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Journal

Journal of Neuroscience, 43(39)

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Publication Date

2023-09-27

DOI

10.1523/JNEUROSCI.2192-22.2023

Peer reviewed

Behavioral/Cognitive

Dissociable Neural Mechanisms Underlie the Effects of Attention on Visual Appearance and Response Bias

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A prominent theoretical framework spanning philosophy, psychology, and neuroscience holds that selective attention penetrates early stages of perceptual processing to alter the subjective visual experience of behaviorally relevant stimuli. For example, searching for a red apple at the grocery store might make the relevant color appear brighter and more saturated compared with seeing the exact same red apple while searching for a yellow banana. In contrast, recent proposals argue that data supporting attention-related changes in appearance reflect decision- and motor-level response biases without concurrent changes in perceptual experience. Here, we tested these accounts by evaluating attentional modulations of EEG responses recorded from male and female human subjects while they compared the perceived contrast of attended and unattended visual stimuli rendered at different levels of physical contrast. We found that attention enhanced the amplitude of the P1 component, an early evoked potential measured over visual cortex. A linking model based on signal detection theory suggests that response gain modulations of the P1 component track attention-induced changes in perceived contrast as measured with behavior. In contrast, attentional cues induced changes in the baseline amplitude of posterior alpha band oscillations (~9-12 Hz), an effect that best accounts for cue-induced response biases, particularly when no stimuli are presented or when competing stimuli are similar and decisional uncertainty is high. The observation of dissociable neural markers that are linked to changes in subjective appearance and response bias supports a more unified theoretical account and demonstrates an approach to isolate subjective aspects of selective information processing.

Key words: alpha; attention; contrast; EEG; response bias; visual perception.

Significance Statement

Does attention alter visual appearance, or does it simply induce response bias? In the present study, we examined these competing accounts using EEG and linking models based on signal detection theory. We found that response gain modulations of the visually evoked P1 component best accounted for attention-induced changes in visual appearance. In contrast, cue-induced baseline shifts in alpha band activity better explained response biases. Together, these results suggest that attention concurrently impacts visual appearance and response bias, and that these processes can be experimentally isolated.

Introduction

Selective information processing, or selective attention, leads to faster and more accurate processing of sensory stimuli that are cued to be behaviorally relevant (Posner, 1980; Desimone and Duncan, 1995; Egeth and Yantis, 1997; Serences and Yantis, 2006; Carrasco, 2011; Anton-Erxleben and Carrasco, 2013; Buschman and Kastner, 2015; Sprague et al., 2015). While the effects of attention on the efficiency of sensory processing are well established, the impact of selective attention on subjective perceptual experience has long been debated (von Helmholtz, 1866; James, 1890; Fodor, 1984; Pylyshyn, 1999; Raftopoulos, 2001; Carrasco et al., 2004; Schneider, 2006, 2011; Prinzmetal et al., 2008; Schneider and Komlos, 2008; Firestone and Scholl, 2014, 2015a,b; Beck and Schneider, 2017; Itthipuripat et al., 2019a). In the past two decades, a growing body of psychophysical evidence suggests that attended stimuli are perceived differently than physically identical, but unattended, stimuli (e.g., attended stimuli might be perceived as higher contrast or more saturated than unattended stimuli) (Carrasco et al., 2004, 2008; Tse, 2005; Ling and Carrasco, 2007; Fuller et al., 2008, 2009; Prinzmetal et al., 2008; Störmer et al., 2009; Anton-Erxleben et al., 2010, 2011; Cutrone et al., 2014; Firestone and Scholl, 2014, 2015a,b; Störmer and Alvarez, 2016; Carrasco and Barbot, 2019). That said, others have argued that attention does not alter perceptual experience and that reports of such effects are instead attributable to cue-induced response biases. For example, subjects are more inclined to respond that an attended stimulus has a higher contrast than an unattended stimulus, despite having an equivalent subjective perceptual experience of the two stimuli (Schneider, 2006, 2011; Prinzmetal et al., 2008; Schneider and Komlos, 2008; Beck and Schneider, 2017; Schneider and Malik, 2021a,b; Marić and Domijan, 2022).

As a partial resolution to this debate, recent studies suggest that the relative influence of selective attention on visual appearance and response bias may depend on low-level stimulus attributes, such as luminance and contrast (Schneider, 2006, 2011; Carrasco et al., 2008; Prinzmetal et al., 2008; Schneider and Komlos, 2008; Beck and Schneider, 2017; Itthipuripat et al., 2019a). When attended and unattended stimuli are near or below detection thresholds, attentional cues may not alter the perceived contrast because there is not enough baseline visual information to upregulate. Thus, reported differences in the perceived contrast of the attended stimulus must be because of response bias (Prinzmetal et al., 2008). However, Carrasco and colleagues have argued that cue-induced response biases do not substantively impact measurements of the subjective experience of suprathreshold stimuli (Carrasco et al., 2008; Anton-Erxleben et al., 2010, 2011). This argument is based on the premise that attention has a larger impact on neural responses evoked by suprathreshold stimuli because they provide sufficient sensory evidence to guide perceptual judgments (di Russo et al., 2001; Kim et al., 2007; Lee and Maunsell, 2009; Itthipuripat et al., 2014a,b, 2017, 2018, 2019b; Sawetsuttipan et al., 2023). Nonetheless, rendering two suprathreshold stimuli at similar contrast levels will increase uncertainty and may induce a bias to report that a cued stimulus is higher contrast, independent of the actual subjective experience (Schneider, 2006, 2011; Schneider and Komlos, 2008; Beck and Schneider, 2017). Thus, isolating changes in subjective perceptual experience is challenging as there are a variety of scenarios that might promote, or mask, the contributions of response biases.

To address this issue, we recently conducted a psychophysical study that systematically measured both cue-induced response biases and changes in the perceived contrast of attended and unattended visual stimuli across a wide range of contrast levels (Itthipuripat et al., 2019a). Our findings revealed that, when both the attended and unattended stimuli had very low or very high contrasts, subjects tended to guess that the cued stimulus had a higher contrast than the uncued stimulus, consistent with the cue-induced response bias hypothesis (Itthipuripat et al., 2019a; see also Schneider, 2006, 2011; Prinzmetal et al., 2008; Schneider and Komlos, 2008; Beck and Schneider, 2017). However, the most noticeable changes in perceived contrast occurred at low-to-mid-level contrasts, consistent with prior results demonstrating that attention can alter visual appearance (Itthipuripat et al., 2019a; see also Carrasco et al., 2008; Anton-Erxleben et al., 2010, 2011). While these findings suggest that attention can alter contrast appearance in certain circumstances and induce response bias in others, here we assessed different neural markers of visual processing to determine whether there are dissociable neural mechanisms that can be quantitatively linked to these two processes. If so, this would further suggest that attention impacts changes in appearance as well as changes in response bias and that both processes contribute to overall patterns observed in psychophysical data.

Using a paradigm adopted from our recent experimental work (see Fig. 1) (see also Itthipuripat et al., 2019a), we conducted an EEG study where we simultaneously measured attentional modulations of two different EEG markers of early visual processing: the amplitude of the P1 component and the amplitude of alpha (α) band oscillations (9-12 Hz) over posterior occipital electrodes. We focused on these neural markers because selective attention modulates the amplitude of the P1 component (van Voorhis and Hillyard, 1977; Mangun and Hillyard, 1990; Woldorff et al., 1997; Hillyard and Anllo-Vento, 1998; Foster et al., 2021) and because α oscillations track changes in the spatial focus of selective attention (van Voorhis and Hillyard, 1977; Mangun and Hillyard, 1990; Woldorff et al., 1997; Foxe et al., 1998; Hillyard and Anllo-Vento, 1998; Fries et al., 2001, 2008; Sauseng et al., 2005; Kelly et al., 2006, 2009; Klimesch et al., 2007; Foster et al., 2016, 2017, 2021). To assess the relationship between attention-related neural modulations of these markers and changes in behavior, we used quantitative linking models based on signal detection theory (SDT) (Tanner and Swets, 1954; Pestilli et al., 2011; Cutrone et al., 2014; Itthipuripat et al., 2014a, 2017; Itthipuripat and Serences, 2016).

Our results indicate that attention-related modulations of the P1 amplitude were predictive of attentional effects on perceived contrast at low-to-mid-level stimulus contrasts. In contrast, changes in α band activity were associated with response bias in the psychophysical data when cued and uncued stimuli were both rendered in either very low or very high contrasts. Together, our findings suggest that dissociable neural mechanisms underlie the effects of attention on visual appearance and response bias. More importantly, these dissociable neural modulations demonstrate that changes in appearance and changes in response bias simultaneously operate — to varying degrees depending on bottom-up stimulus factors — in the context of selective information processing.

Materials and Methods

Subjects

We recruited 22 neurologically healthy male and female human observers who had normal or corrected-to-normal vision from the local community at the University of California–San Diego. In accordance with the local institutional review board at University of California–San Diego, subjects provided written informed consent before participating in the study. Two subjects terminated their participation before completing the experiment, resulting in 20 subjects included in the final analysis
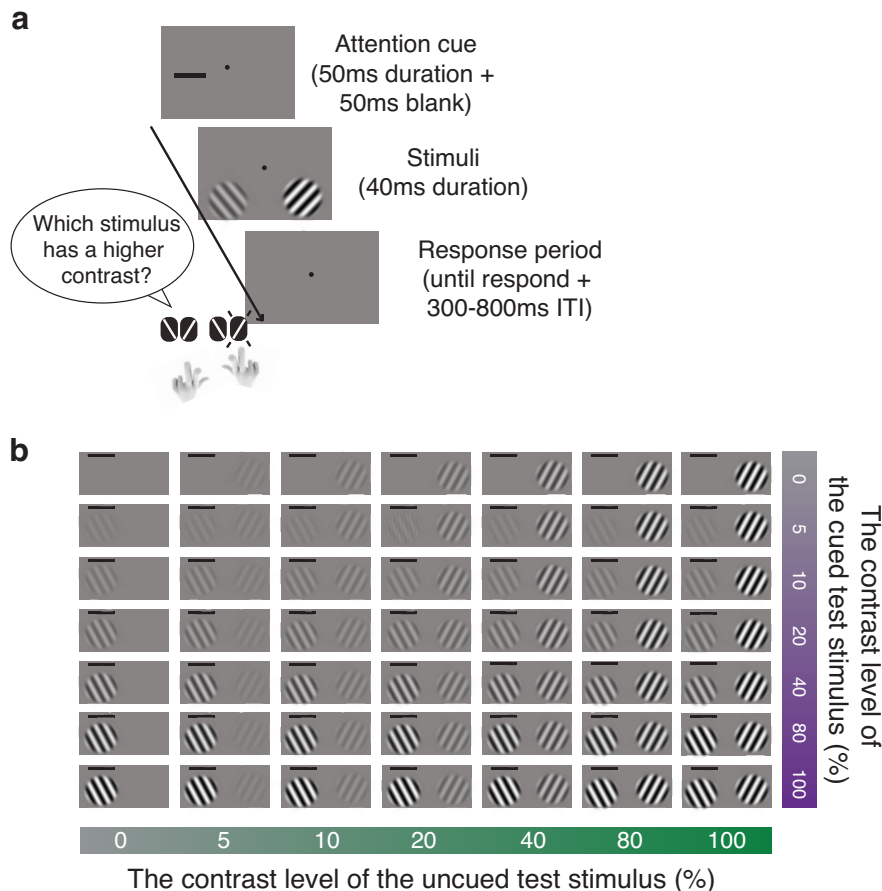
Figure 1. Task and stimuli. *a*, The attention-cueing comparative contrast judgment task (see a similar method in Itthipuripat et al., 2019a). Subjects had to report the orientation of the stimulus they perceived as having a higher contrast. *b*, Depiction of all contrast pairs in the cue-left condition. The same fully crossed contrast manipulation was also used in the cue-right condition. The values in the horizontal gray-green box are the possible contrast levels used for the uncued test stimuli. The contrast values in the vertical gray-purple box represent the contrast levels of the cued test stimuli.

(9 female, 18-25 years old, 2 left-handed). Given that we used a single-session EEG recording approach unlike previous studies that used a multiple-recording session approach, the sample size of 20 we used in the present study was relatively higher than those used in the prior studies (*N* values = 3-14 in Pestilli et al., 2011; Itthipuripat et al., 2014a,b, 2017; Sawetsuttipan et al., 2023).

Experimental design and statistical analysis

Stimuli and task. We presented stimuli using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and MATLAB (The MathWorks) 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 (see Fig. 1) (Itthipuripat et al., 2019a). In this task, they were asked to judge the relative apparent contrast of two Gabor stimuli (spatial frequency = 3 c/°, SD of the Gaussian envelope = 2.18°, stimulus radius = 6.53°) that were presented in the left and right lower quadrants (eccentricity = 13.74°). Subjects reported whether the stimulus with the higher contrast was tilted 45° clockwise (CW) or counterclockwise (CCW) from vertical. Responses were made by pressing one of four buttons on a standard QWERTY keyboard. The responses 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 consisting of 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 40 ms

(50% left-cued and 50% right-cued trials). The contrast values of the two stimuli were fully crossed and drawn from seven contrast levels (0%, 5%, 10%, 20%, 40%, 80%, 100% Michelson contrasts). There was no response deadline. Following a button press response, there was an intertrial interval 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 location (left or right), left stimulus contrast (7 levels from 0% to 100%), and right stimulus contrast (7 levels from 0% to 100%).

Analysis of behavioral data. Past psychophysical studies that examined the effects of attention on visual appearance typically presented one stimulus (either in the left or the right hemifield) at a fixed level of contrast (termed as the "standard contrast"). Another stimulus would be simultaneously presented on the other side of fixation and at a variable contrast level (termed the "test contrast") (e.g., Carrasco et al., 2004, 2008; Ling and Carrasco, 2007; Fuller et al., 2008, 2009; Störmer et al., 2009; Anton-Erxleben et al., 2010, 2011). This method yields an estimate of the relative perceived contrast of each test stimulus compared with the standard stimulus, which can be expressed as the probability $p(test > standard)$ for each test stimulus chosen over a given standard stimulus.

In the present study, we adopted a slightly modified approach using a fully crossed design where the contrasts of the cued and the uncued stimuli were drawn from a full range of contrast values (0%, 5%, 10%, 20%, 40%, 80%, and 100%). To make contact with previous research, we computed the probability that each stimulus (termed here the stimulus of interest or the test stimulus) was reported as having a higher contrast than the stimulus on the opposite side of the screen (termed here the paired or the standard stimulus). This calculation was performed

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 performed two types of analyses where the probability values were based on all trials (all-trials condition) or only on trials where the reported orientation of the test contrast was "correct" (i.e., correct-only conditions). When the test stimulus was rendered at 0% contrast, we randomly labeled the direction of the orientation offset (CW or CCW) before 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% test contrast trials.

Next, we fit the probability functions 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 (NR) equation using a maximum likelihood estimation method as follows:

$$P(c) = G_r \times \frac{C^q}{C^q + G_c^q} + B \qquad (1)$$

where $P(c)$ is $p(\text{test} > \text{standard})$ for a given test contrast value (c). 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 (see, e.g., Carandini and Heeger, 2011). 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 NR function, termed a baseline-input model (Cutrone et al., 2014), because in prior work we found that it yielded worse fits compared with the baseline shift model and the baseline-input model gave B values that were out of the realistic range (i.e., values that were ≫1), making it difficult to interpret the results (Itthipuripat et al., 2019a). If there is an increase in contrast appearance driven by the attentional cue, we expect an increase in contrast gain or a decrease in G_c, which will result in a leftward shift of the psychometric function (see Fig. 2a) (see also Carrasco et al., 2004; Itthipuripat et al., 2019a). A decrease in G_c leads to a leftward shift because G_c is the denominator of the NR function so as G_c decreases $P(c)$ will increase at the low-to-mid-level contrast values. That said, if the cue only induces response bias, there should be an increase in the baseline-offset (B) of the psychometric function without concurrent changes in contrast gain (see Fig. 2b). Since the probability values of the psychometric function cannot exceed 1, an increase in the baseline-offset parameter should result in smaller values of response gain (G_r) as the slope of the psychometric function will get necessarily smaller. The attentional cue could also induce changes in both subjective appearance and response bias. This would lead to a decrease in G_c, an increase in B, and an accompanying decrease in G_r (see Fig. 2c).

Next, we used two-way repeated-measures ANOVAs to evaluate main effects of attention and main effects of standard contrast, as well as interactions between these factors on the B, G_r, and G_c parameters that best characterize the observed psychometric functions (see Fig. 3).

EEG recording and preprocessing. EEG data were recorded using a 512 Hz sampling rate with a Biosemi ActiveTwo system containing 64 pin-type active EEG electrodes and 8 flat-type active external electrodes that were made of sintered Ag-AgCl. The 64 pin-type electrodes were mounted on the elastic head caps with the 10-20 layout that is in accordance with the international 10-20 system (Jasper, 1958; Chatrian et al., 1975, 1985; American EEG Society, 1980a,b,c,d). Two flat-type external electrodes were placed on top of the left and right mastoids. Two additional external electrodes were placed near the outer canthi of the left and right eyes to monitor horizontal eye movements. To monitor blinks and vertical eye movements, four more external electrodes were placed on the forehead just above the left and right eyebrows and on the cheeks right below the left and right eyes. To reduce the impedance of the

electrodes, high conductive gel was applied to all EEG and external electrodes to ensure good contact with the skin. We kept signal offsets below 20 mV relative to the CMS-DRL reference, which is standard practice for the Biosemi ActiveTwo system. While EEG signals were being recorded, subjects were asked to minimize blinks, eye movements, and head and body movements. They were seated on a comfortable chair in a dimly lit sound-attenuated electromagnetically shielded room.

EEGLAB version 2019.1 and in-house MATLAB (R2020a) scripts were used to preprocess the EEG data offline. First, the continuous EEG data were rereferenced 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 2000 ms after the cue onset. Next, we used independent component analysis (Bell and Sejnowski, 1995; Makeig et al., 1996) to correct prominent eye blink and muscle artifacts. Finally, we used visual inspection and threshold rejection to discard epochs contaminated by residual eye blinks and saccades ($>\pm$50-200 μV deviation from zero, with thresholds chosen for each individual subject), horizontal eye movements ($>\pm$50-75 μV deviation from zero), muscle activity, or drifts (8.8946% of trials were rejected, $\pm$9.2797% SEM).

The visually evoked P1 component and α band oscillations. To examine the effects of attention on visual information processing, our study focused on two EEG signals believed to reflect different aspects of visual cortical processing: the P1 component and the α band oscillations ($\sim$9-12 Hz). The P1 component is an early evoked response thought to originate from extrastriate visual areas. Its amplitude is known to be enhanced by selective attention (van Voorhis and Hillyard, 1977; Mangun and Hillyard, 1990; Woldorff et al., 1997; Hillyard and Anllo-Vento, 1998). Notably, attention-induced increases in the P1 amplitude have been associated with improved perceptual detection and discrimination as well as increases in perceived contrast (Mangun and Hillyard, 1990; Störmer et al., 2009, 2019; Itthipuripat et al., 2014a, 2017). On the other hand, selective attention has been found to reduce the amplitude of α band oscillations in posterior occipital electrodes contralateral to the attended location (Foxe et al., 1998; Fries et al., 2001, 2008; Sauseng et al., 2005; Kelly et al., 2006, 2009; Klimesch et al., 2007). The reduction in α amplitudes has been shown to track changes in response bias (i.e., response criterion), but not changes in perceptual sensitivity (Limbach and Corballis, 2016; Benwell et al., 2017, 2018, 2020; Iemi et al., 2017; Foster and Awh, 2019). While previous studies have associated changes in the amplitude of the P1 and α band activity with changes in perceived contrast, they have not taken into account potential contributions from response bias in their psychophysical measurements (Störmer et al., 2009, 2019; Balestrieri and Busch, 2022).

Following the EEG preprocessing steps described in the previous section, 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 versus right cued stimuli (2 conditions) × 7 cued contrast levels (0%-100%) × 7 uncued contrast levels.

Next, we averaged the stimulus-locked EEG data in each of these conditions to obtain the ERPs. At this step, the ERPs contained both cue-evoked and bilateral stimulus-evoked responses. Therefore, we adopted the ERP subtraction method to (1) isolate the early sensory responses associated with a single stimulus from the bilateral stimulus presentation and (2) subtract the cue-related response from the stimulus-evoked ERPs, under the assumption that these stimulus- and cue-related responses combine linearly (see similar methods in Greenwood and Goff, 1987; Iragui et al., 1993; Kiss et al., 1998; Chica et al., 2010; Itthipuripat et al., 2014a, 2017, 2019b; Störmer et al., 2019).

As illustrated in Figures 4 and 5a, 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%). We also extracted the stimulus evoked responses related to the uncued stimuli of different contrast levels by subtracting the ERPs on trials where the uncued stimulus was rendered
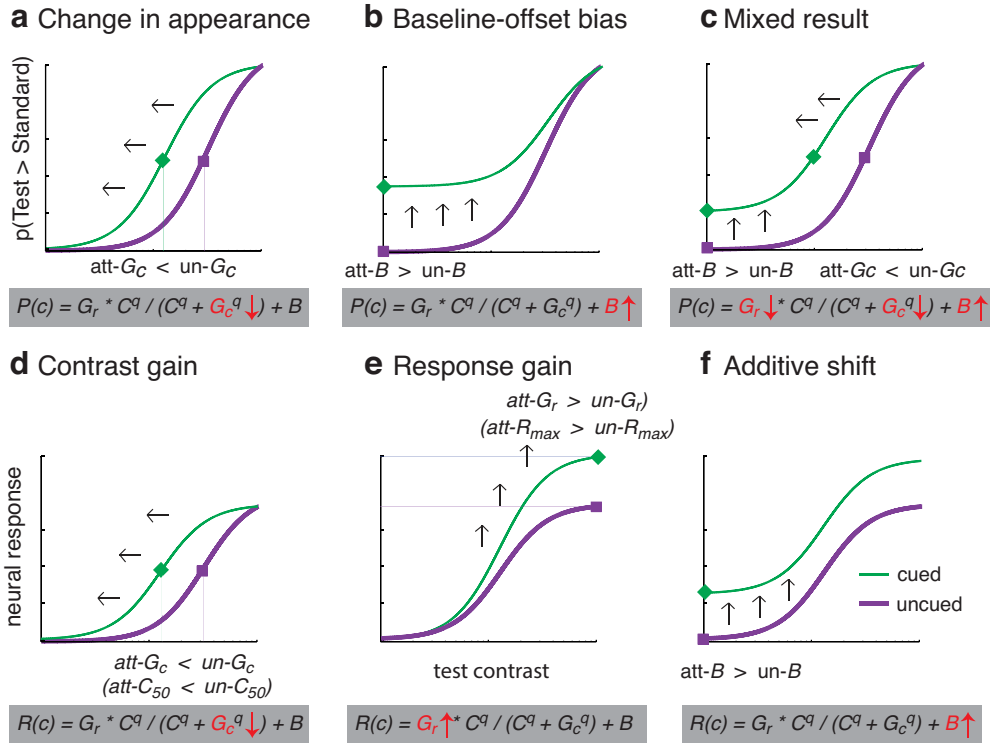
Figure 2. Predictions. ***a-c***, Alternative predictions for the behavioral results. ***a***, Attention increases the perceived contrast of visual stimuli via a leftward shift in the behavioral CRFs. In this scenario, attention should only decrease the contrast gain factor (G_c) and there should not be any changes in the baseline-offset (B) or response gain (G_r). ***b***, Attention induces a baseline-offset response bias (B; upward shift at the baseline-offset) without changes in a leftward shift of the CRFs (i.e., no change in G_c). This corresponds to a bias to respond to the cued stimulus without a change in subjective appearance. ***c***, Attention could induce changes in both subjective appearance and response bias as indexed by changes in both G_c and B, respectively. ***d-f***, Alternative predictions for the neural CRFs. Since the estimated G_r and G_c parameters could extend beyond the realistic range of stimulus contrast values ($>$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 semisaturation 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 semisaturation contrast factor (C_{50}). ***e***, Alternatively, attention could increase the multiplicative response gain, corresponding to the slope of the neural CRFs, as indexed by the maximum neural response (R_{max}). ***f***, Last, 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. Gray boxes below individual figures contain the NR equation (Eq. 1) with the parameters that change in each scenario marked in red and the arrows indicating the direction of changes.

at 0% contrast. These steps allowed us to isolate a P1 component, which we obtained the signals from five contralateral posterior occipital electrodes (O2, PO4, PO8, P2, and P4 for the left stimulus and O1, PO2, PO6, P1, and P3 for the right stimulus). These electrodes were selected because they had the highest baseline-subtracted P1 amplitude collapsed across attention conditions and contrast levels. The time window of the P1 was selected around the peak of the subtracted P1 data collapsed across attention conditions and contrast levels (i.e., 60-90 ms after stimulus). Next, we computed the mean amplitude of the P1 component over 60-90 ms, in each cue and contrast condition from individual subjects. The electrodes and time window of the P1 component in this present study were consistent with those used in previous studies that examined attentional modulations of the P1 component and early sensory-evoked responses (van Voorhis and Hillyard, 1977; Mangun and Hillyard, 1990; Woldorff et al., 1997; Hillyard and Anllo-Vento, 1998; Störmer et al., 2009, 2019; Itthipuripat et al., 2014a, 2017). Then, we plotted the mean amplitude values as a function of test contrast, resulting in a P1-based contrast response function (CRF) for each attention condition and standard contrast level (see Fig. 5a).

Next, we fit the P1-based CRFs with the NR equation (Eq. 1) to determine whether these P1-based CRFs underwent contrast gain, multiplicative response gain, or changes in baseline-offset (see Fig. 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 three free parameters, including the contrast gain (G_c), response gain (G_r), and baseline-offset parameters (B). We used the root mean squared error method to fit the neural data instead of using the maximum likelihood estimation method like we did for fitting the behavioral

data because the neural responses are continuous values unlike the behavioral outputs that are discrete values. Here the exponent q of the NR equation was fixed at 2 (Carandini and Heeger, 2011). 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. The contrast gain parameter (G_c) was constrained so that it could vary only between 0% and 100% contrast (i.e., the realistic range of the physical contrast value).

Hypothetically, a decrease in G_c will lead to an increase in contrast gain or the neural CRF shifting horizontally in the leftward direction (see Fig. 2d). On the other hand, an increase in G_r will lead to an increase in multiplicative response gain or the slope of the neural CRF (see Fig. 2e). Alternatively, an increase in B will lead to an increase in the baseline-offset of the neural CRF or an additive shift in overall neural activity of the function without changing its slope (see Fig. 2f). 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 semisaturation 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 main effects of attention (cued vs uncued), main effects of standard contrasts (0%-100%), and their interactions on the B, C_{50}, and R_{max} (see Fig. 5b).

Since the ERP subtraction method relied on an assumption of linear summation, we evaluated whether similar patterns of attentional modulations of the P1-based CRFs were obtained without performing the
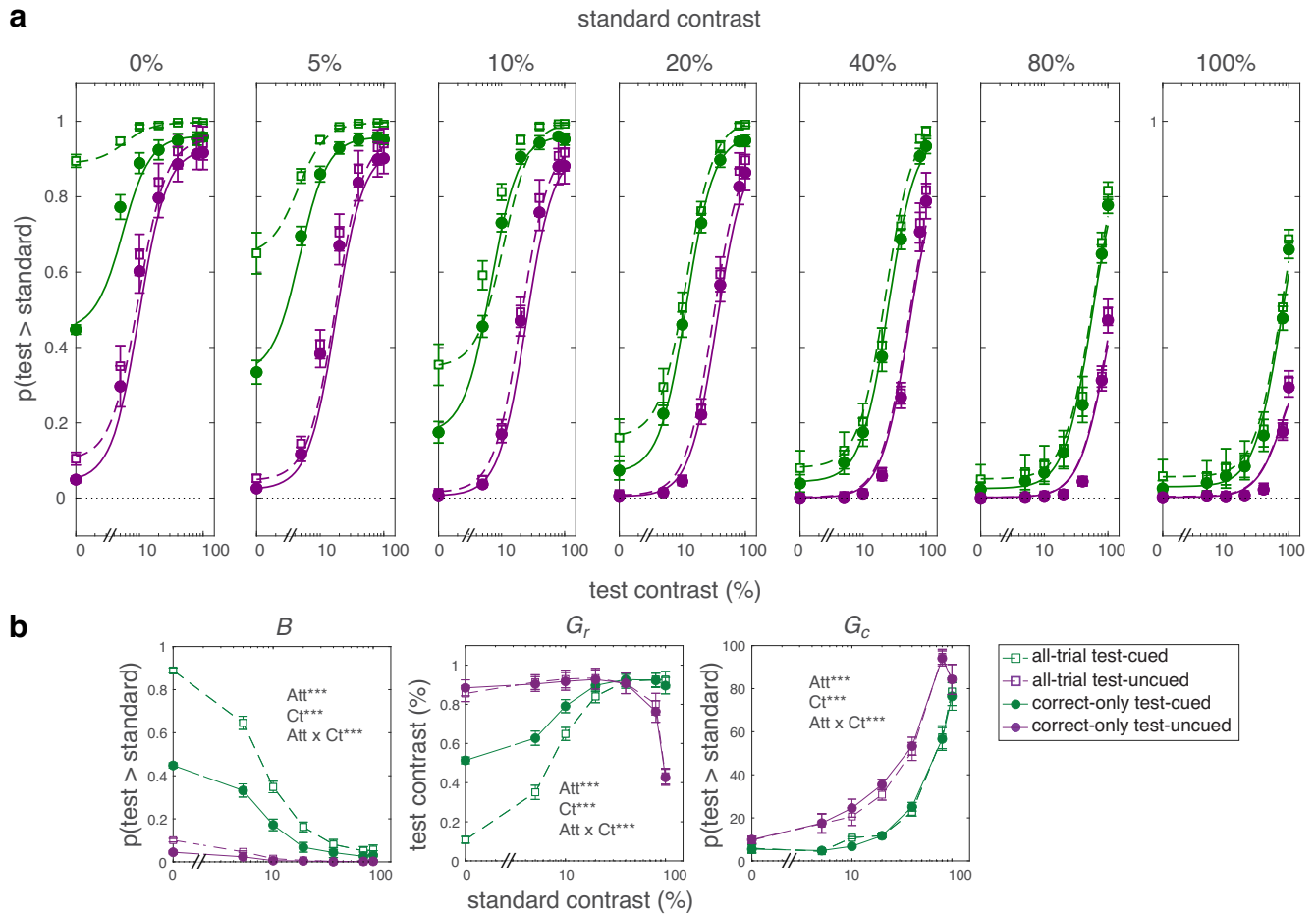
Figure 3. Behavioral data. *a*, The probability that subjects reported the test stimulus (i.e., the stimulus of interest, either cued or uncued) as having a higher contrast than the standard stimulus (i.e., the paired cued or uncued stimulus) termed here as *p* (test > standard) plotted as a function of test contrast for all possible standard contrast levels. *b*, The corresponding best-fit parameters from an NR function. Left, 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) (Prinzmetal et al., 2008; Itthipuripat et al., 2019a). 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. Middle, The response gain parameter (*G_r*) controls the slope of the psychometric function. *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* (Left). 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 (i.e., 80%-100%). Right, 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. Error bars indicate the within-subject SEMs ($\pm$1 SEMs). Att∗∗∗, Ctt∗∗, and Att × Ctt∗∗∗ represent the significant main effects of attention, standard contrast, and the interaction between the two factors, respectively (all *p* values < 0.001).

subtraction. To do so, we obtained the nonsubtracted P1 responses at the same set of electrodes and time windows as those of the subtracted P1 data and plotted them as a function of test contrast. We then performed the same fitting procedure and statistical analysis to test whether the nonsubtracted P1-based CRFs underwent contrast gain, multiplicative response gain, or changes in baseline-offset (see Fig. 5c,d).

In order to assess cue-induced changes in in posterior α band activity, we first wavelet-filtered the artifact-corrected epoched EEG data using a Gaussian filter centered at 1-40 Hz (in 1 Hz steps) with a fractional bandwidth of 0.2 Hz and computed the absolute value of the wavelet coefficients to obtain a measure of amplitude for each frequency. This resulted in event-related time-frequency representations from 1 to 40 Hz (see Fig. 6) (see also Canolty et al., 2006, 2007; Itthipuripat et al., 2013).We then selected the data from 9 to 12 Hz and sorted them into each of the 98 experimental bins. As illustrated in Figure 7, for each of these experimental bins, we then computed the mean percent change in α amplitude relative to baseline activity from 200 to 600 ms before the cue onset (or 300 to 700 ms before the stimulus onset) using the following equation:

$$Percent\ signal\ change = \frac{\alpha\ amplitude - Baseline\ activity}{Baseline\ activity} \times 100\%$$

(2)

To obtain α-based CRFs, we then took the averaged values of the α data from 100 to 700 ms after the cue onset (0-600 ms after the stimulus onset) across the same set of contralateral posterior electrodes used in the P1 analysis. We then plotted mean α amplitudes as a function of test contrast for each attention condition and each standard contrast level for each subject (see Fig. 8a). Since the poststimulus reduction in α band activity occurred over an extended temporal epoch, we averaged over a longer time window (i.e., 0-600 ms after stimulus onset) compared with the window used for the P1 component. Also, the electrodes and time window of the α band activity used in the present study were consistent with those used by prior studies (e.g., Foxe et al., 1998; Fries et al., 2001, 2008; Sauseng et al., 2005; Kelly et al., 2006, 2009; Klimesch et al., 2007; Nelli et al., 2017). The α-based CRFs were then fit with an NR equation (Eq. 1). The fitting routine was similar to that conducted in the P1 data analysis, except that the seed value for G_r was determined based on the
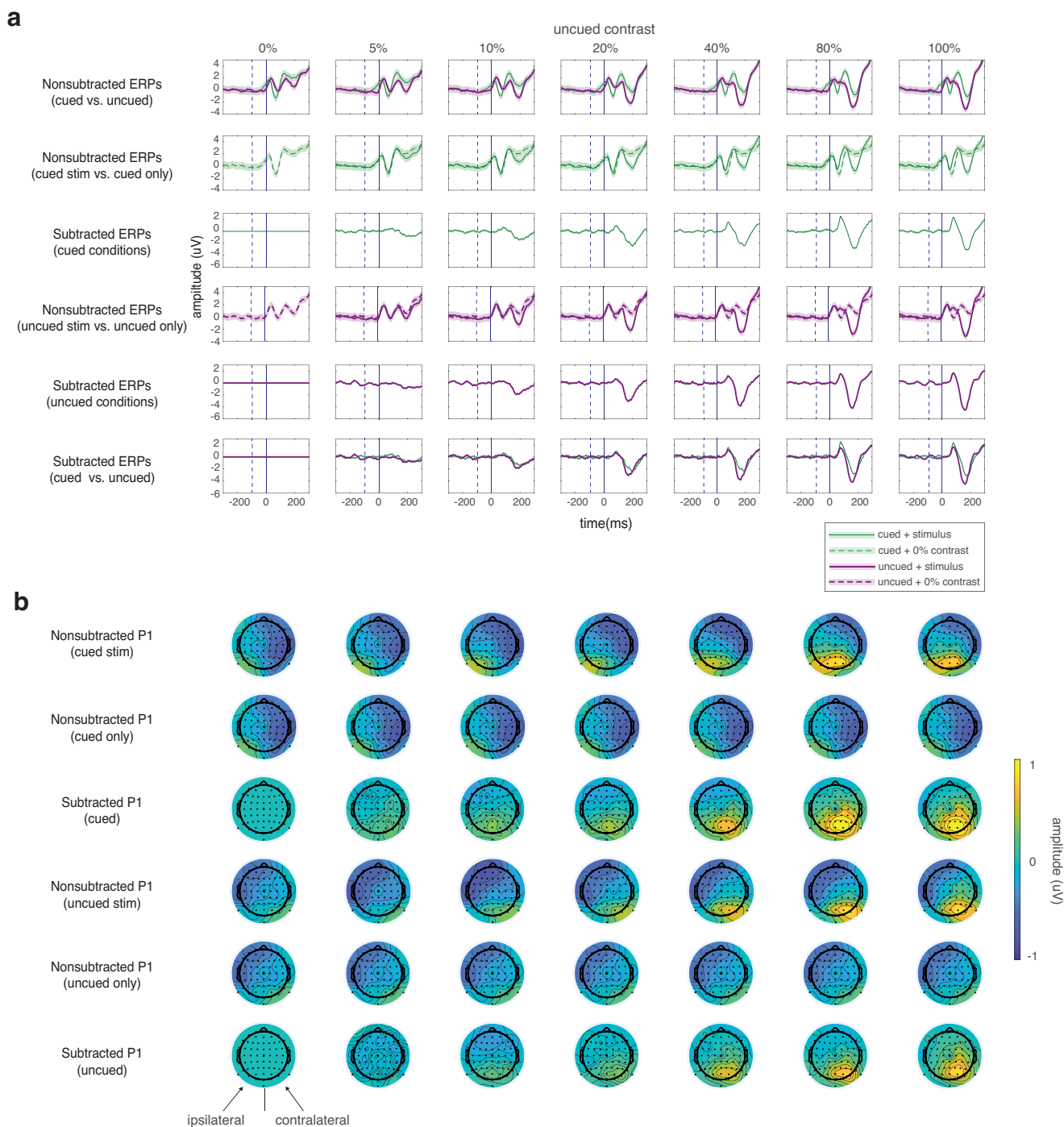
Figure 4. Isolating the P1 component related to a single visual stimulus from ERPs elicited by the cue and the bilateral stimulus array. *a*, ERP traces represent the subtraction method. Shaded areas represent the within-subject SEMs where the mean values between attention conditions were removed before computing the SEMs. First row, Nonsubtracted ERPs contralateral to the cued and uncued locations shown in green and purple traces, respectively. These ERP traces were obtained from the posterior occipital electrodes (see Materials and Methods). Vertical dashed and solid black lines indicate the cue and stimulus onsets, respectively. In the second row, We subtracted ERPs contralateral to the cue alone (green dashed traces) from ERPs contralateral to the cue paired with the stimuli of 0%-100% contrasts (i.e., the cued-stimulus conditions; green solid traces). Both cue-only and cued-stimulus conditions were paired with uncued stimuli of 0%-100% contrasts on the opposite visual hemifield, and the responses associated with these uncued stimuli should also be subtracted out. In the third row, we show that this subtraction method results in the subtracted ERPs related to a single cued stimulus without responses related to the cue itself or the uncued stimulus presented on the opposite visual hemifield. Fourth and fifth rows, The ERP subtracting method for the uncued condition and the resulting subtracted ERPs contralateral to the uncued stimulus. Sixth row, The overlay between the subtracted ERPs contralateral to the cued and uncued stimuli, shown in green and purple, respectively. The amplitude of the P1 component increased with attention, especially at the high test contrast levels, implicating response gain mechanisms. *b*, Corresponding topographical maps of the P1 amplitude averaged across ~60-90 ms after stimulus. The head model was reconfigured so that the left and right sides of the head model represent contralateral and ipsilateral channels, respectively.
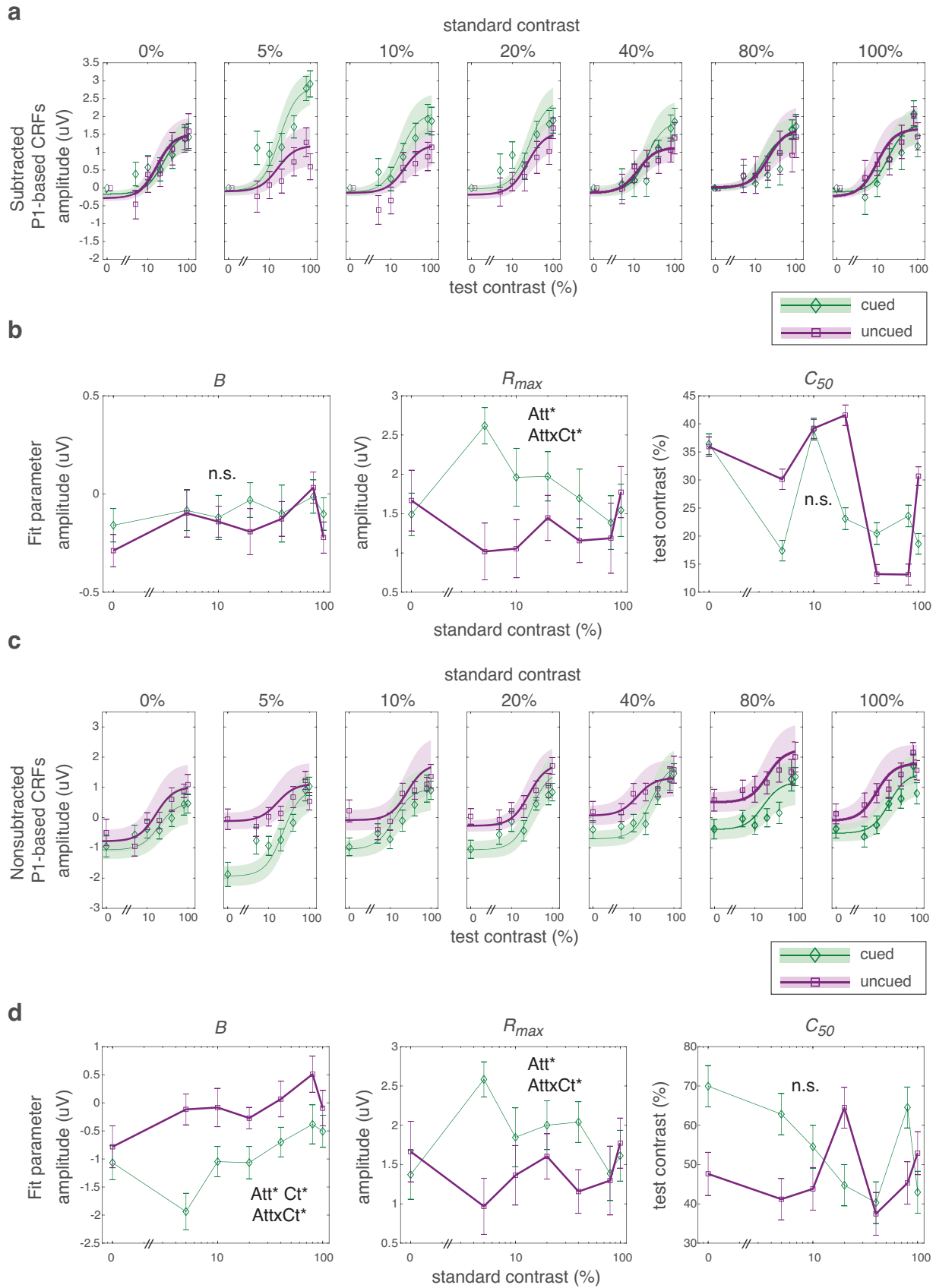
Figure 5. ***a***, The baseline-subtracted P1-based CRFs plotted separately for the cued and uncued conditions across different levels of standard contrast. Attention enhanced the multiplicative response gain of the P1 data. ***b***, The corresponding best-fitting parameters from the NR function. Left, There were no differences in the baseline-offset. Middle, Attention selectively enhanced response gain indexed via an increase in the maximum response of the P1 component (R_{max}), which was larger at low-to-mid-level standard contrasts. Right, There were no differences in the level at which the P1 amplitude reached half-maximum (C_{50}). ***c***, ***d***, The nonsubtracted P1-based CRFs and corresponding best-fitting parameters. Overall, the data are qualitatively similar to

difference between the minimum and maximum values of the postcue α activity across all test contrast levels because of the fact that the α band activity got smaller as a function of test contrast (instead of larger like the P1). Finally, we used two-way repeated-measures ANOVAs to test main effects of attention (cued vs uncued), main effects of standard contrasts (0%-100%), and their interactions on the B, C_{50}, and R_{max} (see Fig. 8b).

Recent research has suggested that traditional practices for analyzing changes in the power or the amplitude of brain oscillations may not truly reflect changes in the periodic components of the underlying oscillations. Instead, apparent changes in amplitude might reflect changes in the slope of the aperiodic 1/f noise in EEG signals (Donoghue et al., 2020). Thus, we performed an auxiliary analysis where we fit the precued and poststimulus power spectra of EEG signals recorded from the contralateral posterior occipital sites (see Fig. 7c) using the FOOOF function (i.e., fitting oscillations & one over f) (Donoghue et al., 2020). This fitting procedure allowed the parametrization of the periodic components of α band oscillations, including log power, central frequency, and bandwidth as well as the aperiodic components of the 1/f, including the aperiodic exponent and offset (see Fig. 9a-e). Before using the FOOOF function, we converted α amplitude into α power (squared amplitude). Finally, we used four-way repeated-measures ANOVAs to test the main effects of period (precued vs poststimulus periods), attention (cued vs uncued), test contrast, and standard contrast as well as their interactions on each of these periodic and periodic exponents.

Since we found a significant three-way interaction between period, attention, and test contrast on the log α power, we subtracted the precue baseline from the poststimulus α activity and fit the neural CRFs based on the log α power with respect to the precue baseline (see Fig. 8f) using the NR equation (Eq. 1). Last, we performed two-way repeated-measures ANOVAs to test main effects of attention (cued vs uncued), main effects of standard contrasts (0%-100%), and their interactions on the B, C_{50}, and R_{max} (see Fig. 9g).

Modeling behavioral data using attentional modulations of the P1 and α band activity. Next, we examined how different patterns of attentional modulations, specifically attention-induced increases in multiplicative response gain of the P1-based CRF and attentional modulations of the baseline-offset of the α-based CRF 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 (Itthipuripat et al., 2019a) (see Fig. 2a,e). However, this did not account for the baseline-offset in response biases (Itthipuripat et al., 2019a). 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 (Itthipuripat et al., 2019a) (see Fig. 2b,f). Based on these results, we hypothesized that the multiplicative gain of the P1-based CRFs (see Fig. 5) should account for attention-induced increases in contrast appearance as reflected by the leftward shifts of the psychometric functions which occurred predominantly when the standard stimuli were rendered at low-

to-mid-level contrasts (see Figs. 2a, 3b-right). On the other hand, modulations of baseline-offsets in the α-based CRFs (see Fig. 8) should better account for changes in the baseline-offset response bias in the behavioral data (Itthipuripat et al., 2019a) (see Figs. 2b, 3b-left).

To test these predictions, we adopted a quantitative linking model based on SDT (Cutrone et al., 2014; Itthipuripat et al., 2019a). In brief, we estimated our psychophysical data, or $p(test > standard)$, based on the amplitude difference between neural responses (either the P1 data, the α 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), shared across all experimental conditions (see Fig. 10a).

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 because of 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:

$$Normalized\, Data = \frac{Data - min(Data)}{max(Data) - min(Data)} \qquad (3)$$

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 α-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 α-based CRFs were the result 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 α band activity was generally reduced as a function of attention and stimulus contrast, we flipped the sign of the simulated α-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 α 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 α model, we computed the sum of the normalized P1-based and α-based CRFs separately for individual attention conditions and standard contrast levels.

To compare the predictive power of different linking models (e.g., the P1-only model, the α-only model, and the combined model), we conducted a cross-validation and bootstrapping analysis. For each modeling iteration, we first shuffled the trial order of the data from each subject and then assigned the first 80% of trials in the shuffled data to a training set and the last 20% trials into a holdout set (note: using the term "holdout" set here as opposed to the more common "test" set to avoid confusion with the "test stimulus" and "standard stimulus" terminology used elsewhere). Training data and holdout data from each subject were then combined to create a meta-training set and a meta-holdout set. We then computed the magnitude of the P1 response and α response for each contrast and attention condition using only data from the training set (following methods described above). Assuming a maximum likelihood decision rule, p (test > standard) based on the behavioral data from the holdout dataset was estimated based on the probability that the test-evoked neural response was higher than the standard-evoked neural response in the training dataset in 1000 simulated trials for individual contrast levels and attention conditions, where each simulated trial was

←

the baseline subtracted data shown in *a*, *b*, except that the baseline of the nonsubtracted data was reduced with attention (*d*, left). This was because of the overlapping temporal windows between the negative-going N1 component associated with the cue and the positive-going P1 component associated with the stimulus in the nonsubtracted data. Ctt∗, Att∗, and Att × Ctt∗ represent significant main effects of contrast and attention, as well as a significant interaction between attention and standard contrast, respectively (p values < 0.05). *a*, *c*, The fit curves were not obtained by fitting the grand-averaged P1-based CRF data per se (i.e., *a*, *c*, diamonds and squares). Instead, they were reconstructed based on the averaged fit parameters computed at the individual-subject level (*b*, *d*, diamonds and squares). We did this so that the fit curves represent the statistics we performed on the fit parameters obtained from fitting individual subjects' data. *b*, *d*, Error bars indicate within-subject SEMs where the mean value of each attention condition was subtracted before computing the SEMs. *a*, *c*, Shaded areas of the fit curves in represent the variation of the fit data across subjects based on within-subject SEMs of fitting parameters shown in *b*, *d*.
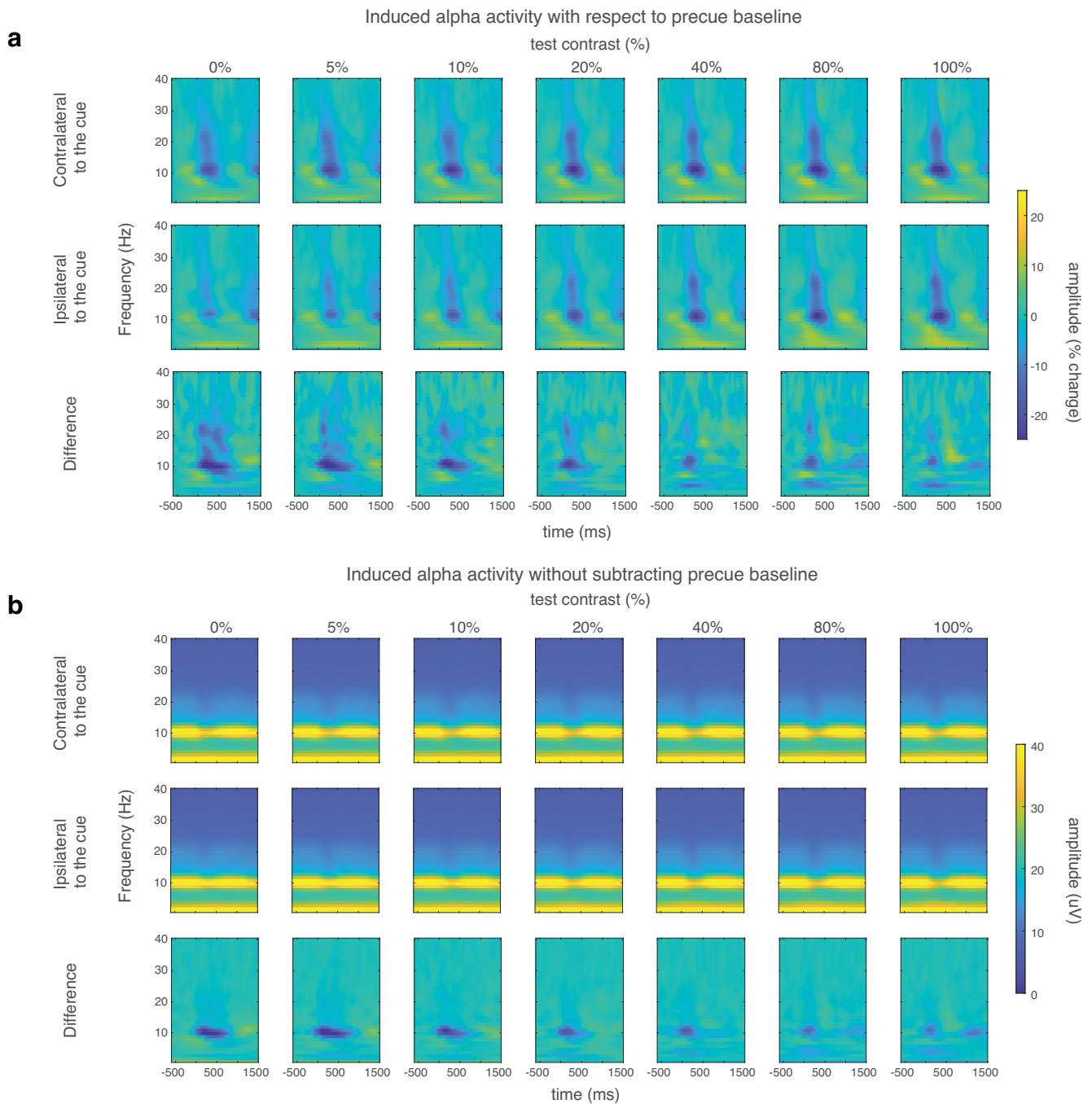
Figure 6. Time-frequency representations of induced EEG oscillations. ***a***, Changes in induced EEG amplitude with respect to precue baseline. ***b***, Non–baseline-corrected data.

generated by sampling from normal distributions with means derived from the training dataset and SDs derived from exhaustively sampling noise values from 0 to 0.7 in 71, 0.01-increments to maximize log-likelihood estimates. This procedure was then repeated 5 times with successive blocks of 20% of trials from each subject used as a holdout set (i.e., fivefold cross-validation). We then took the average of the log-likelihood estimates and goodness-of-fit (R^2) across all 5 folds. After one fivefold cross-validation iteration was complete, we reshuffled the data from each subject and then repeated the exhaustive process of assigning 80% of trials to a training set and 20% to a holdout set. This process was repeated 1000 times, with each iteration yielding different results because the trial shuffling and cross-validation procedure ensured that different trials went into each training and holdout dataset on each iteration. Finally, we created bootstrap distributions based on these 1000 iterations to derive 95% CIs

associated with the predictions of the linking models as well as the corresponding log-likelihood estimates and R^2 values. We could directly compare R^2 values and log-likelihood estimates of different models because all of these models only had one free parameter, which was the neuronal noise shared across all standard and test contrast levels as well as across the different attention conditions. To evaluate the difference between the performance of the P1 and α models, we compiled the bootstrap distributions of the differences in the R^2 and log-likelihood estimates between the two models and computed the percentage of values in the tails of this distribution that were more or <0 (two-tailed) (see Fig. 10b-d). We also performed a similar statistical analysis to compare the performance of each of the P1 and the α models in relation to the combined model.

In addition, we ran an additional analysis where the weights of the P1 and α data were varied systematically before computing the combined
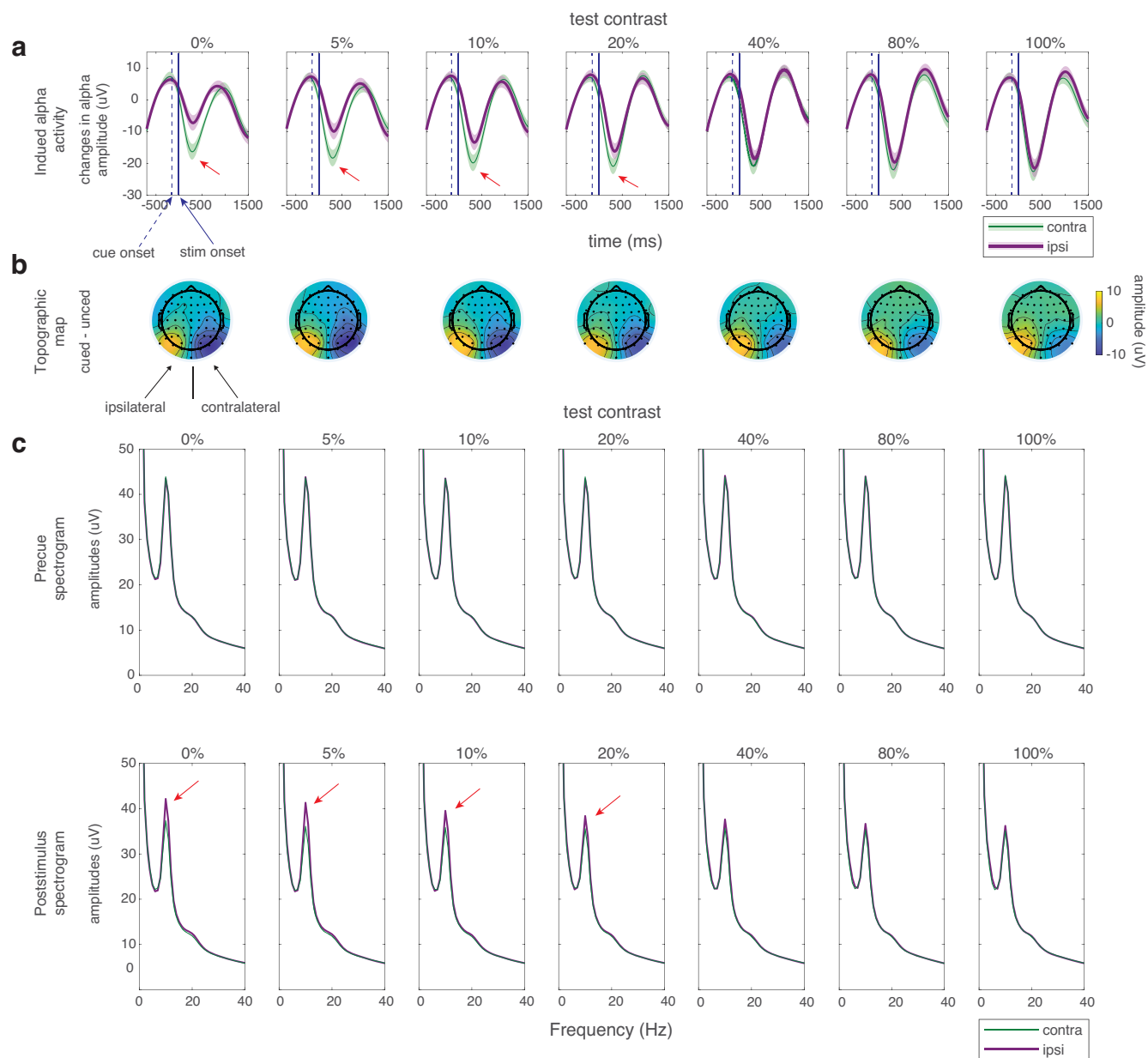
Figure 7. Postcue reduction in α band activity. ***a***, Attentional cues induced a reduction in α amplitude in the posterior occipital electrodes that were contralateral to the stimulus of interest. In these plots, the cue onset and stimulus onsets were at −100 ms (the vertical black dotted lines) and 0 ms (the vertical black solid lines), respectively. The α data were baseline-corrected from −600 to −200 ms before cue onset. ***b***, Topographical maps represent the difference in the α amplitude between the cued and unced conditions at different test contrast levels. ***c***, EEG spectrograms represent non–baseline-corrected α oscillations during the precue and the poststimulus periods (top and bottom rows, respectively). Attention decreased the amplitude of the induced α band activity during the poststimulus period; this was especially apparent at the low-to-mid levels of test contrasts (0%-20%) but not at higher levels of test contrast (40%-100% contrasts). Red arrows indicate robust differences in α amplitude during the poststimulus period.

response to examine the relative contributions of the P1 and α data at explaining changes in the psychophysical data. To do so, we ran an auxiliary analysis where the weights of the P1 and α data were varied systematically before computing the combined response. Specifically, we multiplied the normalized P1 and the normalized α-based CRFs with two different sets of weights (0, 1, 2, ..., 10 for the P1's weight and 10, 9, 8, ..., 0 for the α's weight), yielding 11 models with different combinations of weights associated with the P1 and α data. After summing the weighted responses, we normalized the summed activity again to control for the range of minimal and maximal response values across these 11 models. The model with the P1 weight set to 0 and the α weight set to 10 is equivalent to the α model in the main analysis. The model with the α weight set to 0 and the P1 weight set to 10 is equivalent to the P1 model in the main analysis. The model with equal weights for both the P1 and the α data are equivalent to

the combined model in the main analysis. Here, we performed similar cross-validation and bootstrapping procedures similar to those conducted in the main analysis to compare the predictability of different models.

It is important to note that, in our modeling routine, the neuronal noise parameter, or the SD 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. This assumption is based on the previously established modeling methods (Cutrone et al., 2014; Itthipuripat et al., 2019a). At the first glance, this assumption may seem counter to some previous findings from single-unit studies in nonhuman primates, which demonstrated that attention could change neuronal noises or trial-by-trial variability of neuronal activity (Mitchell et al., 2007, 2009; Cohen and Maunsell, 2009; Cohen and Kohn, 2011; Niebergall et al., 2011; Luo and Maunsell, 2015). That said, studies in humans that used
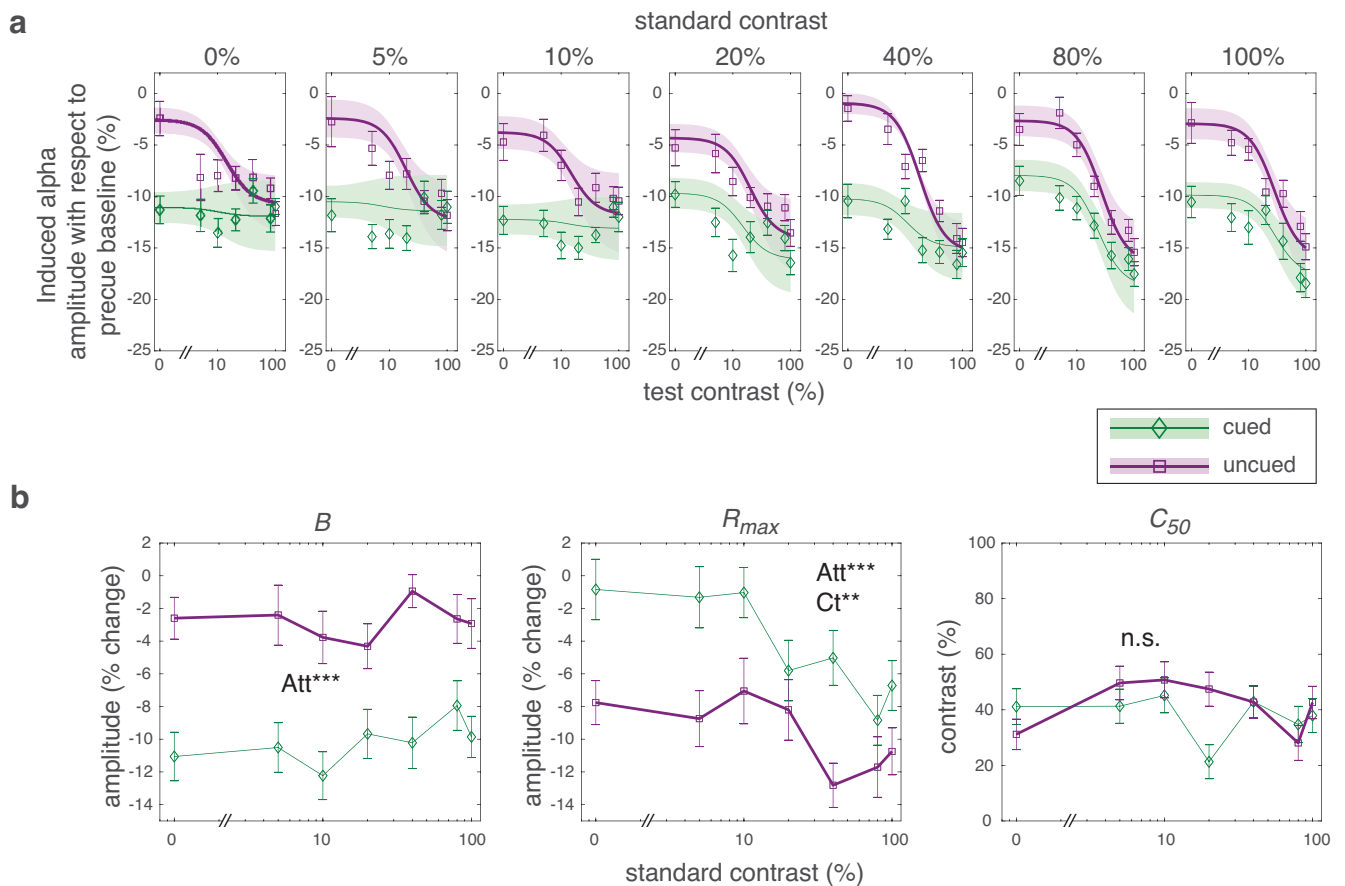
Figure 8. *a*, α amplitude plotted as a function of test contrast separately for different attention conditions and levels of standard contrast. Attention induced a shift in the baseline-offset of α band oscillations, regardless of standard contrast. *b*, The corresponding best-fit parameters from an NR function (Eq. 1). Left, Overall, attention decreased the baseline-offset (*B*) of the neural CRFs, consistent with a reduction in the amplitude of α oscillations. The degree of baseline modulation was comparable across standard contrasts. Middle, Attention-related reductions in α amplitude became smaller as test contrast increased (e.g., "pinching" patterns at 100% test contrast in *a*), leading to a smaller negative slope of α-based CRFs in the cued compared with the uncued condition (i.e., R_{max} became less negative with attention). However, R_{max} became more negative with increasing standard contrast. Right, There were no differences in the semisaturation constant (C_{50}) across test or standard contrast levels. Att∗∗∗ and Ctt∗∗ represent the significant main effects of attention (*p* values < 0.001) and standard contrast, respectively (*p* < 0.01). *a*, The fit curves were not obtained by fitting the grand-averaged α-based CRF data per se (i.e., *a*, diamonds and squares), but they were reconstructed from the averaged fit parameters computed at the individual-subject level (*b*, diamonds and squares). We did this so that the fit curves represent the statistics we performed on the fit parameters obtained from fitting individual subjects' data. *b*, Error bars indicate the within-subject SEMs where the mean value of each attention condition was removed before computing the SEMs. *a*, Shaded areas of the fit curves represent the variation of the fit data across subjects based on within-subject SEMs of fitting parameters shown in *b*.

quantitative linking models to study the relationship between attention effects on behavior and population-level neural activity, such as EEG and fMRI, have reported negligible contributions of trial-by-trial variability of EEG/fMRI activity on the attentional modulations of behavioral data (e.g., Pestilli et al., 2011; Hara and Gardner, 2014; Itthipuripat et al., 2014a). In one recent EEG study from our group, we found that noise varied across conditions only when human subjects underwent extended training (~10 testing sessions spread over ~1 month of training) (Itthipuripat et al., 2017). To prevent potential training effects on noise modulations in the present study, we only had human subjects perform an 1 h task in 1 d, which did not require extensive training as protocols used in our recent human EEG study (Itthipuripat et al., 2017) and in the aforementioned monkey studies, where subjects were trained for many months (Mitchell et al., 2007, 2009; Cohen and Maunsell, 2009; Cohen and Kohn, 2011; Niebergall et al., 2011; Luo and Maunsell, 2015). Therefore, under the limited amount of behavioral training, it is reasonable to assume that neuronal noise levels were approximately the same across different experimental conditions, at least at the level measured with EEG.

Results

The present study investigated the neural mechanisms that underlie the effects of attention on perceived contrast and response bias.

We used a comparative judgment task where the contrast of cued and uncued visual stimuli was fully crossed and systematically manipulated from 0% to 100% Michelson contrast (Fig. 1; see Materials and Methods) (Itthipuripat et al., 2019a). 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 CRF) and to quantitatively link the attentional modulations of neural CRFs to changes in perceived contrast and response bias in the psychometric data (Fig. 2).

Attention induces changes in contrast appearance and response bias as measured with behavior

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

Changes in the periodic components of alpha oscillations and the aperiodic components of the 1/f noise
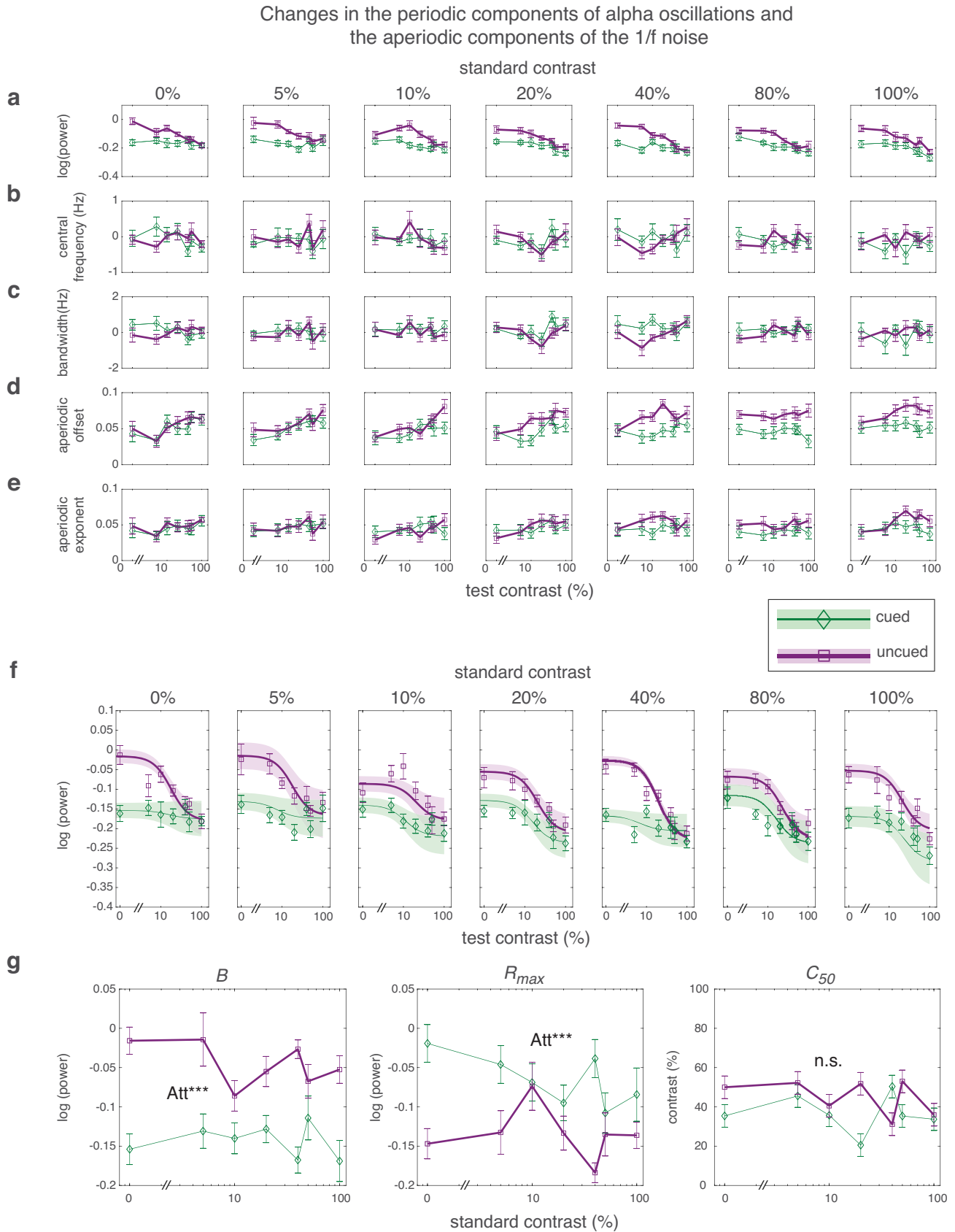
Figure 9. The periodic parameters of the induced α oscillations (i.e., log power, central frequency, and bandwidth) and the aperiodic parameters of the spectral data after stimulus onset (i.e., the offset and exponent of the 1/f component). **a-e**, The log power, central frequency, bandwidth, aperiodic offset, and aperiodic exponent parameters across different attention conditions and levels of test and standard contrasts. **f**, α log power 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 α band oscillations, regardless of standard contrast. **g**, The corresponding best-fit parameters from an NR function. Overall, the results were consistent with the

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. For purposes of data exposition, we always refer to the stimulus being held constant in a plot as the standard stimulus and the stimulus being varied in a plot as the test stimulus. Thus, in the example above, the 5% contrast cued stimulus would be the standard stimulus that is compared with 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 green and data associated with the uncued stimulus in purple.

To better quantify these behavioral data, we fit each psychophysical function using an NR equation (Eq. 1) 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 Fig. 2a-c; Materials and Methods) (Heeger, 1992; Geisler and Albrecht, 1997; Kim et al., 2007; Itthipuripat et al., 2019a). Here, we used changes in the baseline-offset (B) to track the magnitude of cue-induced response biases because reporting the contrast of the cued stimulus as higher than the contrast of the uncued stimulus, when the cued stimulus was rendered at 0% contrast, likely reflects bias (because no stimulus was actually presented) (Prinzmetal et al., 2008; Itthipuripat et al., 2019a). On the other hand, we used changes in contrast gain (G_c) to index changes in contrast appearance because this parameter controls left/right translations along the x axis, which would be expected if the actual physical contrast of the test stimuli increased or decreased, respectively. We focused on G_c instead of the point of subjective equality (PSE) because others have suggested that PSE overestimates changes in contrast appearance when there are significant amounts of cue-induced response bias (Schneider, 2006, 2011; Prinzmetal et al., 2008; Schneider and Komlos, 2008; Itthipuripat et al., 2019a; Schneider and Malik, 2021b).

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 contrast and stimulus uncertainty (i.e., whether the test and standard stimuli were rendered at the similar contrasts) (Itthipuripat et al., 2019a). When there was a 0% contrast stimulus presented at both the cued and the uncued locations, subjects were more likely to report that the cued location had a higher contrast than the uncued location (although no stimulus was presented on either side in this condition, see Fig. 3a, leftmost panel). 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 standard stimulus increased. To statistically evaluate these effects, we performed a two-way repeated-measures ANOVA with attention (cued vs uncued) and the contrast of the standard as factors. There were 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: $F_{(6,114)} = 114.94$, $p < 0.001$. An analogous ANOVA was also performed on only the correct trials (i.e., we only counted the responses on trials where subjects correctly discriminated the orientation offset of the chosen visual stimulus). This analysis revealed the same pattern of results: there were 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 standard stimulus on B: $F_{(6,114)} = 128.96$, p values < 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 revealed that attention effects on B were significant for standard contrast levels of 0%, 5%, 10% and 20% ($t_{(19)}$ values $= 3.26$-24.00 and 2.88-24.57 for all trials and correct-only trials, respectively, all p values ≤ 0.0042, Holm–Bonferroni-corrected). However, differences in B were not significant for standard contrast levels of 40%, 80% and 100% ($t_{(19)}$ values $= 1.36$-1.80 and 1.38-1.88 for all trials and correct-only trials, respectively, all p values ≥ 0.0751). Overall, these results suggest that attention induced significant response bias, especially for low-contrast standard stimuli.

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: $F_{(1,19)}$ values $= 48.08$ and 35.42, p values < 0.001, a significant main effect of standard contrast: $F_{(6,114)}$ values $= 111.89$ and 103.21, p values < 0.001, and a significant interaction between the two factors: $F_{(6,114)}$ values $= 9.64$ and 9.34 for all trials and correct-only trials respectively, with p values < 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% ($t_{(19)}$ values $= -2.77$ to -9.15 p values ≤ 0.0122, Holm–Bonferroni-corrected), but were not significant for standard contrast levels of 0%, 10%, and 100% contrasts ($t_{(19)}$ values $= 1.36$-1.80, p values ≥ 0.0153, not passing the corrected threshold of 0.0125). For the correct-only trials, attentional modulations of G_c were significant for standard contrast levels of 10%-80% contrast ($t_{(19)}$ values $= -9.15$ to -2.77, p values ≤ 0.0122, Holm–Bonferroni-corrected) but were not significant for standard contrast levels of 0% and 100% contrast ($t_{(19)}$ values $= -0.96$ and -2.14, p values ≥ 0.0457, not passing the corrected threshold of 0.025). These results suggest that attention alters contrast appearance but does so primarily at low-to-mid-level contrasts.

The lack of a significant contrast gain modulation (G_c) at the highest standard contrast was in part because the psychometric functions in this condition did not reach the maximum possible value of 1 (i.e., p(stimulus of interest > paired stimulus) was <1). Thus, attentional modulations of the psychophysical functions at the highest standard contrast (100%) manifested as an increase in the response gain parameter (G_r), corresponding to a steeper slope ($t_{(19)}$ values $= 10.93$ and 10.23 for all trials and
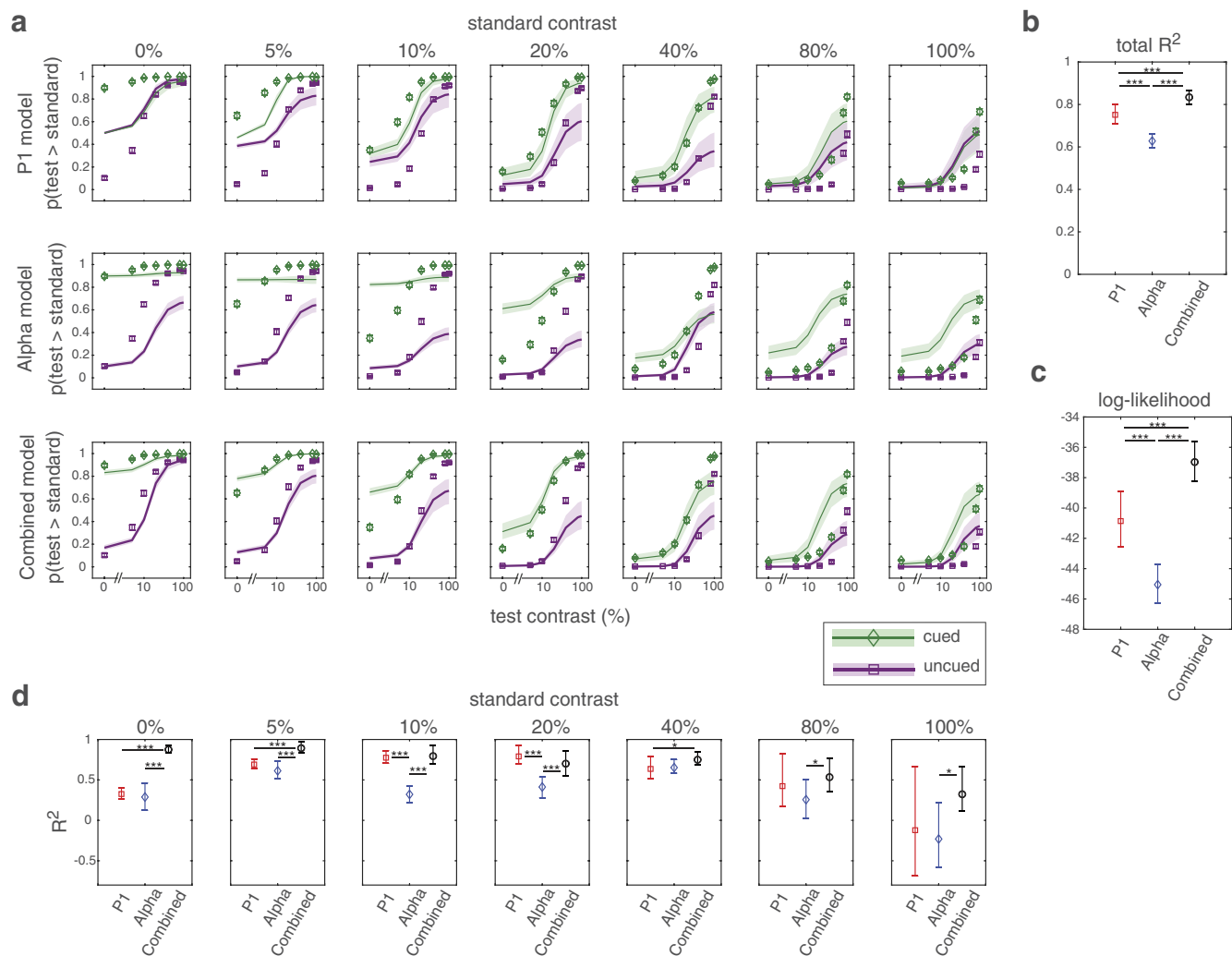
Figure 10. *a,* Cross-validation results (fivefold) of the linking models that predicted the effects of attention on behavioral responses based on attentional modulations of neural data. Top row, Modeling based on attentional gain modulations of the early visual P1 component (i.e., the P1 model) better captured the psychometric data overall but did not predict changes in the baseline-offset at low standard contrast levels (0%-5%). Middle row, In contrast, attention-induced changes in α band activity (i.e., the α model) tracked large modulations in the baseline-offsets of the psychometric functions across all standard contrast levels. Bottom row, Modeling that used both P1 and α data (i.e., the combined model) did the best at predicting the pattern of attentional modulations of the psychophysical data. Fit lines indicate the linking-model predictions from fivefold cross-validation bootstrapped 1000 times. Shaded areas of the fit lines represent 95% CIs (two-tailed) from the bootstrap distributions of the linking-model predictions. Diamonds and squares represent the observed behavioral data averaged across fivefolds and 1000 resampling iterations. These observed behavioral data were obtained from the independent dataset (20% of trials) from the EEG data used to train the linking models (the other 80% of the trials). Error bars indicate 95% CIs (two-tailed) from the bootstrap distributions of the observed data in the test or "holdout" set. *b,* The goodness-of-fit (i.e., R^2 values) of the resampled cross-validation predictions based on the P1 data, the α data, and the combination of the P1 and α data (i.e., the combined model), represented as a red square, a blue diamond, and a black circle, respectively. Error bars indicate the 95% CIs (two-tailed) from the bootstrap distributions of the R^2 values. *c,* Log-likelihood estimates of the resampled cross-validation predictions from the linking models. Error bars indicate the 95% CIs (two-tailed) from the bootstrap distributions of the log-likelihood estimates. *d,* Same as in *b,* but data presented separately for individual standard contrast levels. Significant differences between modeling performance from the cross-validation and bootstrapping analysis: $*p < 0.05$; $***p < 0.001$. To examine the relative contributions of the P1 and α data at explaining changes in the psychophysical data, we performed an additional analysis that varied the weights of the P1 and α data before computing the combined response used for predicting behavioral data (see Extended Data Fig. 10-1).

correct-only trials, respectively, *p* values < 0.001, two-tailed, Holm–Bonferroni-corrected). A recent study demonstrated that attention-induced gain changes measured at high standard contrasts might not exclusively reflect changes in appearance per se. Instead, these gain changes might be influenced by response bias related to high stimulus uncertainty as 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) (Itthipuripat et al., 2019a).

Possible neural mechanisms driving attention-related changes in stimulus appearance

Several neural mechanisms have been proposed to explain attention-related modulations in information processing and attention-

related changes in perceptual performance and stimulus appearance (Fig. 2*d-f*) (Reynolds et al., 2000; di Russo et al., 2001; Martínez-Trujillo and Treue, 2002; Carrasco et al., 2004; Williford and Maunsell, 2006; Buracas and Boynton, 2007; Kim et al., 2007; Murray, 2008; Lee and Maunsell, 2009; Reynolds and Heeger, 2009; Herrmann et al., 2010; Lauritzen et al., 2010; Pestilli et al., 2011; Wang and Wade, 2011; Cutrone et al., 2014; Hara and Gardner, 2014; Itthipuripat et al., 2014b, 2015, 2017, 2018, 2019a,b; Sprague et al., 2018). 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 (Fig. 2*d*) (Reynolds et al., 2000; Martínez-Trujillo and Treue, 2002; Carrasco et al., 2004; Itthipuripat et al., 2014b). 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 (Fig. 2e) (di Russo et al., 2001; Kim et al., 2007; Lee and Maunsell, 2009; Itthipuripat et al., 2014b, 2017, 2018, 2019b; Sawetsuttipan et al., 2023). Last, an additive baseline shift would suggest that attention can lead to increases in the baseline activity of neural CRFs in a manner that is invariant to stimulus contrast (Fig. 2f) (Williford and Maunsell, 2006; Buracas and Boynton, 2007; Murray, 2008; Pestilli et al., 2011; Cutrone et al., 2014; Hara and Gardner, 2014; Sprague et al., 2018; Itthipuripat et al., 2019b).

Although few studies have directly linked these attention-related changes in neural activity with subjective visual appearance, prior psychophysical studies have used ideal-observer models to determine which modulations of hypothetical neural CRFs might best explain attention-induced changes in the perceived contrast of visual stimuli. One of the earliest studies adopting this approach demonstrated that response gain (i.e., Fig. 2e) and contrast gain (i.e., Fig. 2d) failed to explain attention-induced changes in perceived contrast compared with a model that only incorporated a baseline-offset at low contrasts (and compression at higher contrasts, referred to as activity gain) (Cutrone et al., 2014). However, this study did not take into account the potential for response bias driven by exogenous cues, especially when the visual stimulus was absent at the cued location (i.e., effects of attention on 0% contrast stimuli). Recently, we systematically tracked attentional effects on both perceived contrast and response bias and found that cue-induced response biases for 0% contrast stimuli were largely explained by shifts in the baseline-offset of hypothetical neural CRFs (Itthipuripat et al., 2019a). In contrast, attention-induced changes in appearance for low-to-mid contrast stimuli were better explained by changes in response gain (Itthipuripat et al., 2019a). However, there is still a lack of neural evidence that can inform linking models to relate neural data with perceptual experience. Here we tested whether (1) dissociable patterns of attentional modulations in different neural markers of visual processing, such as the P1 component and α band activity, could be observed; and (2) if dissociable neural components explain attention-induced changes in contrast appearance and response bias measured with behavior. Our modeling approach was based on SDT and adopted from previous psychophysical studies (Cutrone et al., 2014; Itthipuripat et al., 2019a). The primary difference was that we used EEG data in the present study — the P1 and α band activity — instead of using hypothetical neural CRFs. Thus, we could directly link changes in behavioral responses with concurrent modulations in simultaneously collected EEG data.

Motivation for linking the amplitude of P1 and α band responses with behavior

Here, we targeted two EEG indices that are thought to track different aspects of visual information processing: (1) the P1 component, which is an early visually evoked potential that peaks ~60-90 ms ms after stimulus onset; and (2) the amplitude of posterior occipital α band oscillations (i.e., EEG oscillations in the ~9-12 Hz band). We used these two EEG markers because they have been previously linked to bias in subjective contrast perception (Störmer et al., 2009, 2019; Balestrieri and Busch, 2022). That said, we hypothesized that the attentional modulations of the visual P1 component and α 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 (van Voorhis and Hillyard, 1977; Mangun and Hillyard, 1990; Woldorff et al., 1997; Hillyard and Anllo-Vento, 1998), and attentional gain of

P1 amplitude has been linked to improved detection and discrimination for low-level visual features, such as contrast and object shape (Mangun and Hillyard, 1990; Itthipuripat et al., 2014a, 2017). Recent studies have also found that selective attention induces a multiplicative response gain of neural CRFs based on P1 amplitude (see Fig. 2e), and quantitative models suggest that these gain modulations predict attention-related changes in perceptual contrast discrimination thresholds (Itthipuripat et al., 2014a, 2017). 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 with uncued visual stimuli (Störmer et al., 2009, 2019). Although changes in subjective experience were not quantitatively linked to changes in P1 amplitude using a formal linking model, this finding (Störmer et al., 2009, 2019), coupled with suggestive earlier work (Itthipuripat et al., 2014b, 2017; Störmer et al., 2019), is consistent with the hypothesis that multiplicative response gain of the P1 is tightly coupled with attention-induced changes in perceived contrast (Itthipuripat et al., 2019a).

In addition to changes in perceived contrast, attention is also thought to influence other aspects of behavioral performance that may be more closely tracked by other neural markers, such as α band oscillations. 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 (Schneider, 2006, 2011; Schneider and Komlos, 2008; Beck and Schneider, 2017; Itthipuripat et al., 2019a; Schneider and Malik, 2021b). A large corpus of prior studies demonstrates that endogenous attention cues decrease α amplitude in posterior visual areas contralateral to the attended visual field (Foxe et al., 1998; Fries et al., 2001; Sauseng et al., 2005; Rihs et al., 2007; Yamagishi et al., 2008; Kelly et al., 2009; Händel et al., 2011; Bosman et al., 2012; Keefe and Störmer, 2021). Recent studies using exogenous cues presented at the peripheral locations also report similar cue-induced decreases in contralateral α band activity. Together, these findings suggest that lateralized α activity reflects visuo-cortical biasing across both exogenous and endogenous attention (Song et al., 2014; Keefe and Störmer, 2021).

In addition to these well-documented topographic modulations related to the locus of spatial attention, we hypothesized that α might also track attention-induced changes in response bias. First, past studies have found that α 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 (Limbach and Corballis, 2016; Benwell et al., 2017, 2018, 2020; Iemi et al., 2017; Foster and Awh, 2019). Second, attention has been shown to reduce the amplitude of contralateral posterior occipital α 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 (Itthipuripat et al., 2019b; Foster et al., 2021). Consistent with this idea, recent studies have found that attention shifts the baseline-offset of CRFs based on the amplitude of α oscillations, reflecting a shift in general arousal or responsiveness that does not interact with the actual intensity of the stimulus (Fig. 2f) (Itthipuripat et al., 2019b; Foster et al., 2021). Based on these observations, we predicted that a shift in the baseline-offset of α-based CRFs would be systematically linked with attention-induced response bias (Itthipuripat et al., 2019a).

Attention amplifies response gain of the early visually evoked P1 component

We first sought to isolate stimulus-specific P1 activity from activity evoked by the presentation of the attention cue. Thus, we computed ERPs from trials where the cue was followed by 0% contrast cued and uncued stimuli (termed cue-only trials). We then subtracted this cue-only ERP from the ERPs evoked on trials that contained a cue plus a stimulus. This subtraction was performed separately for stimulus-present trials from each attention condition and contrast level (Fig. 4a; see Materials and Methods) (see similar methods in Greenwood and Goff, 1987; Iragui et al., 1993; Kiss et al., 1998; Chica et al., 2010; Itthipuripat et al., 2014a, 2017, 2019b; Störmer et al., 2019). This procedure yielded a clear P1 component that peaked ~60-90 ms after stimulus over posterior occipital electrodes that were contralateral to the stimulus of interest. 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 (Fig. 5a). Then, we fit these P1-based CRFs with an NR equation (Eq. 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_c parameters can potentially go beyond the realistic range of stimulus contrast (≫100%), the contrast gain parameter was allowed to vary only between 0% and 100% contrast (i.e., the realistic range of the physical contrast value). Moreover, 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 semisaturation contrast (C_{50} or the contrast at which the response reached half-maximum), respectively (see Early sensory-evoked response).

As illustrated in Figure 5a, the best fit curves from the NR equation (Eq. 1) explain the observed baseline-subtracted P1-based CRFs reasonably well (goodness-of-fit $R^2 = 0.7977$). Importantly, we found that attention increased the maximum response (i.e., R_{max}) of the P1-based CRF (main effect of attention: $F_{(1,19)} = 4.46$, $p = 0.0482$) (Fig. 5b). In addition, there were larger attentional modulations at the low-to-mid-level standard contrasts (5%-20%) compared with when the standard was absent (0% contrast) and when the standard had a higher contrast (40%-100%). This gave rise to a significant interaction between attention and the contrast of the standard stimulus ($F_{(6,114)} = 2.24$, $p = 0.0441$). Importantly, attention had a selective effect on the R_{max} parameter of the P1 response, as there were no changes in any other parameters (Fig. 5b; main effect of attention: $F_{(1,19)} = 2.20$, $p = 0.1546$ for B, $F_{(1,19)} = 1.51$, $p = 0.2973$ for C_{50}; main effect of standard contrast level: $F_{(6,114)} = 1.05$, $p = 0.3961$ for B, $F_{(6,114)} = 1.91$, $p = 0.0854$ for C_{50}; interaction between the attention and standard contrast: $F_{(6,114)} = 0.24$, $p = 0.9614$ for B; $F_{(6,114)} = 1.03$, $p = 0.4079$ for C_{50}). The elevated response gain of the P1-based CRFs (i.e., R_{max}) 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 (Fig. 3b). The best fit curves illustrated in Figure 5a were not obtained by fitting the P1-based CRF data after averaging across all subjects (i.e., Fig. 5a, diamonds and squares). Instead, the best fit curves were reconstructed based on the averaged fit parameters computed at the individual-subject level (Fig. 5b, diamonds and squares). We adopted this approach so that the best fit curves better represent the statistics we performed on the parameters obtained from fitting individual subjects' data separately.

Since the ERP subtraction method is based on the assumption that the stimulus- and cue-evoked responses linearly sum (Greenwood and Goff, 1987; Iragui et al., 1993; Kiss et al., 1998; Chica et al., 2010; Itthipuripat et al., 2014a, 2017, 2019b; Störmer et al., 2019), we did additional analyses to determine whether a similar pattern of response gain modulations was observed without performing the ERP subtraction (Fig. 5c,d). Overall, we found that the NR equation (Eq. 1) fit the nonsubtracted CRF data slightly better than the subtracted CRF data with $R^2 = 0.8305$. In addition, the overall pattern of attentional modulations were consistent across the subtracted and nonsubtracted data: there were still a significant main effect of attention ($F_{(1,19)} = 5.03$, $p = 0.0371$) and a significant interaction between attention and standard contrast on R_{max} ($F_{(6,114)} = 2.57$, $p = 0.0225$). However, attention and the contrast of the standard had no significant impact on the C_{50} parameter and the two factors did not interact (all F values ≤ 1.91, p values = 0.1030-0.5503).

For the baseline-offset parameter (B), we found that the attention cue reduced the baseline value of the nonsubtracted P1-based CRF (it became more negative), resulting in a significant main effect of attention on the baseline-offset ($F_{(1,19)} = 5.88$, $p = 0.0255$). This was expected because the stimulus-elicited P1 component overlaps with the early negative N1 component evoked by the cue that was presented just 100 ms before stimulus onset (see Fig. 4a) (see also similar results in Itthipuripat et al., 2019b). The baseline-offset value also increased as a function of standard contrast ($F_{(6,114)} = 2.87$, $p = 0.0121$). This is also expected because the nonsubtracted responses contained positive evoked potentials elicited by both test and standard stimuli. The increased baseline-offset values as a function of contrast observed at the contralateral posterior-occipital sites could be a result of the spread of activity elicited by the standard stimulus from the opposite hemisphere (see topographic maps showing more spread of activity for the nonsubtracted P1 data in Fig. 4b), and this is why we subtracted out the baseline activity to isolate brain activity related to the stimulus of interest (i.e., the test stimulus). We also found a significant interaction between attention and standard contrast on the baseline values of the nonsubtracted P1 CRFs ($F_{(6,114)} = 2.82$, $p = 0.0136$). This interaction was driven by a higher degree of attention-induced reduction in baseline values on trials with low compared with high standard contrasts and compared with 0% standard contrast.

Overall, there was a consistent pattern of response gain modulations in the baseline-subtracted and non–baseline-subtracted P1 data, suggesting that the baseline subtraction method did not change the pattern of modulations of the response gain in early sensory responses.

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

Next, we examined the effects of attention on the contralateral posterior occipital α band activity (i.e., EEG oscillations at ~9-12 Hz), another commonly used neural index of visuospatial attention (Foxe et al., 1998; Fries et al., 2001, 2008; Sauseng et al., 2005; Kelly et al., 2006, 2009; Klimesch et al., 2007; Rihs et al., 2007; Bosman et al., 2012; Foster et al., 2016, 2017; Samaha et al., 2016; Voytek et al., 2017; Hakim et al., 2019; Itthipuripat et al., 2019b; Wang et al., 2021). Consistent with previous observations, we found a significant cue-related reduction in the amplitude of α oscillations, compared with a precue baseline period, that grew more pronounced as the contrast of the test stimulus increased. These α amplitude modulations were most prominent

over the posterior occipital electrodes that were contralateral to the stimulus of interest (Figs. 6 and 7).

Figure 8 shows the α data plotted as a function of both test and standard contrast levels to form CRFs. Overall, the best fit curves from the NR equation (Eq. 1) explain the observed α data reasonably well (goodness-of-fit $R^2 = 0.8289$). In contrast to the P1 data, we found that attention cues modulated the baseline-offset (B) of the neural CRFs based on the postcue reduction of the posterior occipital α activity (main effect of attention; $F_{(1,19)} = 39.35$, $p < 0.001$). These lateralized α changes likely reflect a mixture of low-level sensory-evoked activity elicited by the peripheral visual cues as well as α changes because of attentional biases. This cue-induced reduction in α band activity occurred to a comparable degree across all standard contrast levels (no main effect of standard contrast level: $F_{(6,114)} = 0.71$, $p = 0.6384$; no interaction between attention and standard contrast: $F_{(6,114)} = 0.65$, $p = 0.6912$). Since the degree of cue-induced modulation of α amplitude was relatively more robust at the low compared with the high test contrasts, the R_{max} parameters describing the α-based CRFs became less negative with attention (i.e., the negative slope of the α-based CRFs became shallower, main effect of attention: $F_{(1,19)} = 18.96$, $p = 0.0003$). On the other hand, R_{max} became more negative with increasing standard contrast (main effect of standard contrast: $F_{(6,114)} = 3.83$, $p = 0.0016$). However, there was no interaction between attentional cue and contrast on R_{max} ($F_{(6,114)} = 1.00$, $p = 0.4314$). While there were attention-induced changes in response gain modulations, these modulations occurred in opposition to the effects related to the contrast of the test stimulus, resulting in the CRFs pinching/saturating at the highest test contrast. Thus, unlike the P1-based CRFs where the slope of cued condition was steeper than that of the uncued condition, the slope of the cued α-based CRF was actually shallower than the uncued α-based CRF. Interestingly, past studies have reported a similar pattern of results in fMRI data measured in early visual cortex, suggesting that increases in baseline responses and reductions in response gain at high contrast levels may reflect the influence of top-down attention and response saturation induced by overly strong stimulus inputs into early visual areas, respectively (e.g., Pestilli et al., 2011; Itthipuripat et al., 2019b). Finally, there was no main effect of the attention cue or the contrast of the standard on the semisaturation contrast parameter (C_{50}), and no interaction between the two factors (all F values ≤ 0.98, all p values ≥ 0.4391). Overall, the shift in the baseline-offset of the α-based CRFs was consistent with the robust baseline-offset response bias observed in the behavioral data (Fig. 3).

Based on recent work, it is plausible that the attention effects on the α band activity reflect changes in aperiodic components of EEG signals rather than a change in the amplitude of a true oscillation (Donoghue et al., 2020). For example, a global rotation of the 1/f fall-off of the EEG power spectrum might lead to erroneous conclusions that energy in a specific frequency band increased or decreased. To address this issue, we ran additional analyses to independently examine attention effects on the periodic and aperiodic components of α oscillations following the algorithm described by Donoghue et al. (2020). First, we obtained the spectrogram from the contralateral posterior occipital electrodes during the precue baseline and the poststimulus period (Fig. 7c). Next, we fit the spectrogram in each experimental condition, each time period, and each subject using the FOOOF toolbox developed by Donoghue et al. (2020). This step yielded estimates of the periodic components of α oscillations, including log power, central frequency, bandwidth, as well as the aperiodic

offset and exponent. We then computed the differences between these periodic and aperiodic parameters across the stimulus versus precue periods to estimate changes of these parameters with respect to the precue baseline (Fig. 9a-e).

The modulatory pattern of the log power of the α band activity was very similar to the main analysis where we found attention reduced the α band amplitudes more prominently at the baseline-offset (i.e., 0% test contrasts), and this pattern of data was consistent across all standard levels (Fig. 9a). We found a significant main effect of period, showing that α log power decreased significantly during the stimulus period compared with the precue baseline ($F_{(1,19)} = 51.12$, $p = 0.0004$). Importantly, we found significant interactions between attention and period ($F_{(1,19)} = 389.26$, $p < 0.0001$), and between the attention, period, and test contrast ($F_{(6,114)} = 7.86$, $p < 0.0001$) with no main effect of standard contrast and no interactions between standard contrast and any other factors (p values > 0.1038). This set of statistical results could be described by the significant reduction in log α power during the stimulus period with respect to the precue period.

Next, we fit the neural CRFs based on log α power to compare the response gain, contrast gain, and baseline-offsets across attention and standard contrast conditions. We found results similar to the main α-based CRF analysis (compare Figs. 8a, b and 9f, g). Specifically, we found that attention significantly increased the baseline-offset of the CRF based on the reduced α log power with respect to the precue baseline ($F_{(1,19)} = 38.65$, $p < 0.0001$). Since the reduction of log α power saturated at high test contrast levels, we found no differences in attentional modulations at high test contrasts. This led to a decrease in the response gain parameter that controls the slope of the α-based CRFs ($F_{(1,19)} = 16.27$, $p = 0.0007$). Importantly, there were no significant main effects of standard contrast and no interactions between attention and standard contrast on the baseline-offset and response gain parameters (p values > 0.065), suggesting that the patterns of attention modulations of the α-based CRFs were independent of the level of standard contrast. In addition, there were no changes in contrast gain (p values > 0.1143). Together, the main analysis of the neural CRFs based on α amplitude and this additional analysis of log α power, which separated out the periodic components of α band oscillations from the aperiodic components of the 1/f activity, provides converging evidence that the attentional modulations of α amplitude/power undergo the baseline shift in the neural CRFs.

The other periodic components, including the central frequency and bandwidth of α band oscillations, reduced significantly during the stimulus period with respect to the precued baseline ($F_{(1,19)}$ values $= 51.12$ and 8.78 with p values $= 0.0004$ and 0.0252, respectively) (Fig. 9b,c). For the central frequency, there were no significant interactions between period and any of other factors, including attention, test contrast, and standard contrast, suggesting that the reduction in the central frequency α band oscillations with respect to the precued baseline was not modulated by attention, test contrast, or standard contrast (p values > 0.223). For the bandwidth parameter, however, attention also interacted significantly with period because of a higher degree of bandwidth reduction with respect to the precue baseline in the uncued compared with the cued conditions ($F_{(1,19)} = 6.75$, $p = 0.0407$). That said, there were no significant interactions between period and the other factors, including test and standard contrasts (p values > 0.1616).

The modulatory patterns of aperiodic components of the 1/f were different from the patterns of periodic components of the α

band oscillations reported above (see Fig. 9d,e). Both the aperiodic offset and exponent increased during the stimulus period compared with the precue baseline ($F_{(1,19)}$ values $=1600.71$ and 3542.80, respectively, p values ≤ 0.0001). The increased aperiodic offset and exponent with respect to the precue baseline increased as a function of test contrast (the interaction between period and test contrast: $F_{(6,114)}$ values $= 10.92$ and 5.81, p values < 0.0001 and $= 0.0003$), but they decreased with attention (the interaction between period and attention: $F_{(1,19)}$ values $= 20.69$ and 6.45, p values $= 0.0039$ and 0.044). Unlike the α log power data, the degree of attentional modulations in the aperiodic offset and exponent were larger at high compared with lower test contrasts. Together, our results suggest that changes in the amplitude/power of α band activity could not be explained by the modulatory patterns of the aperiodic components of the 1/f activity.

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 link patterns of attentional modulations of the P1-based and α-based CRFs and the pattern of attentional modulations in the psychometric data (see Materials and Methods) (see Tanner and Swets, 1954; Boynton et al., 1999; Pestilli et al., 2011; Cutrone et al., 2014, 2018; Itthipuripat et al., 2014b, 2015, 2017). The linking model used the patterns of attentional modulations of the observed P1-based and α-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 SDT 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) (Tanner and Swets, 1954; Boynton et al., 1999; Pestilli et al., 2011; Cutrone et al., 2014; Itthipuripat et al., 2014a, 2017, 2019a). 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 α-based CRFs (termed here as the α-based model; see details in Materials and Methods). The amplitude of α band activity generally got smaller with attention and stimulus contrast (see Fig. 8) (see also Itthipuripat et al., 2019b; Foster et al., 2021). Therefore, we flipped the sign of the normalized α-based CRFs before estimating p (test $>$ standard). Last, we compared the results with those predicted by a model that sums the normalized P1-based CRFs and the normalized α-based CRFs (with the flipped sign) to predict the behavioral data based on the sum of the normalized P1 and α 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) and log-likelihood estimates to compare how well they predicted the psychophysical data.

The fivefold cross-validation bootstrapping results demonstrated that the P1-based model accounted for the psychophysical data reasonably well, especially at the low-to-mid-level contrasts (Fig. 10). That said, the P1 model could not capture changes in the baseline-offset in the behavioral data at lower

standard contrast levels. This resulted in poorer model fits at these contrast levels. The P1 model also performed poorly at higher standard contrast levels. This poor fit occurred because attentional modulations of the P1-based R_{max} parameter diminished with increasing standard contrast, although the attentional modulations of the psychophysical data remained robust at these contrast levels (Fig. 3).

Compared with the P1-based model, the α-based model performed significantly worse at predicting the pattern of the behavioral data in general (p values < 0.001 for differences in both log-likelihood estimates and R^2). This is because the α-based model could only capture attention-induced changes in the baseline-offset of the psychometric functions at the low standard contrast levels, which only accounted for a small fraction of the variance in the overall behavioral data. That said, when we used the combination of the P1 and α data to predict the psychometric functions (i.e., the combined model), we were able to predict the pattern of the behavioral responses significantly better than using the P1 data or the α alone (p values < 0.001 for differences in log-likelihood estimates and R^2 between the combined and α models as well as between the combined and P1 models). This improvement in model performance was because the combined model better captured the baseline-offset response bias at the low and high standard contrast levels.

When modeled separately for each standard contrast level (Fig. 10d), we found that the P1 and α models were equally bad at predicting the data at low standard contrast levels and performance did not differ between the models (p values $= 0.1000$ and 0.3480 for 0% and 5% standard contrasts). Moreover, the combined P1$+\alpha$ model performed significantly better than either the P1 (p values $= 0$ for both 0% and 5% standard contrasts) or the α model on its own (p values $= 0$ for both 0% and 5% standard contrasts) (see the first two columns of Fig. 10a). This occurred because the baseline-offset modulations of the α-based CRFs help the combined model better account for changes in the baseline-offset response bias in the psychometric data. On the other hand, for the intermediate standard contrast levels, the P1 model performed very well and significantly better than the α model (p values $= 0$ for 10% and 20% standard contrasts). The combined model, therefore, did not perform significantly better than the P1 model alone (p values $= 0.8160$ and 0.1660 for 10% and 20% standard contrasts) (see the third and fourth columns of Fig. 10a). Additionally, no differences between model performance were observed between the P1 and α models at higher standard contrast levels (p values $= 0.4060$–0.8720). For 40% standard contrast, the combined model was significantly better than the P1 model ($p = 0.0140$, passing the Holm–Bonferroni-corrected threshold of 0.0167), but it did not perform significantly better than the α model ($p = 0.1040$). For 80% and 100% standard contrasts, the combined model was slightly better than the P1 model at explaining attentional modulations at of the psychometric functions (see the last two columns of Fig. 10a); however, the two models did not significantly differ (p values $= 0.1740$–0.6060). Nonetheless, the combined model was marginally and significantly better than the α model at the 80% and 100% contrast levels, respectively (p values $= 0.0280$ and 0.0140 with a Holm–Bonferroni-corrected threshold of 0.0167).

In addition, we ran an auxiliary analysis where the weights of the P1 and α data were varied systematically before computing the combined response to examine the relative contribution of the P1 and α data at explaining changes in the psychophysical data (Extended Data Fig. 10-1). Overall, the results were consistent with the main analysis where the combined model was

significantly better than the P1 or the α model. The R^2 and log-likelihood estimates were the highest for the model with 6:4 P1/α weight ratio. However, this model was not significantly better than the combined model with equal weighting of the P1 and α data. Together, these results suggest that, under the assumption of linear summation with equal weights given to the P1 and α data, the attentional modulations of these neural markers sufficiently account for attention-induced changes in contrast appearance and response bias. Specifically, the response gain modulations of the P1 component explained attention-induced changes in perceived contrast at the low-mid-level standard contrasts but changes in the baseline-offset of α band activity underlie cued-induced response bias at very low and very high standard contrasts.

Discussion

The present study focused on investigating the relationship between attentional modulations of two well-known neural markers for visual information processing — the P1 component and the α 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 α-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 (Itthipuripat et al., 2014a). In contrast, the baseline-offset of the α-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% (compare Prinzmetal et al., 2008; Itthipuripat et al., 2019a). This shift in baseline-offset of the α 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 (Itthipuripat et al., 2019a).

The current P1 data and the accompanying modeling results are consistent with a theory proposed in a previous study that the gain amplification of early visual responses can account for the effect of attention on the subjective appearance of visual stimuli (Störmer et al., 2009, 2019). 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) (Sundberg et al., 2009; Andersen et al., 2012; Khayat and Martinez-Trujillo, 2015).

We found that attention selectively increased the multiplicative 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, has been consistently observed across many studies where subjects performed visual detection and discrimination tasks (Mangun and Hillyard, 1991; Morgan et al., 1996; Hillyard and Anllo-Vento, 1998; Müller et al., 1998; di Russo et al., 2001; Kim et al., 2007; Wang and Wade, 2011; Itthipuripat et al., 2014a,b, 2017, 2018, 2019b; Foster et al., 2021). 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 (Kantrowitz et al., 2009; Calderone et al., 2013; Ribeiro et al., 2014; Hou et al., 2016; Lygo et al., 2021). Based on these results and our recent findings, determining whether these populations experience the same attention-related changes in perception as measured with behavior may provide an additional test of the link between early gain amplification and subjective experience.

It is possible that our results may be influenced by sensory interactions between the exogenous cue and visual stimuli rather than the attentional effects of the cue per se. However, we view this possibility as unlikely given that our experimental design aimed to minimize potential confounds related to sensory interaction effects. For example, Schneider (2006) has argued that the psychophysical effects of exogenous cues on visual appearance were because of sensory interactions. In support of this idea, he found that white and black exogenous cues had opposite effects on contrast appearance, with the white cue enhancing perceived contrast and the black cue reducing it (Schneider, 2006). However, Carrasco's group later provided evidence arguing against this sensory interaction hypothesis (Ling and Carrasco, 2007; Carrasco et al., 2008). Specifically, they manipulated cue polarity and demonstrated that both black and white cues increased the perceived contrast of visual stimuli (Ling and Carrasco, 2007; Carrasco et al., 2008). Carrasco's group proposed that the sensory interaction effects observed by Schneider (2006) were potentially influenced by the experimental design. Schneider (2006) presented attention cues in the form of circular rings at the same eccentricity as the stimulus location, which could act as forward metacontrast masks causing sensory interactions. In contrast, Carrasco's group presented a small cue nearby, but not overlapping, with a much larger visual stimulus to minimize potential confounds from sensory interactions (Ling and Carrasco, 2007; Carrasco et al., 2008). To avoid potential confounds from sensory interactions, we adopted Carrsaco's design, where we presented a black thin line above a much larger circular grating with no spatial overlap. The consistency of our experimental design and results with Carrasco's group supports the notion that attention, rather than sensory interactions, is the primary driver of the observed behavioral and neural effects in the present study.

In contrast to the P1 results, where attention modulated response gain, we observed that attention mainly changed the baseline-offset of contralateral α band activity measured in the posterior occipital electrodes. This contralateral reduction in α band activity has been previously used to track the allocation of spatial attention following endogenous and exogenous cues (Foxe et al., 1998; Fries et al., 2001, 2008; Sauseng et al., 2005; Kelly et al., 2006, 2009; Klimesch et al., 2007; Rihs et al., 2007; Bosman et al., 2012; Song et al., 2014; Foster et al., 2016, 2017; Samaha et al., 2016; Voytek et al., 2017; Foster and Awh, 2019; Hakim et al., 2019; Keefe and Störmer, 2021). The reduction of α 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 (Foxe et al., 1998; Fries et al., 2001, 2008; Sauseng et al., 2005; Kelly et al., 2006, 2009; Klimesch et al., 2007; Rihs et al., 2007; Bosman et al., 2012; Song et al., 2014; Foster et al., 2016, 2017; Samaha et

al., 2016; Nelli et al., 2017; Voytek et al., 2017; Foster and Awh, 2019; Hakim et al., 2019; Itthipuripat et al., 2019b; Keefe and Störmer, 2021). Moreover, the topographic patterns of α reduction contain information about the attended location, even in the absence of visual stimuli (Sauseng et al., 2005; Kelly et al., 2009; Foxe and Snyder, 2011; Rohenkohl and Nobre, 2011; Bosman et al., 2012; Foster et al., 2016, 2017; Green et al., 2017; Foster and Awh, 2019). Consistent with these studies, recent studies have found that attention shifted the baseline-offset of α-based CRFs where no visual stimuli were presented (Itthipuripat et al., 2019b; Foster et al., 2021). That said, we found that the magnitude of baseline modulations of the α-based CRFs was unaffected by the standard contrasts of the paired stimuli.

It is important to note that the amplitude of the induced α oscillations decreased below the precue baseline for both of the cued and uncued locations, which could be because of the behavioral task that pittings cue-driven exogenous attention against endogenous attention and working memory required to compare the contrast levels of the two grating stimuli (compare Foxe et al., 1998; Fries et al., 2001; Sauseng et al., 2005; Rihs et al., 2007; Yamagishi et al., 2008; Kelly et al., 2009; Händel et al., 2011; Bosman et al., 2012; Song et al., 2014; Foster et al., 2016; Itthipuripat et al., 2019a; Keefe and Störmer, 2021). The degree of α amplitude reduction also increased as a function of test contrast, especially for the uncued condition. These distinct patterns of attention and contrast modulations of α amplitudes suggest that changes induced by α oscillations reflect complex interactions between exogenous attention, endogenous and processing of incoming sensory inputs that occurred before influencing bias in postperceptual decision- and sensorimotor-related processing.

Interestingly, the overall pattern of the α band data observed here is similar to the pattern of BOLD activity observed in similar tasks. This is consistent with the idea that α band activity is highly correlated with modulations of the BOLD response recorded in human visual cortex (Conner et al., 2011; Hermes et al., 2017). Past studies using fMRI have shown that spatial attention increased BOLD activity in retinotopically organized areas in early visual cortex overlapped with the attended locations, even when visual stimuli were not physically presented (Kastner et al., 1999), resulting in an additive shift in the baseline response of the BOLD CRF in a manner similar to the attentional modulation of the α-based CRF (Buracas and Boynton, 2007; Murray, 2008; Pestilli et al., 2011; Hara and Gardner, 2014; Sprague et al., 2018; Itthipuripat et al., 2019b). Consistent with the present study, attentional modulations of BOLD CRFs were unaffected by the contrast level of the paired or nontarget stimulus (Sprague et al., 2018). Previous fMRI studies have also shown that baseline shifts of BOLD CRFs were not able 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 (Pestilli et al., 2011; Hara and Gardner, 2014). Our modeling results of the α 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 α amplitude have been associated with modulations of postperceptual processing, such as changes in decision criterion, confidence, and visual awareness, but not changes in perceptual sensitivity (Limbach and Corballis, 2016; Benwell et al., 2017, 2018, 2020; Iemi et al., 2017; Samaha et al., 2017; Iemi and Busch, 2018; Foster and Awh, 2019).

Most studies reporting an attention-induced baseline shift in CRFs based on α band and fMRI activity used endogenous cues to guide attention. However, we used exogenous cues in the present study. Thus, changes in the baseline-offset of α-based CRFs could also reflect bottom-up stimulus processing or visual priming associated with the peripheral cues. Related to this possibility, prior studies have argued that changes in visual appearance could be because of low-level sensory interactions between the cue and the stimulus, independent of an attention effect (Schneider, 2006). That said, some of these α changes are likely of attentional nature given our experimental design and given that recent studies have found similar lateralized α activity using auditory cues (Störmer et al., 2016; Keefe and Störmer, 2021).

Given the current design of our study, there are important limitations that should be considered when interpreting the findings. First, unlike past studies where fMRI and EEG signals were recorded across multiple sessions and days (e.g., Pestilli et al., 2011; Itthipuripat et al., 2014a,b, 2017; Sawetsuttipan et al., 2023), we only recorded one session of EEG over 1-1.5 h. This limited the amount of trials for each experimental condition in the current design, especially given that we had to have many conditions to measure EEG signals across a full range of stimulus contrast. Accordingly, the sensory-evoked responses at the individual-subject level are noisier than those obtained in the multiple-session studies. That said, we limited our recording session to only one session intentionally because previous work has shown that training can attenuate attentional modulations of the P1 and can alter the magnitude of neural noise (Itthipuripat et al., 2017). Thus, we chose to use a relative larger sample size ($N = 20$) than prior work that measured attention modulations of the neural CRFs across multiple-recording sessions (N values = 3-14 in Pestilli et al., 2011; Itthipuripat et al., 2014a,b, 2017; Sawetsuttipan et al., 2023).

Second, the ERP subtraction method used to isolate the P1 evoked by the cue from the P1 evoked by the stimulus relies on the assumption of linear summation (Greenwood and Goff, 1987; Iragui et al., 1993; Kiss et al., 1998; Chica et al., 2010; Itthipuripat et al., 2014a, 2017, 2019b; Störmer et al., 2019). It is possible that neural responses related to the exogenous cue and the contrast of visual stimulus may interact in a nonlinear fashion (e.g., multiplicative reduction of the cue-only response as a function of stimulus contrast). Indeed, we found that the standard contrast jointly modulated the degree of attentional modulations on the response gain of the P1-based CRFs such that attentional modulations at high contrasts were compressed. That said, these attentional modulations of response gain of the P1 data were consistent between the subtracted and nonsubtracted P1 data, which in part validated the linear summation assumption of the ERP subtraction method. Last, our combined model that linked attentional modulations of the P1 and α band activity to the behavioral data also relies on the assumption of linearity, which we assumed for simplicity. However, it is important to note that P1 and α waves are typically analyzed and interpreted separately because of their different origins and functional interpretations. To our knowledge, the overall validity of summing the P1 and α band responses has not been explored previously in the literature. Thus, it is possible that the attentional modulations of the P1 and α band activity might not equally contribute to changes in the psychophysical data. Thus, we performed an auxiliary analysis where we systematically varied the weights of the P1 and α before combining the signals. We found that varying these weights did not make the linking model significantly better than the combined model with equal weighting of the P1 and α,

suggesting that, at least under the assumption of linearity, attentional modulations of the P1 and α band activity reasonably account for attention-induced changes in contrast appearance and response bias.

In line with our findings, recent neurophysiological studies in monkeys have found dissociate neural mechanisms that underlie the effects of attention on sensitivity and criterion in a visual detection task (Luo and Maunsell, 2015, 2019). Specifically, attentional modulations in neural activity in V4 were correlated with changes in sensitivity but not with changes in criterion (Luo and Maunsell, 2015). Consistent with these monkey studies, human EEG studies, have found that attentional modulations of the P1 component, thought to be generated from the extrastriate visual areas, are tightly associated with attention-induced changes in behavioral sensitivity in low-level visual features, such as contrast and object shape (Mangun and Hillyard, 1990; Itthipuripat et al., 2014a, 2017). The present study added that changes in the response gain of the P1 component were directly linked to changes in the perceived contrast of a visual stimulus and were not related to response bias. Alternatively, changes in the baseline activity of the α band activity track the influence of attentional cues on response bias. The present study did not directly measure sensitivity and criterion; thus, the comparisons between these behavioral measures and more subjective aspects, such as contrast appearance and response bias, should be interpreted with caution; and the direct links between changes in neural activity and these behavioral measurements need further investigations.

In contrast to modulatory patterns in early sensory responses, the attentional modulations of neural activity measured in the lateral PFC were correlated with changes in both perceptual sensitivity and response criterion (Luo and Maunsell, 2018, 2019). To further explore brain processes outside visual cortex, we also measured the anterior directing-attention negativity (ADAN) and the lateralized readiness potential (LRP), thought to that track the activity of frontal and pre-motor areas involved in response selection and preparatory motor activity, respectively (see ADAN and LRP analyses and results on Open Science Framework: https://osf.io/4kmcv/) (compare Eimer, 1993, 1995; Verleger et al., 2000; Eimer et al., 2002; Praamstra et al., 2005; van der Lubbe et al., 2006; Green et al., 2008; Störmer et al., 2009; Schankin and Schubö, 2010; Baines et al., 2011; Cosman et al., 2016; Faugeras and Naccache, 2016). We found similar patterns of response bias in the ADAN and LRP emerging at ∼250-500 ms and ∼750-1000 ms after stimulus onset, respectively. Interestingly, response bias could be observed at very low and very high contrast levels, where we observed no attentional modulations of the P1 data. It is important to also note that past studies have also proposed that ADAN might track the shift of visual spatial attention as ADAN often emerges right after spatial attention cues (e.g., Nobre et al., 2000; Eimer et al., 2002; Macaluso et al., 2003). That said, many studies have argued that ADAN involves multiple neural generators that support response-selection mechanisms, such as saccadic movements and motor-related preparatory processes, rather than attention itself (Eimer, 1995; see also Praamstra et al., 2005; van der Lubbe et al., 2006; Green et al., 2008). The consistent response bias patterns in the ADAN and LRP results are thus likely to support the premise that response-selection mechanisms involve multiple neural subcomponents in the frontal and premotor brain areas.

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, the baseline-offset modulations of α band activity correspond to biases driven by the attentional cue. Moreover, under circumstances where there is prominent response bias, exogenous cues can directly trigger the cascading of cue-related neural signals from the frontal to premotor area to bias motor responses without modulating the early visuocortical processing of sensory inputs.

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