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Double Dissociation of Spontaneous Alpha-Band Activity and Pupil-Linked Arousal on Additive and Multiplicative Perceptual Gain

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Perception is a probabilistic process dependent on external stimulus properties and one's internal state. However, which internal states influence perception and via what mechanisms remain debated. We studied how spontaneous alpha-band activity (8–13 Hz) and pupil fluctuations impact visual detection and confidence across stimulus contrast levels (i.e., the contrast response function, CRF). In human subjects of both sexes, we found that low prestimulus alpha power induced an “additive” shift in the CRF, whereby stimuli were reported present more frequently at all contrast levels, including contrast of zero (i.e., false alarms). Conversely, prestimulus pupil size had a “multiplicative” effect on detection such that stimuli occurring during large pupil states (putatively corresponding to higher arousal) were perceived more frequently as contrast increased. Signal detection modeling reveals that alpha power changes detection criteria equally across the CRF but not detection sensitivity (d'), whereas pupil-linked arousal modulated sensitivity, particularly for higher contrasts. Interestingly, pupil size and alpha power were positively correlated, meaning that some of the effect of alpha on detection may be mediated by pupil fluctuations. However, pupil-independent alpha still induced an additive shift in the CRF corresponding to a criterion effect. Our data imply that low alpha boosts detection and confidence by an additive factor, rather than by a multiplicative scaling of contrast responses, a profile which captures the effect of pupil-linked arousal. We suggest that alpha power and arousal fluctuations have dissociable effects on behavior. Alpha reflects the baseline level of visual excitability, which can vary independent of arousal.

Key words: alpha-band oscillations; arousal; confidence; perception; pupillometry

Significance Statement

Nearly a century ago, brain waves ~8–13 Hz (the “alpha-band”) were discovered and linked to visual processing and cortical arousal. However, the precise way that alpha activity shapes perception and relates to arousal is unsettled. We recorded pupillometry and EEG while subjects detected and reported confidence for visual stimuli with varying intensity. Stimuli occurring during states of high alpha were seen less often, regardless of intensity level, suggesting alpha exerts subtractive inhibition on perception and confidence. Pupil size (a proxy for arousal) was found to correlate with alpha yet, surprisingly, has a different effect on perception. Small pupil lowered perceptual sensitivity more as stimulus intensity increased. Our findings reveal distinct effects of alpha activity and arousal on visual perception.

Introduction

Perception is known to be shaped by both internal states of an observer and external stimulus properties (von Helmholtz, 1924). During near-threshold stimulation, for example, internal states

strongly govern whether the stimulus is perceived. Prior experiments have revealed that ongoing alpha-band (8–13 Hz) oscillations reliably predict such trial-to-trial variability in perception [reviewed in Samaha et al. (2020)]. Specifically, states of low alpha power have frequently been associated with an increased probability of stimulus detection (Ergenoglu et al., 2004; Hanslmayr et al., 2007; Romei et al., 2008; Busch et al., 2009; Mathewson et al., 2009; Lange et al., 2013; Weisz et al., 2014; Samaha et al., 2017a). Recently, signal detection theory (SDT) analyses have found that low alpha power leads to a liberal shift in criterion and no effect of alpha on d' (Limbach and Corballis, 2016; Craddock et al., 2017; Iemi et al., 2017; Iemi and Busch, 2018). Complementary findings using discrimination tasks generally find that low alpha

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increases subjective reports of visibility and confidence without changing discrimination accuracy/sensitivity (Benwell et al., 2017, 2022; Samaha et al., 2017b, 2022; Waschke et al., 2019; Di Gregorio et al., 2022). However, a few recent studies have reported d' effects (Zhou et al., 2021; Balestrieri and Busch, 2022).

Despite intensive research, whether alpha impacts criterion or sensitivity has rarely been studied across the varying stimulus levels defining one's psychometric function. In a SDT framework, the function linking changes in stimulus contrast to detection (contrast response function, CRF) could undergo different alpha-related gain modulation. As simulated in Figure 1, additive gain would add (when alpha is low) a constant amount to the internal sensory distributions. This manifests as an upward shift in the detection CRF, a leftward shift in confidence judgments, a downward shift in criteria, and no change in detection sensitivity (Fig. 1A). Alternatively, multiplicative gain would multiply (when alpha is low) the response distributions in proportion to their input strength such that weak responses (absent or sub-threshold stimuli) would receive negligible boosts and stronger (higher contrast) responses would receive larger boosts. Multiplicative gain manifests as an increase in detection for higher contrast stimuli, a selective boost in confidence for high contrast stimuli, and a change in sensitivity that grows with stimulus contrast (Fig. 1B). If alpha exerts multiplicative gain, then effects should manifest principally at suprathreshold contrast levels, yet most studies have used near-threshold stimuli, potentially missing this effect. To conclude that alpha exerts only additive gain (i.e., just a criterion shift) could be premature if based primarily on near-threshold perception. To date, only one study attempted to adjudicate these models; however, they did not include stimulus-absent trials, precluding a SDT analysis (Chaumon and Busch, 2014).

Moreover, prior work has neglected other perceptually relevant factors that may covary with ongoing alpha power. Specifically, some studies have shown that spontaneous pupil fluctuations [putatively reflecting arousal-linked neuromodulatory systems (Joshi et al., 2016)] are positively correlated with ongoing alpha

power, posing a possible confound (Hong et al., 2014; Montefusco-Siegmund et al., 2022; Pfeffer et al., 2022). For instance, pupil increases are generally taken to reflect greater arousal, which may enhance performance (Allen et al., 2016; Urai et al., 2017; Larsen and Waters, 2018; Waschke et al., 2019), and in vision studies, increasing pupil size provides more retinal lightfall, which increases detection in peripheral vision (Mathôt and Ivanov, 2019; Eberhardt et al., 2022). Thus, recent work highlights the need to investigate alpha fluctuations that are independent of contemporaneous pupil changes (Podvalny et al., 2019, 2021).

Here, 30 observers detected and reported confidence in stimuli whose contrast levels were tailored to each individual's CRF while the alpha activity and pupil diameter were simultaneously monitored. We found that prestimulus occipital alpha power exerted an effect most consistent with additive, rather than multiplicative, gain. In contrast, prestimulus pupil fluctuations exerted multiplicative effects on behavior. Importantly, controlling for pupil size, alpha was still found to exert additive gain, consistent with criterion but not sensitivity changes.

Materials and Methods

Subjects

Thirty-three participants (24 female; mean age, 21.6) were recruited for this study from the University of California. All participants provided written consent and were compensated a \$20 Amazon gift card as well as course credit for attending. All participants reported normal or corrected vision. Three participants were excluded from the final analysis due to equipment malfunction ($n = 1$), inability to sufficiently perform the task ($n = 1$), and early termination of the study ($n = 1$), leaving a sample size of 30 for the analysis reported here. A final sample size of 30 subjects was chosen a priori based on previous studies investigating the effects of the prestimulus alpha power on detection using a signal detection framework (Limbach and Corballis, 2016; Iemi et al., 2017; Iemi and Busch, 2018; Zhou et al., 2021). The racial/ethnic identity of this sample was 46.6% non-Hispanic White, 20% Latinx/Hispanic, 20% Asian, and 13.3% mixed race. Data will be made available through the SamahaLabUCSC Open Science Framework repository upon publication (<https://osf.io/une4c/>).

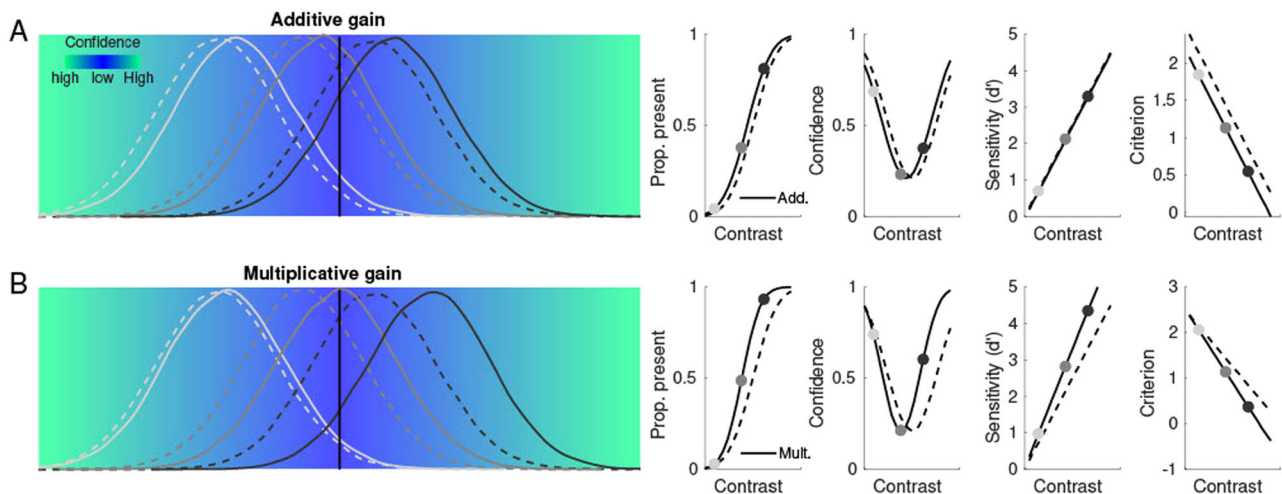


Figure 1. SDT interpretation of the psychometric function and confidence. Each stimulus intensity level gives rise to an internal response which can be characterized as coming from a Gaussian distribution. When an internal response on a given trial surpasses the decision criterion (vertical line in panels **A** and **B**), the observer reports that a stimulus was present. Here, three stimulus intensity levels are highlighted as three distributions with increasing means (from light to dark lines). A standard framework for confidence in SDT is to assume that confidence on a given trial is a function of the “distance-to-criterion” of a sample of evidence, illustrated here in the color gradient. We simulated detection reports, confidence, sensitivity, and criterion across varying stimulus intensities for two different states of prestimulus alpha power (the solid line representing low alpha power). **A**, Behavioral predictions under an additive gain model whereby low alpha adds the same constant to each distribution regardless of stimulus intensity. **B**, Predicted behavior under multiplicative gain, whereby the mean of each distribution is multiplied by a constant, producing larger increases as stimulus intensity grows.

Stimuli

The experiment was implemented in MATLAB (MathWorks), and all stimuli were generated using Psychophysics Toolbox 3 (Kleiner, 2007). Stimuli were presented on a uniform gray background (~ 50 cd/m²) on a gamma-corrected VIEWPixx EEG monitor (1,920 × 1,080 resolution, 120 Hz refresh rate). Participants were seated in a dimly lit room ~ 74 cm away from the screen with their head stabilized on a chin rest. The target Gabor patch had a spatial frequency of 1.8 cycles per degree of visual angle (DVA) and spatial SD of 0.5 DVA. The target location was either in the top-right or top-left visual field, 5 DVA above the fixation, and 5 DVA in either direction (Fig. 2). An individual's threshold level (i.e., the Michelson contrast value at which they reported perceiving the target $\sim 50\%$ of the time) was determined using a one-up/one-down staircase procedure prior to the main task. The staircase relied on routines from the PALAMEDES toolbox (Prins and Kingdom, 2019). The threshold level was then multiplied by a range of values (0, 0.6, 0.8, 1, 1.4, 1.8) to produce a set of contrast levels spanning the CRF, including stimulus absent (0).

Procedure

Participants performed 800 trials of a yes–no visual detection task with confidence ratings. A target Gabor was presented for 8 ms at a random location either in the top-left or top-right visual field and random contrast level (sampled with equal probability from the range specified above). After a 600 ms delay, participants were cued via a fixation color change to provide their detection and confidence response via a single button press. The right hand indicated that the participant perceived the target with four confidence levels (1, “I’m guessing I saw the target”; 4, “I’m certain I saw the target”), and the left hand indicated that they did not perceive the target with reciprocal confidence levels (Fig. 2).

Prior to the main task, participants performed one practice block (50 trials) of the task as well as one block (100 trials) of an up/down staircase procedure. The average of the last 30 reversals provided the estimate of an individual's threshold value (mean threshold value, 18.1% contrast). The total experiment time was ~ 3 h.

EEG acquisition and preprocessing

EEG data were recorded using a 64-channel Ag/AgCl gel-based active electrode system (actiCHamp Plus, Brain Products). Electrode FCz served as the online reference and AFz as the ground. The data were pre-processed using custom MATLAB scripts (version R2022a) and the EELAB toolbox (Delorme and Makeig, 2004). First, a high-pass filter

was applied at 0.1 Hz, and the data were downsampled to 500 Hz and then rereferenced to the median of all electrodes. Then, the epoched data were visually inspected, and trials with excessive noise, muscle artifacts, or ocular artifacts were rejected. Because we were specifically interested in spontaneous pupil activity and its link to EEG signals, we did not use the independent component analysis to remove eyeblink artifacts but instead rejected any trial with an eyeblink or eye movement appearing within a 1 s window centered on stimulus onset. An average of 125 trials was removed (range, 24–301). Channels with excessive noise were removed and spherically interpolated (average of four channels; range, 2–11). Lastly, the data were rereferenced to the average.

Single-trial prestimulus alpha power and residual alpha power

Single-trial prestimulus alpha power was estimated using a fast Fourier transform on a prestimulus window of -450 to 50 ms relative to stimulus onset (as close as we could estimate to stimulus processing but prior to any evoked responses). Single-trial prestimulus signals were Hamming tapered and zero padded (by a factor of 5) to increase frequency resolution. The power spectrum was averaged over the six occipital electrodes showing the highest 8–12 Hz power at the group level (Fig. 3B). Using those electrodes, we then averaged over each individual's peak alpha frequency (IAF) ± 2 Hz (range, 7.58–13.16 Hz). For one participant who did not show a peak in the power spectrum in that range, an IAF of 10 was assigned. Using a fixed alpha frequency range of 8–12 Hz for all participants led to comparable results (data not shown).

Once alpha power was determined for each trial, these data were binned into four quartiles of ascending power (1, lowest power trials; 4, highest power trials). Primary analyses in this study considered the two most extreme bins, that is, 1 and 4, as the high and low prestimulus alpha power conditions. Behavioral data were then sorted according to these high and low alpha bins.

Alpha power independent of pupil size was estimated by taking the single-trial residuals of a linear model predicting the prestimulus alpha power from the prestimulus pupil size. The residuals of this model were then grouped in the same manner as alpha power (i.e., four bins of ascending power) for the purposes of examining the behavior in these bins.

Pupillometry acquisition and preprocessing

Eye-tracking data were recorded using a binocular 2,000 Hz TRACKPixx3 tabletop eye-tracker placed ~ 55 cm in front of the participant and below the stimulus presentation monitor. The eye-tracker was calibrated at the

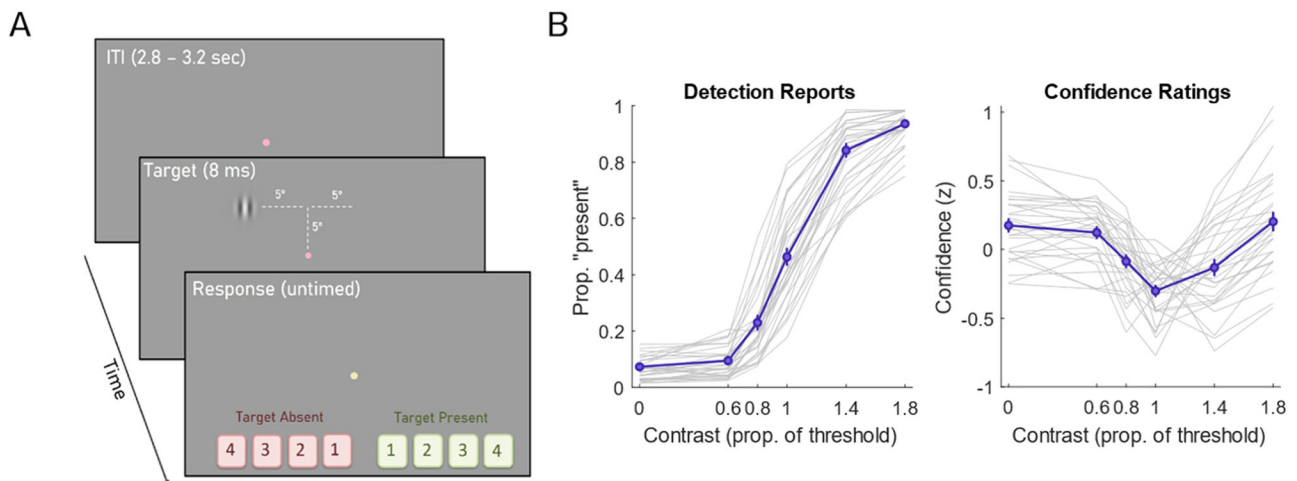


Figure 2. Task schematic and behavior. **A**, After a variable intertrial interval, a brief Gabor patch (“target”) was presented either in the top-left or top-right visual field and observers ($n = 30$) reported whether they detected it or not along with their confidence, using a single button press (note that the dashed lines and text in this schematic were not displayed to observers). The target varied in contrast randomly from trial-to-trial between 0 (absent) and 1.8 times each individual's 50% detection threshold (estimated prior to the main task via an adaptive procedure). **B**, The left panel shows the CRF linking stimulus contrast to the proportion of “present” reports for each observer (gray line) and the group average (purple line). The right panel shows the mean confidence rating (z-scored) at each contrast level for individual observers and the group. The U-shaped confidence curve indicates that confidence increased as the stimulus became more clearly present or more clearly absent; a contrast of 1 indicates the 50% threshold level where uncertainty was highest and confidence was appropriately rated as lowest. Note that in all plots, we display normalized confidence to more clearly see the within-subject variation, but all statistical tests were performed on raw confidence ratings. Error bars indicate ± 1 SEM.

beginning of each block using the default TRACKPixx3 calibration routine. Triggers sent into the EEG system were synchronized with the eye data using a DATAPixx3. The epoched eye data were then aligned with the EEG data, and any trials rejected in the EEG preprocessing stage were also removed from the eye data.

Single-trial pupil size

The average prestimulus pupil size on a given trial was determined by first assessing the median pupil value of both eyes between a -450 and 50 ms prestimulus window. We then checked that the median value was within a biologically plausible range ($10 < \text{value} < 40$ pixels); otherwise, if both pupils did not fall within the range of plausible pupil sizes, that trial was omitted from the analysis (grand total of 70 omitted trials). If the value of both pupils fell within the plausible range, the average of both eyes was used to estimate the given trial's pupil size. And if only one pupil was within the plausible range, then that one constituted the median pupil size of the given trial. The single-trial average pupil sizes were then z -scored within each block to account for possible blockwise differences in the efficacy of the eye-tracker calibration or the head position of the participants. The z -scored, single-trial pupil size estimate was then binned into four quartiles of ascending size (1, smallest pupil size trials; 4, largest pupil size trials).

Signal detection measurements

Detection reports. For each contrast level and alpha/pupil bin, we computed the proportion of trials where the subject reported detecting the stimulus. On stimulus-absent trials, this proportion corresponds to the false alarm rate (FAR). For all other contrast levels, this proportion corresponds to the hit rate (HR). For all SDT measures, a log-linear correction (Stanislaw and Todorov, 1999) was applied to the detection reports in order to accommodate the perfect performance at any given contrast level and alpha bin.

Criterion. Criterion (c) was calculated by adding the z -transformed HR to the z -transformed FAR and multiplying it by $-1/2$. The formula for calculating c is as follows:

$$c = -1/2(z(\text{HR}) + z(\text{FAR})).$$

Sensitivity. Sensitivity (d') was calculated by subtracting the z -transformed FAR by the z -transformed HR. The formula for calculating d' is as follows:

$$d' = z(\text{HR}) - z(\text{FAR}).$$

Generalized linear model (GLM). The GLM for an analogous parameterization of SDT measurements uses a probit link function for estimating the probability of the response "seen" based on stimulus presence (stimpres), prestimulus alpha power (alphapow), and the interaction term of these two (stimpres:alphapow). The coefficients outputted by this model are used for the SDT calculations:

$$\text{probit}(\text{resp}) \sim \beta_0(\text{y-intercept}) + \beta_1(\text{stimpres}) + \beta_2(\text{alphapow}) + \beta_3(\text{stimpres:alphapow}).$$

The intercept (β_0) of this model can be understood in the context of whether or not the stimulus was presented (the effect of which is β_1) and is represented as either 0 (absent) or 1 (presented). In the case of stimulus absence, β_0 represents the FAR. In the case of stimulus presence, $\beta_0 + \beta_1$ represents the HR. The effect that alpha power has on the probability of saying "seen"—irrespective of stimulus presence—is represented by β_2 . And the effect that alpha power has on reports given the stimulus presence is β_3 .

GLM criterion. C was computed by taking the negative of the sum of the intercept and alpha power coefficient and subtracting that by

half the product of the stimulus presence coefficient by the interaction coefficient:

$$c = -(\beta_0 + \beta_2) - (\beta_1 + \beta_3).$$

GLM sensitivity. d' was calculated by adding the stimulus presence coefficient to the interaction coefficient:

$$d' = \beta_1 + \beta_3.$$

GLM alpha power on criterion. The effect of alpha power on criterion was computed by subtracting the negative of the alpha power coefficient from half of the interaction coefficient:

$$-\beta_2 - 1/2(\beta_3).$$

GLM alpha power on sensitivity. The effect of alpha power on sensitivity was the interaction coefficient β_3 .

Naka-Rushton model fitting

To further characterize the changes in the detection CRF due to prestimulus alpha and pupil levels, we fit the detection CRF using a four-parameter Naka-Rushton model (Ling and Carrasco, 2006). This model has the following form:

$$\text{Response} = \frac{R \max * C^n}{C^n + c50^n} + M,$$

where C is the stimulus contrast (expressed here as the proportion of threshold), $R\max$ is the saturation point, $c50$ is the contrast at half the saturation level (threshold), the exponent n is the function's slope, and M is an overall offset added to the response (offset).

The model was fit using the least-square estimation, and parameters were compared between high and low alpha or big and small pupil states using a nonparametric bootstrap procedure. Specifically, we fit the model to a group-averaged CRF from a given condition based on a random sample of participants (with replacement). Repeating this process 10,000 times for each condition separately generated distributions of parameter estimates for high and low alpha or big and small pupil, which were then subtracted to generate difference distributions for each parameter. These difference distributions were then compared against zero to compute a p value by counting the number of bootstrap samples above/below zero and dividing by the total number of bootstraps. Confidence intervals on the difference in parameters were taken as the 2.5th and 97.5th percentile of each difference distribution.

Results

We first determined which frequencies in our data were relevant for predicting perception by sorting trials according to whether the stimulus was reported as "seen" or "unseen" (collapsing all contrast levels) and testing for differences between these two states across the prestimulus power spectrum (from 3 to 40 Hz) derived from posterior channels with maximal alpha power [see Materials and Methods, Generalized linear model (GLM)]. As seen in Figure 3A, stimuli which were reported as "seen" showed significantly lower power in a relatively narrow frequency range from 6 to 14 Hz as compared with "unseen" stimuli. The fact that this effect was narrowband in nature supports the claim that oscillatory alpha activity predicts stimulus detection. To further interrogate the mechanisms by which alpha influences detection across the CRF, we estimated the prestimulus alpha power on single trials and computed four behavioral metrics: the proportion of "seen" responses, mean confidence ratings, sensitivity (d'), and criterion (c) for high and low prestimulus alpha power bins and for each contrast level.

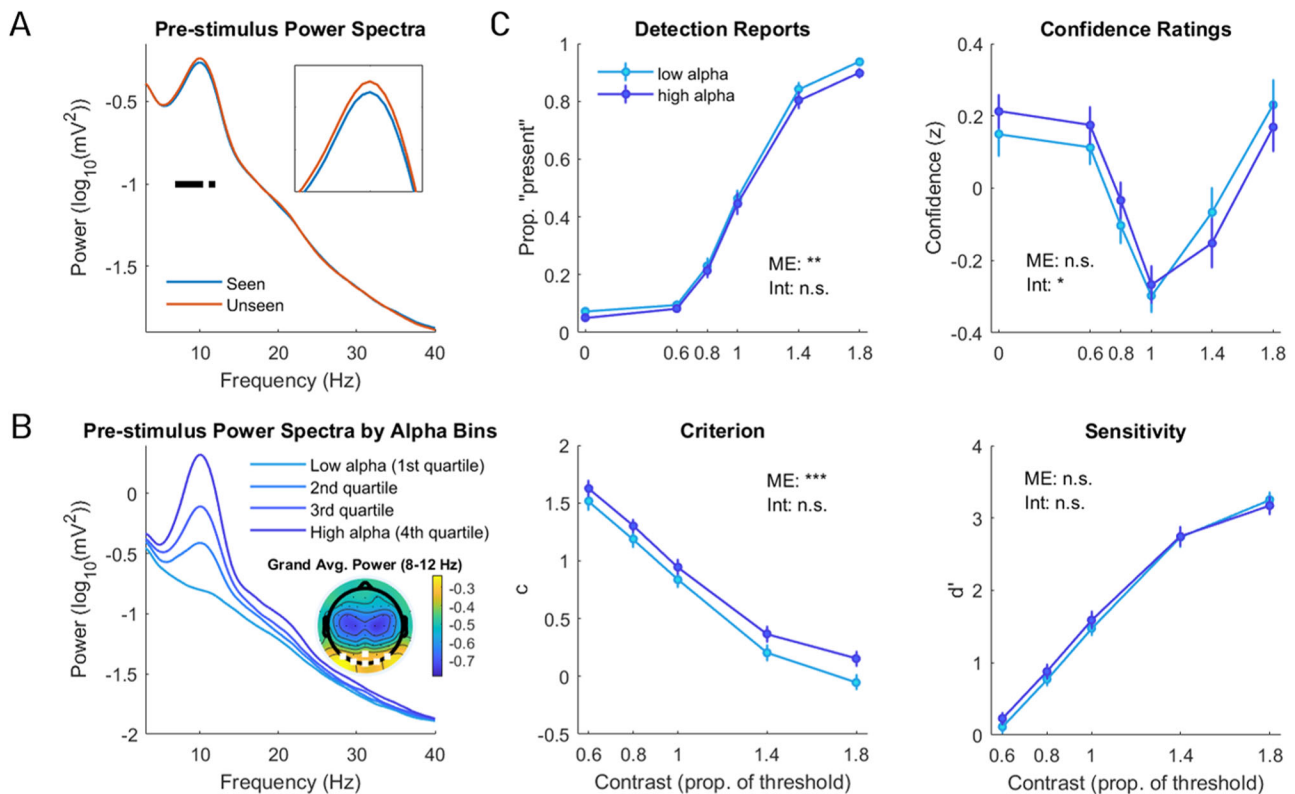


Figure 3. Additive effects of prestimulus power on behavior. **A**, The grand average prestimulus power spectrum from occipital channels reveals higher alpha power preceding unseen compared with seen trials, collapsing across all contrast levels. The black squares represent statistically significant differences (false discovery rate-corrected), showing a relatively narrowband effect limited to the alpha range (magnified in the inset figure). **B**, The grand average power spectrum for each alpha bin used in our analyses. The inset topoplotted map displays the grand average 8–12 Hz power with white dots indicating the electrodes used for all subsequent analyses. **C**, Detection reports showing the proportion of trials reported “present” by contrast level and prestimulus alpha power bin. Confidence depicts the average (z -scored) confidence rating of each contrast level for both high and low prestimulus alpha states. Criterion and sensitivity (d') are shown in the two bottom graphs. Overall, states of low prestimulus alpha power induced a main effect (ME) on detection reports without an interaction (int), boosting detection approximately equally across contrast levels leading to a constant criterion shift at all contrast levels and no interaction or impact on d' . Low prestimulus alpha also translated the confidence curve leftward, boosting confidence for suprathreshold stimuli and reducing it for subthreshold contrasts, thus leading to a significant interaction between alpha and contrast. The effects of ongoing alpha on all four behavioral markers best resemble those predicted by the additive model. Error bars indicate ± 1 SEM. * denotes $p < 0.05$; ** denotes $p < 0.01$; *** denotes $p < 0.001$.

Prestimulus alpha power

We first analyzed detection reports (i.e., the proportion of “seen” responses) as a function of alpha power (high, low) and stimulus contrast (six levels) using a two-by-six repeated-measure ANOVA (for full ANOVA tables with every effect, see <https://osf.io/une4c/>; below we focus on the hypothesis-relevant effects). The additive model predicts that low prestimulus alpha increases detection across all contrast levels equally, corresponding to a main effect in an ANOVA framework without an interaction. In contrast, the multiplicative model predicts that alpha power interacts with contrast such that the boost in detection during low alpha is stronger in high compared with low contrasts.

As seen in Figure 3C, we observed a modest though approximately equal effect of alpha on stimulus detection across all contrast levels, leading to a significant main effect of alpha on the proportion of “seen” responses ($F_{(1,145)} = 10.44$; $p = 0.003$). The direction of this effect is consistent with literature showing an inhibitory function of alpha, whereby states of high prestimulus alpha power led to lower detection reports (Samaha et al., 2020). In contrast with the predictions of the multiplicative model, we found no evidence for an interaction between alpha power and contrast level ($F_{(5,145)} = 0.53$; $p = 0.75$), which suggests that prestimulus alpha power exerts an effect on detection that is uniform across contrast levels. Taken together, the influence of alpha on detection across the CRF is more consistent with an additive, rather than the multiplicative, account of alpha.

The confidence rating data we collected can also help arbitrate between additive and multiplicative effects since, according to a standard SDT implementation of confidence (Fig. 1), additive gain should shift the U-shaped confidence curve rightward by a constant when alpha power is low. This would mean that, when alpha is high, subjects feel more confident for weak stimuli (i.e., more confident that they are not detecting) and less confident for strong stimuli (i.e., less confident that they are detecting). This pattern should manifest as “crossover” interaction in an ANOVA since the direction of the alpha effect flips depending on the contrast level. Multiplicative gain also predicts an interaction between alpha and contrast level although with a qualitatively different pattern, whereby the effect of alpha is largely restricted to higher contrast levels (i.e., not a “crossover” pattern).

As seen in Figure 3C, the effect of prestimulus alpha on confidence appears to flip in direction right around the threshold level of contrast such that participants are more confident in weak stimuli and less confident in strong stimuli when alpha is low. This crossover pattern resulted in a significant interaction effect ($F_{(5,145)} = 2.71$; $p = 0.023$) and a nonsignificant main effect of alpha ($F_{(1,145)} = 0.59$; $p = 0.449$). The pattern of the effect of alpha on confidence across the CRF most closely resembles that of the additive model.

Based on our simulation (Fig. 1), the clearest dissociation between the additive and the multiplicative models is their predicted effect on sensitivity (d') and criterion (c). Since the additive

model equally boosts the HR and the FAR, no change in d' is expected at any contrast level (no main effect or interaction); however, a change in criterion is expected, and this effect should be approximately equal across contrast levels (a main effect, no interaction). On the other hand, the multiplicative model predicts an interactive effect of alpha on d' and criterion, such that during states of low alpha, sensitivity is boosted more the higher the contrast. Our pattern of ANOVA results precisely follows that of the additive model predictions.

Specifically, our results showed a significant main effect of alpha power ($F_{(1,116)} = 15.82$; $p < 0.001$) on criterion, accompanied by no interaction effect ($F_{(4,116)} = 1.49$; $p = 0.211$), suggesting that the impact of alpha on criterion was approximately constant across the CRF. This effect can be seen in Figure 3C, and the direction is consistent with prior work suggesting that low alpha power induces a more liberal criterion, making participants report seeing stimuli more frequently, regardless of their actual presence.

Our analysis on sensitivity did not reveal a significant main effect of alpha power ($F_{(1,116)} = 0.31$; $p = 0.583$) nor interaction between alpha and contrast level ($F_{(4,116)} = 1.49$; $p = 0.211$). These results are visible in Figure 3B by the overlapping d' measurement at each contrast level for both high and low prestimulus alpha power. Our results show that spontaneous states of high and low prestimulus alpha power did not influence sensitivity, even at higher contrast levels.

Taken together, these results provide an additional support that spontaneous prestimulus alpha power changes the detection rate by way of a criterion shift and not a sensitivity shift. Moreover, the effect of alpha power on criterion appears equal across the CRF, supporting the additive model.

In sum, the pattern of alpha effects across all four behavioral indicators were predicted best by the additive gain model. States of low alpha led to a uniform increase in detection reports inducing both HR and FAR increases, confidence ratings showed a crossover interaction which depended on both alpha power and stimulus intensity, criterion showed a uniform change across stimulus intensities (with low alpha having a relatively more liberal criterion), and sensitivity was unaffected by changes in alpha at any contrast level.

GLM for prestimulus alpha power

The previous analysis considered the highest and lowest alpha power quartiles which somewhat arbitrarily classifies trials as “high” and “low” alpha trials while excluding all other trials. This approach aided in visualization of the effects, ease of interpretation, and consistency with prior literature (Iemi et al., 2017, 2022; Iemi and Busch, 2018); however, we wanted to confirm that these effects were not due to the specific binning procedure used and still hold when utilizing the complete dataset. We therefore implemented an alternative measurement of SDT using a GLM with a probit link function (DeCarlo, 1998). Equivalent SDT measurements of c and d' can be computed in a GLM framework [see Materials and Methods, Generalized linear model (GLM)], though they are somewhat less standard in the literature.

The results of the GLM analysis supported our initial findings and provided a reason to believe that our binning procedure did not mask any potentially weaker effects nor create any artifactual ones. Parameter estimates corresponding to the effect of prestimulus alpha power on criterion and sensitivity were derived separately for each contrast level and participant. To assess the main effect of alpha power on c and d' , we collapsed over contrast levels and used a t test to determine if the parameter estimates were different from zero. This revealed a statistically significant

change in criterion [$t_{(29)} = 3.191$; $p = 0.003\%$; 95% CI, (0.040, 0.187)] but not in d' [$t_{(29)} = 0.546$; $p = 0.59\%$; 95% CI, (−0.133, 0.231)]. A one-way ANOVA assessed whether the parameter estimates capturing the effect of alpha on criterion and sensitivity changed with contrast level and found no statistically significant effects (criterion, $F_{(4,29)} = 1.99$; $p = 0.1$; d' , $F_{(4,29)} = 2.01$; $p = 0.097$), indicating a lack of an interaction and a relatively constant influence of alpha across the CRF.

Pupil size

We next sought to better understand how spontaneous pupil fluctuations may have affected perception. The pupil responds to both external stimuli (e.g., luminance changes) and internal states (e.g., relaxation) and is often used as a proxy for arousal, termed pupil-linked arousal (Joshi et al., 2016; Joshi and Gold, 2020). As our analysis focused on prestimulus pupil states, just as in the case of alpha, single-trial variation in pupil size from our data likely reflects changes in internal cognitive states rather than external stimuli. This allowed us to address whether internally driven states of pupil-linked arousal impacted stimulus detection in our paradigm and via what mechanisms (additive or multiplicative gain).

To estimate single-trial pupil diameter, we averaged over the same time window of data (−450 to 50 ms relative to stimulus onset) and implemented the same binning procedure used for the alpha analysis, which classified the pupil size high and low pupil states based on the first and fourth quartiles. We then analyzed all four behavioral measures (detection, confidence, criterion, and sensitivity) using repeated-measure ANOVAs with the pupil size (high and low) and contrast level as predictors.

Figure 4A shows the effect of prestimulus pupil size across all behavioral metrics. In contrast to the effect of alpha, we observed a significant main effect of pupil size on detection ($F_{(1,145)} = 16.3$; $p < 0.001$) as well as a significant interaction with contrast level ($F_{(5,145)} = 8.32$; $p < 0.001$). This effect shows that on trials when participants happened to have a larger pupil size, they reported perceiving the stimulus more often but only for higher contrast levels (i.e., participants were not producing more false alarms). This pattern of results is more consistent with the pupil exerting a multiplicative as opposed to additive effect on the CRF. Profiles of the other behavioral metrics bore this out as well.

Specifically, large pupil led to a boost in confidence ratings but primarily for stronger stimulus intensities, resulting in a significant interaction effect ($F_{(5,145)} = 3.28$; $p = 0.008$) and no main effect ($F_{(1,145)} = 2.92$; $p = 0.1$). Large pupil also led to an apparent liberal shift in criterion which was more pronounced for higher contrast levels, leading to a significant interaction effect ($F_{(4,116)} = 3.72$; $p = 0.007$) as well as a main effect ($F_{(1,116)} = 5.77$; $p = 0.023$). This criterion effect, however, could be understood to originate from a multiplicative change in sensitivity since, as the distributions increase along the internal evidence axis, they become further from the criterion (producing an apparent shift in the “relative” criterion measured by standard SDT; Fig. 1). This seems to be the case as an interactive effect of pupil on d' was clear, whereby large pupil increased sensitivity particularly at high contrasts ($F_{(4,116)} = 3.72$; $p = 0.007$). A significant main effect of pupil on d' was also evident ($F_{(1,116)} = 17.12$; $p < 0.001$). In other words, this apparent shift in criterion could simply be the result of highly similar FAR between the two pupil states with differing HR as is predicted by the multiplicative gain model in Figure 1B. Thus, whereas spontaneous changes in alpha power produce an additive effect on the CRF that alters criterion, pupil changes occurring at the same moment in time lead to a multiplicative effect that boosts sensitivity.

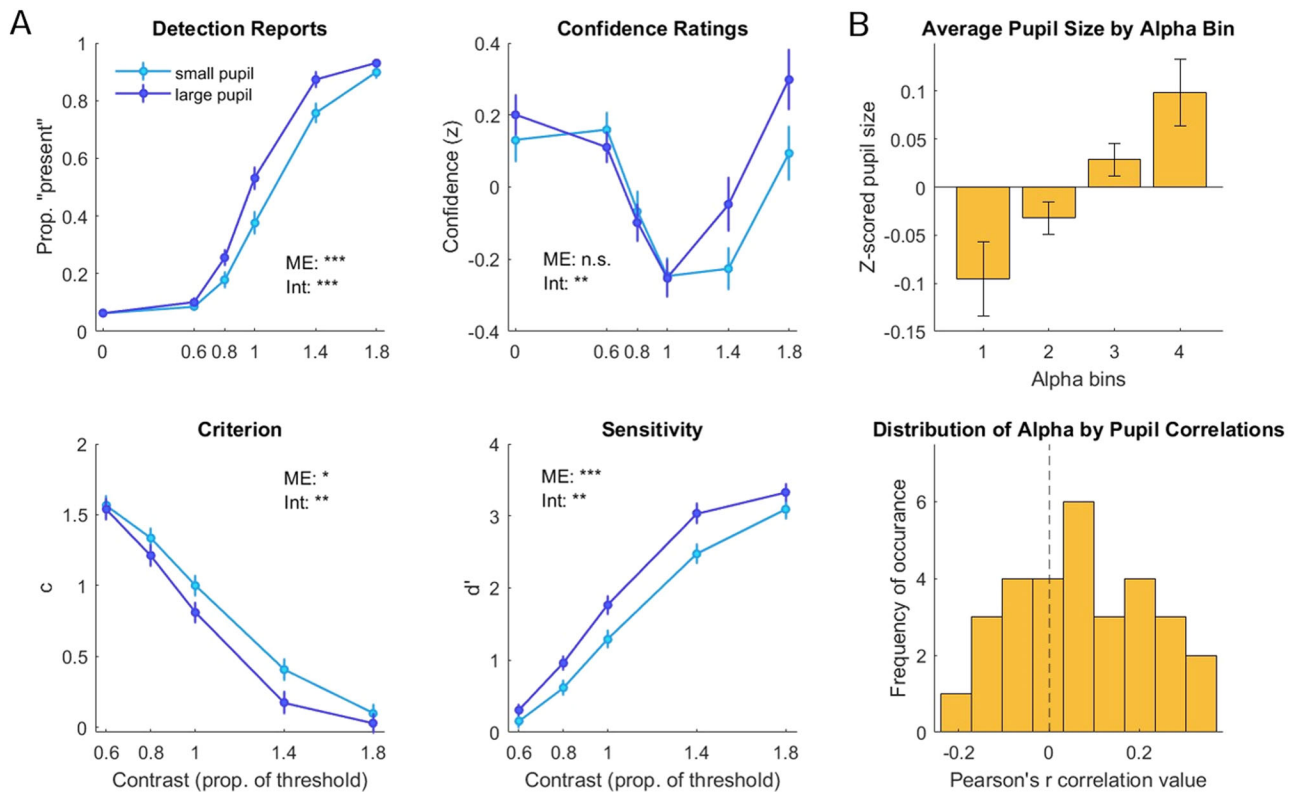


Figure 4. Multiplicative effects of prestimulus pupil size on behavior **A**, Large prestimulus pupils lead to more frequent stimulus detection, particularly at higher contrasts, without increasing false alarms. This effect corresponds to a boost in sensitivity that interacts with contrast level and is mirrored in a criterion shift with similar profile. Confidence on high prestimulus pupil trials was also selectively boosted at supra- but not subthreshold contrasts, as predicted by multiplicative gain. **B**, The top panel shows the group-level, z-scored prestimulus pupil size for each prestimulus alpha power quartile, depicting a positive linear relationship between spontaneous alpha and pupil size. The bottom panel depicts the distribution of single-trial correlations between prestimulus alpha and pupil for each subject, which tends toward positive correlations. Error bars indicate ± 1 SEM. * denotes $p < 0.05$; ** denotes $p < 0.01$; *** denotes $p < 0.001$.

We next sought to understand how these opposing effects might be related. This question has particularly interesting theoretical implications since both spontaneous pupil fluctuations and spontaneous alpha power are often taken as proxies of internal states of arousal or attention, respectively, that are predictive of task performance (Kelly et al., 2009; Kelly and O'Connell, 2013; Urai et al., 2017; van Kempen et al., 2019; Waschke et al., 2019; Podvalny et al., 2021). To this end, we used the same alpha quartiles as used in the previous analysis of behavior but instead computed the normalized prestimulus pupil size at each alpha level. As seen in Figure 4B, there is an apparent positive linear relation between spontaneous alpha fluctuations and contemporaneous pupil changes, with a significant increase in pupil at the highest compared with the lowest alpha level [$t_{(29)} = -2.759$; $p = 0.01\%$; 95% CI, $(-0.337, -0.050)$]. This relationship was corroborated by a single-trial correlation analysis, whereby alpha and pupil were correlated on single trials separately for each participant. As shown in Figure 4B, most subjects had a positive correlation, the distribution of which was significantly different from zero at the group level [$t_{(29)} = 2.861$; $p = 0.008\%$; 95% CI, $(0.022, 0.133)$].

The strengths of the single-trial correlations were quite small, yet the direction of this effect is somewhat surprising. Namely, states of higher alpha power are generally related to states of larger pupil size, which suggests that these two positively correlated indices of internal states actually have opposing effects on behavior, given the previously observed results. That is, while states of low alpha power have higher detection on average and an additive scaling of the CRF, states of low pupil have

lower detection on average and a multiplicative scaling of the CRF, yet the two are positively related. We therefore reasoned that the correlated and contemporaneous pupil effects could perhaps be influencing the observed effect of alpha on detection behavior, which is not something most other studies have controlled for.

Residual alpha power

The goal of this analysis was to see whether or not the effects of alpha power on detection was modified by alpha's relationship with the pupil size. Residual alpha power was estimated by taking the single-trial residuals of a linear model predicting prestimulus alpha power using prestimulus pupil size. The residuals of this model were then binned in the same manner as alpha power, that is, four bins of ascending power, and the analysis similarly considered the two most extreme bins (high and low) as predictors of behavior.

Consistent with our initial findings, we observed a significant main effect of residual alpha power on detection ($F_{(1,145)} = 10.78$; $p = 0.003$) with no evidence of an interaction ($F_{(5,145)} = 0.38$; $p = 0.861$; Fig. 5B). This suggests that, in our dataset, measurements that better isolate alpha power, such as controlling for pupil-linked arousal, still provide evidence for an additive effect of alpha on perception. Moreover, the crossover effect of alpha on confidence ratings held when residualizing for the pupil (Fig. 5B) shows a significant interaction effect ($F_{(5,145)} = 2.7$; $p = 0.023$) and no main effect ($F_{(1,145)} = 0.41$; $p = 0.527$). As further predicted by the additive model, residual alpha had a main effect on criterion ($F_{(1,116)} = 19.97$; $p < 0.001$) coupled

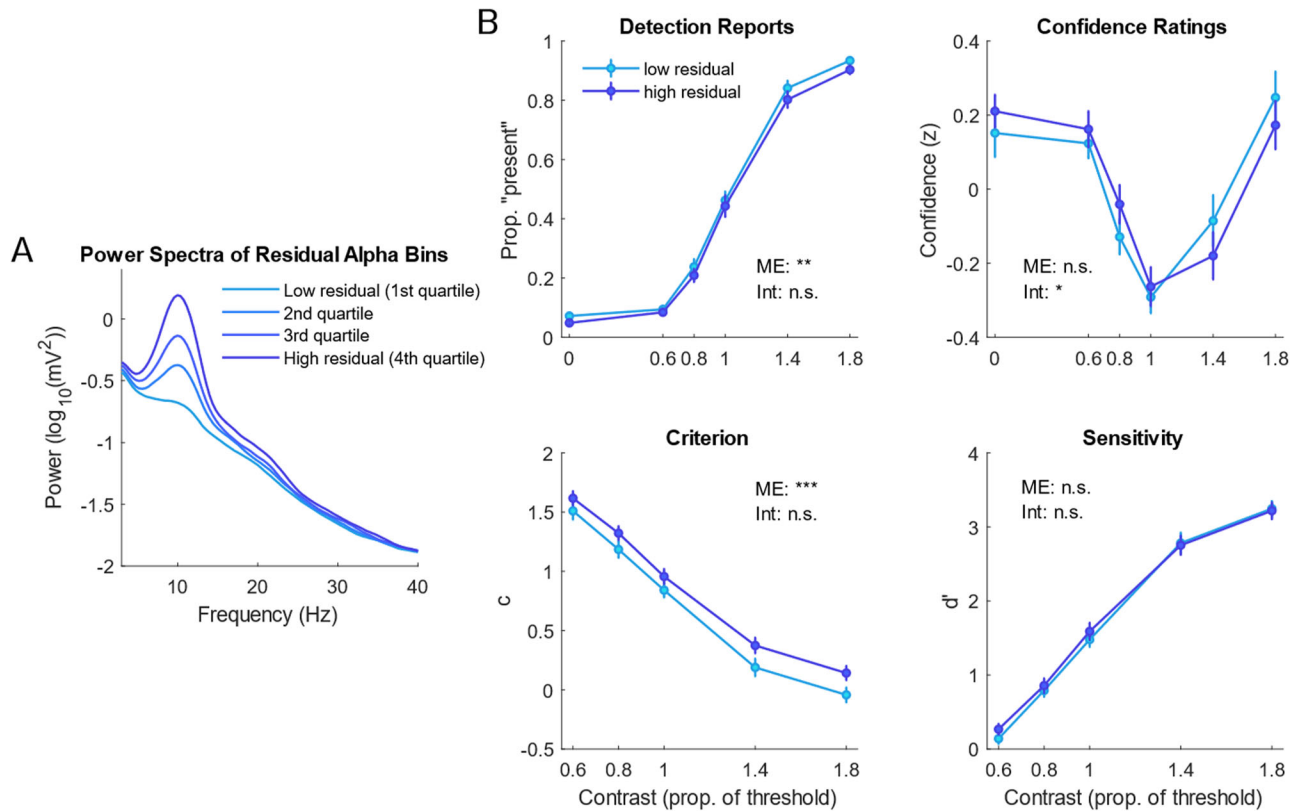


Figure 5. Pupil-independent prestimulus alpha fluctuations exert additive gain. **A**, The grand average prestimulus power spectrum for trials in each pupil-independent alpha quartile. **B**, The effects of residual (pupil-independent) alpha power on detection, confidence, criterion, and sensitivity are indicative of additive gain with a main effect on detection reports and criterion, a contrast-by-alpha interaction on confidence, and no effect of alpha on d' . Error bars indicate ± 1 SEM. * denotes $p < 0.05$; **denotes $p < 0.01$; ***denotes $p < 0.001$.

with a nonsignificant interaction ($F_{(5,116)} = 1.05$; $p = 0.387$) and no main effect ($F_{(1,116)} = 0.29$; $p = 0.591$) or interaction ($F_{(5,116)} = 1.05$; $p = 0.387$) on d' .

Controlling for the time on task

One possible concern is that both behavior and physiological measures might systematically change over the duration of the experiment (Benwell et al., 2019). Thus, any correlation between them could be confounded by the time on task. To assess this, we next tested for possible effects of block number on each of the physiological and behavioral measurements by fitting a line to the (rank-scored) measures for each subject and testing the slope against zero at the group level using a t test (Fig. 6A,B). We found a steady increase in alpha power across blocks [$t_{(29)} = 4.79$; $p < 0.001\%$; 95% CI, (0.205, 0.51)] but no significant change in pupil size [$t_{(29)} = 1.92$; $p = 0.06\%$; 95% CI, (-0.012, 0.376)]. We found a statistically significant change in criterion [$t_{(29)} = 2.39$; $p = 0.023\%$; 95% CI, (0.027, 0.345)], which indicated a shift to be more conservative in later blocks, and no significant block effect in either d' [$t_{(29)} = -1.23$; $p = 0.23\%$; 95% CI, (-0.267, 0.069)] or confidence [$t_{(29)} = -0.43$; $p = 0.67\%$; 95% CI, (-0.26, 0.168)].

In light of the fact that both alpha power and criterion changed over blocks, we ran two control analyses to see if the block effect accounted for the link between the alpha and behavior. First, we repeated the binning analysis but using within-block z -scoring of alpha power, prior to binning, so that across-block variance was eliminated (Fig. 6C). The results of this control analysis mirrored the results from our main analysis, revealing a main effect of alpha power on detection ($F_{(1,145)} = 4.2$; $p = 0.050$) with no interaction effect across contrast levels ($F_{(5,145)} =$

0.64; $p = 0.67$). This change was driven by a main effect of alpha on criterion ($F_{(1,145)} = 5.64$; $p = 0.024$) but not d' ($F_{(1,145)} = 0.31$, $p = 0.58$), with no interaction effect on either ($F_{(5,145)} = 1.62$; $p = 0.173$). The interaction effect of alpha on confidence was trending although not significant ($F_{(1,145)} = 2.12$; $p = 0.066$) and continued to show no main effect ($F_{(1,145)} = 0.41$; $p = 0.53$).

As a second control analysis, we restricted our binning procedure to just the final four blocks of the experiment, since we observed a stable alpha power throughout the second half of the task (Fig. 6A). This analysis further reinforced our findings, demonstrating a main effect of alpha on detection ($F_{(1,145)} = 5.94$; $p = 0.02$) with no interaction ($F_{(5,145)} = 0.34$; $p = 0.88$) that is explained by a main effect of alpha on criterion ($F_{(1,116)} = 7.6$; $p = 0.01$) but not d' ($F_{(1,116)} = 0.22$; $p = 0.65$) with no interaction of either effect with contrast levels ($F_{(4,116)} = 0.44$; $p = 0.78$). Alpha power continued to demonstrate a significant interaction effect with contrast levels in predicting confidence ($F_{(1,145)} = 2.29$; $p = 0.049$) with no overall main effect ($F_{(1,145)} = 0.01$; $p = 0.92$), aligning with the additive model predictions.

Model-based analysis

We have presented our data using an ANOVA framework because it captures the additive and multiplicative effects as modeled in a signal detection framework and can be applied to all four of the behavioral metrics we derived. However, the ANOVA framework does not distinguish between two distinct forms of multiplicative effects on the CRF commonly studied in perception research, namely, contrast gain or response gain (Ling and Carrasco, 2006; Chaumon and Busch, 2014). This motivated a model-based analysis of the detection CRF.

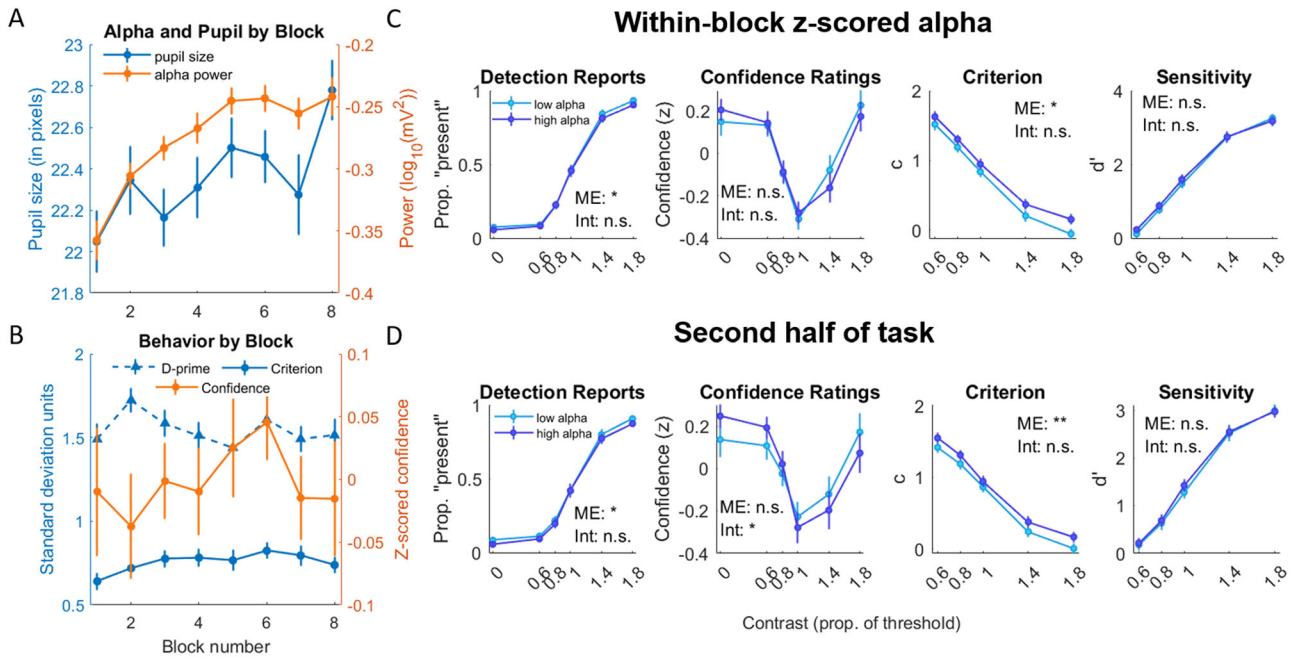


Figure 6. Control analyses for time on task. **A**, Average alpha power and pupil size for each block which revealed a significant increase in alpha, but not pupil, as the task progressed. **B**, Average d' , criterion, and confidence for each block, collapsed across contrast levels. A significant increase in criterion, but not d' or confidence, was found. **C**, To assess whether the correlation between criterion and alpha could be explained by time on task, we z-scored within block the alpha estimates, eliminating blockwise variation. This control produced a similar pattern of results to our main analysis, with a significant main effect of alpha on detection due to a change in criterion and not d' , with no interaction effect. Alpha did not show any main or interaction effect on confidence. **D**, As alpha power and criterion were stable across the last four blocks, an analysis on the second half of the task reproduced the additive effect of alpha on detection. Namely, a main effect of alpha power on detection with no interaction across contrast levels, a main effect on criterion but not d' and no interaction on either, and an interaction effect of alpha on confidence with no interaction. Error bars indicate ± 1 SEM. * denotes $p < 0.05$; ** denotes $p < 0.01$.

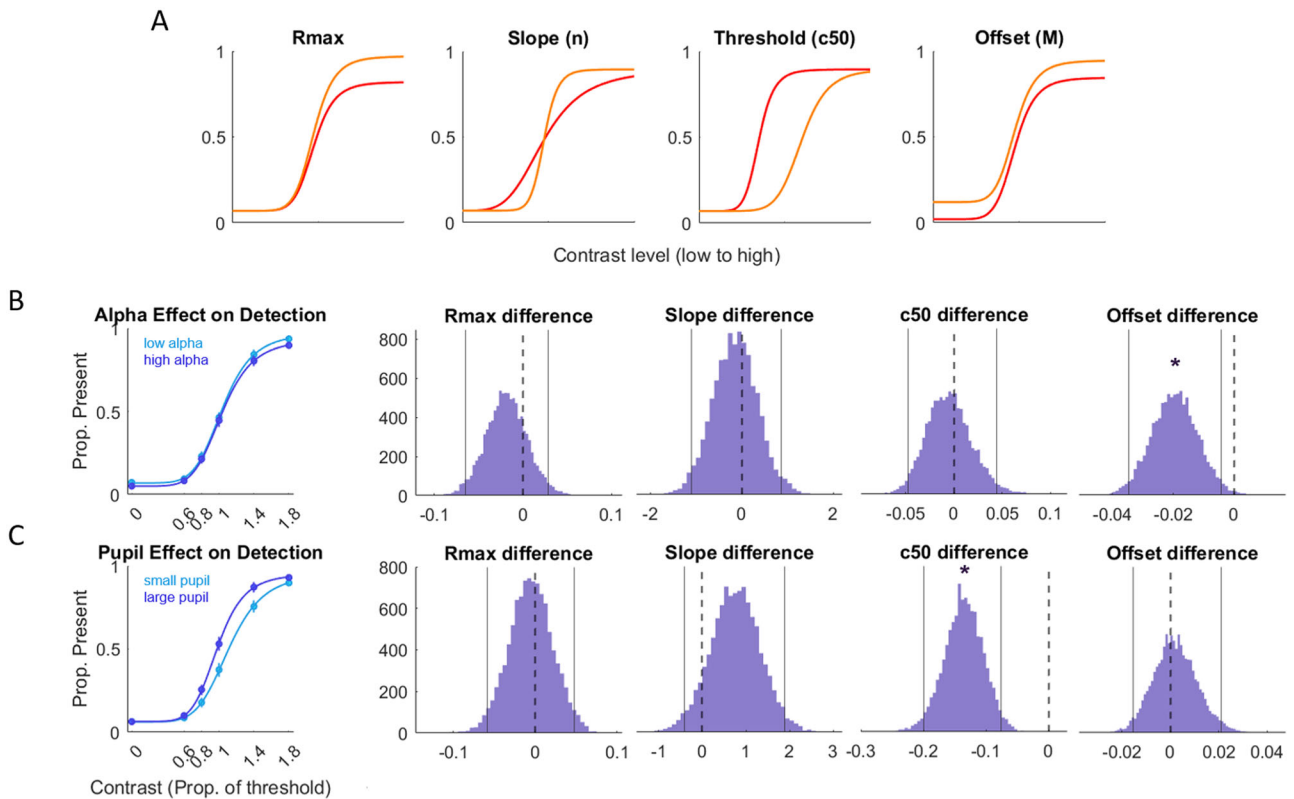


Figure 7. A Naka–Rushton model of the detection reports is consistent with alpha exerting additive gain and pupil exerting contrast gain. **A**, The four parameters of the Naka–Rushton model. R_{max} controls the saturation point of the CRF, n changes the slope, c_{50} indicates the threshold value, and M sets an overall baseline offset. **B**, The difference distribution (high minus low) for each parameter from 10,000 bootstrap iterations. A difference distribution of zero means the parameter estimates for high and low alpha (big and small pupil) were the same. A significant difference in the offset parameter ($p_M = 0.012$) is consistent with an additive effect of alpha. **C**, A significant difference in the c_{50} parameter ($p_{c50} < 0.001$) is consistent with a contrast gain effect of pupil. Note however that we did not design our experiment to ensure subceiling detection in each participant, which may have limited our ability to observe an effect on R_{max} .

We used a four-parameter Naka–Rushton equation to fit the detection data (Fig. 7): the response is $\frac{R_{\max} * C^n}{C^n + c50^n} + M$, whereby R_{\max} controls the saturation point, n dictates the slope, $c50$ defines the threshold value, and M indicates the offset. The signature of the additive model is a change in the offset parameter. Contrast gain is typically inferred from a change in threshold sensitivity ($c50$), whereas response gain is inferred from a change in R_{\max} (Ling and Carrasco, 2006; Chaumon and Busch, 2014).

When we fit the model to the detection CRF for high and low alpha, the only parameter which changed significantly between the two fits was the offset parameter M ($p_M = 0.012$; $p_{R_{\max}} = 0.40$; $p_n = 0.78$; $p_{c50} = 0.79$; Fig. 7B). As expected from our main analysis, this pattern supports the additive account of alpha. When fitting the pupil data, only the threshold parameter ($c50$) significantly changed between fits ($p_{c50} < 0.001$; $p_{R_{\max}} = 0.84$; $p_n = 0.19$; $p_M = 0.83$; Fig. 7C) which indicates a contrast gain effect induced by pupil changes. We note, however, that these results should be interpreted cautiously as a typical experimental design feature important for distinguishing contrast and response gain is ensuring that detection is below the ceiling at the highest contrast level so that changes in R_{\max} can be adequately captured. We did not design our task with this constraint, and about one-third of our subjects reached ceiling levels at the highest contrast. Thus, we cannot fully rule out an effect of pupil size on response gain.

Discussion

Gain modulation of sensory responses allows the brain to dynamically shape how it responds to external stimuli as a function of ongoing internal brain states. Alpha-band oscillations are the most prominent form of intrinsically generated brain activity seen in the human EEG, and, despite having been discovered nearly a century ago (Berger, 1929), the precise modulatory effect of alpha activity on perception has remained unclear. Here we show that states of high (low) ongoing alpha activity suppress visual detection via a constant subtractive (additive) factor, corresponding to a reduction of stimulus detection that is approximately equal across all stimulus intensity levels. In direct contrast, we find that pupil fluctuations, known to partly reflect arousal-related neuromodulatory activity, multiplicatively scale visual detection, such that large prestimulus pupil states boost visual detection more for higher contrasts. Importantly, isolating fluctuations in alpha power from contemporaneous pupil changes still led to the observation of an additive effect of low alpha on detection.

Our findings have important implications for understanding how ongoing alpha activity shapes perceptual behavior. The additive gain we observed suggests that states of low alpha should not lead to any change in perceptual sensitivity (d') since low alpha boosts detection reports even in the absence of any stimulus (i.e., false alarms). This is indeed what our SDT analyses revealed and is congruent with multiple recent studies showing an effect of alpha on detection criterion but not sensitivity (Limbach and Corballis, 2016; Craddock et al., 2017; Iemi et al., 2017; Iemi and Busch, 2018; Vigué-Guix and Soto-Faraco, 2023). Our results build on this prior literature by showing that the effect of alpha on detection criterion is not restricted to just the case of threshold stimuli but is also observed across the range of contrast levels spanning each individual's CRF and also by showing that the criterion effect holds after controlling for the correlation between ongoing alpha and pupil size. Our findings also shed light on the computations underlying confidence in visual detection. According to some accounts, confidence is computed as the probability of being correct, which should increase along with d' (Meyniel et al., 2015; Sanders et al., 2016; Adler and

Ma, 2018; Geurts et al., 2022). However, our results show that confidence increases along with alpha-induced criterion shifts even with no accompanying change in d' . This could naturally come about if observers use a “distance-to-criterion” computation as illustrated in Figure 1. When alpha is low and an additive factor is applied equally to stimulus-present and stimulus-absent distributions, high contrast stimuli become further from the decision criterion (leading to higher confidence), and low contrast/absent stimuli get closer to the criterion (leading to lower confidence). Thus, our analysis of prestimulus brain states adds to the growing body of behavioral evidence that confidence is not computed as the Bayesian probability of being correct (Rahnev et al., 2011; Zylberberg et al., 2012, 2014; Koizumi et al., 2015; Samaha et al., 2016, 2019; Adler and Ma, 2018; Li and Ma, 2020; Maniscalco et al., 2021; Samaha and Denison, 2022; Xue et al., 2024).

Collectively, our findings support the idea that the ongoing alpha power reflects the overall excitability of the visual cortex, a concept which is at least partly dissociable from the notion of arousal, since we find the two have differing effects on perceptual behavior. In line with the recently proposed baseline excitability model (BSEM; Samaha et al., 2020), the alpha-induced change in cortical excitement can be described as a baseline shift, which is hypothesized to influence signal-detecting neural populations even in the absence of any stimulus. In this scenario, the baseline increase would push the firing rate closer to the detection criterion, increasing the chances of perceiving a weak stimulus (i.e., a hit) while simultaneously increasing the chances of weakly perceiving something which was not there (i.e., a false alarm). In contrast, we propose that the spontaneous changes in pupil size can be taken as a proxy of internal arousal, partly distinct from changes in visual cortical excitement. Pupil-linked arousal is widely believed to be modulated by the locus ceruleus–norepinephrine system and/or the superior colliculus (Joshi et al., 2016; Larsen and Waters, 2018; Joshi and Gold, 2020) and may be relatively unlinked with stochastic variation in visual cortical excitability. The effect of pupil-linked arousal on behavior exhibited a gain response which could involve multiple cellular mechanisms including changes in synaptic input or membrane conductance (Ferguson and Cardin, 2020). On the other hand, the additive impact of alpha on detection may be explained by different cellular mechanisms such as shunting inhibition (Ferguson and Cardin, 2020).

By varying contrast levels in the present study, we were able to provide stronger evidence than most prior work in favor of BSEM. Since the multiplicative account predicts the largest sensitivity changes at higher contrast levels, any prior work used as evidence for BSEM may have missed these sensitivity changes due to the use of near-threshold stimuli only. In contrast, our data found criterion but not sensitivity changes at higher contrasts, as predicted by BSEM. However, a handful of studies have reported that spontaneous alpha power can increase sensitivity in certain cases. In addition to finding an effect of alpha on subjective contrast appearance, Balestrieri and Busch (2022) also observed that low prestimulus alpha led to an increase in contrast sensitivity in spatial two-alternative forced-choice discrimination task. One possibly relevant difference is that our study examined the pupil-independent effect of alpha on detection, motivated by the positive correlation found between alpha power and pupil size in our data and by others (Podvalny et al., 2021). The coupling of alpha and pupil suggests that high alpha power co-occurs with states of large pupil. Interestingly, recent work suggests that whereas larger pupils improve detection performance by virtue of increased retinal light-fall (which we also observed), larger pupils were also detrimental to fine-grained discrimination performance, presumably because

smaller pupils result in less optical distortion and higher acuity (Mathôt and Ivanov, 2019). One possibility, then, is that the decrease in contrast discrimination sensitivity observed by Balestrieri and Busch (2022) during states of high alpha power could be partially explained by concomitant increases in pupil size. This speculative account should be explored in future studies examining contrast discrimination while controlling for pupil effects on alpha.

Zhou et al. (2021) similarly found an effect of alpha power on contrast sensitivity in a discrimination task querying whether a backward-masked stimulus had been a grating or noise. The effect on d' was found in only one of their conditions when a conservative detection criterion was experimentally induced and did not replicate in their liberal criterion condition. Notably, their analysis of prestimulus power targeted brain areas which were feature-specific to the target stimulus; this differs from papers looking at global alpha changes, which we presume reflect target and nontarget excitability fluctuations (Samaha et al., 2020; although the authors also found d' effects when using a searchlight analysis). Another difference is that Zhou et al. (2021) experimentally manipulated participant's decision criterion to either be conservative or liberal, which is in contrast to the design of most other works looking at spontaneous fluctuations in criterion as a function of alpha. This raises the possibility that experimental control over participant's criterion could mask otherwise natural variation in trial-to-trial criterion setting.

Lastly, one other study investigating alpha power's role in perception across the CRF presented results which are at odds with our findings. Chaumon and Busch (2014) showed evidence of a multiplicative effect of prestimulus alpha power on detection. This study used a go/no-go task paradigm to report stimulus presence which means participants only responded when they perceived the stimulus (and withheld a response when they did not) and they did not include stimulus-absent trials and thus could not compute SDT measures. We suggest that task demands in their study may explain these inconsistent results. Since the go/no-go paradigm requires additional effort (albeit quite small) to actively report "seen" as opposed to doing nothing to passively report "unseen," this may have created an additional bias such that participants were less inclined to report stimulus presence at low contrasts but when the stimulus was more obvious (at high contrasts) they were more willing to engage in the more effortful behavior, leading to a multiplicative-like pattern. Overall, the literature would benefit not only from additional studies measuring the perceptual effects of alpha across the CRF but also from studies investigating potential differences in the effects of alpha during specific paradigms or task demands.

Much about the stochastic processes underlying perception is still unknown. Here, we provide evidence that spontaneous fluctuations in alpha-band power and pupil size have distinct and separable effects on perception. From this, we postulate that measurements of pupil and alpha reflect different dimensions of internal state fluctuations (cortical excitement in alpha and arousal in pupil) which differentially shape the trial-to-trial variability in our perception.

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