

Alpha oscillations reflect suppression of distractors with increased perceptual load

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ABSTRACT

Attention serves an essential role in cognition and behavior allowing us to focus on behaviorally-relevant objects while ignoring distraction. Perceptual load theory states that attentional resources are allocated according to the requirements of the task, i.e., its 'load'. The theory predicts that the resources left to process irrelevant, possibly distracting stimuli, are reduced when the perceptual load is high. However, it remains unclear how this allocation of attentional resources specifically relates to neural excitability and suppression mechanisms. In this magnetoencephalography (MEG) study, we show that brain oscillations in the alpha band (8–13 Hz) implemented the suppression of distracting objects when the perceptual load was high. In parallel, high load increased the neuronal excitability for target objects, as reflected by rapid invisible frequency tagging. We suggest that the allocation of resources in tasks with high perceptual load is implemented by a gain increase for targets, complemented by distractor suppression reflected by alpha-band oscillations closing the 'gate' for interference.

1. Introduction

In multi-element environments, selective attention is required to allocate resources in accordance with task demand (e.g. Carrasco, 2011; Nobre and Kastner, 2014). Perceptual load theory is a highly influential framework arguing that while attentional resources are limited, they are allocated to all stimuli within capacity. Thus, the level of perceptual demand in the task, namely its 'perceptual load' determines distractor processing (Lavie, 2005, 1995; Lavie et al., 2014). In low load tasks, when task processing does not take up full capacity, irrelevant distractors are nevertheless perceived (due to a 'spillover' of resources), while high perceptual load tasks exhaust perceptual capacity in the processing of task-relevant stimuli and result in inattentive blindness to distractors (e.g., Cartwright-Finch and Lavie, 2007). Perceptual load is operationally defined based on both the number of different stimuli that need to be perceived in a task, and the perceptual demand in the task-relevant processing of each stimulus (Lavie, 1995; Lavie and Tsai, 1994). Much research established that tasks of increased perceptual load, so defined, result in reduced distractor processing. For example, search tasks with increased relevant set size, or increased target/non-target similarity, result in reduced processing of task-irrelevant distractors, compared to smaller set sizes, or dissimilar

search items (e.g., Lavie and Cox, 1997). Similarly, manipulations perceptual load through increased demand on perceptual discrimination, for example, embedding the target signal within a noise mask, or requiring subtle discrimination between target features (e.g. length, shape, location), or their combination, also result in reduced distractor perception and associated neural response (e.g., Bahrami et al., 2007; Lavie, 1995; Remington et al., 2014; Yi et al., 2004), in comparison to low load conditions only requiring simple feature detection (e.g., blue versus green).

A different body of research has demonstrated that neuronal oscillations are strongly modulated by attention (Jensen and Hanslmayr, 2020). However, it remains unclear how these oscillations serve to support the allocation of resources associated with perceptual load theory. The brain signals most strongly associated with the allocation of attentional resources are neuronal oscillations in the alpha-band (8–13 Hz) (Foxe et al., 1998; Jia et al., 2019; Van Diepen et al., 2019; Vanni et al., 1997; Worden et al., 2000). It remains an open question what drives modulations in the alpha-band, although a subcortical route has been suggested (Mazzetti et al., 2019; Saalman et al., 2012; Vijayan and Kopell, 2012). Visual tasks using a simple cue directing attention to one hemifield typically result in a hemispheric lateralization of power in the alpha band over parieto-occipital regions, with decreased power

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contralateral to the selected object (the target) and a relative increase contralateral to the irrelevant object (the distractor) (Kelly et al., 2006; Okazaki et al., 2014; Thut, 2006; Worden et al., 2000). As alpha-band oscillations have been shown to reflect functional inhibition (Jensen and Mazaheri, 2010; Klimesch et al., 2007), the primary role of alpha oscillations is thought to be the suppression of the processing pathway of the irrelevant items as well as engaging the attended pathway by a decrease in alpha power. As mentioned earlier, perceptual load theory predicts a reduction of resources for distractors with increased task processing load (Bruckmaier et al., 2020). It remains unclear how the theory relates to modulations in the alpha band. In fact, as more salient distractors necessitate the need for suppression (Awh et al., 2003; Theeuwes, 1992), alpha band power increases may also be driven by the nature of the distractor. While some research demonstrates an increase in alpha-band power to anticipated distractors (Bonnefond and Jensen, 2012; Haegens et al., 2012; Händel et al., 2011; Okazaki et al., 2014; Payne et al., 2013), other studies question the role of alpha oscillations in distractor suppression during spatial attention (Foster and Awh, 2019). Indeed, while the pattern of alpha-band activity tracks the spatial deployment of attention (Popov et al., 2019), this pattern does not seem to be consistently driven by the anticipated location of distractors (Noonan et al., 2016; van Moorselaar and Slagter, 2019). Furthermore, a body of behavioral studies have concluded that flexible allocation of distractor suppression is minimal or absent, and points to a slower, spatially fixed, mechanism that is learnt with experience (Ferrante et al., 2018; Wang and Theeuwes, 2018a, 2018b). This has led to the proposal that suppression of distractors and the facilitation of targets rely on different mechanisms (Noonan et al., 2016).

It remains unknown how target-facilitation and distractor-suppression are implemented at the neuronal level. In the past, alpha-band oscillations have been linked to gain control, i.e. the multiplicative modulation in response strength to a stimulus which is reflected by neuronal excitability (Jensen and Mazaheri, 2010; Pfurtscheller, 2001), where states of high alpha band power are associated with low cortical excitability (Romei et al., 2008). However, recent evidence from MEG studies using rapid invisible frequency tagging, which, like the steady-state visual evoked potential (SSVEP), is a proxy for neuronal visual excitability (Müller and Hillyard, 2000), suggests that the relation between neuronal excitability and alpha power may not hold when considering trial-by-trial fluctuations (Zhigalov and Jensen, 2020). Similarly, in a recent EEG study (Gundlach et al., 2020), early visual gain, as indexed by the SSVEP, did not show any dependency on fluctuations in alpha-band power in a selective attention task. These findings were complemented by an EEG study (Antonov et al., 2020) reporting increased target processing, as indexed by SSVEP, but no reduction in distractor processing, despite increased alpha band power contralateral to a distractor. This questions a direct link between alpha oscillations and stimulus gain; rather alpha oscillations might implement a gating mechanism just downstream to early sensory regions (Zhigalov and Jensen, 2020), modulating functional connectivity between regions, rather than the gain within the processing region (Jensen and Mazaheri, 2010).

In the current MEG study, we set out to investigate target facilitation and distractor suppression in the context of perceptual load and the role of alpha-band oscillations in sensory gain control versus downstream gating. By using an endogenously cued spatial attention task (Dugué et al., 2020) based on a study by Zhigalov et al. (2019), manipulating target load as well as distractor saliency, we aimed to uncover how target-load and distractor-saliency modulate posterior alpha oscillations as well as neuronal excitability. To assess neuronal excitability, and therewith gain control, we used *Rapid Invisible Frequency Tagging* ('RIFT', Zhigalov et al., 2019) applied to the target and distractor stimuli at different frequencies. The use of MEG allowed for localizing the neuronal sources of alpha oscillations (Hari and Salmelin, 1997) and the RIFT signal. In line with perceptual load theory, we hypothesized that if an increased load of the target drives the allocation of spatial attention,

this would be reflected by an increase in alpha band power contralateral to the distractor. Likewise, we expected RIFT power, reflecting neuronal excitability, to be reduced contralateral to the distractor in the case of high target load (Handy et al., 2001; Jacoby et al., 2012; Parks et al., 2011). We also hypothesized that, if spatial attention reflects the suppression of anticipated distractors, the saliency of the distractor is a driving factor. Increased distractor saliency should result in increased alpha-band power and a decrease in RIFT power contralateral to the distractor. These hypotheses, pre-registered at <https://osf.io/ha4vw/>, are not mutually exclusive. Note that we did not test the pre-registered hypothesis on phase coding in this study. However, as an additional point of exploration not covered in the pre-registration, recent findings have highlighted the possibility that alpha-band oscillations do not implement gain modulation but rather gating in downstream regions. We therefore also investigated that if alpha band oscillations implement stimulus gain, RIFT power should show the inverse pattern of modulations of alpha-band power. If, however, alpha oscillations implement gating downstream to early visual regions, these modulations may be independent (see Zhigalov and Jensen, 2020 for an extended discussion).

2. Materials and methods

2.1. Participants

N = 35 healthy volunteers (25 females, mean age 24.0 years, age range 18–37) participated in the study. Inclusion criteria: English proficient, aged 18–40, right-handed, no history of mental health, normal or corrected to normal vision. Exclusion criteria: history of epilepsy/seizures, medication, MRI contraindications, exceeding scanner weight limits. In line with the criteria set out in our pre-registration (<https://osf.io/ha4vw/>, 1/10/2018), five subjects were not entered into the main analysis due to failure of one or more of the criteria: Poor data quality due to MEG artifacts and/or subject (eye) movement, resulting in a rejection of more than 1/3 of the trials (4 rejections), marginal frequency tagging response (1 rejection). The study was approved by the science, technology, engineering and mathematics ethical review committee of the University of Birmingham. All subjects signed an informed consent before participation and were paid 15GBP per hour.

2.2. Stimuli and procedure

During MEG acquisition, subjects performed a cued change detection task (Fig. 1A) with face stimuli shown to work well with rapid invisible frequency tagging. To allow more space in the bottom half of the screen, the fixation was shifted upwards by 20% of the screen. While fixating, subjects were presented with two face stimuli (circular, 8° visual angle diameter, 7° eccentricity from fixation to stimulus center) in the left and right lower quadrant of the screen. After 1000 ms, a directional cue (presented for 350 ms) appeared at the location of the fixation spot (0.7° height and width) to instruct which hemifield is to be attended. After a variable 1000–2000 ms interval, a change occurred in the eyes of both face stimuli (the pupil shifted 25% of the eye width horizontally such that the gaze of the presented face stimuli shifted left or right). The direction of gaze change was varied randomly for either of the two presented faces. The faces with the new gaze were shown for 150 ms and subsequently disappeared. The subject's task was to identify the change in the cued face and respond as quickly as possible by button press using either the left (leftward gaze) or right (rightward gaze) index finger on a set of MEG compatible button boxes (NAtA technologies, Coquitlam, BC, Canada).

Perceptual load of the target was increased by embedding the target stimulus within a noise mask, as in Yi et al. (2004), where this has been shown to be an effective perceptual load manipulation. The same noise mask manipulation was used to orthogonally vary the saliency of the distractor stimulus, see Fig. 1C. To maintain the same distribution of

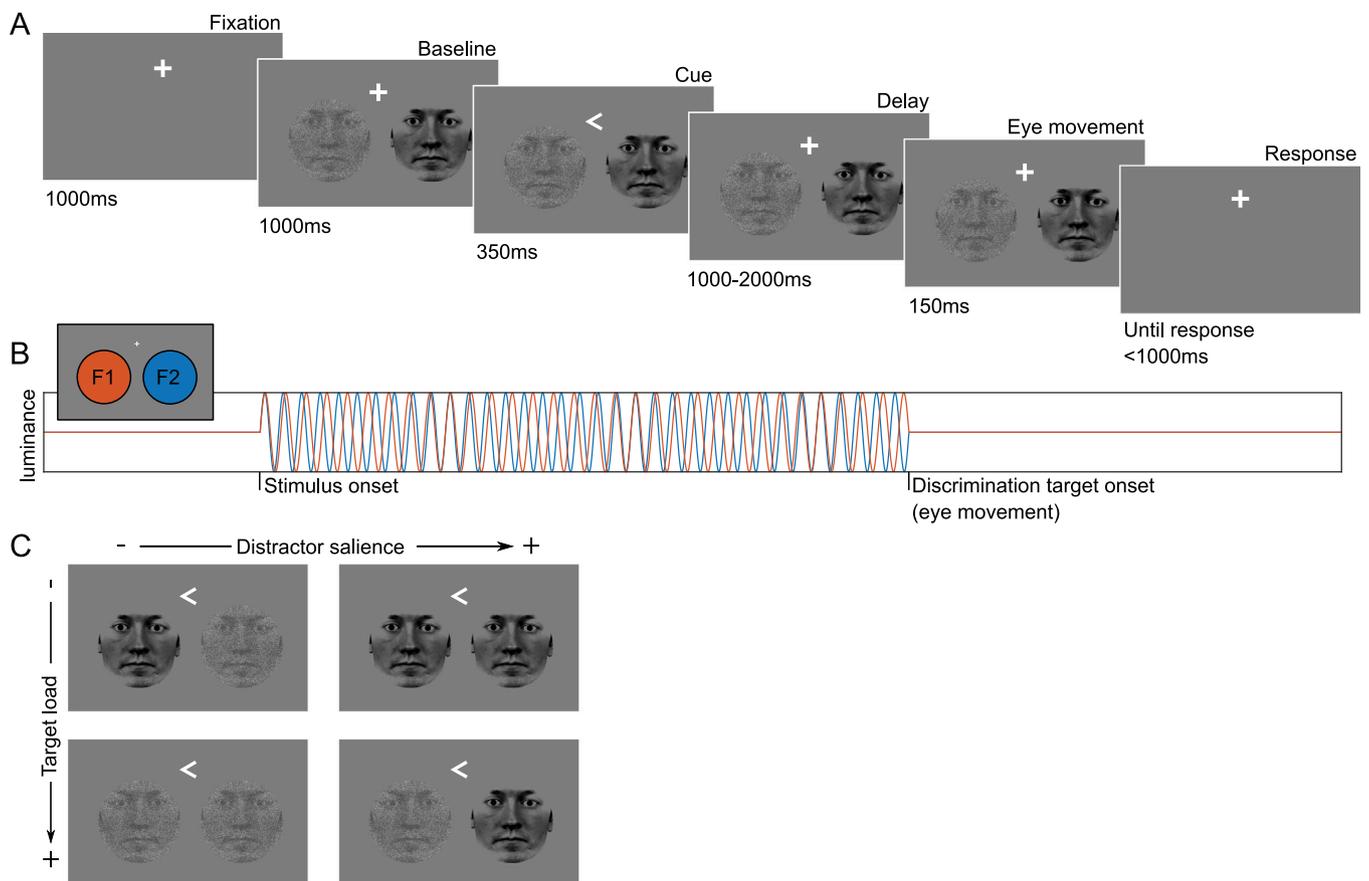


Fig. 1. Overview of the cued discrimination task. A) After fixation, subjects were presented with two face stimuli. A directional cue indicated the target stimulus. After a variable delay, a small eye movement occurred in the face stimuli. Subjects indicated the direction of the eye movement by button press. B) The luminance of the white portions of the stimuli flickered at 63 and 70 Hz (rapid invisible frequency tagging; RIFT), from stimulus onset until the eye movement change of the stimuli. C) The cued target stimuli were masked with noise or not (respectively high versus low perceptual target load). Likewise, the uncued distractors were masked with noise or not (respectively low versus high salient distractors). Noise levels were increased for illustration purposes and stimulus sizes are not to scale.

pixel intensities, and thus frequency tagging power, the noise mask was created by shuffling 50% of the face pixels to a random location. These manipulations allowed for modulating the target load as well as distractor saliency. Eight different face identities were used. The same faces were used in the left and right hemifield for every trial, although the left and right face were mirror symmetric from the fixation point, and the 8 identities were randomized across trials. Stimuli were presented using a Windows 10 computer running Matlab R2017a and Psychtoolbox 3 (Brainard, 1997). Stimuli were projected using a VPixx PROPixx projector (VPixx technologies, Saint-Bruno, Canada) in Quad RGB mode (1440 Hz) with an effective resolution of 960×540 pixels. A projection screen was placed 148 cm from the participant, spanning 71 cm, resulting in a visual angle of 25.6°. The left and right face stimuli were ‘frequency tagged’, i.e., the luminance of the all non-black parts of the face stimuli oscillated sinusoidally at a fixed frequency, see Fig. 1B. The tagging frequencies used were 63 Hz and 70 Hz, which are above the flicker fusion threshold, and the ‘flicker’ was thus effectively invisible to the subject and, importantly, did not create an imbalance in stimulus salience.

2.3. Data acquisition

The ongoing MEG data were recorded using the TRIUX™ system from MEGIN (MEGIN, Stockholm, Sweden) with subjects in upright position. This system has 102 magnetometers and 204 planar gradiometers. These are placed at 102 locations, each having one magnetometer and a set of two orthogonal gradiometers. The vertical EOG, eye tracker data (EyeLink 1000, SR research Ltd., Ottawa, Canada) and

polhemus (Polhemus, Colchester, USA) scalp surface data were acquired together with the MEG data. For accurate source localization, an anatomical T1 MRI scan was acquired for each participant (Philips Achieva 3T, 23 subjects, Siemens Magnetom Prisma 3T, 10 subjects) if not available from a previous source. The MEG data was lowpass filtered at 330 Hz, sampled at 1000 Hz and stored for offline analysis. Subjects completed 2 blocks of 256 trials, 512 trials total, lasting approximately 45 min excluding short breaks or 60 min including breaks.

2.4. Data analysis

Reaction times (RTs) were obtained from the subjects’ button box responses. RTs shorter than 100 ms or longer than 1000 ms were excluded, as well as trials with eye movements (inspected using EyeLink eye tracker data) larger than 3° . Behavioral data from rejected MEG data trials was rejected to keep consistency between the behavioral and electrophysiological data. All data were sorted by condition (target load condition \times distractor saliency) and averaged per participant. To assess the effect of distractor interference per target load condition, the distractor interference index (DI) was calculated as:

$$DI_{\text{low target load}} = RT(\text{low load})_{\text{salient distractor}} - RT(\text{low load})_{\text{non-salient distractor}}$$

$$DI_{\text{high target load}} = RT(\text{high load})_{\text{salient distractor}} - RT(\text{high load})_{\text{non-salient distractor}}$$

MEG data were analyzed using the Fieldtrip software package (Oostenveld et al., 2011) and custom scripts in the Matlab environment. In short, Raw MEG sensor data were demeaned and high-pass filtered at 1 Hz. For the cue-locked analysis, data were segmented in 3.3 s epochs,

with 2.3 s prior and 1 s after cue offset. For discrimination onset-locked analysis, data were segmented 4 s epochs, with 3 s prior and 1 s after onset of the discrimination target (eye movement of the face stimuli). Independent component analysis (ICA), using the 'runica' algorithm was used to 'project out' artefacts after removal of trials with gross incidental artifacts (e.g. jumps) and noisy sensors (sustained gross artifacts) manually. Component removal was restricted to ocular, cardiac and muscle artefacts. After ICA clean up, residual artifacts were identified by visual inspection. Trials containing clear residual artifacts and deviations from fixation larger than 3° (inspected using EyeLink eye tracker data) and eye blinks (inspected using vertical EOG) in the critical – 1 to 1 s interval relative to the cue offset, or the – 1.5 to 0 s interval relative to the discrimination target onset were rejected. On average 13.7% (*SD* 8.0) of the trials were rejected. Removed sensors were interpolated using a weighted neighbor estimate.

For *frequency domain analysis*, data were analyzed separately for the high frequency range (50–100 Hz) and the low frequency range. For the high frequencies, power modulations were estimated using a fixed 500 ms sliding time-window, with steps of 1 ms and a 4 s zero padding to obtain integer frequency bins, resulting in a frequency smoothing of ~ 3 Hz. A single taper approach was taken to avoid spectral smearing of the narrow frequency of interest (the tagging frequencies). Power was calculated using FFT after the application for a 500 ms Hanning taper. For the lower frequencies, a 3-cycle time-window (e.g. 300 ms for 10 Hz) was used with 1 ms steps and next power of 2 zero padding for efficiency, resulting in a frequency smoothing of ~ 4 –6.5 Hz in the alpha range (8–13 Hz). After frequency domain analysis, the planar bidirectional gradiometers were summed. From the resultant spectral estimates, *power time courses* were extracted for every subject and condition from a sensor cluster. For both alpha range and RIFT time courses, the four sensors that showed the strongest attentional modulation at group level (i.e. attention left minus right after cue offset) were chosen. Time courses were normalized using a relative baseline based on the pre-cue baseline 350 ms after stimulus onset until 400 ms before cue offset (600 ms total) per hemifield and frequency.

Statistical analyses were performed with the SPSS statistical software package (IBM) and JASP (JASP team). To test for the behavioral effect of perceptual load, *behavioral data* (reaction times) were entered into an ANOVA with factors 'target load' and 'distractor salience'. The same analyses were conducted for the mean alpha band power extracted from the sensors contralateral to targets and distractors, 500 ms after cue onset until the earliest time at which the discrimination could appear (1350 ms after cue onset). This interval was chosen to avoid contamination from evoked responses from the cue and discrimination stimulus, which could occur in the 1350–2350 ms interval. To support evidence for the null hypothesis in case of non-significant findings, the Bayesian equivalent analysis was performed to provide Bayes factors in favor of the null hypothesis (BF_{01}) using matched models (Jarosz and Wiley, 2014; van Doorn et al., 2021).

To establish a link between behavior and electrophysiology, correlations between the behavioral distractor interference (DI) and RIFT/alpha power were calculated using the same time window as the main ANOVA analysis (500–1350 ms after cue onset), across subjects, using Spearman rank correlation.

Source localization was performed to identify the regions producing the power modulations. In each subject, the scalp surface obtained from the Polhemus digitization was combined with the MRI T1 scan to obtain an individual realistic single-shell head model. These were subsequently used for source estimation using the dynamical imaging of coherent sources (DICS) beamformer approach (Gross et al., 2001). The brain volume was divided into a 5 mm grid. Oscillatory activity of interest was estimated using DPSS tapers with a frequency smoothing of 3 Hz and a center frequency of 10.5 Hz for the alpha band and 63/70 Hz with 2 Hz smoothing for RIFT. All source analyzes focused on the same time window as the main ANOVA: 500–1350 ms after cue offset. A common filter was estimated by pooling across all conditions that were

contrasted. For alpha band sources, contrasts were created by subtracting the power in the time window of interest for both conditions and normalizing by the sum of power for these conditions. For RIFT sources, a contrast was first made with the same pre-cue baseline period as in the time-course analysis, 650 ms after stimulus onset until 400 ms before cue offset. Contrasts of interest were subsequently created from the baselined source estimates. For visualization, contrasts for attention right were mirrored along the y-axis, normalized to non-flipped MNI space and averaged with the attention left condition.

3. Results

3.1. Behavior

The behavioral effect of the perceptual load was reflected in the subjects' reaction times (Fig. 2A). A repeated measures ANOVA on the reaction times with factors 'target load' and 'distractor salience' revealed a significant main effect of 'target load' ($F_{(1,29)} = 132.1$, $p < .001$, *partial* $\eta^2 = .82$), demonstrating that the participants responded slower to high compared to low target loads, as would be expected with a higher level of noise on the target stimulus. There was also a main effect of 'distractor salience' ($F_{(1,29)} = 6.7$, $p = .015$, *partial* $\eta^2 = .19$) meaning that participants responded slower to the target in the presence of a salient compared to a noisy distractor. This shows that the salient distractors were indeed effective in interfering with performance. Critically, a significant interaction was found between 'target load' and 'distractor salience' ($F_{(1,29)} = 12.9$, $p = .001$, *partial* $\eta^2 = .31$). This is explained by slower target-responses in the presence of salient compared to noisy distractors ($M_{low} = 15.3$ ms *SEM* = 3.3 ms, $M_{high} = -4.07$ ms *SEM* = 3.6 ms, two-tailed paired samples t-test $t = 4.7$, $p < .001$), but only when the target load was low (Fig. 2B). When the target load was high, we observed no effect of distractor salience ($p > .27$, $BF_{01} = 2.9$, indicating anecdotal to substantial evidence for the null hypothesis). Thus, distractor interference was eliminated in conditions of high target load, as predicted by perceptual load theory.

3.2. Effects of spatial cuing

3.2.1. Alpha band power

To test the effects of directed attention and select sensors for the subsequent analysis, we compared trials where attention was cued to the left with trials cued to the right hemifield (Fig. 3A). The time-frequency representations of power modulations as well as the topographic representation show the typical hemispheric lateralization of alpha power (Kelly et al., 2006; Worden et al., 2000), i.e., relatively lower alpha power contralateral to the target and higher power contralateral to the distractor. The marked locations in the topographic plot indicate the selected sensors of interest that showed the largest attentional modulation. Fig. 3B shows the time-course of the alpha power relative to a pre-cue baseline, locked to the cue (left), and discrimination target onset (right). Importantly, the alpha power increased contralateral to the distractor, but not the target.

3.2.2. Rapid invisible frequency tagging (RIFT)

Both target and distractor stimuli flickered at either 63 or 70 Hz, i.e. were 'frequency tagged' (Fig. 1B). As can be seen in Fig. 3C–D, RIFT power related to the target showed a sustained increase after cue onset relative to distractor power, indicating that RIFT power was sensitive to attentional modulations. Unlike alpha band power, attentional selection was reflected in increased RIFT power and can thus be considered a proxy for neuronal excitability associated with attentional gain. Note that we found a general decrease of RIFT power over time, regardless of condition or direction of attention, which is why the RIFT power after cue onset is generally below baseline.

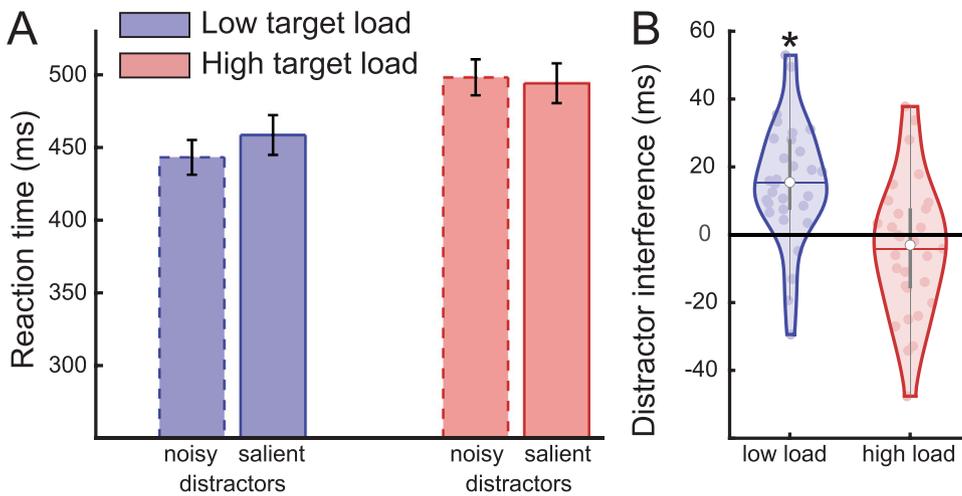


Fig. 2. Behavioral results (reaction times to targets) of the discrimination task. (A) When considered per condition, participants responded slower to high (red) compared to lower (blue) target loads. Error bars denote the standard error of the mean (SEM). (B) Distractor interference (salient compared to noisy distractors) was significant when the target load was low, but not when the target load was high. These findings are consistent with perceptual load theory. The mean is denoted by the horizontal line, the median is denoted by the white dot and interquartile range by the grey vertical bar.

3.3. Effects of perceptual load and distractor salience

By increasing the load of the target, distractor interference was abolished (see Fig. 2B). Next, we related this behavioral finding to neural inhibition (as reflected by alpha amplitude) and excitability (as measured with frequency tagging amplitude). For the alpha band we hypothesized that attentional modulations may be implemented by either a stronger suppression of the distractor with high target load, as reflected by increased alpha-band power contralateral to the *distractor*, or increased resources allocated to the target, as reflected by decreased alpha band power contralateral to the *target*, or both. RIFT power, reflecting neuronal excitability or gain, was hypothesized to show the opposite pattern to alpha band power, with target load increases being associated with decreased RIFT related to distractor processing, increased RIFT related to target processing or both. We also tested the hypothesis that distractor salience drives the distractor suppression effects.

3.3.1. Alpha band power

Alpha band power contralateral to the target. An ANOVA was performed on target-related alpha band power in the 500–1350 ms interval after cue offset with factors ‘target load’ and ‘distractor salience’. The first 500 ms post-cue data were discarded to avoid the evoked response of the cue. There were no significant main effects of ‘target load’ ($F_{(1,29)} = 2.44, p = .13, BF_{01} = 1.5$) or ‘distractor salience’ ($F_{(1,29)} = 0.68, p = .42, BF_{01} = 3.9$) (Fig. 4A, left) and no interaction ($F_{(1,29)} = 0.26, p = .61, BF_{01} = 3.4$). Bayes factors, calculated to establish the level of evidence in favor of the null hypothesis, provided substantial evidence for the null hypothesis for the factors ‘distractor salience’ and the interaction while providing only anecdotal evidence for the null hypothesis for the load factor. Thus, there is substantial evidence against distractor salience and its interaction with load modulating alpha band power contralateral to the target stimulus. However, due to the weak evidence against the load factor, we cannot exclude perceptual load as a factor in modulating alpha band power contralateral to the target.

Alpha band power contralateral to the distractor. The same 2 by 2 ANOVA applied to the alpha band power contralateral to the distractor revealed a significant interaction between ‘target load’ and ‘distractor salience’ for alpha band power contralateral to the distractor ($F_{(1,29)} = 12.6, p = .001, \text{partial } \eta^2 = .30$) (see Fig. 4A, right). We hypothesized that the effect may be driven by the load of the target. Indeed, post hoc tests revealed a significant increase in alpha power with increased target load when the distractors were salient (two-tailed paired samples t-test, $t = -2.97, p = .006$, significant with Bonferroni corrected $\alpha = 0.0125$) but not when distractors were noisy (two-tailed paired samples t-test, $t = 1.14, p = .27, BF_{01} = 2.9$), see Figs. 4B and 4D for this effect over

time. This shows that the perceptual load of the target indeed drove alpha band power increases contralateral to the distractor, but only when the distractor was salient. Source modeling (Fig. 4E) localized this load-driven alpha band increase in the extrastriate cortical areas (peak MNI coordinate: $x: -36, y: -84, z: 8$, BA 18/19), extending into the fusiform gyrus (BA 37). The warm color denotes the sources reflecting the increase in alpha power (high versus low targets) contralateral to the distractor.

Next, we asked if the target load-driven modulation in distractor-alpha power predicted behavior. To this end, we consider behavioral interference, i.e. the increase in reaction time caused by an increase in distractor salience relative to the modulation of alpha-band power contralateral to the distractor. The modulation of alpha power contralateral to the distractor due to increased target load showed a significant positive correlation ($r_{\text{spearman}} = 0.37, p = .048$) with the behavioral interference caused by the distractor (Fig. 4F). This positive correlation demonstrates that subjects with larger distractor interference effects in the low target load conditions had a larger difference in distractor-alpha power when comparing high and low target-loads. Thus, a greater increase in alpha power contralateral to the distractor with high perceptual load may be required to suppress a more salient distractor that produces larger behavioral interference in conditions of low perceptual load; this is also consistent with the target load effects found on alpha power only for the salient (but not for the noise masked) distractors.

Our results show that attentional modulations are driven by the load of the target. However, as hypothesized and evident from the omnibus ANOVA, the salience of the distractor could drive alpha-band modulations. When target load was high, post-hoc paired samples tests showed that alpha band power for the distractor was significantly increased when distractors were salient relative to noisy (two-tailed paired samples t-test, $t = 3.13, p = .004 < \alpha = 0.0125$). This effect, however, may not occur with low target load (two-tailed paired samples t-test, $t = -1.81, p = .081 > \alpha = 0.0125, BF_{01} = 1.2$), see Fig. 4C. Fig. 4G shows the time-course of alpha-band power contralateral to distractors with high target load. A clear increase in alpha band power was observed when distractors were salient, but only when the target load was high. However, these modulations of alpha power did not correlate with the observed behavioral effect (distractor interference, $r_{\text{spearman}} = 0.07, p = .72$). This suggests that the difference in alpha power between noisy and salient distractors, although significant, was of limited behavioral relevance in the light of our paradigm. This may be due to the inability of the noisy distractor to cause interference, making the level of associated alpha power, and suppression, less relevant.

In summary, when the perceptual load increased, alpha band power contralateral to the distractor increased, reducing behavioral distractor interference seen with low perceptual load. The salience of the distractor

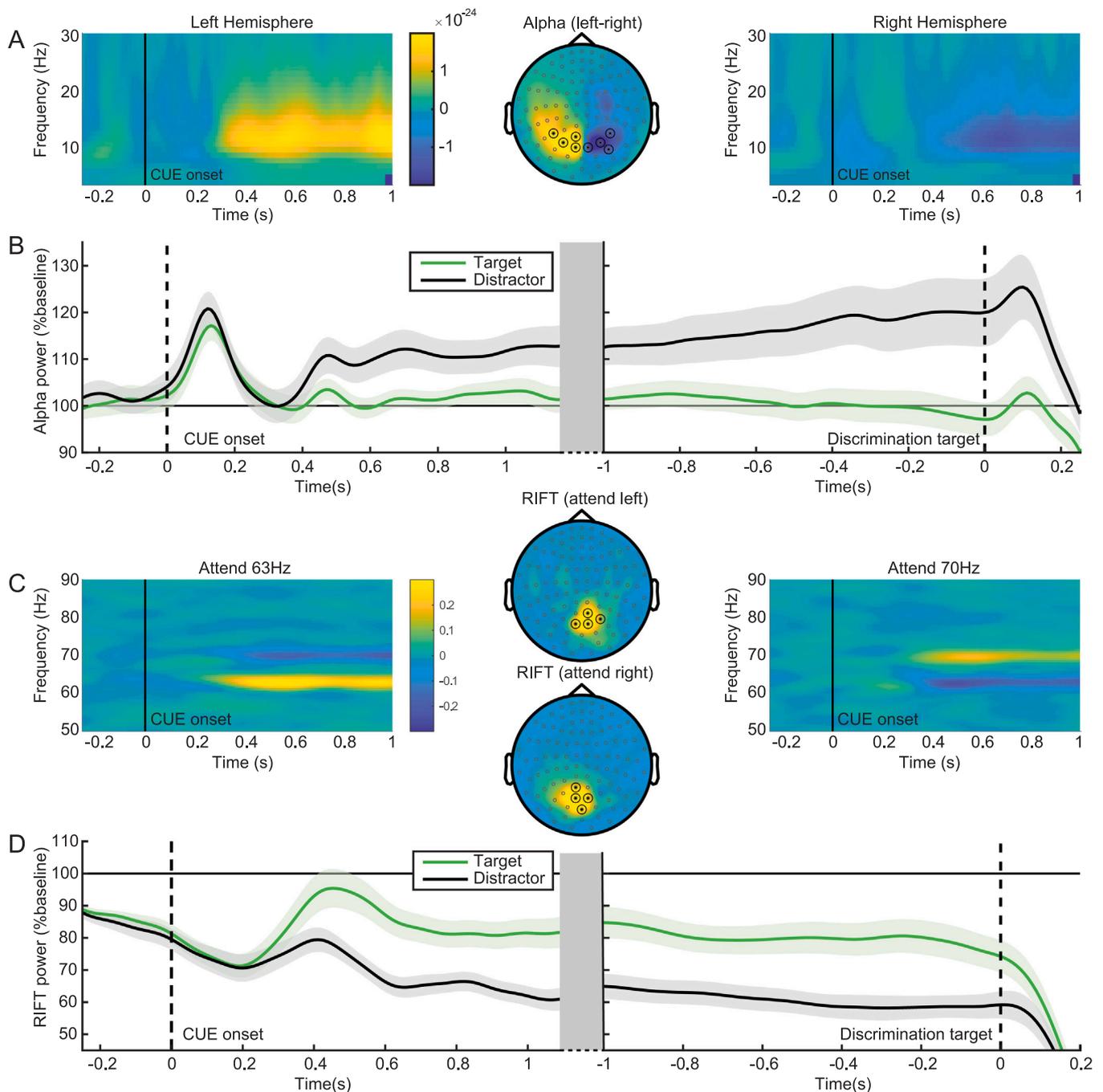
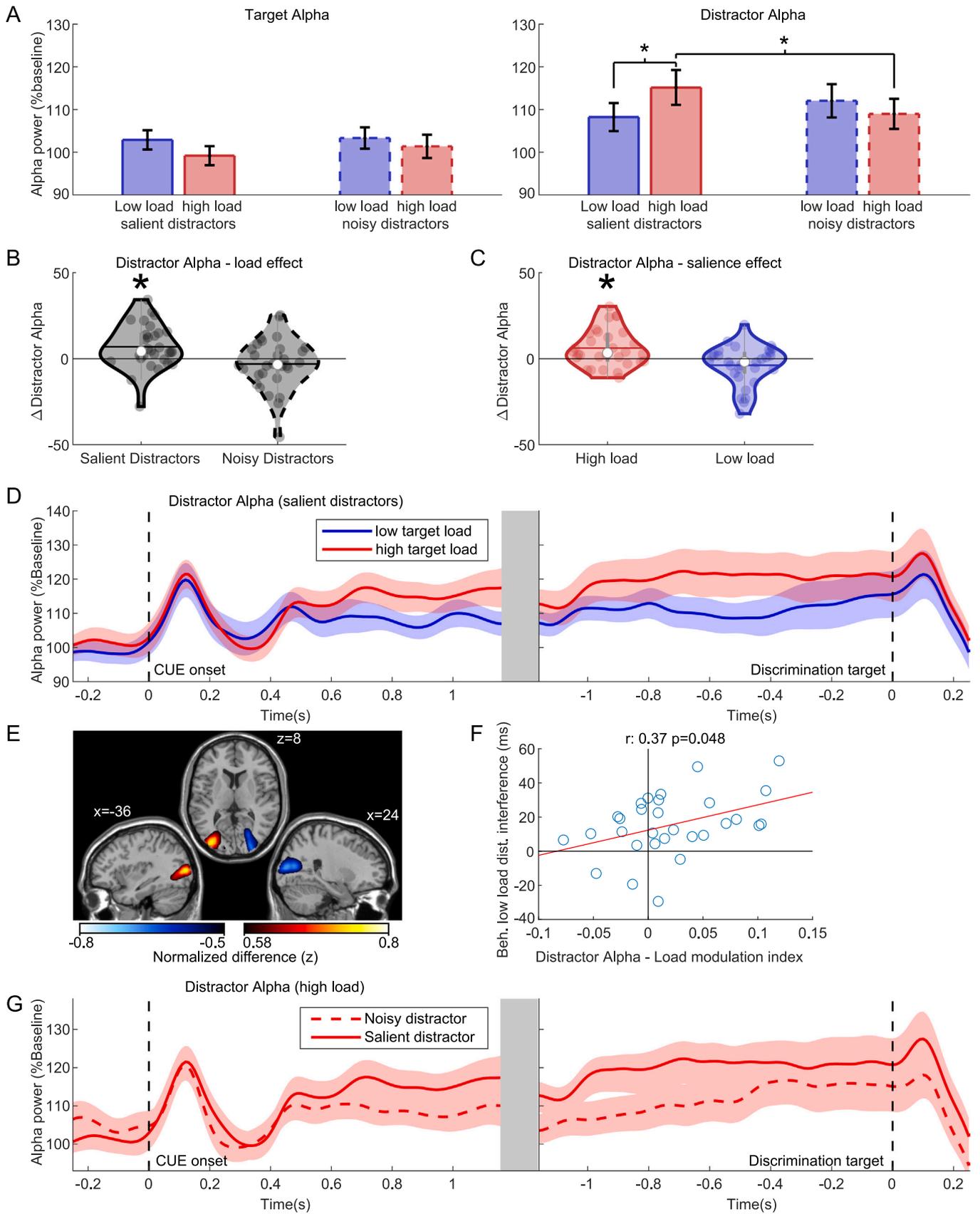


Fig. 3. Attentional modulation and sensor selection. A) Alpha band (8–13 Hz) modulations were quantified by considering the left versus right directional cues. The modulations in time-frequency representation of power showed a sustained alpha power increase ipsi-laterally to the cued hemifield (left) and a power decrease contralaterally (right). The topographic map demonstrated a power modulation over parieto-occipital areas; the marked location indicates the sensors used in the subsequent analyses. B) Time-courses of the alpha band power relative to pre-cue baseline contralateral to target (green) and distractor (black). We show this with respect to Cue onset (left) and discrimination target onset (right). Shaded areas denote the standard error of the mean (SEM). C) Rapid invisible frequency tagging (RIFT) power modulations. The time-frequency representations show an increase in power contralateral to the target and a decrease contralateral to the distractor. The target was flickering at 63 Hz (left) and 70 Hz (right). The topographic plot (center) shows these modulations to be over central occipital areas. The marked location indicates the sensors used in the subsequent analyses. D) Time-courses of the RIFT power relative to pre-cue baseline for target frequencies (green) and distractor frequencies (black) with respect to Cue onset (left) and discrimination target onset (right). Shaded areas denote the standard error of the mean (SEM).

is important, as this perceptual load effect only occurred with salient distractors. High salience of the distractor also increased alpha band power associated with the distractor. However, the alpha band power increased due to perceptual load correlates with behavior, whereas the distractor salience did not. This indicates that perceptual load may be the key driving factor of alpha band modulations related to the distractor, whereas sufficient distractor salience is a pre-condition.

3.3.2. Rapid invisible frequency tagging

RIFT target power associated with the target. As for the alpha band, an ANOVA was performed on the RIFT power averaged in the 500–1350 ms interval after cue onset across all conditions. Analysis of RIFT-power associated with the target (see Fig. 5A), revealed a significant *main effect* of ‘target load’ ($F_{(1,29)} = 27.3, p < .001, \text{partial } \eta^2 = .49$), where overall RIFT power was stronger with high ($M = 0.87, \text{SEM} = 0.046$)



(caption on next page)

Fig. 4. Effects of target load and distractor salience in the alpha band. A) Average alpha band power per condition, contralateral to target (left) and distractor (right) for high (red) and low (blue) target load conditions with noisy (dashed) or salient (solid) distractors 500–1350 ms after cue onset. Error bars denote the standard error of the mean (SEM). B) The effect of target load (high-low target load) for salient and noisy distractors. The mean is denoted by the horizontal line, the median is denoted by the white dot and interquartile range by the grey vertical bar. C) The effect of distractor salience (high-low salience) with high and low target load. D) Distractor-alpha power time courses for high (red) and low (blue) target load locked to cue onset (left) and discrimination target onset (right). Importantly the distractor-alpha was larger for high compared to low target-loads, consistent with the hypothesis that alpha power implements the distractor suppression according to perceptual load theory. Shaded areas denote the standard error of the mean (SEM). E) Source modeling of the distractor-alpha modulation of high versus low target loads (cue-locked, 500–1350 ms) collapsed over left and right attention displayed as attention to the left (left hemisphere is contralateral to distractor). Plot shows top and bottom 1% values in the grid-points. F) Correlation between average load modulation index (distractor alpha (high load – low load)/high load + low load), cue-locked, 500–1350 ms after cue onset) of distractor alpha and behavioral distractor interference ($RT_{noisy} - RT_{salient}$) under low target load. This shows that the larger the difference in distractor alpha power (i.e. lower alpha power with low load), the larger the behavioral distractor interference. G) Distractor alpha power time courses for salient and noisy distractors relative to cue onset (left) and discrimination target onset (right) under high target load. Shaded areas denote the standard error of the mean (SEM).

compared to low target load ($M = 0.80$, $SEM = 0.043$). Additionally, there was a significant interaction between ‘target load’ and ‘distractor salience’ ($F_{(1,29)} = 4.44$, $p = .044$, $partial \eta^2 = .13$) reflecting a stronger effect of target load in the presence of salient distractors (two-tailed paired samples t-test, $t = -7.83$, $p < .001 < \alpha = 0.0125$ Bonferroni corrected) compared to noisy distractors (two-tailed paired samples t-test, $t = -2.37$, $p < .025 > \alpha = 0.0125$); see Fig. 5B. Thus, with salient distractors, target RIFT power with high load was higher than under low load, as can be seen in Fig. 5A and B. This shows that neuronal excitability associated with the target processing increased with target load. Alternatively, this may point to decreased target processing due to distractor interference when the load was low and distractors were salient. The time-course of target RIFT for high and low target load, shown in Fig. 5C, clearly shows a higher RIFT power with high target load, which was especially pronounced shortly following cue offset (0.35 s). Source modeling revealed this increase to be very focal and generated in the primary visual cortex (peak MNI coordinate: x:8, y:-90, z:6, BA 17), extending only slightly beyond (BA18); see Fig. 5D. Note that, due to the very focal nature of the source, the top 1% values may contain artifactual clusters, such as the frontal cluster. While not significant, there was a trend towards a negative correlation between the target RIFT distractor effect (i.e., the difference in target power with salient versus noisy distractors) and the behavioral distractor interference with low target load which was absent with high target load (Fig. 5E). This may suggest that the target RIFT power was reduced when salient distractors were present when the target load was low, but the distractors have no effect when the target load was high, as predicted by perceptual load theory.

Testing for effects of distractor salience yielded no significant effects (two-tailed paired samples t-test, low load $t = -1.99$, $p = .057 > \alpha = 0.0125$, $BF_{01} = 0.9$; high load $t = 0.71$, $p = .48 > \alpha = 0.0125$, $BF_{01} = 4.1$), showing substantial evidence that distractor salience did not directly influence input gain of target processing with high load, but involvement with low load could not be precluded. Thus, this pattern strengthens the existing effect of perceptual load.

RIFT power associated with the distractor. Analysis of RIFT power associated with the distractor (Fig. 6A) yielded a significant main effect of ‘distractor salience’ ($F_{(1,29)} = 5.67$, $p = .024$, $partial \eta^2 = .16$), where RIFT power overall was stronger for noisy distractors ($M = 0.67$, $SEM = 0.029$) than salient distractors ($M = 0.64$, $SEM = 0.032$). Additionally, there was a significant main effect of ‘target load’ ($F_{(1,29)} = 4.63$, $p = .04$, $partial \eta^2 = .14$), where RIFT power was higher when target load was high ($M = 0.67$, $SEM = 0.027$) compared to low ($M = 0.64$, $SEM = 0.033$), possibly indicating a generic gain increase when target load was high, as this also occurs for the target. Finally, we observed a significant interaction between ‘target load’ and ‘distractor salience’ ($F_{(1,29)} = 15.17$, $p < .001$, $partial \eta^2 = .35$).

Testing for effects of target load on distractor RIFT revealed a significant effect of target load with noisy distractors (two-tailed paired samples t-test, $t = -7.24$, $p < .001$, $\alpha = 0.0125$ Bonferroni corrected) but not with salient distractors (two-tailed paired samples t-test,

$t = 0.88$, $p = .39 > \alpha = 0.0125$, $BF_{01} = 3.6$). When distractors were noisy, distractor RIFT power increased with higher target load; see Figs. 6B and 6E for the time-courses. Here, no significant correlations were found with respect to behavioral distractor interference with both low and high target load (all $p > .5$). As can be seen in Fig. 6A, the distractor RIFT effects seemed to be driven by an increase in RIFT power when load was high and distractors noisy. This may be due to a general increase in RIFT power with high target load when distractors did not need to be suppressed, as the same effect is present for target RIFT power with noisy distractors, although this effect did not survive multiple comparisons correction (low load: $M = 0.82$, high load $M = 0.87$, two-tailed paired samples t-test $t = -2.37$, $p = .025$ uncorrected).

Testing for distractor salience effects revealed significant difference between noisy and salient distractors when the target load was high (two-tailed paired samples t-test, $t = 4.80$, $p < .001 < \alpha = .0125$), but not when target load was low (two-tailed paired samples t-test, $t = 0.71$, $p = [0.48TS8201] > \alpha = .0125$, $BF_{01} = 4.1$), see Figs. 6C and 6F the time-course. Thus, distractor power was modulated by saliency, with reduced RIFT power for salient distractors, but only when the target load was high. This may indicate that salient distractors were more suppressed than noisy distractors, as also evidenced by increased alpha power for salient distractors in the same condition. Here, no behavioral correlations were observed ($r_{spearman} = -0.08$, $p = [0.69]$). Source modeling indicates that this modulation occurred centrally, in early visual cortex (MNI: x:-10, y:-82, z:10, BA 17), see Fig. 6D; cooler colors. For comparison, the salience-driven alpha modulation, depicted by the warmer colors, has a source more lateral in early visual cortex (BA 17, MNI x:-10, y:-98, z:8). Interestingly, although the modulation of RIFT and alpha band power both occurred in the early visual cortex, the sources do not seem to overlap, where the alpha band modulation is located slightly more lateral and posterior.

4. Discussion

Our results show that increasing the perceptual load of a target stimulus increases alpha band power contralateral to distractors. This finding is aligned with predictions from perceptual load theory in the sense that the alpha power increase likely reflects distractor suppression with increased target load. In further support of the theory, the alpha power increase contralateral to the distractor as a function of target load predicted behavioral measures reflecting the ability to reduce distractor interference, i.e., lower load-related increase in alpha band power contralateral to the distractor was predictive of larger distractor interference effects on reaction times. Rapid invisible frequency tagging (RIFT) increased contralateral to targets with high perceptual loads, suggesting increased stimulus gain. Increasing the salience of the distractor stimulus also increased distractor related alpha band power and decreased RIFT associated with the distractor, but only when the target load was high. We did not observe an inverse pattern between RIFT power and alpha modulations, suggesting that alpha power may not implement gain control. Furthermore, source modeling showed that both RIFT and alpha power modulations originate from visual cortex,

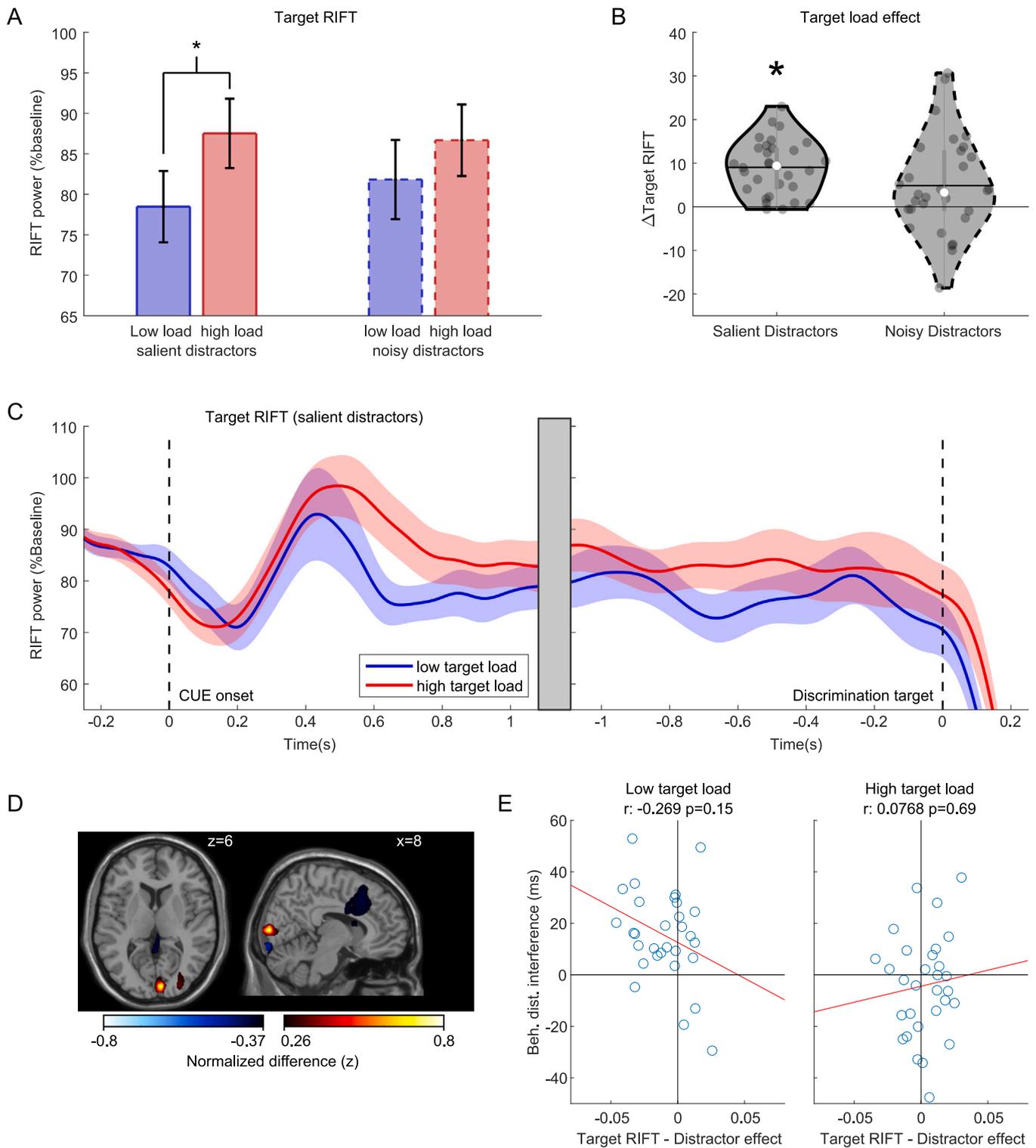


Fig. 5. Load effects in RIFT power. A) Target RIFT power per condition. Average RIFT power related to the frequencies of the target for high (red) and low (blue) target load conditions with noisy (dashed) or salient (solid) distractors 500–1350 ms after cue onset. Error bars denote standard error of the mean (SEM). B) Highlight of the significant effect of target load in target RIFT power (high-low target load) for salient and noisy distractors. The mean is denoted by the horizontal line, the median is denoted by the white dot and interquartile range by the grey vertical bar. C) Target RIFT power time courses for high (red) and low (blue) target load relative to cue onset (left) and discrimination target onset (right). Importantly the target RIFT power was elevated for high compared to low target-loads which is consistent with an increase in neuronal excitability in the target with an increased perceptual load. Shaded areas denote the standard error of the mean (SEM). D) Source modelling of the relative baseline target-RIFT modulation of high versus low target loads (cue-locked, 500–1350 ms, shown in B) collapsed over left and right attention, displayed as attention to the left (right hemisphere is contralateral to target). Plot shows top and bottom 1% of the values in the grid-points. E) Correlations between average distractor effect $(\text{Target RIFT}_{\text{salient}} - \text{Target RIFT}_{\text{noisy}}) / (\text{Target RIFT}_{\text{salient}} + \text{Target RIFT}_{\text{noisy}})$ cue-locked, (500–1350 ms after cue onset) and behavioral distractor interference $(\text{RT}_{\text{noisy}} - \text{RT}_{\text{salient}})$ of target RIFT with respect to low (left) and high (right) target load.

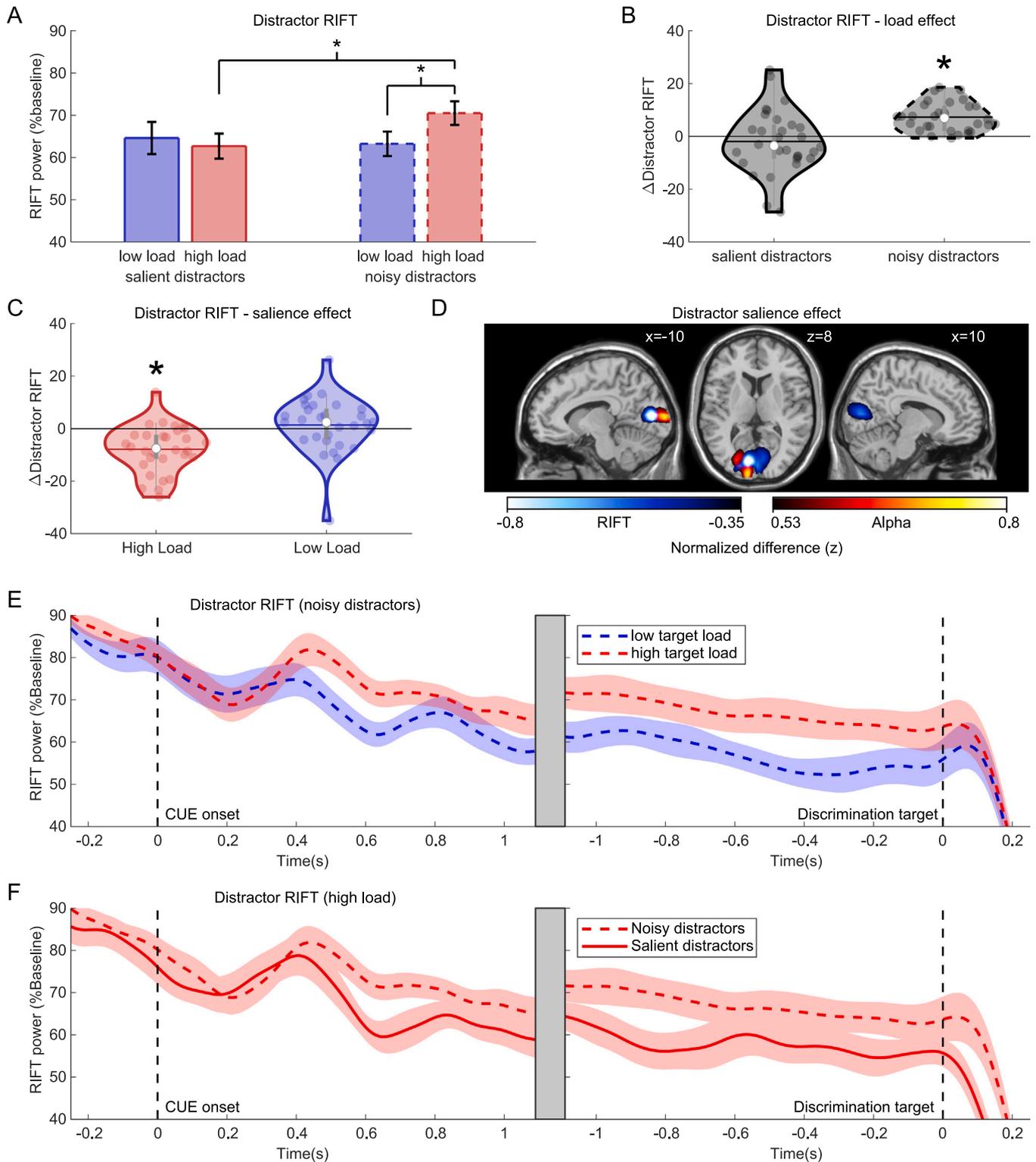


Fig. 6. Effects in distractor RIFT. **A**) Average distractor RIFT power related to the target for high (red) and low (blue) target load conditions with noisy (dashed) or salient (solid) distractors 500–1350 ms after cue onset. Error bars denote standard error of the mean (SEM). **B**) Effect of target load (high-low target load) for salient and noisy distractors. The mean is denoted by the horizontal line, the median is denoted by the white dot and interquartile range by the grey vertical bar. **C**) The effect of distractor salience (high-low salience) for high and low target load. **D**) Source modelling of the salient minus noisy distractor difference under high load 500–1350 ms after cue onset. Cooler colors denote the decrease in RIFT power, while warmer colors show the alpha power increase. Contrasts were collapsed over left and right attention and displayed as attention to the left (left hemisphere is contralateral to distractor). Plot shows top and bottom 1% of the values in the grid-points. **E**) Noisy distractors-RIFT power time courses with high and low target load relative to cue onset (left) and discrimination target onset (right) under high target load. Shaded areas denote the standard error of the mean (SEM). **F**) Distractor RIFT power time courses for salient and noisy distractors relative to cue onset (left) and discrimination target onset (right) under high target load. Shaded areas denote the standard error of the mean (SEM).

but sources do not overlap, indicating a distinct cortical origin. Taken together, this indicates that attentional resource allocation driven by the *target* serves to modulate the brain activity associated with both target and distractor processing. This modulation seems to be associated with two complementary mechanisms: a gain increase of the target, as indexed by RIFT, and an increase of distractor alpha band power, possibly implementing gating at a later stage.

4.1. Perceptual load results in increased distractor suppression reflected by increased alpha band activity

The results are consistent with the framework of perceptual load theory (Lavie, 1995). In particular, we showed that when the perceptual load of the target is increased, alpha band power contralateral to the distractor increased, as well as RIFT related to the target. Thus, the perceptual load of the *target* dictates the resource allocation supporting the task. Behavioral results demonstrated a significant interference effect on reaction times produced by salient compared to noisy distractors. Importantly, this interference effect interacted with perceptual load: high load eliminated the salient distractor interference effect as predicted by load theory. The electrophysiological findings similarly indicated an increase in alpha band power contralateral to the distractor under high target load which occurred when the distractor was salient, but not when it was noisy. Taken together this pattern suggests that the alpha power increase under high load results in the suppression of interfering (salient) distractions. The positive correlation, between the strength of modulation of distractor alpha power due to increased target load and the level of behavioral interference caused by the salient (versus noise-masked) distractors, further supports this conclusion. Given the proposed inhibitory role of alpha-band oscillations (Jensen and Mazaheri, 2010; Jia et al., 2019; Klimesch et al., 2007; Vanni et al., 1997), this suggests a reduction or suppression of the resources available for distractor processing under high target load. It is debated whether the pattern of alpha lateralization with cued attention is due to an alpha power decrease contralateral to target (e.g. Ikkai et al., 2016) or an increase contralateral to distractor (e.g. Kelly et al., 2006; Worden et al., 2000). In our study, we found only a modest decrease in alpha band power contralateral to target, which did not reach significance, and a significant increase contralateral to the distractor. Thus, resource allocation to the target (consistent with increased target RIFT power) may be assisted, or even occur, by reducing resources for distracting stimuli, abolishing interference with a high perceptual load. This is in line with an fMRI study by Torralbo et al. (2016) that measured BOLD responses under high and low perceptual load. The authors showed increased BOLD responses in early visual cortex to target stimuli with increased load. Importantly, BOLD responses were decreased for irrelevant distractor stimuli. BOLD responses are typically negatively correlated with alpha-band power (Goldman et al., 2002; Pang and Robinson, 2018; Scheeringa et al., 2009). Similarly, using spectroscopy, Bruckmaier et al. (2020) recently showed increased cellular metabolism for attended target and a reduction for unattended stimuli with increased perceptual load. Our current results can thus be taken to support the idea that the previously observed resource reduction for the distractor due to increased target load is supported, or even implemented, by an increase in alpha-band power. Similarly, the allocation of resources related to an increase in target load, may be implemented by an increase in early visual gain, as indexed by the target-related RIFT power.

4.2. The effect of distractor salience

Our results show that suppression of distractor stimuli only occurred when these stimuli were salient and interfering and task demands (load) were high. This is somewhat expected, given that distractor suppression is thought to be an important part of maintaining task performance (Gaspelin and Luck, 2018; Hickey et al., 2019; Jensen and Mazaheri, 2010). However, it has recently been questioned to what extent

distractor anticipation and processing results in an alpha power increase. van Moorselaar and Slagter (2019); see also Vissers et al., 2016) found no alpha power modulations related to anticipated (repeated) distractor locations. Likewise, Noonan et al. (2016) showed that anticipatory suppression of distractors did not occur when the location of an upcoming distractor was known. Although the location of the distractor was not varied in our study (beyond that it could occur in either hemifield), we did find evidence for increased alpha-band power contralateral to the distractor, dependent on both distractor salience and target load. This co-occurred with a reduction of distractor-related RIFT power. The dependence on distractor salience highlights that the nature of the distractor stimulus *did* seem to be important for the alpha power modulation and thus possibly the distractor suppression. Critically, the dependence on target load specifically reflected that an increase in distractor-alpha power was only found when the perceptual load of the target processing was high. During low perceptual load, the salient distractors produced behavioral interference effects, and there was no evidence for alpha suppression, similar to the findings in Noonan et al. (2016) and van Moorselaar and Slagter (2019). Indeed, the tasks used in both of these previous studies (i.e., simple feature-based discrimination of different shapes, triangle versus square, or relatively large orientation differences), were akin to tasks in the low load conditions in prior research (e.g. Lavie, 1995 Experiment 2b) as well as in our paradigm. Thus, the difference between our findings and those of Noonan et al. (2016) as well as van Moorselaar and Slagter (2019) could be explained by differences in the perceptual load of the target. This leads to a clear prediction: increasing the perceptual load in either of these studies (e.g., a condition requiring discrimination between very similar orientations, each embedded within a noise mask) would result in increased alpha power associated with the distractors and thus reduced distractor interference at the behavioral level. This could be an interesting avenue for future research.

4.3. Attentional modulations consist of early gain and downstream gating

Using frequency tagging it has recently been suggested that alpha-band oscillations do not impose gain control in early visual regions (Antonov et al., 2020; Gundlach et al., 2020), but rather that they implement a gating mechanism in downstream visual areas (Jensen and Mazaheri, 2010; Zhigalov and Jensen, 2020). The gain versus gating notion would explain why we did not find a consistent inverse pattern of modulations of alpha power and RIFT. We only found an inverse pattern when contrasting distractor salience levels, but not target load. Note that an MEG study by Molloy et al. (2015) did find reduced alpha power with high perceptual load, both pre- and post- stimulus onset. However, it is unclear whether this was a generic effect or specific to target facilitation. In line with our current findings, Zhigalov and Jensen (2020) found no evidence for trial-by-trial correlations between RIFT and alpha band power, again supporting that gain control is not implemented by means of inhibitory alpha oscillations. Given that we found the neuronal sources of the RIFT signal in early visual cortex, gain control of the target stimuli seems to involve primary visual cortex. The sources of the alpha band power contralateral to the distractor were identified in visual areas just outside of the calcarine sulcus and extended into fusiform areas. As such, our findings suggest that distractor suppression and target facilitation are driven by different neuronal mechanisms (Noonan et al., 2016). However, it remains to be further uncovered how these two mechanisms (gating related to distractor suppression, versus gain related to the effects of target load) relate to the push-pull resource allocation mechanism proposed in load theory and supported by both fMRI and more recently spectroscopy work (Bruckmaier et al., 2020; Pinsk et al., 2004; Schwartz et al., 2005; Torralbo et al., 2016).

5. Conclusions

We conclude that the perceptual load of a target stimulus is a key

driving factor of attentional modulations. Higher target loads lead to suppression of distracting stimuli, reflected by increased distractor-related alpha-band oscillations. Simultaneously, the gain associated with target processing increased. This resulted in a reduction of behavioral distractor interference. Attentional modulations are driven by the target load and distractor salience, with target facilitation and distractor suppression working together to achieve a behaviorally favorable outcome and are thus not mutually exclusive. We thus conclude that while perceptual load increased the gain associated with target processing, alpha oscillations reflected greater distractor suppression with high perceptual load.

Code availability

The analysis pipeline and experiment scripts are available at https://github.com/tgutteling/Perceptual_Load_Experiment.

CRedit authorship contribution statement

Tjerk Gutteling: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. **Lonieke Sillekens:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft. **Nilli Lavie:** Conceptualization, Writing – review & editing. **Ole Jensen:** Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition.

Competing Interest Statement

The authors declare no competing interests.

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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References

- Antonov, P.A., Chakravarthi, R., Andersen, S.K., 2020. Too little, too late, and in the wrong place: alpha band activity does not reflect an active mechanism of selective attention. *Neuroimage* 219, 117006. <https://doi.org/10.1016/j.neuroimage.2020.117006>.
- Awh, E., Matsukura, M., Serences, J.T., 2003. Top-down control over biased competition during covert spatial orienting. *J. Exp. Psychol. Hum. Percept. Perform.* 29, 52–63. <https://doi.org/10.1037/0096-1523.29.1.52>.
- Bahrami, B., Lavie, N., Rees, G., 2007. Attentional load modulates responses of human primary visual cortex to invisible stimuli. *Curr. Biol.* 17, 509–513. <https://doi.org/10.1016/J.CUB.2007.01.070>.
- Bonnefond, M., Jensen, O., 2012. Alpha oscillations serve to protect working memory maintenance against anticipated distracters. *Curr. Biol.* 22, 1969–1974. <https://doi.org/10.1016/j.cub.2012.08.029>.
- Brainard, D.H., 1997. The psychophysics toolbox. *Spat. Vis.* 10, 433–436.
- Bruckmaier, M., Tachtsidis, I., Phan, P., Lavie, N., 2020. Attention and capacity limits in perception: a cellular metabolism account. *J. Neurosci.* 40, 6801–6811. <https://doi.org/10.1523/JNEUROSCI.2368-19.2020>.
- Carrasco, M., 2011. Visual attention: the past 25 years. *Vis. Res.* <https://doi.org/10.1016/j.visres.2011.04.012>.
- Cartwright-Finch, U., Lavie, N., 2007. The role of perceptual load in inattention blindness. *Cognition* 102, 321–340. <https://doi.org/10.1016/j.cognition.2006.01.002>.
- Dugué, L., Merriam, E.P., Heeger, D.J., Carrasco, M., 2020. Differential impact of endogenous and exogenous attention on activity in human visual cortex. *Sci. Rep.* 10. <https://doi.org/10.1038/s41598-020-78172-x>.
- Ferrante, O., Patacca, A., Di Caro, V., Della Libera, C., Santandrea, E., Chelazzi, L., 2018. Altering spatial priority maps via statistical learning of target selection and distractor filtering. *Cortex* 102, 67–95. <https://doi.org/10.1016/j.cortex.2017.09.027>.
- Foster, J.J., Awh, E., 2019. The role of alpha oscillations in spatial attention: limited evidence for a suppression account. *Curr. Opin. Psychol.* <https://doi.org/10.1016/j.copsyc.2018.11.001>.
- Foxe, J.J., Simpson, G.V., Ahlfors, S.P., 1998. Parieto-occipital approximately 10 Hz activity reflects anticipatory state of visual attention mechanisms. *Neuroreport* 9, 3929–3933.
- Gaspelin, N., Luck, S.J., 2018. The role of inhibition in avoiding distraction by salient stimuli. *Trends Cogn. Sci.* <https://doi.org/10.1016/j.tics.2017.11.001>.
- Goldman, R.I., Stern, J.M., Engel Jr, J., Cohen, M.S., 2002. Simultaneous EEG and fMRI of the alpha rhythm. *Neuroreport* 13, 2487–2492. <https://doi.org/10.1097/01.wnr.0000047685.08940.d0>.
- Gross, J., Kujala, J., Hamalainen, M., Timmermann, L., Schnitzler, A., Salmelin, R., 2001. Dynamic imaging of coherent sources: studying neural interactions in the human brain. *Proc. Natl. Acad. Sci. USA* 98, 694–699. <https://doi.org/10.1073/pnas.98.2.694>.
- Gundlach, C., Moratti, S., Forschack, N., Müller, M.M., 2020. Spatial attentional selection modulates early visual stimulus processing independently of visual alpha modulations. *Cereb. Cortex.* <https://doi.org/10.1093/cercor/bhz335>.
- Haegens, S., Luther, L., Jensen, O., 2012. Somatosensory anticipatory alpha activity increases to suppress distracting input. *J. Cogn. Neurosci.* 677–685.
- Händel, B.F., Haarmeier, T., Jensen, O., 2011. Alpha oscillations correlate with the successful inhibition of unattended stimuli. *J. Cogn. Neurosci.* 23, 2494–2502. <https://doi.org/10.1162/jocn.2010.21557>.
- Handy, T.C., Soltani, M., Mangun, G.R., 2001. Perceptual load and visuoocortical processing: event-related potentials reveal sensory-level selection. *Psychol. Sci.* 12, 213–218. <https://doi.org/10.1111/1467-9280.00338>.
- Hari, R., Salmelin, R., 1997. Human cortical oscillations: a neuromagnetic view through the skull. *Trends Neurosci.* [https://doi.org/10.1016/S0166-2236\(96\)10065-5](https://doi.org/10.1016/S0166-2236(96)10065-5).
- Hickey, C., Pollicino, D., Bertazzoli, G., Barbaro, L., 2019. Ultrafast object detection in naturalistic vision relies on ultrafast distractor suppression. *J. Cogn. Neurosci.* 31, 1563–1572. https://doi.org/10.1162/jocn_a_01437.
- Ikkai, A., Dandekar, S., Curtis, C.E., 2016. Lateralization in alpha-band oscillations predicts the locus and spatial distribution of attention. *PLoS One* 11. <https://doi.org/10.1371/journal.pone.0154796>.
- Jacoby, O., Hall, S.E., Mattingley, J.B., 2012. A crossmodal crossover: opposite effects of visual and auditory perceptual load on steady-state evoked potentials to irrelevant visual stimuli. *Neuroimage* 61, 1050–1058. <https://doi.org/10.1016/j.neuroimage.2012.03.040>.
- Jarosz, A.F., Wiley, J., 2014. What are the odds? A practical guide to computing and reporting Bayes factors. *J. Probl. Solving* 7, 2. <https://doi.org/10.7771/1932-6246.1167>.
- Jensen, O., Hanslmayr, S., 2020. The role of alpha oscillations for attention and working memory. In: Poeppel, D., Mangun, G.R., Gazzaniga, M.S. (Eds.), *The Cognitive Neurosciences*, 6th ed. The MIT Press.
- Jensen, O., Mazaheri, A., 2010. Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front. Hum. Neurosci.* 4, 186. <https://doi.org/10.3389/fnhum.2010.00186>.
- Jia, J., Fang, F., Luo, H., 2019. Selective spatial attention involves two alpha-band components associated with distinct spatiotemporal and functional characteristics. *Neuroimage* 199, 228–236. <https://doi.org/10.1016/j.neuroimage.2019.05.079>.
- Kelly, S.P., Lalor, E.C., Reilly, R.B., Foxe, J.J., 2006. Increases in alpha oscillatory power reflect an active retinotopic mechanism for distractor suppression during sustained visuospatial attention. *J. Neurophysiol.* 95, 3844–3851. <https://doi.org/10.1152/jn.01234.2005>.
- Klimesch, W., Sauseng, P., Hanslmayr, S., 2007. EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res. Rev.* 53, 63–88. <https://doi.org/10.1016/j.brainresrev.2006.06.003>.
- Lavie, N., 2005. Distracted and confused?: selective attention under load. *Trends Cogn. Sci.* <https://doi.org/10.1016/j.tics.2004.12.004>.
- Lavie, N., 1995. Perceptual load as a necessary condition for selective attention. *J. Exp. Psychol. Hum. Percept. Perform.* 21, 451–468.
- Lavie, N., Beck, D.M., Konstantinou, N., 2014. Blinded by the load: attention, awareness and the role of perceptual load. *Philos. Trans. R. Soc. B Biol. Sci.* 369, 20130205. <https://doi.org/10.1098/rstb.2013.0205>.
- Lavie, N., Cox, S., 1997. On the efficiency of visual selective attention: efficient visual search leads to inefficient distractor rejection. *Psychol. Sci.* 8, 395–396. <https://doi.org/10.1111/j.1467-9280.1997.tb00432.x>.
- Lavie, N., Tsai, Y., 1994. Perceptual load as a major determinant of the locus of selection in visual attention. *Percept. Psychophys.* 56, 183–197. <https://doi.org/10.3758/BF03213897> (1994 562).
- Mazzetti, C., Staudigl, T., Marshall, T.R., Zumer, J.M., Fallon, S.J., Jensen, O., 2019. Hemispheric asymmetry of globus pallidus relates to alpha modulation in reward-related attentional tasks. *J. Neurosci.* 39, 9221–9236. <https://doi.org/10.1523/JNEUROSCI.0610-19.2019>.
- Molloy, K., Griffiths, T.D., Chait, M., Lavie, N., 2015. Inattention deafness: visual load leads to time-specific suppression of auditory evoked responses. *J. Neurosci.* 35, 16046–16054. <https://doi.org/10.1523/JNEUROSCI.2931-15.2015>.
- Müller, M.M., Hillyard, S., 2000. Concurrent recording of steady-state and transient event-related potentials as indices of visual-spatial selective attention. *Clin. Neurophysiol.* 111, 1544–1552. [https://doi.org/10.1016/S1388-2457\(00\)00371-0](https://doi.org/10.1016/S1388-2457(00)00371-0).

- Nobre, A.C., Kastner, S., 2014. *The Oxford handbook of attention*. Oxford Library of Psychology. Oxford University Press, New York, NY, US.
- Noonan, M.P., Adamian, N., Pike, A., Printzlau, F., Crittenden, B.M., Stokes, M.G., 2016. Distinct mechanisms for distractor suppression and target facilitation. *J. Neurosci.* 36, 1797–1807. <https://doi.org/10.1523/JNEUROSCI.2133-15.2016>.
- Okazaki, Y.O., De Weerd, P., Haegens, S., Jensen, O., 2014. Hemispheric lateralization of posterior alpha reduces distracter interference during face matching. *Brain Res.* 1590, 56–64. <https://doi.org/10.1016/j.brainres.2014.09.058>.
- Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.-M., 2011. FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput. Intell. Neurosci.* 2011, 156869 <https://doi.org/10.1155/2011/156869>.
- Pang, J.C., Robinson, P.A., 2018. Neural mechanisms of the EEG alpha-BOLD anticorrelation. *Neuroimage* 181, 461–470. <https://doi.org/10.1016/j.neuroimage.2018.07.031>.
- Parks, N.A., Hilimire, M.R., Corballis, P.M., 2011. Steady-state signatures of visual perceptual load, multimodal distractor filtering, and neural competition. *J. Cogn. Neurosci.* 23, 1113–1124. <https://doi.org/10.1162/jocn.2010.21460>.
- Payne, L., Guillory, S., Sekuler, R., 2013. Attention-modulated alpha-band oscillations protect against intrusion of irrelevant information. *J. Cogn. Neurosci.* 25, 1463–1476. https://doi.org/10.1162/jocn_a.00395.
- Pfurtscheller, G., 2001. Functional brain imaging based on ERD/ERS. *Vis. Res.* 41, 1257–1260.
- Pinsk, M.A., Doniger, G.M., Kastner, S., 2004. Push-pull mechanism of selective attention in human extrastriate cortex. *J. Neurophysiol.* 92, 622–629. <https://doi.org/10.1152/JN.00974.2003>.
- Popov, T., Gips, B., Kastner, S., Jensen, O., 2019. Spatial specificity of alpha oscillations in the human visual system. *Hum. Brain Mapp.* 40, 4432–4440. <https://doi.org/10.1002/hbm.24712>.
- Remington, A., Cartwright-Finch, U., Lavie, N., 2014. I can see clearly now: the effects of age and perceptual load on inattentive blindness. *Front. Hum. Neurosci.* 8. <https://doi.org/10.3389/FNHUM.2014.00229>.
- Romei, V., Brodbeck, V., Michel, C., Amedi, A., Pascual-Leone, A., Thut, G., 2008. Spontaneous fluctuations in posterior α -band EEG activity reflect variability in excitability of human visual areas. *Cereb. Cortex* 18, 2010–2018. <https://doi.org/10.1093/cercor/bhm229>.
- Saalmann, Y.B., Pinsk, M.A., Wang, L., Li, X., Kastner, S., 2012. The pulvinar regulates information transmission between cortical areas based on attention demands. *Science* 337 (80), 753–756. <https://doi.org/10.1126/science.1223082>.
- Scheeringa, R., Petersson, K.M., Oostenveld, R., Norris, D.G., Hagoort, P., Bastiaansen, M. C.M., 2009. Trial-by-trial coupling between EEG and BOLD identifies networks related to alpha and theta EEG power increases during working memory maintenance. *Neuroimage* 44, 1224–1238. <https://doi.org/10.1016/j.neuroimage.2008.08.041>.
- Schwartz, S., Vuilleumier, P., Hutton, C., Maravita, A., Dolan, R.J., Driver, J., 2005. Attentional load and sensory competition in human vision: modulation of fMRI responses by load at fixation during task-irrelevant stimulation in the peripheral visual field. *Cereb. Cortex* 15, 770–786. <https://doi.org/10.1093/cercor/bhh178>.
- Theeuwes, J., 1992. Perceptual selectivity for color and form. *Percept. Psychophys.* 51, 599–606. <https://doi.org/10.3758/BF03211656>.
- Thut, G., 2006. Band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *J. Neurosci.* 26, 9494–9502. <https://doi.org/10.1523/JNEUROSCI.0875-06.2006>.
- Torralbo, A., Kelley, T.A., Rees, G., Lavie, N., 2016. Attention induced neural response trade-off in retinotopic cortex under load. *Sci. Rep.* 6, 33041. <https://doi.org/10.1038/srep33041>.
- Van Diepen, R.M., Foxe, J.J., Mazaheri, A., 2019. The functional role of alpha-band activity in attentional processing: the current zeitgeist and future outlook. *Curr. Opin. Psychol.* <https://doi.org/10.1016/j.copsyc.2019.03.015>.
- van Doorn, J., van den Bergh, D., Böhm, U., Dablander, F., Derks, K., Draws, T., Etz, A., Evans, N.J., Gronau, Q.F., Haaf, J.M., Hinne, M., Kucharský, S., Ly, A., Marsman, M., Matzke, D., Gupta, A.R.K.N., Sarafoglou, A., Stefan, A., Voelkel, J.G., Wagenmakers, E.J., 2021. The JASP guidelines for conducting and reporting a Bayesian analysis. *Psychon. Bull. Rev.* <https://doi.org/10.3758/s13423-020-01798-5>.
- van Moorselaar, D., Slagter, H.A., 2019. Learning what is irrelevant or relevant: expectations facilitate distractor inhibition and target facilitation through distinct neural mechanisms. *J. Neurosci.* 39, 6953–6967. <https://doi.org/10.1523/jneurosci.0593-19.2019>.
- Vanni, S., Revonsuo, A., Hari, R., 1997. Modulation of the parieto-occipital alpha rhythm during object detection. *J. Neurosci.* 17, 7141–7147. <https://doi.org/10.1523/jneurosci.17-18-07141.1997>.
- Vijayan, S., Kopell, N.J., 2012. Thalamic model of awake alpha oscillations and implications for stimulus processing. *Proc. Natl. Acad. Sci. USA* 109, 18553–18558. <https://doi.org/10.1073/pnas.1215385109>.
- Vissers, M.E., van Driel, J., Slagter, H.A., 2016. Proactive, but not reactive, distractor filtering relies on local modulation of alpha oscillatory activity. *J. Cogn. Neurosci.* 28, 1964–1979. https://doi.org/10.1162/jocn_a.01017.
- Wang, B., Theeuwes, J., 2018a. Statistical regularities modulate attentional capture. *J. Exp. Psychol. Hum. Percept. Perform.* 44, 13–17. <https://doi.org/10.1037/xhp0000472>.
- Wang, B., Theeuwes, J., 2018b. How to inhibit a distractor location? Statistical learning versus active, top-down suppression. *Atten. Percept. Psychophys.* 80, 860–870. <https://doi.org/10.3758/s13414-018-1493-z>.
- Worden, M.S., Foxe, J.J., Wang, N., Simpson, G.V., 2000. Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *J. Neurosci.* 20, RC63.
- Yi, D.J., Woodman, G.F., Widders, D., Marois, P., Chun, M.M., 2004. Neural fate of ignored stimuli: dissociable effects of perceptual and working memory load. *Nat. Neurosci.* 7, 992–996. <https://doi.org/10.1038/nn1294>.
- Zhigalov, A., Herring, J.D., Herpers, J., Bergmann, T.O., Jensen, O., 2019. Probing cortical excitability using rapid frequency tagging. *Neuroimage* 195, 59–66. <https://doi.org/10.1016/j.neuroimage.2019.03.056>.
- Zhigalov, A., Jensen, O., 2020. Alpha oscillations do not implement gain control in early visual cortex but rather gating in parieto-occipital regions. *Hum. Brain Mapp.* hbm.25183. <https://doi.org/10.1101/2020.04.03.021485>.