with a response gain account. Similarly, the comparative data from the present study suggests that changes in perceived contrast also increase multiplicatively as a function of the standard contrast, but our data suggest that this happens across a wider range of contrast levels. The psychophysical data showing a larger effect of attention on contrast appearance at higher contrasts are naturally consistent with response gain modulations of the hypothetical neural CRFs. Consistent with this idea, our quantitative modeling based on SDT also suggests that response gain can best explain the increased degree of changes in contrast appearance at the highest standard contrasts (Figure 7b and Table 1). However, the response gain model did not capture modulations induced by changes in the baseline-offset at low standard contrasts, suggesting that response gain selectively indexes changes in contrast appearance. A previous neurophysiological study using electroencephalography (EEG) reported an attention-induced amplification of an early visually evoked potential (i.e., the visual P1 component) in response to attention-induced changes in contrast appearance (Störmer et al., 2009). Interestingly, when attentional modulations of the P1 component were measured parametrically as a function of stimulus contrast, we have consistently observed patterns of the P1 data showing multiplicative response gain (Itthipuripat et al., 2017; Itthipuripat, Ester, et al., 2014; Itthipuripat et al., 2019). Collectively, these results support the idea that response gain may play an especially important role in supporting changes in contrast appearance.

Unlike our comparative data, Zhou et al. (2018) recently found that attention-induced changes in perceived contrast were attenuated as the standard contrast increased from 15% to 60%, consistent with an increase in contrast gain. We speculate that the seemingly disparate findings between our present study and Zhou et al. may have been driven by differences in stimulus properties as suggested by the normalization model of attention (NMA; Herrmann et al., 2010; Itthipuripat, Garcia, et al., 2014; Lee & Maunsell, 2009; Reynolds & Heeger, 2009; Zhang et al., 2016). The NMA predicts that attention increases response gain when the stimulus is big and the attention is highly focused, whereas attention increases contrast gain when the stimulus is small relative to the focus of attention (Herrmann et al., 2010; Itthipuripat, Garcia, et al., 2014; Lee & Maunsell, 2009; Reynolds & Heeger, 2009; Zhang et al., 2016). Although it is hard to estimate the size of attention field in individual studies, the stimulus size in the recent study that showed an increase in contrast gain is much smaller (1° in radius; Zhou et al., 2018) than the stimuli used in studies suggesting that attention increases response gain (~2°–6° in radius; the present study; Carrasco et al., 2004).

Counter to the response and contrast gain accounts, Cutrone et al. (2014) reported that the magnitude of attention-induced changes in contrast appearance were comparable across 5%–80% standard contrast levels. According to their SDT-based modeling, they found that these changes in contrast appearance could be best explained by a baseline input mechanism, which posits that attention increases the magnitude of sensory signals at low contrasts without changing responses at high contrasts (Cutrone et al., 2014). However, the good fit of the baseline input model may be due in part to the fact that they did not account for potential changes in baseline-offset response bias, which the present study found to be most prominent at low

contrasts. Importantly, our SDT modeling suggests that the baseline-input mechanism captured most of this baseline-offset response bias at low contrasts, but the model performed relatively worse than the response gain model at predicting attentional modulations of the comparative data at higher contrasts (Figure 7c, Table 1). Thus, an additive-like elevation of neural responses across all contrast levels was required to account for both baseline-offset response bias and changes in contrast appearance. Accordingly, the additive baseline shift model in which attention increases neural activity in the same degree across all contrast levels was best at predicting the behavioral data across the full range of standard contrasts because it can account for both response-offset bias and attention-induced changed in contrast appearance (Figure 7d and Table 1).

Although we assume that the increase in the baseline offset parameter (B) indexes response bias, it is possible that attention strengthens the neural representation at the cued location even when the visual stimulus is not present. This could potentially make the cued location appear to have a higher luminance contrast. Consistent with this possibility, studies have shown that attention can also lead to an increase in neural activity measured in early visual cortex even when the stimulus is absent, giving rise to the additive baseline shift of the neural CRFs (Buracas & Boynton, 2007; Itthipuripat et al., 2019; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Murray, 2008; Pestilli et al., 2011; Sprague et al., 2018; Williford & Maunsell, 2006). This type of attentional modulation has been consistently observed in previous studies using fMRI), standing in contrast with several EEG studies that found either response or contrast gain modulations in early sensory evoked responses (e.g., the P1 component and steady-state visually evoked potential or SSVEP; Di Russo et al., 2001; Itthipuripat et al., 2017; Itthipuripat et al., 2018; Itthipuripat, Ester, et al., 2014; Itthipuripat, Garcia, et al., 2014; Kim et al., 2007; Lauritzen, Ales, & Wade, 2010; Wang & Wade, 2011).

Recently, we have conducted a study that used both fMRI and EEG to measure attentional modulations as a function of contrast in the same subjects performing the same behavioral task (Itthipuripat et al., 2019). First, we found that the additive baseline shifts of the fMRI-based CRFs were generally inconsistent with the multiplicative response gain modulations of the P1- and SSVEP-based CRFs (Itthipuripat et al., 2019). However, the patterns of fMRI results were consistent with attentional modulations of a later sustained negative-going event-related potential and slow-going EEG oscillations at alpha frequencies (~10 Hz) measured in the contralateral posterior occipital electrodes (Itthipuripat et al., 2019). We speculate that the additive shifts of these neural measurements may reflect the augmentation of the spatially specific neural represen-

tation, which could possibly make the cued location looked like it was higher in luminance contrast. Although this explanation might be possible, we argue that this potential change in perceptual experience induced by 0% contrast baseline shifts is unlikely related to the contrast appearance of the visual stimulus itself as subjects might perceive a light gray blob at the cued location, but it is unlikely that they would perceive a low-to-medium contrast grating at an empty cued location.

A lack of the baseline-offset response bias at high standard contrasts in the comparative judgment data does not necessarily mean that there was no response bias that arises from stimulus uncertainty at high contrasts, especially when the cued and uncued stimuli were rendered at similar suprathreshold contrast values. Therefore, we collected data from an equality judgment task that has been suggested to be less prone to this type of response bias (Schneider, 2006, 2011; Schneider & Komlos, 2008). We found that there were still changes in perceived contrast at 5% and 10% standard contrasts as indexed by changes in C_{max} of the equality functions. Additionally, the degree of changes was comparable to changes in G_c obtained from the data in the comparative judgment task. However, at higher standard contrasts, changes in C_{max} were negligible. These results suggest that the robust changes in appearance at high standard contrasts observed in the comparative judgment task might be partly influenced by response bias driven by stimulus uncertainty. That said, the interpretation of the equality data must be considered with caution because others have argued that the equality judgment task is less sensitive than the comparative judgment task in terms of tracking changes in appearance and that the equality judgment task is prone to changes in criterion settings (Anton-Erxleben et al., 2010, 2011).

Previous studies have shown that the effect of attention on visual appearance is not limited to just brightness and contrast, but is also evident in other visual domains, including spatial characteristics (frequency, gap size, positional repulsion), color (saturation but not hue), temporal features of visual stimuli (temporal frequency, motion coherence, and speed), and high-level features (e.g., facial attractiveness and emotion) (Abrams, Barbot, & Carrasco, 2010; Anton-Erxleben, Herrmann, & Carrasco, 2013; Cutrone, Heeger, & Carrasco, 2018; Fortenbaugh, Prinzmetal, & Robertson, 2011; Gobell & Carrasco, 2005; Kirsch, Heitling, & Kunde, 2018; Klein, Harvey, & Dumoulin, 2014; Mishra & Srinivasan, 2017; Pratt & Turk-Browne, 2003; Störmer & Alvarez, 2016; Suzuki & Cavanagh, 1997). Moreover, some of these appearance effects have been shown in behavioral tasks when attention was drawn either exogenously or endogenously toward stimulus locations (Abrams et al., 2010;

Barbot, Liu, Kimchi, & Carrasco, 2018; Carrasco et al., 2004; Cutrone et al., 2018; Gobell & Carrasco, 2005; Liu, Abrams, & Carrasco, 2009; Suzuki & Cavanagh, 1997). Our results suggest that stimulus visibility and uncertainty are two important factors that influence response bias. Thus, positive results from previous studies that only used the comparative judgment method and do not account for the potential contribution of response bias induced by visibility and uncertainty may not completely capture changes in appearance across other visual features. Future research could adopt experimental and analytic methods similar to those used here to determine if interactions between the effects of attention-induced changes in appearance and response bias are similarly expressed in other visual domains and tasks in which endogenous attention is manipulated.

In summary, we found that stimulus visibility and uncertainty regulated the balance between spatial attention effects on stimulus appearance and response bias. In particular, when visual stimuli were near threshold, attention-induced significant changes in contrast appearance that were consistently observed across both comparative and equality judgment tasks. However, there was also substantial baseline-offset response bias at near-threshold contrasts and another type of response bias driven by uncertainty due to the attended and unattended stimuli having similar suprathreshold contrasts. Over all, these results help resolve debates about the impact of attention on appearance and decision bias, and they also provide useful insights about how basic properties of visual stimuli interact with spatial attention to influence visual perception and decision making.

Keywords: attention, appearance, vision, response bias, uncertainty

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