Dissociable neural mechanisms of selective visual information processing underlie the effects of attention on visual appearance and response bias

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Abstract

It has been debated if attention can penetrate early perceptual representations to alter visual appearance or it simply induces response biases. Here, we tested these alternative accounts by evaluating attentional modulations of EEG responses recorded from human subjects while they compared the perceived contrasts of cued and uncued visual stimuli of varying physical contrasts. We found that attention enhanced the response gain of neural contrast response functions (CRFs) computed based on the amplitude of the P1 component, an early visually evoked potential. Quantitative models suggested that the response gain of the P1-based CRFs could account for attention-induced changes in perceived contrast. Instead, attentional cues induced changes in the baseline offset of the CRFs based on 9-12Hz alpha-band oscillations and these baseline-offset changes better accounted for cue-induced response biases. Together, these results suggest that different neural mechanisms underlie the effects of attention on perceptual experience and on response biases.

Introduction

Selective attention refers to the set of mechanisms that supports faster and more accurate processing of behaviorally relevant sensory information compared to irrelevant stimuli [1–8]. Many past studies suggest that – in addition to faster and more accurate processing – attention also penetrates early sensory processing to alter the subjective experience of visual stimuli [9–30] . In contrast, others have argued that attention does not alter perception and that reports of changes in subjective experience instead reflect cue-induced response biases [18,22,31–36].

In a recent study, we argued that attentional effects on visual appearance and on response biases co-existed and were expressed to varying degrees depending on the overall levels of stimulus contrast and decision uncertainty (determined by the degree of contrast difference between the cued and uncued stimuli [22] . For example, subjects often guessed that a cued stimulus had a higher contrast than an uncued stimulus when the cued and uncued stimuli were rendered at very low contrasts or at very high contrasts [22] However, changes in perceived contrast were most evident at intermediate contrast levels [17,18,22] .

While our recent findings suggest that attention can alter contrast appearance in certain circumstances and induce response bias in others, it is unclear whether changes in perceived contrast and response bias reflect different underlying neural processes. This is in part due to a lack of quantitative links between different neural markers of visual information processing and the effects of attention on visual appearance and response bias. To address this gap, we concurrently measured attentional modulations of two EEG signals that track early visual processing – the P1 component and the amplitude of posterior alpha oscillations – as well as EEG signals that track response preparation (the lateralized readiness potential or LRP). We then used a signal-detection-theory-based model to assess how cue-related modulations of each signal maps onto behavioral changes in perceived contrast and response bias [23,37–40] .

First, we found that cue-related modulations of the visually evoked P1 component predicted behaviorally assessed effects of attention on perceived contrast at low-to-mid-level of stimulus contrast. In contrast, we found that changes in alpha amplitude tracked response bias in the psychometric data when the cued and uncued stimuli rendered at either a very low or a very high contrast. Finally, we found that the LRP tracked response biases at both low and high contrast levels, even in the absence of attentional modulations of the P1 component, consistent with the LRP being an index of response-planning [41–45] . Together, these findings suggest that dissociable neural markers of information processing track attention-induced changes in subjective appearance and response-related attentional modulations of behavior.

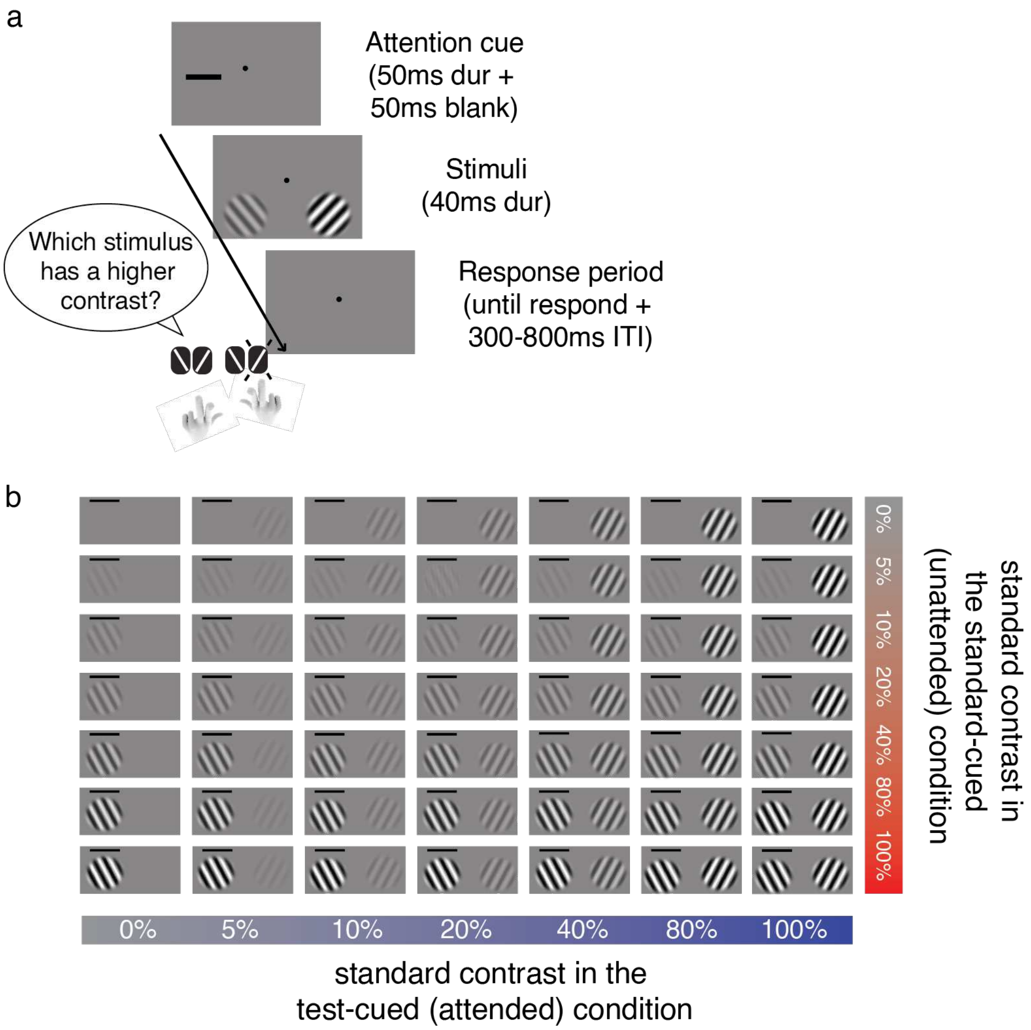


Figure 1. Task and stimuli. **(a)** The attention-cueing comparative contrast judgment task. Subjects were tasked with reporting the orientation of the stimulus they perceived as having a higher contrast. **(b)** Depiction of all contrast pairs in the cue-left condition. Note that the same fully-crossed contrast manipulation was also used in the cue-right condition.

Results

Study Design

The present study investigated the neural mechanisms that underlie the effects of attention on perceived contrast and response bias. We employed a comparative judgment task where the contrast of cued and uncued visual stimuli were fully crossed and systematically manipulated from 0%-100% Michelson contrast (Figure 1; see ref[22]and Materials and Methods). In this task, subjects used button press responses to report whether the cued or the uncued visual stimulus subjectively appeared to have a higher contrast value. EEG signals and behavioral responses were concurrently measured across the full range of contrast values for both cued and uncued stimuli. The simultaneous recording of the behavioral and EEG data allowed us to examine attentional modulations of behavioral and neural responses as a function of contrast (i.e., the neural contrast response function, or CRF) and to quantitatively link the attentional modulations of neural CRFs to changes in perceived contrast and response bias in the psychometric data (Figure 2).

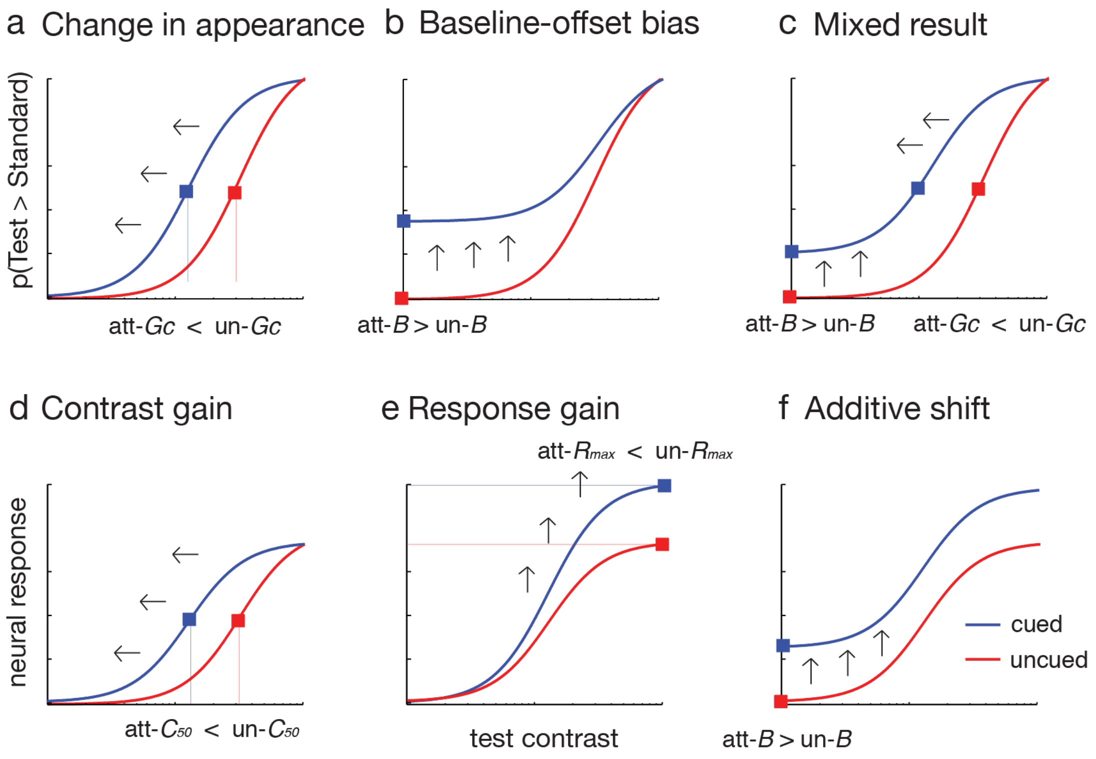


Figure 2. Predictions. **(a-c)** Alternative predictions for the *behavioral* results. (a) Attention increases the perceived contrast of visual stimuli via a leftward shift in the behavioral contrast response functions. In this scenario, attention should only decrease the contrast gain factor (G_c) and there should not be any changes in the baseline offset (B) or response gain (G_r). (b) Attention induces baseline-offset response bias (B; additive upward shift) without changes in a leftward shift of the CRFs (i.e. no change in G_c). This corresponds to a response bias for the cued stimulus without a change in perceived contrast. (c) Attention could induce changes in both subjective appearance and response bias as indexed by changes in both G_c and B, respectively. **(d-e)** Different patterns of attentional modulations in the neural contrast response functions (CRFs) measured over visual cortex. Since the estimated G_r and G_c parameters could extend beyond the realistic range of stimulus contrast (>100%), the response gain and contrast gain of neural CRFs were reparameterized as the maximal response (R_{max} or the response at 100% contrast minus the baseline offset) and the semi-saturation contrast (C_{50} or the contrast at which the response reached half maximum), respectively. (d) Attention increases neural contrast sensitivity or contrast gain as indexed by changes in the semi-saturation contrast factor (C_{50}). Alternatively, attention could increase the multiplicative response gain or the slope of the neural CRFs as indexed by the maximum neural response (R_{max}). Lastly, attention could shift the baseline offset of the neural CRFs so that overall responses to the cued stimulus are enhanced in a manner that is independent of stimulus contrast. One past modeling study from our group suggests that the response gain mechanism (panel e) is sufficient to account for psychophysical changes in contrast appearance (panel a). However, a change in the baseline of neural CRFs (panel f) is

required to explain changes in the behavioral baseline-offset response bias (panel b) (see ref[22]), That said, there is still no neural evidence that validates these modeling predictions.

Attention induces changes in contrast appearance and response bias

To examine the effects of attention on changes in perceived contrast and response bias, we performed two complementary analyses that compared the probabilities of reporting either the cued or the uncued stimulus as having a higher contrast. First, we computed the probability of reporting a cued stimulus at each contrast level as having a higher perceived contrast than the uncued stimulus at all other contrast levels. For example, we computed the probability of reporting a 5% contrast cued stimulus as having a higher contrast than a 0%, 5%, 10%, …, 100% uncued stimulus and we repeated this exhaustive analysis for each possible contrast level of the cued stimulus. We then performed an analogous analysis quantifying the probability of reporting an uncued stimulus at each contrast level as having a higher perceived contrast when it was paired with a cued stimulus of all possible contrast values. Note that for purposes of data exposition, we always refer to the stimulus being held constant as the standard stimulus and the stimulus being varied as the test stimulus. Thus, in the example above, the 5% contrast cued stimulus would be the standard compared against uncued test stimuli that ranged in contrast systematically from 0% to 100%. Importantly, both the cued and uncued stimuli served as standard and test stimuli depending on the nature of the analysis being performed. This allowed us to plot summary data for cued and uncued stimuli on the same axes as shown in Figure 3, with data from the cued stimulus plotted in blue/cyan and data associated with the uncued stimulus in red/magenta.

To better quantify these behavioral data, we fit each psychometric function using a Naka-Rushton (NR) function [22,46–48] to estimate the baseline offset (*B)*, contrast gain (G_c), and response gain (G_r), which control the baseline, the horizontal position (e.g. leftward shift), and the slope of the behavioral CRFs, respectively (see Figures 2a-c and Methods and Materials). Here, we used changes in the baseline offset (*B*) to track cue-induced response bias on the basis that reporting the cued contrast as higher contrast than the uncued stimulus when the cued stimulus was 0% contrast must reflect bias[22] . On the other hand, we used changes in contrast gain (G_c) to index changes in contrast appearance. We focused on G_c instead of the point of subjective equality (PSE) because it has previously been suggested that PSE overestimates changes in contrast appearance when there were significant amounts of cue-induced response bias [18,22,32–35].

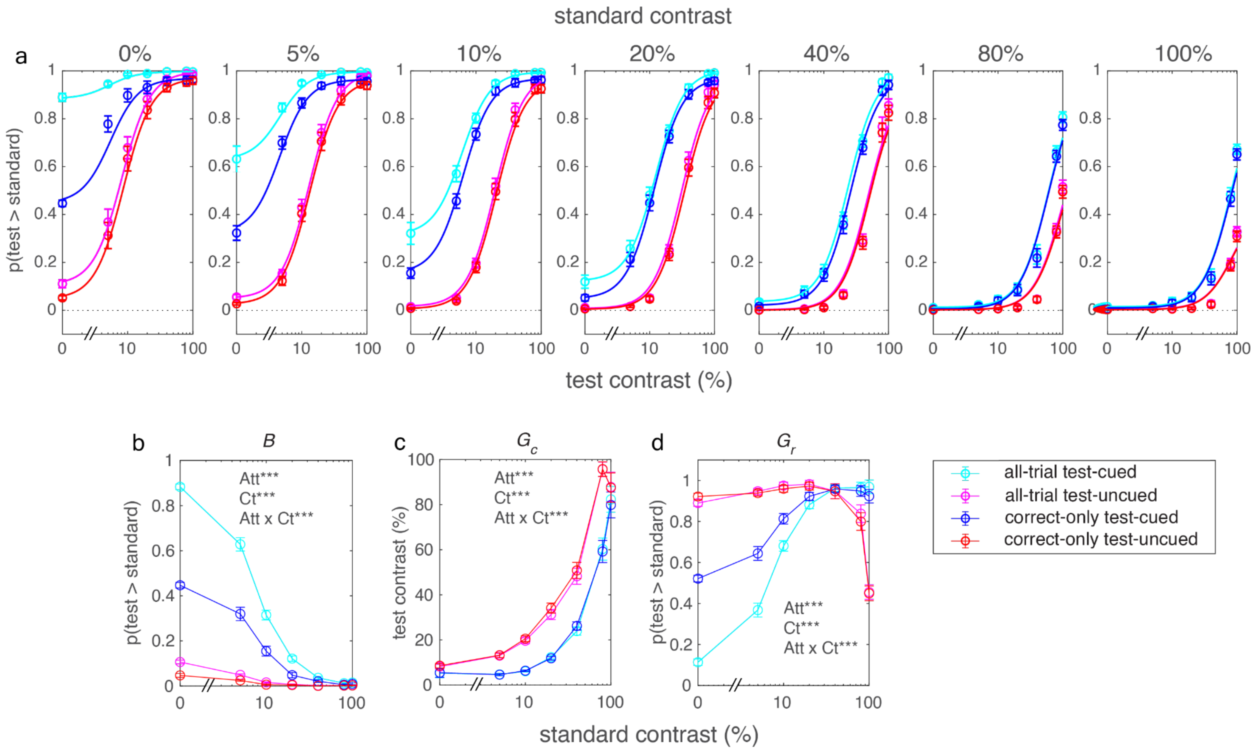


Figure 3. Behavioral data. **(a)** The probability that subjects reported the test stimulus (i.e., the stimulus of interest, either cued or uncued) as having a higher contrast than the standard stimulus (i.e., the paired cued or uncued stimulus) plotted as a function of test contrast for all possible standard contrast levels. We used *B* to index the baseline-offset response bias that the cued stimulus had a higher contrast than the uncued stimulus even when the cued stimulus was not physically present (i.e., presented at 0% contrast) [18,22]. **(b)** Overall, we found a significant attention-induced increase in response bias when the contrast of the standard was relatively low, with a decreasing effect of response bias as the contrast of the standard increased. **(c)** The contrast gain parameter (G_c) controls the horizontal position of the psychometric function, which we used to index changes in contrast appearance. Attention reduced G_c, as indexed by a leftward shift in the psychometric functions, which should correspond to an increase in perceived contrast, predominantly at low-to-mid-levels of standard contrast. **(d)** The response gain parameter (G_r) controls the slope of the psychometric function. Note that G_r and *B* are conflated because behavioral response probabilities could not exceed 1. At low-to-mid level standard contrasts, there were large attentional effects on *B* (panel b). Thus, this increase in B must also lead to a decrease in slope, or G_r, given the fixed ceiling of the psychometric response functions. Instead, attention increased G_r without changing *B* at higher contrasts (ie., 80%-100%). Error bars represent the within-subject standard errors of the mean (±1 SEMs). Att***, Ctt**, and Att x Ctt*** represent the significant main effects of attention, standard contrast, and the interaction between the two factors, respectively (all p's <0.001).

Consistent with a recent report from our group, we found that the effects of attention on contrast appearance and response bias depend on the overall level of stimulus contrasts and stimulus uncertainty (i.e., whether the stimuli were rendered at the same contrast)[22]. When there was no stimulus presented at the cued and the uncued locations, subjects were more likely to report that the cued location had a higher contrast than the uncued location (even though no stimuli were presented, see the leftmost panel of Figure 3a). This response bias resulted in an increase in the baseline-offset parameter (*B*) of the psychometric function. Importantly, this response-bias-induced baseline-offset became smaller as the contrast of the uncued stimulus increased. To statistically evaluate these effects, a repeated measures two-way ANOVA with attention (cued vs. uncued) and the contrast of the standard as factors revealed a significant main effect of attention on *B*: $F(1, 19) = 60.82$, $p < 0.001$, a significant main effect of the contrast of the standard stimulus on *B*: $F(6, 114) = 159.93$, $p < 0.001$, and a significant interaction between attention and the contrast of the standard stimulus on *B:* $F(6, 114) = 114.94$, $p < 0.001$. A separate ANOVA was also performed on only the correct trials (i.e., we only counted the comparative responses in trials where subjects correctly discriminated the orientation offset of the chosen visual stimulus) and revealed the same pattern of results: there was a significant main effect of attention on B: $F(1, 19) = 61.73$, $p < 0.001$, a significant main effect of the contrast level of the paired or standard stimulus on *B*: $F(6, 114) = 128.96$, p's < 0.001, and a significant interaction between attention and the contrast of the standard stimulus on *B*: $F(6, 114) = 100.88$, $p < 0.001$. Post-hoc paired t-tests showed that the attention effects on *B* were significant for standard contrast levels of 0%, 5%, 10% and 20% (t(19)'s = 3.26-24.00 and 2.88-24.57 for all trials and correct-only trials, respectively, all p's $\leq$ 0.0042, Holm-Bonferroni corrected). However, differences in B were not significant for standard contrast levels of 40%, 80% and-100% (t(19)'s = 1.3612-1.8034 and 1.38-1.88 for all trials and correct-only trials, respectively, all p's $\geq$ 0.0751). Overall, these results suggest that attention indeed induced response bias especially when the contrasts of the standard stimuli were relatively low and attention-induced response bias reduced as the standard contrasts increased.

To measure changes in contrast appearance, we next examined attentional modulations of the contrast gain parameter (G_c) that controls the horizontal shift of the psychometric functions. We found that attention reduced the G_c parameter which led to a leftward shift of the psychometric functions. However, these leftward shifts were most pronounced at low-to-middle standard contrast levels and then became smaller as the standard contrast approached 100%. A two-way repeated measures ANOVA on G_c with attention and standard contrast as factors revealed a significant main effect of attention: F(1, 19)'s =48.08 and 35.42, p's < 0.001, a significant main effect of standard contrast: F(6, 114)'s = 111.89 and 103.21, p's < 0.001, and a significant interaction between the two factors: F(6, 114)'s = 9.64 and 9.34 for all trials and correct-only trials respectively, with p's < 0.001. Post-hoc paired t-tests showed that in the all-trial analysis, attention effects on G_c were significant for standard contrast levels of 5%, 20%, 40%, and 80% (t(19)'s = -2.7713 to -9.1541 p's $\leq$ 0.0122, Holm-Bonferroni corrected), but were not significant for standard contrast levels of 0%, 10% and 100% contrasts (t(19)'s = 1.3612-1.8034, p's $\geq$ 0.0153, not passing the corrected threshold of 0.0125). For the correct-only trials, the attention effects on G_c were significant for the standard contrast levels of 10%-80% contrast (t(19)'s =-9.1541 to -2.7713, p's $\leq$ 0.0122, Holm-Bonferroni corrected) but were not significant for the standard contrast levels of 0% and 100% contrast (t(19)'s = -0.9563 and -2.1384, p's $\geq$ 0.0457, not passing the corrected threshold of 0.025). These results suggest that attention could also alter contrast appearance but the appearance effects were restricted to low-to-mid-level contrasts.

The lack of a significant contrast gain modulation (G_c) at the highest standard contrast was in part due to the fact that the psychometric functions in this condition did not reach the maximum possible value of 1 (i.e., p(stimulus of interest > paired stimulus) was less than 1). Thus, attentional modulations of the psychometric functions at the highest standard contrast (100%) manifested as an increase in the response gain parameter (G_r), corresponding to a steeper slope of the psychometric functions (t(19)'s = 10.93 and 10.23 for all trials and correct-only trials, respectively, p's <0.001, 2-tailed). Note that a recent study has shown that attention-induced gain changes measured at high standard contrasts might not purely reflect changes in appearance per se and could be influenced by response bias driven by high stimulus uncertainty (i.e., subjects were unsure which of the two already high contrast stimuli had a slightly higher contrast, thus they were biased to follow the attentional cue) (see ref [22]).

Possible mechanisms of attention-related changes in appearance

Several neural mechanisms have been proposed to explain attention-related modulations in information processing and attention-related changes in stimulus appearance (Figures 2d-f) [17,23,38,48–67]. The contrast gain account posits that attention shifts the neural CRFs horizontally to the left, consistent with attention increasing the contrast sensitivity of neural responses that respond to cued stimuli (Figure 2d) [17,55,59,60]. In addition, multiplicative response gain models posit that attention can amplify neural activity to increase the slope of neural CRFs, thereby increasing sensitivity to detect small differences in contrast (Figure 2e) [48,51,55,61–63] . Lastly, the additive shift account suggests that attention can lead to increases in the baseline activity of neural CRFs (Figure 2f) [23,38,54,64–67]. In the following sections, we examined how each of these mechanisms might best link attentional modulations of the P1 event-related potential (EPR) component and of the amplitude of alpha band oscillations as recorded over human visual cortex.

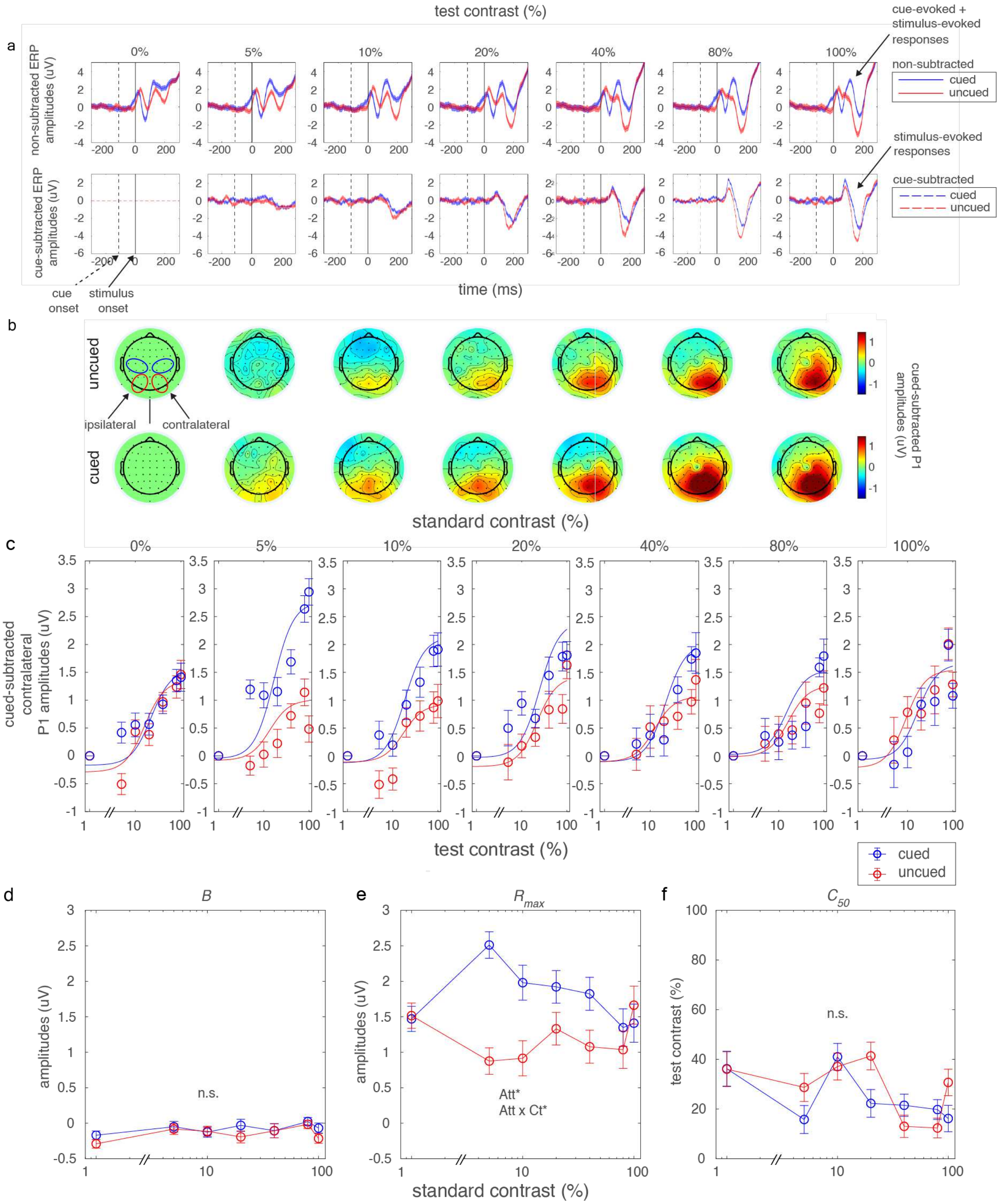
Predictions for linking neural responses and behavior

Here, we targeted two EEG indices that are thought to track different aspects of visual information processing: (i) the P1 component, which is an early visually evoked potential that peaks approximately 100ms after stimulus onset and (ii) the amplitude of posterior occipital alpha-band oscillations (i.e., EEG oscillations in the ~9-12Hz band). We used these two EEG markers because they have been previously linked to bias in subjective contrast perception [29,68,69]. That said, we hypothesized that the attentional modulations of the visual P1 component and alpha band activity would differentially relate to the effects of attention on visual contrast appearance and response bias for several reasons. First, attention enhances the amplitude of the P1 component [70–73] and attentional gain of P1 amplitude has been linked to improved detection and discrimination for low-level visual features like orientation [39,62,73]. Recent studies have also found that selective attention induces a multiplicative response gain of neural CRFs based on P1 amplitude (see Figure 2e) and quantitative models suggest that these gain modulations predict attention-related changes in perceptual contrast discrimination thresholds [39,62]. Importantly – especially for the present experiment – attentional gain of P1 amplitude has been previously related to an increase in the perceived contrast of cued compared to uncued visual stimuli [29,69]. Although changes in subjective experience were not quantitatively linked to changes in P1 amplitude using a formal linking model, this finding [29,69] – coupled with suggestive earlier work [26,55,62,69] – is consistent with the hypothesis that multiplicative gain of the P1 is tightly coupled with attention-induced changes in perceived contrast [22].

In addition to changes in perceived contrast, attention is also thought to influence other aspects of behavioral performance. For example, prior work suggests that attention cues – particularly the peripheral cues used in most comparative judgment tasks – can induce a bias such that subjects are more likely to select the cued stimulus as having a higher contrast, independent of the perceptual experience of the subject [22,31–35]. We hypothesized that these attention-induced changes in response bias might be related to modulations in the amplitude of oscillatory activity in the alpha band. First, past studies have found that alpha amplitude at the time of stimulus onset predicts shifts in response bias (i.e., response criterion) but not shifts in perceptual sensitivity in some visual detection and discrimination tasks [74–79]. Second, attention has been shown to reduce the amplitude of contralateral posterior occipital alpha band oscillations even in the absence of visual stimuli, suggesting that it may simply reflect top-down inputs from downstream areas in visual cortex onto early sensory areas and does not tract the interaction between attention and sensory inputs [49,80]. Consistent with this idea, recent studies have found that attention shifts the baseline offset of CRFs based on the amplitude of alpha oscillations, reflecting a shift in general arousal or responsiveness that does not interact with the actual intensity of the stimulus (Figure 2f [49,80]. Based on these observations, we predicted that a shift in the baseline offset of alpha-based CRFs would be systematically linked with attention-induced response bias [22]. Finally, even though a recent study has previously linked alpha band modulations to bias in subjective contrast perception [68], it did not examine response bias that prominently occurred with low contrast stimuli [11,18,22] and did not rule out the possibility that response bias could also occur even with near- and supra-theshold stimuli [18,31–35,49].

Attention amplifies response gain of the P1 response

To obtain the stimulus-specific P1 activity, we first subtracted the event-related potentials (ERPs) elicited in trials with a cue followed by 0%-contrast cued and uncued stimuli (termed as the cue-only trials) from the ERPs evoked by trials with a cue plus the stimulus in each attention condition and contrast level (Figure 4a in the top row; see refs [39,62] and Materials and Methods). After this procedure, we observed a clear P1 component that peaked ~60-90ms post-stimulus over posterior occipital electrodes that were contralateral to the stimulus of interest (Figure 4a in the bottom row). Next, we plotted the mean amplitude of the isolated P1 component as a function of stimulus contrast (i.e., test contrast) to obtain the P1-based CRFs for each attention condition and contrast level of the standard stimulus (Figure 4c). Then, we fit these P1-based CRFs with a Naka-Rushton equation (Equation 1) to examine changes in the baseline offset (B), response gain (G_r) and contrast gain (G_c) of the neural CRFs. Since the estimated G_r and G_c parameters can potentially go beyond the realistic range of stimulus contrast (>>100%), we reparameterized the response gain and contrast gain of neural CRFs as the maximal response (R_{max} or the response at 100% contrast minus the baseline offset) and the semi-saturation contrast (C_{50} or the contrast at which the response reached half maximum), respectively (see Materials and Methods, section Early Sensory Evoked Response).



a
test contrast (%)
0%
5%
10%
20%
40%
80%
100%
non-subtracted ERP amplitudes (uV)
cue-subtracted ERP amplitudes (uV)
cue-evoked + stimulus-evoked responses
non-subtracted
cued
uncued
stimulus-evoked responses
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-200
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time (ms)
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b
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C_{50}
test contrast (%)
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standard contrast (%)
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10
100

Figure 4. The P1 component across cue and standard contrast conditions. **(a: top row)** The non-subtracted ERPs from the contralateral posterior occipital electrodes (see the red circle on the right hemisphere of the head model in **(b)**). These non-subtracted ERPs contained both cue-evoked and stimulus-evoked responses. Note that in these plots the cue onset and stimulus onsets were at -100 ms (vertical black dotted lines) and 0 ms, respectively (vertical black solid lines). The data were baseline-corrected from -200 to 0ms before the cue onset. **(a: bottom row)** The extracted stimulus-evoked potentials obtained after subtracting the cue-only condition (the leftmost panel from the top row of panel a) from all other stimulus contrast conditions. We observed a P1 component peaking ~60-90 ms with its amplitude increasing as a function of the contrast of the test stimulus. Moreover, attention increased the P1 amplitude at high test stimulus contrast levels. All shaded areas represent within-subject SEMs. **(b)** Topographical maps of the P1 amplitude averaged across ~60-90ms post-stimulus. The rings mark each of 5 electrodes over the contralateral/ipsilateral posterior occipital sites where the P1 (Figure 4) and alpha data were analyzed (Figure 5; red rings) and on the contralateral/ipsilateral central sites where the LRP data were analyzed (Figure 7; blue rings). **(c)** The P1-based contrast-response functions (CRFs) plotted separately for the cued and uncued conditions across different levels of standard contrast. Attention enhanced the multiplicative response gain of the P1 data. **(d-f)** The corresponding best-fitting parameters from the NR function. **(d)** There were no differences in the baseline offset. **(e)** Attention selectively enhanced response gain indexed by an increase in the maximum response of the P1 component (R_{max}), which were relatively more robust at low-to-mid-level standard contrasts. **(f)** There were no differences in the semi-saturation contrast level or the level at which the P1 amplitude reached half maximum (C_{50}). Error bars represent the within-subject SEMs where the mean values between attention conditions were removed before computing the standard errors. Att* and Att x Ctt* represent the significant main effect of attention ($p < 0.05$) and the trending interaction between attention and standard contrast, respectively ($p = 0.053$). n.s.= non-significant.

Overall, we found that attention increased the maximum response (i.e., R_{max}) of the P1-based CRF (main effect of attention: $F(1, 19) = 6.26$, $p = 0.0217$). In addition, there were larger attentional modulations at the low-to-mid-level standard contrasts (5%-20%) compared to when the standard was absent (0% contrast) and when the standard had a higher contrast (40%-100%) (Figure 4e). This gave rise to a trending interaction between attention and the contrast of the standard stimulus ($F(6, 114) = 2.16$, $p = 0.0586$). Post-hoc paired t-tests showed significant and marginal attentional modulations at the low-to-mid-level standard contrasts ($t(19)$'s = 4.33, 2.04, and 2.00 with p's = 0.0002, 0.0280, and 0.0297 for 5%, 10%, 20% contrasts, 1-tailed due to the predicted directions of the modulations with Holm-Bonferroni corrected threshold of 0.0071) but not at 0% contrast ($t(19) = 0.37$ with $p = 0.3581$, 1-tailed) or high standard contrast levels ($t(19)$'s = 1.26, 0.36, and 0.20 with p's = 0.1113, 0.3612, and 0.4215 for 40%, 80%, 100% contrasts, 1-tailed).

Importantly, attention had a selective effect on the R_{max} parameter of the P1 response, as there were no changes in any other parameters (Figures 4d and f; main effect of attention: $F(1, 19) = 2.17$, $p = 0.1572$ for B, $F(1, 19) = 0.99$, $p = 0.3329$ for C_{50}; main effect of standard contrast level: $F(6, 114) = 1.25$, $p = 0.2856$ for B, $F(6, 114) = 1.53$, $p = 0.1741$ for C_{50}; interaction between the attention and standard contrast: $F(6, 114) = 0.20$, $p = 0.9756$ for B; $F(6, 114) = 0.96$, $p = 0.4544$ for C_{50}). The slightly elevated response gain of the P1-based CFRs at low-to-mid-level contrast levels was consistent with the fact that changes in appearance, as indexed by changes in contrast gain (G_c), were observed most prominently at these contrast levels.

Attention induces an additive shift in the amplitude of posterior occipital alpha oscillations

Next, we examined the effects of attention on the contralateral posterior occipital alpha band activity (i.e., EEG oscillations at ~9 –12 Hz), another commonly-used neural index of visuospatial attention [49,81–95] . Past studies have found that alpha amplitude modulations track the relevance of visual stimuli in a topographically selective manner. For example, covert spatial attention induced by endogenous cues decreases alpha amplitude in the posterior occipital areas contralateral to the attended visual field and increases alpha amplitude in areas contralateral to the unattended visual field [81,82,84,86,88,89,96–98]. Recent studies using exogenous cues presented at the peripheral locations also observed similar cue-induced decreases in alpha band activity in the posterior occipital area to the cued locations, suggesting that lateralized alpha activity reflects visuocortical biasing across both exogenous and endogenous attention [98,99]. Consistent with these previous observations, we found a significant cue-related reduction in the amplitude of alpha oscillations – compared to a pre-cue baseline period – that was also modulated by the contrast of the test stimulus. These alpha amplitude modulations were most prominent over the posterior occipital electrodes that were contralateral to the stimulus of interest (Figures 5a-b).

Figure 5c shows the alpha data plotted as a function of both test and standard contrast levels to form CRFs. In contrast to the P1 data, we found that attention cues modulated the baseline offset (B) of the neural CRFs based on the post-cue reduction of the posterior occipital alpha activity (main effect of attention; $F(1, 19) = 45.07$, $p < 0.001$). Note that these lateralized alpha changes likely reflect a mixture of low-level sensory-evoked activity elicited by the peripheral visual cues themselves as well as alpha changes due to attentional biases. This cue-induced reduction in alpha band activity occurred to a comparable degree across all standard contrast levels (no main effect of standard contrast level: $F(6, 114) = 0.62$, $p = 0.7172$; no interaction between attention and standard contrast: $F(6, 114) = 0.60$, $p = 0.7334$). Since the degree of cue-induced modulation of the alpha amplitude was relatively more robust at the lower compared to the higher test contrasts, the R_{max} parameters describing the alpha-based CRFs became less negative with attention (i.e., the negative slope of the alpha-based CRFs became shallower, main effect of attention: $F(1, 19) =1 9.73$, $p = 0.0003$). On the other hand, R_{max} became more negative with increasing standard contrast (main effect of standard contrast: $F(6, 114) =3.87$, $p = 0.0015$). However, there was no interaction between attentional cue and contrast on R_{max} ($F(6, 114) =0.99$, $p = 0.4361$). For the semi-saturation contrast parameter (C_{50}), there was no main effect of attention cue, no main effect of standard contrast, and no interaction between the two factors ($F(1, 19) = 0.51$, $F(6, 114) = 0.49$ and $F(6, 114) = 0.99$, respectively, p's ≥ 0.4372). Overall, the shift in the baseline offset of the alpha-based CRFs was consistent with the robust baseline-offset response bias observed in the behavioral data (Figure 3).

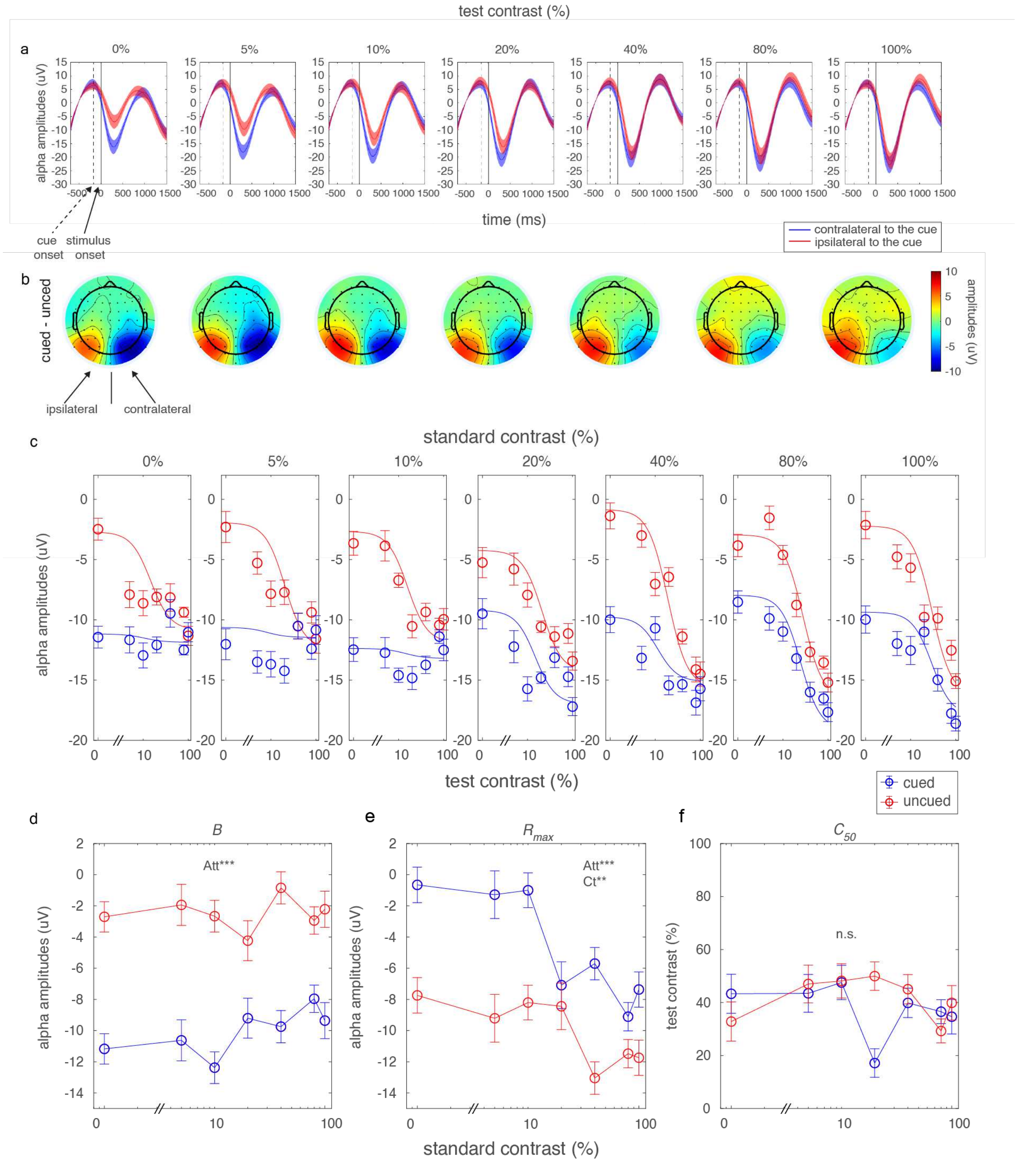

Figure 5. Post-cue reduction in alpha band activity. **(a)** Attentional cues induced a reduction in alpha amplitude in posterior occipital electrodes that were contralateral to the stimulus of interest. Note that in these plots, the cue onset and stimulus onsets were at -100 ms (the vertical black dotted lines) and 0 ms (the vertical black solid lines), respectively. The alpha data were baseline-corrected from -600 to -200 ms before cue onset. **(b)** Topographical maps showing the difference in the alpha amplitude between the cued and uncued conditions at different test contrast levels. **(c)** Alpha amplitude plotted as a function of test contrast separately for different

attention conditions and levels of standard contrast. Attention induced a shift in the baseline offset of alpha band oscillations, regardless of standard contrast. **(d-f)** The corresponding best-fit parameters from a Naka-Rushton function. **(d)** Overall, attention decreased the baseline offset (B) of the neural CRFs, consistent with a reduction in the amplitude of alpha oscillations. The degree of baseline modulation was comparable across standard contrasts. **(e)** Attention-related reductions in alpha amplitude became smaller as test contrast increased (e.g., pinching modularity patterns at 100% test contrast in panel a), leading to a smaller negative slope of alpha-based CRFs in the cued compared to the uncued condition (i.e., R_{max} became less negative with attention). However, R_{max} became more negative with increasing standard contrast. **(f)** There were no differences in the semi-saturation constant (C_{50}) across test or standard contrast levels. Error bars represent within-subject SEMs where the mean values between attention conditions were removed before computing the standard errors. Att***and Ctt** represent the significant main effects of attention (p's<0.001) and standard contrast, respectively (p<0.01). n.s. = non-significant.

Quantitative linking models suggest that different attentional modulations of neural data relate to different modulations of behavioral data

Next, we used a quantitative model to make a more formal link between the patterns of attentional modulations of the P1-based and alpha-based CRFs and the pattern of attentional modulations in the psychometric data (see Materials and Methods [23,37,38,53,55,62,100,101]). The linking model used the patterns of attentional modulations of the observed P1-based and alpha-based CRFs to predict changes in contrast appearance and response bias in the observed behavioral data. The model is based on the assumption derived from the signal detection theory where observers' contrast discrimination accuracy relies on the difference in neural responses (ΔR) related to the standard (R_standard(c)) and test stimuli (R_test(c)) divided by the trial-by-trial variability of neural responses (termed as neuronal noise) [22,23,37–39,62,100]. For a given pair of standard and test stimuli, the model computed the probability of a test stimulus being perceived as having a higher contrast than a standard stimulus ((p(test > standard)) using a maximum likelihood decision rule with neuronal noise equally distributed across the standard and test stimuli.

We first stimulated the behavioral data using the normalized P1-based CRFs (termed here as the P1-based model) and compared the simulated results with those predicted using the normalized alpha-based CRFs (termed here as the alpha-based model; see details in Materials and Methods). Note that the amplitude of alpha band activity generally got smaller with attention and stimulus contrast (see Figure 5; also see refs [49,80]). Therefore, we flipped the sign of the normalized alpha-based CRFs before estimating contrast discrimination accuracy. Last, we compared the results with those predicted by a model that sums the normalized P1-based CRFs and the normalized alpha-based CRFs (with the flipped sign) to predict the behavioral data based on the sum of the normalized P1 and alpha responses. For each linking model, neuronal noise was one free parameter shared across all contrast levels and attention conditions. Thus, since each model had the same number of free parameters, we directly compared the goodness of fit of individual models (i.e., R^2 values) to compare how well they predicted the psychophysical data.

Overall, the P1-based model accounted for the psychophysical data reasonably well (median R^2 of the resampling distribution = 0.71), especially at the low-to-mid-level contrasts (median R^2 values = 0.77 and 0.79 for 10% and 20% contrast levels, respectively) (Figure 6). Since there was no baseline offset change in the P1-based CRFs, the P1-model could not capture changes in the baseline-offset in the behavioral data at lower standard contrast levels. This resulted in lower model fits at these contrast levels (median R^2 values = 0.38 and 0.67 for 0% and 5% contrast levels, respectively). The P1-model also performed poorly at the higher standard contrast levels (median R^2 values 0.54, 0.31, and -0.03 for 40%, 80% and 100% contrast levels, respectively). This poor fit occurred because attentional modulations of the P1-based R_{max} parameter diminished with increasing standard contrast, even though the attentional modulations of the psychophysical data remained robust at these contrast levels (Figure 3).

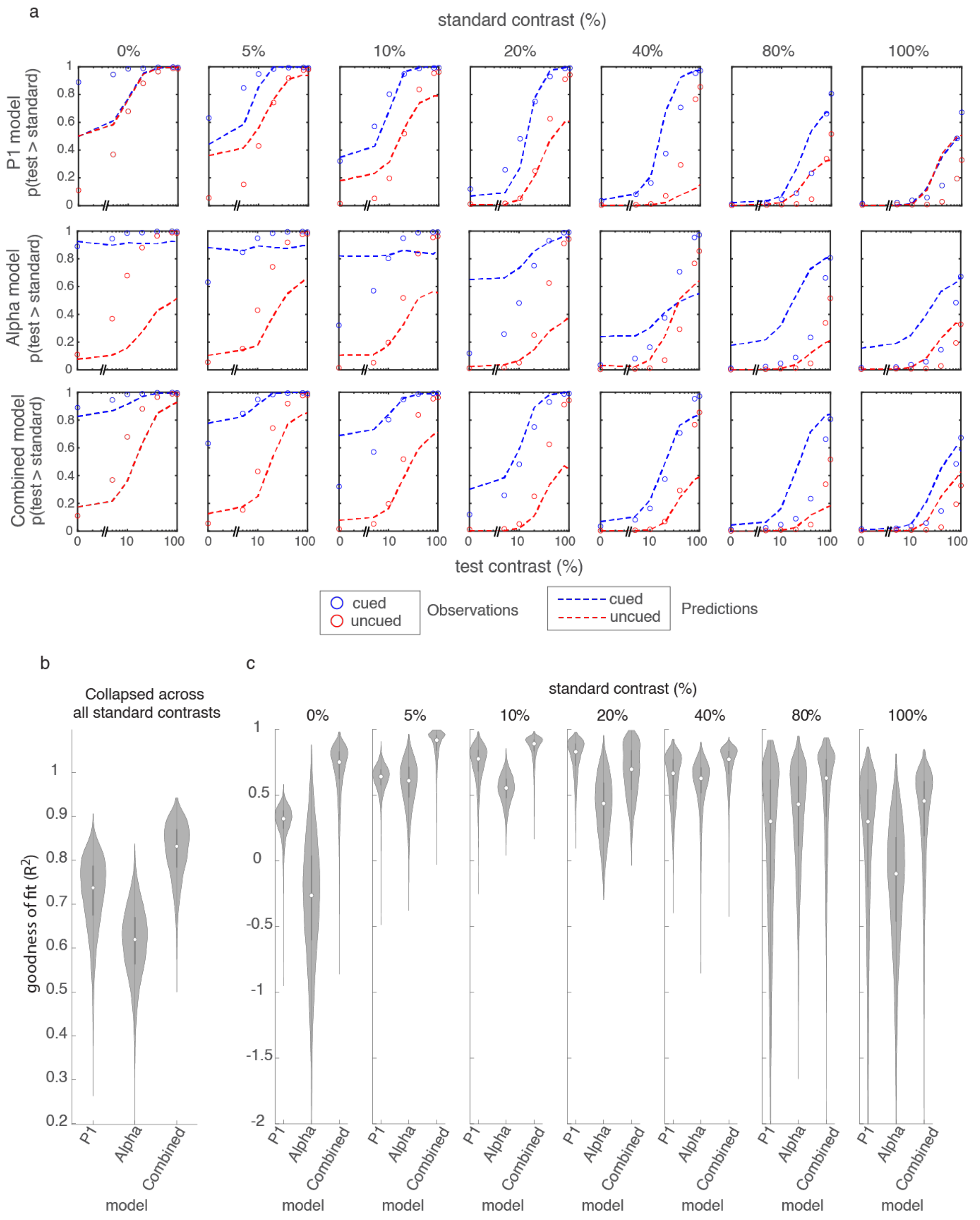

Figure 6. (a) Predicting the effects of attention on behavioral responses based on attentional modulations of neural data. **(top row)** Modeling based on attentional gain modulations of the early visual P1 component better captured the psychometric data overall, but did not predict changes in the baseline offset at low standard contrast levels (0-5%) and did not capture the attention effect on the behavioral data at the 100% standard contrast. **(middle row)** In contrast,

attention-induced changes in alpha band activity tracked large modulations in the baseline offsets of the psychometric functions across all standard contrast levels. **(bottom row)** Modeling that used both P1 and alpha data did the best at predicting the pattern of attentional modulations of the psychophysical data. **(b)** The violin plots showing the goodness of fit of the resampled modeling predictions based on the P1 data, the alpha data, and the combination of the P1 and alpha data (i.e., the combined model), respectively. **(c)** Same as **(b)** but data presented separately for individual standard contrast levels.

Compared to the P1 model, the alpha-based model performed worse at predicting the pattern of the behavioral data in general (median $R^2 = 0.58$ compared to 0.71; both models have only one free parameter which is trial-by-trial variability of the neural activity, i.e., neural noise; see Materials and Methods). This is because the alpha model could only capture attention-induced changes in the baseline-offset at the low standard contrast levels which only accounted for a small fraction of the variance in the overall psychometric data. That said, when we used the combination of the P1 and alpha data to predict the psychometric functions, we were able to predict the pattern of the behavioral responses better than using the P1 data or the alpha alone (median $R^2 = 0.79$ for the combined model compared to median R^2 values of 0.58 and 0.71 for the P1- and alpha- models, respectively). This improvement in modeling performance was due to the fact that the combined model better captured the baseline-offset response bias at the low standard contrast levels (median R^2 values of the combined model vs. the P1 model = 0.72 vs. 0.38 and 0.84 vs. 0.67 for 0% and 5% standard contrasts, respectively) as well as the attentional modulations of the psychometric data at high standard contrast levels (median R^2 values of the combined model vs. the P1 model = 0.74 vs. 0.54 and 0.48 vs. 0.31 and 0.33 and -0.03 for 40%, 80%, and 100% standard contrasts, respectively). Together, these modeling results suggest that the attentional modulations of the P1 component and alpha band activity underlie the different effects of attention on contrast appearance and response bias, respectively. Moreover, attentional modulations of the alpha baseline offset could account for cued-induced biases at both low and high standard contrast levels.

Attention biases motor responses

The P1-modeling data suggest that the multiplicative gain of early visually evoked responses could only account for attention-induced changes in contrast appearance when the standard stimuli were rendered at low-to-mid-level contrasts. While attentional modulations of the P1 data were not observed at 0% or at high standard contrasts, robust attentional modulations of the psychometric functions were still observed at 0% and high standard contrast levels. These results suggest that attention may bias motor responses without modulating early sensory processing under these stimulus conditions.

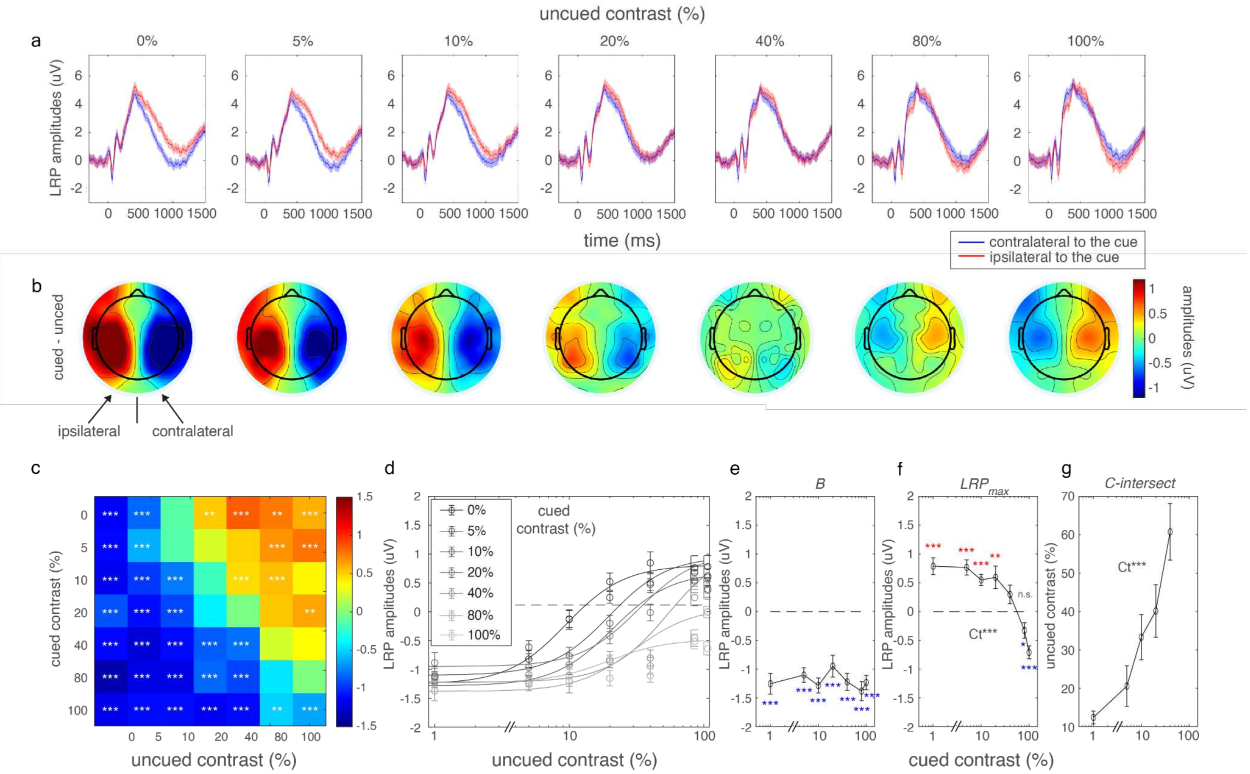

Figure 7. The lateralized readiness potential (LRP). **(a)** The LRP data from lateral central electrodes (see the blue ellipses in Figure 4b) time-locked to stimulus onset. Overall, the LRP was more negative in the electrodes contralateral to the cued hand (blue) compared to the electrodes ipsilateral to the cued hand (red), which is typically interpreted as more response bias towards the cue hand. The negative bias of the LRP toward the cued hand got smaller as the contrast of the uncued stimulus increased. This bias even became positive at high levels of uncued contrast, possibly reflecting response bias to the uncued hand (i.e., there was more overlap between the red and blue ERP traces with increased uncued contrast moving from the left to the right panels). **(b)** Topographical maps of the cued minus uncued conditions averaged from 500-1120 ms after stimulus onset. As the contrast of the uncued stimulus increased, the lateralization of the LRP towards the cued hand became smaller and the sign of the LRP modulation eventually flipped towards the uncued hand. **(c-d)** The cued minus uncued data from the contralateral to the cued hand plotted as a function of the contrast of the cued and uncued stimuli. As the contrast of the cued stimulus increased, higher contrast levels of the uncued stimulus were needed to compete for motor-related activity. **(e-f)** The corresponding best-fitting parameters from a NR function. **(e)** The baseline offset (*B*) values of the LRP-based CRFs were negative across all levels of cued contrast, reflecting response bias towards the cued hand when the cued stimulus of any contrast was presented alone (i.e., paired with the uncued stimulus of 0% contrast). **(f)** The maximal LRP response of the LRP-based CRFs (i.e., responses to the uncued contrast of 100% or uncued-LRP$_{max}$) got smaller as a function of cued contrast, reflecting more influence of the cued stimulus competing with the uncued stimulus of 100% contrast. Here, the positive and negative values of uncued-LRP$_{max}$ mean response bias towards the uncued and cued hand, respectively. When the cued contrasts were 0-20%, they were not strong enough to compete with the uncued stimulus of 100% contrast, thus producing the positive uncued-LRP$_{max}$ values. However, the uncued-LRP$_{max}$ values for 80% and 100% cued contrasts were negative, indicating that the cued stimuli of 80% and 100% contrasts could

compete with the uncued stimuli of 100% contrast for motor responses. At 40% cued contrast, there was no significant motor bias towards either cued or uncued hand (uncued-LRP_{max} was not significantly different from 0), showing comparable influence of the cued stimulus of 40% and the uncued stimulus of 100% at competing for motor responses. **(g)** The uncued contrast that produced no LRP modulations (C-intersect, where the LRP-based CRFs hit 0) increased as a function of cued contrast, suggesting that the uncued stimulus had to be higher contrast to effectively compete for motor-related responses associated with cued stimuli rendered at higher contrasts. Note that we could not estimate C-intersect for the cued contrasts of 80% and 100% because they were beyond the realistic range or responses (>>100%). All shaded areas and error bars represent the within-subject SEMs. *, **, and *** showed significant differences from zero with p's < 0.05, <0.01, and <0.001, respectively (2-tailed, Holm-Bonferroni-corrected). Ctt***'s represent the significant main effects of cued contrast with p's <0.001. n.s. = non-significant.

To test this hypothesis, we further examined the cue- and contrast-related modulations of the lateralized readiness potential (LRP), which is a common EEG index for motor preparation and response bias [41–45]. Overall, we found a strong lateralization of the LRP toward the hand subjects used to respond to the cued location, presumably reflecting the influence of the attentional cue on response bias (main effect of laterality on the LRP amplitude: $F(1, 19) = 100.17$, $p < 0.001$) (Figure 7). However, as the contrast of the uncued stimulus increased, the lateralization of the LRP towards the cued hand became smaller and the sign of the LRP modulation eventually flipped towards the uncued hand, leading to a significant interaction between laterality and the contrast of the uncued stimulus ($F(6, 114) = 48.20$, $p < 0.001$). We also observed a significant three-way interaction between laterality, the contrast of the cued stimulus, and the contrast of the uncued stimulus ($F(36, 684) = 4.53$, $p < 0.001$). This three-way interaction was driven by changes in the lateralization of the LRP as a function of the contrast of the cued stimulus, which occurred at different uncued contrasts.

We then fit the LRP data as a function of the contrast of the uncued stimulus with a NR equation. We found that the baseline offset (B) parameters of the LRP-based CRFs started at negative values around -1 to -1.5 uV for all cued contrast conditions. Paired t-tests showed that B parameters were significantly below 0 for all levels of cued contrasts ($t(19)$'s = -10.12 to -5.49, p's < 0.001, Holm-Bonferroni corrected) and they were comparable across conditions (a repeated-measures ANOVA showed no significant main effect of cued contrast: $F(6, 114) = 0.87$, $p = 0.5219$). We speculate that these negative baseline values reflect response biases toward the cued stimuli specifically when there was no competing stimulus on the uncued side (i.e., 0% uncued contrast), consistent with the cue-induced shifts in the baseline offsets in the psychometric functions and the shifts in alpha band activity.

Nonetheless, as the contrast of the uncued stimulus increased, the LRP became less negative and eventually flipped to positive values, reflecting motor bias towards the uncued side when the relative contrast of the uncued stimulus was high enough. As expected, the LRP reached its maximum when the contrast of the uncued stimulus was rendered at 100% contrast. Interestingly, we found that the maximal LRP response (i.e., the LRP amplitude when the uncued stimulus had 100% contrast or uncued-LRP_{max}) was significantly above 0 only when the cued stimuli were rendered at 0%-20% contrast ($t(19)$'s = 2.39-4.86, p's ≤ 0.0272, 2-tailed, Holm-Bonferroni corrected) but were below 0 (negative) when the cued stimuli had higher contrast values (t(19)'s = -2.8383 and -6.5806, p's = 0.0105 and <0.001 for 80% and 100% contrasts, respectively, 2-tailed, Holm-Bonferroni corrected). This resulted in a significant reduction in uncued-$\mathrm{LRP}_{\max}$ as a function of the contrast of the cued stimulus ($F(6, 114) = 19.28$, $p < 0.001$), which reflects the competitive interaction between the cued and uncued contrasts on response bias. In particular, an uncued stimulus of 100% contrast led to a larger LRP with a positive sign (showing bias towards the uncued stimulus) when the contrast of the cued stimulus was 0%, 5%, 10% or 20%. However, an uncued stimulus of 100% contrast did not lead to a larger LRP when the contrast of the cued stimulus was 40%, 80% or 100% contrast. Moreover, the uncued-$\mathrm{LRP}_{\max}$ values for cued contrasts of 80% and 100% were still negative, suggesting that at these cued contrast levels, an uncued stimulus of 100% contrast did not effectively compete with the cue for response bias. This suggests that changes in psychometric functions at the highest standard contrasts could be due to response bias [22]. Interestingly, these biases in the LRP occurred in the absence of attentional gain modulations of the P1 but in the presence of significant shifts in the amplitude of alpha band oscillations. Together, these data suggest that attention can bias motor responses and can impact behavioral responses at high contrasts without modulating early sensory processing as indexed by the P1 (see Figure 4).

Finally, we obtained the contrast level of the uncued stimulus that produced no LRP modulations (termed here as C-intercept) for each contrast level of the cued stimulus. As expected, the C-intercept increased as the cued contrast increased (main effect of cued contrast on C-intercept: $F(4,76) = 11.09$, $p < 0.001$), reflecting the fact that higher contrasts of the uncued stimulus were needed to compete with a cued stimulus of a given contrast (mean C-intercept values = 12.40, 20.57, 33.34, 40.14, and 60.79% uncued contrast for 0%, 5%, 10%, 20%, and 40% cued contrasts, respectively). Note that we could not estimate the C-intercept values for cued contrast levels of 80%-100% because the uncued-$\mathrm{LRP}_{\max}$ values were negative (i.e., the uncued stimuli of 100% contrast could no longer compete with the cued stimuli). Note that the C-intercept values were much higher than the actual uncued contrasts, showing the additional influence of the presence of a cue on inducing motor bias.

Discussion

The present study investigated the relationship between the attentional modulations of two well-known neural markers for visual information processing-- the P1 component and the alpha band activity – and changes in perceived contrast and response bias. While attention increased the multiplicative response gain (or the slope) of P1-based CRFs, it also shifted the baseline offset of the alpha-based CRFs. Quantitative linking models suggest that the multiplicative response gain of the P1-based CRFs could account for the increase in perceived contrast only when the cued stimuli were rendered at low-to-mid-level contrasts. Notably, the range of contrasts where P1 modulations correspond to changes in perceived contrast fall in a similar range to previous demonstrations of a link between P1 amplitude and contrast appearance [75]. In contrast, the baseline-offset of the alpha-based CRF tracked shifts in the baseline-offset of psychometric functions, consistent with a response bias in favor of the cued stimulus when contrast was very low or 0% [11,18]. This shift in baseline offset of the alpha band activity could also explain response bias driven by high stimulus uncertainty specifically when both the cued and uncued stimuli were rendered at high contrasts [22]. Importantly, the modulations of the LRP tracked both types of response bias (at 0% and at the highest standard contrast levels), which occurred without any attentional gain modulation of the P1 amplitude.

The current P1 data and the accompanying modeling results are consistent with a theory proposed in a previous study that the gain amplification of the early visual response can account for the effect of attention on the subjective appearance of visual stimuli [29,69] . In addition, we found that gain amplification of the P1 and its contribution to changes in contrast appearance were significant only across a specific range of contrasts values for the competing, uncued, stimulus. These observations are consistent with the idea that the gain amplification of sensory responses depends on the strength of bottom-up stimulus inputs (or the contrast of the competing stimulus in our case) [102–104].

We found that attention selectively increased the response gain of the P1-based CRF. Response gain of early visually evoked signals, like the P1 component and the steady-state visually evoked potential (SSVEP), has been consistently observed across many studies where subjects performed visual detection and discrimination tasks [39,48,49,55,58,61–63,72,80,105–107]. The consistency in the response gain modulations observed across these studies, as well as in the present study, suggests that the response gain of the early sensory response is a common neural mechanism that mediates the effects of attention on perceptual performance and on the appearance of visual stimuli. Interestingly, reductions in response gain of early sensory responses have been shown to underlie sensory and attention deficits in clinical populations, such as schizophrenia, neurofibromatosis, and amblyopia [108–112]. Based on these results and our recent findings, it is possible that these patients perceive the world in a manner that is different from the healthy populations due to the reduced influence of attention on gain amplification of early sensory processing.

We also observed different patterns of cue-induced modulations in posterior occipital alpha-band activity that was contralateral to the target of interest. This kind of alpha band modulation has been previously used to track the allocation of spatial attention following endogenous and exogenous cues [79,81–94,98,99]. The reduction of alpha amplitude, which is thought to reflect increased cortical excitability, has also been associated with an increase in the intensity of stimulus inputs and selective attention, and behavioral performance in perceptual decision-making tasks [49,79,81–94,98,99,113]. Moreover, the topographic patterns of alpha reduction contain information about the attended location even in the absence of visual stimuli [79,84,86,89–91,114–116]. Consistent with these studies, recent studies have found that attention shifted the baseline offset of alpha-based CRFs where no visual stimuli were presented [22,74]. That said, we found that the magnitude of baseline modulations of the alpha-based CRFs was unaffected by the contrast level of the paired stimuli.

Interestingly, the overall pattern of the alpha band data observed here is highly similar to the pattern of blood oxygenation level dependent (BOLD) activity observed in similar tasks. This is consistent with the idea that alpha band activity is highly correlated with modulations of the BOLD response recorded in human visual cortex [117,118]. Specifically, many previous studies using functional magnetic resonance imaging (fMRI) have shown that spatial attention induces an additive shift in the baseline response of the BOLD CRF in a manner similar to the attentional modulation of the alpha-based CRF [38,49,54,65–67], but see the effect of feature-based attention on fMRI activity [126]). Consistent with our present study, attentional modulations of BOLD CRFs were unaffected by the contrast level of the paired or non-target stimulus[67]. Previous fMRI studies have also shown that baseline shifts of BOLD CRFs failed to explain multiplicative response gain (the slope) of the hypothetical neural activity needed to account for attention-induced perceptual benefits in variants of attentional-cueing contrast discrimination tasks [38,55]. Note that most studies that reported the attention-induced baseline-offset shifts in the CRFs based on alpha band and fMRI activity used endogenous cues to guide attention. However, we used exogenous cues in the present study. Thus, changes in the baseline offsets in the alpha-based CRFs in our study could also reflect bottom-up stimulus processing or visual priming associated with the peripheral cues. Related to this aspect, studies have argued that changes in visual appearance could be due to low-level sensory interactions between the cue and the stimulus, independent of an attention effect [32]. In this respect, the observed changes in alpha band activity could in part reflect these low-level sensory interactions. That said, some of these alpha changes are likely of attentional nature given that recent studies have found similar lateralized alpha activity using auditory cues [98,119].

Our modeling results of the alpha data suggest an alternative account in which shifts in the baseline offset of neural CRFs might instead mediate preparatory attention and the motor-related processes that give rise to response bias. In line with our modeling results, reductions in alpha amplitude have been associated with modulations of post-perceptual processing such as changes in decision criterion, confidence, and visual awareness, but not changes in perceptual sensitivity [74–79,120,121]. Counter to this perspective, a recent study argued that changes in alpha band activity do indeed account for changes in subjective contrast appearance [68]. However, unlike the present and other studies that have used an exogenous cue to study changes in appearance, this recent study used an endogenous cue under the assumption that there should be relatively less attentional capture and response bias driven by an endogenous compared to an exogenous cue [68]. That said, subjects might still have been more aware of the presence of the cue and the cued stimulus [22,31–34]. Accordingly, this increase in visual awareness, which has also been linked to weak alpha amplitude, could result in response bias without changing visual appearance per se [18,31–35,49,76–78]. This recent study also did not systematically map out modulations of the alpha band activity with changes in appearance and response bias across a full range of stimulus contrast[68]. Therefore, it is difficult to assess if the reported modulations of alpha band activity were associated with changes in subjective contrast perception or cue-induced response bias.

Taken together, our results suggest that the different types of neural computations that support visuospatial attention occur at different stages of visual information processing and they underlie different perceptual and behavioral effects of attention. While an increase in the multiplicative response gain modulations of the early visually evoked potential supports attention-induced changes in perceived contrast, additive shifts of alpha band activity correspond to biases driven by the attentional cue. Moreover, under circumstances where there is prominent response bias, attention can directly trigger a bias in motor responses without modulating the processing of early sensory inputs.

Material and Methods

Subjects

We recruited 22 neurologically healthy male and female human observers who had normal or corrected-to-normal vision from the University of California, San Diego (UCSD). In accord with the local institutional review board at UCSD, they provided written informed consent before participating in our study. Two subjects terminated their participation before completing the experiment, resulting in 20 subjects included in the final analysis (9 female, 18-25 years old, 2 left-handed).The sample size was within the typical range used in these types of studies in which attentional modulations of EEG and psychophysical data are measured across different contrast levels [39,48,49,55,58,62,63,80,122].

Stimuli and task

We presented stimuli using the Psychophysics Toolbox [123,124] and MATLAB (MathWorks, Natick, MA) run on the personal computer with the Windows XP operating system. Participants were seated 60 cm from the gray background CRT monitor (34.51 cd/m2, 120 Hz refresh rate) in a dimly lit sound-attenuated room where they performed the comparative contrast judgment task (Figure 1; see ref[22]). In this task, they were asked to judge the relative apparent contrast of two Gabor stimuli (spatial frequency = 3 c/°, standard deviation of the Gaussian envelope = 2.18°, stimulus radius = 6.53°) that were presented on the left and right of the central fixation point in the left and right lower quadrants (eccentricity = 13.74°). They reported whether the stimulus with the higher contrast was tilted 45° clockwise (CW) or counterclockwise (CCW) from vertical. They responded by pressing one of four buttons on the keyboard, which corresponded to a CCW left stimulus, a CW left stimulus, a CCW right stimulus, and a CW right stimulus with their left middle, left index, right index, and right middle fingers, respectively. To examine the impact of covert spatial attention on subjective reports about the perceived stimulus contrasts, we presented an exogenous cue, which was a horizontal black bar (0.36° × 3.63° length × thickness) located to the left or right of fixation 2.04° above the outer edge of the cued stimulus. The cue was presented for 50 ms followed by a 50-ms blank screen and the two oriented Gabor stimuli, which were presented for 40ms (50% left-cued and 50% right-cued trials). The contrast values of the two stimuli were fully-crossed and independently drawn from seven contrast levels (0%, 5%, 10%, 20%, 40%, 80%, 100% Michelson contrasts). There was no response deadline. Following a button press, there was an intertrial interval (ITI) of 300-800 ms. Trial order was pseudo-randomized so that subjects were unable to predict the cued side or the contrast of each stimulus. Each subject completed 2940 trials in total. There were 30 trials for each combination of cue locations (left or right), left stimulus contrasts (7 levels from 0%-100%), and right stimulus contrasts (7 levels from 0%-100%).

Analysis of behavioral data

Based on the level of stimulus contrast and the cued location, the probability that each stimulus of interest was reported as having a higher contrast was evaluated based on the contrast level of that stimulus, the contrast level of stimulus contrast on the opposite side (i.e., the paired stimulus), and the cued location (Figures 2-3). We labeled the stimulus of interest as the ‘test’ stimulus and the paired stimulus as the ‘standard’ stimulus. Then, we computed the probability that the test stimulus was reported as having a higher contrast, termed here as p(test > standard). We computed this probability separately for cued and uncued test stimuli, as well as when the test stimulus was paired with different contrast levels of the standard stimulus. We used the number of trials in which the reported orientation of the stimulus of interest was ‘correct’ as a numerator while using the number of all trials as a denominator. For the test stimulus of 0% contrast, we randomly labeled the direction of the orientation offset (CW or CCW) prior to the start of the experiment. This was done because no physical stimulus was actually presented in the 0% contrast stimulus condition. The “correct” responses in this condition were then determined based on a match to these randomly assigned labels. The effect of exogenous cues on guessing and baseline-offset response bias was then determined by the difference between the probability of choosing a cued versus an uncued test stimulus on these 0% contrast stimulus conditions.

Next, we fitted the probability values across different test contrasts separately for each standard contrast and each attention condition (cued/uncued), separately for each subject, with a variant of the Naka–Rushton equation using a maximum likelihood estimation method:

$$P(c)= G_r * C^q / (C^q+G_c^q) + B, \qquad \text{(Equation 1)}$$

where P(c) is p(test > standard) for a given test contrast value. Here, B is the baseline offset (indexing response bias), G_c is the contrast gain factor that controls the horizontal shift of the curve (indexing perceived appearance), G_r is the response gain factor that controls the vertical shift of the psychometric function, and q is the exponent fixed at 2 [133]. In addition, we constrained the fit so that $0 \geq G_r \leq 1$, $0 > G_c < 100$, $P(100) \leq 1$, and $P(0) \geq 0$. We did not use another version of the Naka–Rushton function, termed a baseline-input model [23], because our past work using this formula showed that it yielded worse fits compared to the baseline-input model predicted B values, which were out of the realistic range (that were $\gg 1$), making it difficult to interpret the results.

Next, we used two-way repeated-measures ANOVAs to test the main effects of attention and contrast values of standard stimuli as well as interactions between these factors on the parameters B, G_r, and G_c. Then, we used post-hoc pairwise t-tests to examine differences between attention conditions (test cued/standard cued) for each standard contrast (two-tailed) and corrected for multiple comparisons using the Holm-Bonferroni method.

EEG recording and reprocessing

EEG data were recorded with a 64 + 8 channel Biosemi ActiveTwo system at a 512 Hz sampling rate. We kept signal offsets below 20 uV relatively to the CMS-DRL reference. While their EEG signals were being recorded, subjects were asked to minimize blinks, eye movements, and head movements. EEGLAB v2019.1 and in-house MATLAB (R2020a) scripts were used to preprocess the EEG data offline. First, the continuous EEG data were re-referenced to the mean of the left and right mastoid electrodes, followed by the application of 0.25-Hz high-pass and 55-Hz low-pass Butterworth filters (third order). Then, we segmented the continuous EEG data into epochs extending from -1000 ms before to 2,000 ms after the cue onset. Next, we used independent component analysis [125,126] to reject prominent eye blink and muscle artifacts and then discarded epochs contaminated by residual eye blinks and saccades (more than ±50-200 μV deviation from zero, with thresholds chosen for each individual subject), horizontal eye movements (more than ±50-75 μV deviation from zero), muscle activity, or drifts using threshold rejection and visual inspection (8.8946% of trials were rejected, ± 9.2797% SEM).

Early sensory evoked response

Following the EEG preprocessing steps described above, we baseline-corrected the artifact-corrected EEG data to their mean EEG response from -200 to 0 ms relative to the cue onset. We then realigned the epoched EEG data to the onset of the stimulus. The baselined EEG data were then sorted into the following 98 conditions: left vs. right cued stimuli (2 conditions) x 7 cued contrast levels (0%-100%) x 7 uncued contrast levels. Next, we averaged the stimulus-locked EEG data in each of these conditions to obtain the event-related potentials. Note that at this step, the event-related potentials (ERPs) contained both cue-evoked and stimulus-evoked responses. In order to isolate the stimulus-evoked responses related to the cued stimuli from the cue-evoked responses, we subtracted the ERPs from the cue-only trials (0% contrast) from the ERPs related to the cued stimuli of all contrast levels (0%-100%) as shown in Figure 4a (top row). We also extracted the stimulus evoked responses related to the uncued stimuli of different contrast levels by subtracting the ERPs in trials where the uncued stimulus was rendered at 0% contrast. These steps allowed us to isolate a P1 component peaking ~60-90ms after the stimulus onset at contralateral posterior occipital electrodes (Figures 4a-b; O1, PO3, PO4, P1, and P3 for left channels and O2, PO4, PO8, P2, and P4 for right channels). Next, we computed the mean amplitude of the P1 component over 60-90ms across contralateral posterior occipital electrodes in each cue and contrast condition from individual subjects and then plotted them as a function of test contrast. This resulted in a P1-based CRFs for each attention condition and standard contrast level (Figure 4), which were then fit with the Naka–Rushton equation (Equation 1) to determine if these P1-based CRFs underwent contrast gain, multiplicative response gain, or changes in baseline offset (Figures 2d-f). For individual attention conditions and standard contrast levels, this fitting procedure was performed using MATLAB's "fmincon" function to minimize the root mean squared error between the data and the fit function with 3 free parameters including the contrast gain (G_c), response gain (G_r), baseline-offset parameters (B). Here the exponent q of the Naka–Rushton equation was fixed at 2 [127]. The guess values for G_r, G_c, and B were 1% contrast, the difference between the maximum and minimum values of the P1 amplitudes across all test contrast levels, and the minimum value of the P1 amplitude, respectively. Note that the G_c and G_r parameters could in principle exceed the realistic range of stimulus contrast (0 –100% contrast), making it difficult to interpret the results. Therefore, instead of directly comparing these two parameters, we obtained parameters that indicated the contrast at which neural responses reached half their maximum (the semi-saturation constant; C_{50}) and the maximum neural responses relative to baseline (R_{max}) to track changes in contrast gain and response gain, respectively. Finally, we used two-way repeated measures ANOVAs to test the main effect of attention (cued vs. uncued), the main effect of standard contrasts (0%-100%), and their interaction on the B, C_{50}, and R_{max}.

Alpha band activity

In order to assess cue-induced changes in in posterior alpha band activity, we wavelet-filtered the artifact-corrected and epoched EEG data using a Gaussian filter centered at 9-12 Hz with a fractional bandwidth of 0.2 Hz and computed the absolute value of the wavelet coefficients to obtain a measure of amplitude [128–130]. Next, we sorted the data into each of the 98 experimental bins. For each of these experimental bins, we then computed the mean percent change in alpha amplitude relative to baseline activity from 200-600 ms before the cue onset (or 300-700 ms before the stimulus onset) using the following equation:

Percent signal change =
(alpha amplitude - baseline activity) x 100% / baseline activity (Equation 2)

To obtain alpha-based CRFs, we then took the averaged values of the alpha data from 100-700ms after the cue onset (0-600ms after the stimulus onset) across 5 contralateral posterior occipital electrodes (O1, PO3, PO4, P1, and P3 for left channels and O2, PO4, PO8, P2, and P4 for right channels) and plotted them as a function of test contrast for each attention condition and each standard contrast level in individual subjects (Figure 5). The alpha-based CRFs were then fit with a Naka–Rushton equation (Equation 2). The fitting routine was similar to that conducted in the P1 data analysis except that the guessing value for G_r was determined based on the difference between the minimum and maximum values of the post-cue alpha activity across all test contrast levels due to the fact that the alpha band activity got smaller as a function of test contrast. Finally, we used two-way repeated measures ANOVAs to test the main effect of attention (cued vs. uncued), the main effect of standard contrasts (0%-100%), and their interaction on the B, C_{50}, and R_{max}.

Lateralized readiness potential

In addition to examining the effects of attention on the P1 component and alpha band activity, we also monitored changes in the LRP, which has been used as an index for motor preparation [41–45]. First, we obtained the mean ERPs from the central posterior electrodes (C1, C3, C5, CP1, CP3 for left channels and C2, C4, C6, CP2, and CP4 for right channels) (Figure 7). Then, we subtracted the ERPs from the electrodes ipsilateral to the cue from the ERPs from the contralateral electrodes to obtain the LRP which emerged from ~500-1120 ms after the stimulus onset. The negative differences in the LRP are usually interpreted to indicate motor bias toward the cue location, whereas a positive difference reflects motor-related responses toward the uncued location. To examine the effects of cued and uncued contrast as well as their interaction on the LRP data, we performed a two-way repeated measures ANOVA on the LRP differences averaged across a window extending from ~500-1120ms window. In addition, we performed post-hoc pairwise t-tests for individual cued and uncued contrast conditions to test if the mean LRP differences were significantly above or below zero to determine the direction of motor bias toward either the cued or uncued location. We corrected for multiple comparisons using the Holm-Bonferroni method.

We also plotted the LRP differences as a function of uncued contrast for individual cued contrast levels to examine how motor bias to cued stimuli of different contrast levels were mediated by the contrast of the competing stimulus (i.e. the uncued stimulus on each trial). We then fit the LRP-based CRFs for individual cued contrast levels using a Naka–Rushton equation (Equation 1) and MATLAB's "fmincon" function. Then, we estimated the baseline parameter (B) – or the degree of bias toward the cued location when there was no competing stimulus – and the maximal LRP response at the 100% uncued contrast level (uncued-LRP_{max}), and the uncued contrast that produced no LRP modulations (C-intersect). Note that we could not estimate C-intersect for cued contrasts of 80% and 100% because they were beyond the realistic range of responses (>>100%). Next, we used one-way repeated measures ANOVAs to examine the main effect of uncued contrast on B, uncued-$\mathrm{LRP}_{\max}$, and C-intersect. In addition, we performed paired t-tests to determine if the B and uncued-$\mathrm{LRP}_{\max}$ parameters were below or above zero to determine the direction of response bias towards cued vs. uncued locations. Multiple comparisons were corrected using the Holm-Bonferroni method.

Modeling behavioral data using EEG data

We examined how different patterns of attentional modulations, specifically the multiplicative response gain of the P1-based CRFs and the contrast gain of the alpha-based CRFs could be linked to the attentional effects in our psychometric data. We recently demonstrated that quantitative models assuming changes in the response gain of hypothetical neural CRFs can capture attention-induced changes in contrast appearance via modulations in the contrast gain factor (G_r) of the psychometric data. However, this did not account for the baseline-offset in response biases [22]. On the other hand, models assuming shifts in the baseline offset of the hypothetical neural CRFs could better account for cue-induced changes in the baseline-offset response bias in the behavioral data [22]. Based on these results, we hypothesized that the multiplicative gain of the P1-based CRFs should account for the leftward shifts of the psychometric functions which occurred predominantly when the standard stimuli were rendered at low-to-mid-level contrasts. On the other hands, modulations of baseline offsets in the alpha-based CRFs should better account for changes in the baseline-offset response bias in the behavioral data [22].

To test these predictions, we adopted a quantitative modeling method based on signal detection theory (SDT (Cutrone et al., 2014; Itthipuripat et al., 2019a)). Here, we estimated p(test > standard) based on the amplitude difference between neural responses (either the P1 data, the alpha data, or both) evoked by test and standard stimuli that can be drawn from the measured neural CRFs given a certain level of hypothetical neuronal noise (or trial-by-trial variability) (Figure 6). To do this, we first obtained the best fit parameters of the Naka–Rushton equation, including G_r, G_c, and B, which described the P1-based and the alpha-based CRFs of individual subjects. Next, we resampled subject labels with replacement 10,000 times and obtained the G_r, G_c, and, B parameters averaged across these resampled subjects labels and in each iteration, we used these average values to generate a hypothetical P1-based and alpha-based CRF in order to predict the patterns of the behavioral data.

For the P1-based model, we collapsed the G_c and B values across different attention and standard contrast levels so that the same G_c and B values were shared across all of these conditions and could not contribute to changes in the predicted behavioral results. On the other hand, different G_r values obtained from the original fitting routine were assigned to different attention and standard contrast conditions. These steps ensured that the pattern of attentional modulations in the predicted behavioral results were selectively due to changes in response gain of the P1-based CRFs and were not influenced by spurious differences in other factors (B or G_c) that may occur in single-subjects. In each resampled iteration, the simulated P1-based CRFs were normalized using the following formula:

$$Normalized\ Data = Data - \min(Data) / \max(Data) - \min(Data), \qquad \text{(Equation 3)}$$

where min(Data) and max(Data) were the minimum and the maximum values of the simulated P1-based CRFs across all attention and standard contrast conditions.

For the alpha-based model, we only collapsed the G_c parameters across the different attention conditions and standard contrast levels since there were neither main effects of these factors nor their interaction on G_c. That said, different B and G_r values were directly obtained from the original fitting routine and assigned to different attention and standard contrast conditions. Here, both B and G_r were allowed to be different across experimental conditions because the baseline shifts in the alpha-based CRFs were the results of the baseline offset (B) becoming more negative with attention and the response again (G_r) becoming smaller with attention (i.e. G_r became less negative so the negative slope was less steep). Since the amplitude of the alpha band activity was generally reduced as a function of attention and stimulus contrast, we flipped the sign of the simulated alpha-based CRFs and normalized the data using Equation 3. This sign-flipping step allowed us to perform the linking model in the similar way as the P1-based model and to combine the P1 and alpha data to examine the joint contribution of the attentional modulations of these two different electrophysiological signals to predict the effects of attention on the behavioral data. Finally, for the combined P1 and alpha model, we computed the sum of the normalized P1-based and alpha-based CRFs separately for individual attention conditions and standard contrast levels.

For all of these models, in each of the 10,000 iterations we simulated 1,000 trials in which responses to the standard and test stimuli of individual contrasts and attention conditions were randomly drawn from a normal distribution with means obtained from the P1-based CRFs, the alpha-based CRFs, or the combined data. 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(test > standard) was estimated based on the probability at which the test stimulus–related neural response was higher than the standard stimulus–related response in the 1,000 stimulated trials. For each of 10,000 subject-label resampling iterations, we computed the goodness of fit (R^2) for each model and plotted the median R^2 values and the resampling distributions of these different models using the violin plot function [131] to compare their performance (Figure 6). Note that we could directly compare R^2 values of different models because all of these models only had 1 free parameter, which was the neuronal noise shared across all standard and test contrast levels as well as across the different attention conditions.

Figure Legends

Figure 1. Task and stimuli. **(a)** The attention-cueing comparative contrast judgment task. Subjects were tasked with reporting the orientation of the stimulus they perceived as having a higher contrast. **(b)** Depiction of all contrast pairs in the cue-left condition. Note that the same fully crossed contrast manipulation was also used in the cue-right condition.

Figure 2. Predictions. **(a-c)** Alternative predictions for the *behavioral* results. (a) Attention increases the perceived contrast of visual stimuli via a leftward shift in the behavioral contrast response functions. In this scenario, attention should only decrease the contrast gain factor (G_c) and there should not be any changes in the baseline offset (B) or response gain (G_r). (b) Attention induces baseline-offset response bias (B; additive upward shift) without changes in a leftward shift of the CRFs (i.e. no change in G_c). This corresponds to a response bias for the cued stimulus without a change in perceived contrast. (c) Attention could induce changes in both subjective appearance and response bias as indexed by changes in both G_c and B, respectively. **(d-e)** Different patterns of attentional modulations in the neural contrast response functions (CRFs) measured over visual cortex. Since the estimated G_r and G_c parameters could extend beyond the realistic range of stimulus contrast (>100%), the response gain and contrast gain of neural CRFs were reparameterized as the maximal response (R_{max} or the response at 100% contrast minus the baseline offset) and the semi-saturation contrast (C_{50} or the contrast at which the response reached half maximum), respectively. (d) Attention increases neural contrast sensitivity or contrast gain as indexed by changes in the semi-saturation contrast factor (C_{50}). Alternatively, attention could increase the multiplicative response gain or the slope of the neural CRFs as indexed by the maximum neural response (R_{max}). Lastly, attention could shift the baseline offset of the neural CRFs so that overall responses to the cued stimulus are enhanced in a manner that is independent of stimulus contrast. One past modeling study from our group suggests that the response gain mechanism (panel e) is sufficient to account for psychophysical changes in contrast appearance (panel a). However, a change in the baseline of neural CRFs (panel f) is required to explain changes in the behavioral baseline-offset response bias (panel b) [22]. That said, there is still no neural evidence that validates these modeling predictions.

Figure 3. Behavioral data. **(a)** The probability that subjects reported the test stimulus (i.e., the stimulus of interest, either cued or uncued) as having a higher contrast than the standard stimulus (i.e., the paired cued or uncued stimulus) plotted as a function of test contrast for all possible standard contrast levels. We used the parameter B to index the baseline-offset response bias that the cued stimulus had a higher contrast than the uncued stimulus even when the cued stimulus was not physically present (i.e., presented at 0% contrast, as in [18,22]). **(b)** Overall, we found a significant attention-induced increase in response bias when the contrast of the standard was relatively low, with a decreasing effect of response bias as the contrast of the standard increased. **(c)** The contrast gain parameter (G_c) controls the horizontal position of the psychometric function, which we used to index changes in contrast appearance. Attention reduced G_c, as indexed by a leftward shift in the psychometric functions, which should correspond to an increase in perceived contrast, predominantly at low-to-mid-levels of standard contrast. **(d)** The response gain parameter (G_r) controls the slope of the psychometric function. Note that G_r and B are conflated because behavioral response probabilities could not exceed 1. At low-to-mid level standard contrasts, there were large attentional effects on B (panel b). Thus, this increase in B

must also lead to a decrease in slope, or G_r, given the fixed ceiling of the psychometric response functions. Instead, attention increased G_r without changing B at higher contrasts (ie., 80%-100%). Error bars represent the within-subject standard errors of the mean (±1 SEMs). Att***, Ctt**, and Att x Ctt*** represent the significant main effects of attention, standard contrast, and the interaction between the two factors, respectively (all p's <0.001).

Figure 4. The P1 component across cue and standard contrast conditions. **(a: top row)** The non-subtracted ERPs from the contralateral posterior occipital electrodes (see the red circle on the right hemisphere of the head model in **(b)**). These non-subtracted ERPs contained both cue-evoked and stimulus-evoked responses. Note that in these plots the cue onset and stimulus onsets were at -100 ms (vertical black dotted lines) and 0 ms, respectively (vertical black solid lines). The data were baseline-corrected from -200 to 0ms before the cue onset. **(a: bottom row)** The extracted stimulus-evoked potentials obtained after subtracting the cue-only condition (the leftmost panel from the top row of panel a) from all other stimulus contrast conditions. We observed a P1 component peaking ~60-90 ms with its amplitude increasing as a function of the contrast of the test stimulus. Moreover, attention increased the P1 amplitude at high test stimulus contrast levels. All shaded areas represent within-subject SEMs. **(b)** Topographical maps of the P1 amplitude averaged across ~60-90ms post-stimulus. The rings mark each of 5 electrodes over the contralateral/ipsilateral posterior occipital sites where the P1 (Figure 4) and alpha data were analyzed (Figure 5; red rings) and on the contralateral/ipsilateral central sites where the LRP data were analyzed (Figure 8; blue rings). **(c)** The P1-based contrast-response functions (CRFs) plotted separately for the cued and uncued conditions across different levels of standard contrast. Attention enhanced the multiplicative response gain of the P1 data. **(d-f)** The corresponding best-fitting parameters from the NR function. **(d)** There were no differences in the baseline offset. **(e)** Attention selectively enhanced response gain indexed by an increase in the maximum response of the P1 component (R_{max}), which were relatively more robust at low-to-mid-level standard contrasts. **(f)** There were no differences in the semi-saturation contrast level or the level at which the P1 amplitude reached half maximum (C_{50}). Error bars represent the within-subject SEMs where the mean values between attention conditions were removed before computing the standard errors. Att* and Att x Ctt* represent the significant main effect of attention (p <0.05) and the trending interaction between attention and standard contrast, respectively (p = 0.053). n.s.= non-significant.

Figure 5. Post-cue reduction in alpha band activity. **(a)** Attentional cues induced a reduction in alpha amplitude in posterior occipital electrodes that were contralateral to the stimulus of interest. Note that in these plots, the cue onset and stimulus onsets were at -100 ms (the vertical black dotted lines) and 0 ms (the vertical black solid lines), respectively. The alpha data were baseline-corrected from -600 to -200 ms before cue onset. **(b)** Topographical maps showing the difference in the alpha amplitude between the cued and uncued conditions at different test contrast levels. **(c)** Alpha amplitude plotted as a function of test contrast separately for different attention conditions and levels of standard contrast. Attention induced a shift in the baseline offset of alpha band oscillations, regardless of standard contrast. **(d-f)** The corresponding best-fit parameters from a Naka-Rushton function. **(d)** Overall, attention decreased the baseline offset (B) of the neural CRFs, consistent with a reduction in the amplitude of alpha oscillations. The degree of baseline modulation was comparable across standard contrasts. **(e)** Attention-related reductions in alpha amplitude became smaller as test contrast increased (e.g., pinching modularity patterns at 100% test contrast in panel a), leading to a smaller negative slope of

alpha-based CRFs in the cued compared to the uncued condition (i.e., R_{max} became less negative with attention). However, R_{max} became more negative with increasing standard contrast. **(f)** There were no differences in the semi-saturation constant (C_{50}) across test or standard contrast levels. Error bars represent within-subject SEMs where the mean values between attention conditions were removed before computing the standard errors. Att***and Ctt** represent the significant main effects of attention (p's<0.001) and standard contrast, respectively (p<0.01). n.s. = non-significant.

Figure 6. (a) Predicting the effects of attention on behavioral responses based on attentional modulations of neural data. **(top row)** Modeling based on attentional gain modulations of the early visual P1 component better captured the psychometric data overall, but did not predict changes in the baseline offset at low standard contrast levels (0-5%) and did not capture the attention effect on the behavioral data at the 100% standard contrast. **(middle row)** In contrast, attention-induced changes in alpha band activity tracked large modulations in the baseline offsets of the psychometric functions across all standard contrast levels. **(bottom row)** Modeling that used both P1 and alpha data did the best at predicting the pattern of attentional modulations of the psychophysical data. **(b)** The violin plots showing the goodness of fit of the resampled modeling predictions based on the P1 data, the alpha data, and the combination of the P1 and alpha data (i.e., the combined model), respectively. **(c)** Same as **(b)** but data presented separately for individual standard contrast levels.

Figure 7. The lateralized readiness potential (LRP). **(a)** The LRP data from lateral central electrodes (see the blue ellipses in Figure 4b) time-locked to stimulus onset. Overall, the LRP was more negative in the electrodes contralateral to the cued hand (blue) compared to the electrodes ipsilateral to the cued hand (red), which is typically interpreted as more response bias towards the cue hand. The negative bias of the LRP toward the cued hand got smaller as the contrast of the uncued stimulus increased. This bias even became positive at high levels of uncued contrast, possibly reflecting response bias to the uncued hand (i.e., there was more overlap between the red and blue ERP traces with increased uncued contrast moving from the left to the right panels). **(b)** Topographical maps of the cued minus uncued conditions averaged from 500-1120 ms after stimulus onset. As the contrast of the uncued stimulus increased, the lateralization of the LRP towards the cued hand became smaller and the sign of the LRP modulation eventually flipped towards the uncued hand. **(c-d)** The cued minus uncued data from the contralateral to the cued hand plotted as a function of the contrast of the cued and uncued stimuli. As the contrast of the cued stimulus increased, higher contrast levels of the uncued stimulus were needed to compete for motor-related activity. **(e-f)** The corresponding best-fitting parameters from a NR function. **(e)** The baseline offset (*B*) values of the LRP-based CRFs were negative across all levels of cued contrast, reflecting response bias towards the cued hand when the cued stimulus of any contrast was presented alone (i.e., paired with the uncued stimulus of 0% contrast). **(f)** The maximal LRP response of the LRP-based CRFs (i.e., responses to the uncued contrast of 100% or uncued-LRP_{max}) got smaller as a function of cued contrast, reflecting more influence of the cued stimulus competing with the uncued stimulus of 100% contrast. Here, the positive and negative values of uncued-LRP_{max} mean response bias towards the uncued and cued hand, respectively. When the cued contrasts were 0-20%, they were not strong enough to compete with the uncued stimulus of 100% contrast, thus producing the positive uncued-LRP_{max} values. However, the uncued-LRP_{max} values for 80% and 100% cued

contrasts were negative, indicating that the cued stimuli of 80% and 100% contrasts could compete with the uncued stimuli of 100% contrast for motor responses. At 40% cued contrast, there was no significant motor bias towards either cued or uncued hand (uncued-LRP_{max} was not significantly different from 0), showing comparable influence of the cued stimulus of 40% and the uncued stimulus of 100% at competing for motor responses. **(g)** The uncued contrast that produced no LRP modulations (C-intersect, where the LRP-based CRFs hit 0) increased as a function of cued contrast, suggesting that the uncued stimulus had to be higher contrast to effectively compete for motor-related responses associated with cued stimuli rendered at higher contrasts. Note that we could not estimate C-intersect for the cued contrasts of 80% and 100% because they were beyond the realistic range or responses (>>100%). All shaded areas and error bars represent the within-subject SEMs. *, **, and *** showed significant differences from zero with p's < 0.05, <0.01, and <0.001, respectively (2-tailed, Holm-Bonferroni-corrected). Ctt***'s represent the significant main effects of cued contrast with p's <0.001. n.s. = non-significant.

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