Target Enhancement or Distractor Suppression? Functionally Distinct Alpha Oscillators form the Basis of Attention

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Abstract

Recent advances in attention research have been propelled by the debate on target enhancement versus distractor suppression. A predominant neural signature of attention is the modulation of alpha oscillatory power (~10 Hz), which signifies shifts of attention in time, space, and between sensory modalities. However, the underspecified functional role of alpha oscillations limits the progress of tracking down the neuro-cognitive basis of attention. In this short opinion article, we review and critically examine a synthesis of three conceptual and methodological aspects that are indispensable for alpha oscillations as a neural signature of attention. (a) Precise mapping of the anatomical source and the temporal response profile of neural signals reveals distinct alpha oscillators that implement facilitatory versus suppressive components of attention. (b) A testable framework enables unanimous association of alpha modulation with either target enhancement or different forms of distractor suppression (active versus automatic). (c) Links of anatomically and functionally specified alpha oscillators (based on a and b, respectively) to behavior reveal the causal nature of alpha oscillators for attention. The three reviewed aspects substantially enrich study design, data analysis, and interpretation of results to achieve the goal of understanding how anatomically specified and functionally relevant neural oscillators contribute to the implementation of facilitatory versus suppressive components of attention.

Keywords: attention, target enhancement, distractor suppression, alpha rhythm, neural oscillator

1. Introduction

Selective attention allows for the prioritization of target stimuli over concurrent distraction. When listening to a friend in a crowded restaurant, selective attention to what the friend is saying could be accomplished by enhancement of the friend's voice, suppression of background noise, or by a combination of the two. Two conceptual questions that coin current research on selective attention are (a) how the cognitive system implements distractor suppression, and (b) whether distractor suppression is a dedicated and *active* mechanism, or a side-effect of target enhancement, and thus *automatic*.

On the neural level, the implementation of selective attention has been related to the alpha rhythm, which is a prominent neural oscillation at ~10 Hz, easily detectable in human Electro- and Magnetoencephalography (EEG/MEG). Briefly summarized, ample previous work has led to the conclusion that alpha oscillations are involved in the control of attention, by selectively regulating the inhibition/ activation balance across brain networks. Such modulation happens through power (i.e., squared amplitude) modulation and precise timely control of neural activity through oscillatory phase (for reviews, see Foxe & Snyder, 2011; Jensen & Mazaheri, 2010; Klimesch, 2012; Strauß et al., 2014).

In this short opinion article, we focus on the role of selective attention in controlling the balance between the processing of relevant and irrelevant inputs, and its mechanistic implementation in alpha power modulation. De- and increases of alpha power have been associated with the enhancement versus suppression of the activity of neuronal populations, respectively, for instance to favor the selection of one sensory modality over another (e.g. Adrian, 1944; Frey et al., 2014; Fu et al., 2001; Mazaheri et al., 2014) or to favor the processing of sensory inputs from a particular location in space (e.g. Bauer et al., 2012; Sauseng et al., 2005; Worden et al., 2000). Therefore, the alpha rhythm has the potential to implement both, enhancement of relevant information and suppression of irrelevant inputs concurrently (e.g. ElShafei et al., 2018; Wöstmann, Alavash, et al., 2019). However, it has been pointed out that the evidence for the latter is limited at present (Antonov et al., 2020; Foster & Awh, 2018). Here, we review and critically examine recent conceptual and methodological advances necessary to establish a unifying theoretical framework of the functional role of alpha power modulation for selective attention.

2. Functional Specification Requires Anatomical and Temporal Separation

Taking auditory attention as a model, an apparent controversy regarding the role of the alpha rhythm arises from the literature: While some studies find that alpha power recorded at the scalp level decreases during auditory tasks (e.g. Becker et al., 2013; Obleser & Weisz, 2012), other studies find increases in net alpha power (e.g. Dimitrijevic et al., 2017; in younger but not in older listeners: Henry et al., 2017; Wöstmann et al., 2015). Among others, one recent study that recorded from implanted electrodes (Electrocorticography; de Pesters et al., 2016) points to a solution of this controversy: Indeed, alpha power increased and decreased at the same time during an auditory task, however, in different brain regions. In agreement with the longstanding view of co-existing mechanisms for target enhancement and distractor suppression (Houghton & Tipper, 1984), a presumably facilitatory effect of low alpha power was observed in regions directly involved in the processing of auditory information (see also Billig et al., 2019), while a potentially suppressive effect of high alpha power was present in motor and frontal regions. Hence, this apparent controversy can be explained by anatomically separate alpha oscillators, which implement different cognitive functions.

Scalp-level recordings of the alpha rhythm might not allow for such detailed anatomical separation, but, in combination with adequate experimental paradigms, they nevertheless allow to separate functionally different sources of alpha activity. For instance, not only in the auditory domain, but across sensory modalities, recent EEG studies consistently demonstrated that anatomically separate alpha oscillators in parietal and occipital cortex regions fulfill different roles in attention: While (dis)engagement of visual sensory attention modulated alpha power in visual cortex regions, alpha power in parietal cortex regions was modulated when participants attended versus ignored speech items (Wöstmann et al., 2020), and when participants divided attention between modalities or hemifields (Sokoliuk et al., 2019). The anatomical separation of different attention-modulated alpha oscillators supports attention models that posit the existence of a supra-modal hub region (in parietal cortex) that interacts with sensory areas during attentional selection (e.g. Banerjee et al., 2011).

In addition to the anatomical distribution, it is essential to consider the temporal profile of different alpha oscillators. The time course of the alpha power response has been shown to exhibit relatively slow modulations with alternating states of higher versus lower alpha power, which align with temporal expectations (e.g. Herbst & Obleser, 2017; Rohenkohl &

Nobre, 2011; van Ede et al., 2020; Wilsch et al., 2020), with the presentation rate of sensory stimuli (e.g. Wilson & Foxe, 2020; Wöstmann et al., 2016), and with time-varying goals to attend versus ignore external stimuli (e.g. Hanslmayr et al., 2011; Payne et al., 2013; van Diepen et al., 2015). In this regard, the momentary up- versus down-phase of alpha power provides important information about the potential inhibitory versus facilitatory function of the underlying alpha oscillator, respectively. A critical distinction has to be made between pre-stimulus and post-stimulus alpha power. Spontaneous fluctuations in pre-stimulus alpha power have been shown to relate to neural baseline excitability (e.g. Benwell et al., 2017; Iemi et al., 2017; Samaha et al., 2017; Wöstmann, Waschke, et al., 2019). If modulated by attention, pre-stimulus alpha power is a potential neural signature of pro-active attentional filtering (e.g. Vissers et al., 2016), while post-stimulus alpha power modulation rather reflects re-active filtering (for a review on different mechanisms of distractor suppression, see Geng, 2014).

The above-mentioned examples demonstrate that searching for *the* alpha rhythm and its functional implementation in selective attention is too unspecific, leads to apparent discrepancies between studies, and thus limits the progress of models to understand the neuro-cognitive basis of attention. Specific effort needs to be dedicated to the identification and separation of functionally distinct alpha oscillators, which originate from distinct neural sources and exhibit characteristic temporal response profiles.

Notably, further defining features such as individual alpha peak frequency (Haegens et al., 2014) or data-driven separation of veridical oscillatory components from aperiodic background activity (Donoghue et al., 2020) can contribute to the separation of distinct alpha oscillators, based on scalp-level recordings.

3. A Testable Framework for Alpha Oscillations in Distractor Suppression

While the previous section emphasized the importance of precisely localizing an alpha oscillator and examining its temporal response profile – rather than just investigating *the* alpha rhythm – this section describes a testable framework that might be used to link a respective oscillator to a facilitatory or suppressive functional role.

On the neurophysiological level, low and high alpha power are respectively related to enhancement and suppression of neural activity, indicated by negative correlation of alpha power and neuronal firing rate (e.g. Haegens et al., 2011), as well as brain activity measured in functional magnetic resonance imaging (fMRI; e.g. Laufs et al., 2003). Critically, however, the fact that alpha power reflects enhancement and suppression in a neurophysiological sense does not necessarily imply that it implements target enhancement and distractor suppression in a *psychological* sense as well (Aron, 2007). As we explain below, it is necessary to carefully disentangle alpha responses to target, distractor, and neutral control stimuli to resolve the functional roles of alpha oscillators for attention.

In theory, suppression in a neurophysiological sense refers to a relatively reduced neural response to a given stimulus compared to other stimuli. To quantify distractor suppression in a broad sense, neuroscientists typically calculate the difference (or the ratio; e.g. Moran & Desimone, 1985) of the neural response to distracting versus target stimuli. In this sense, distractor suppression indicates that the neural response to the distractor is suppressed relative to the target. However, distractor suppression in the broad sense could either be driven by an enhanced response to the target, or by a reduced response to the distractor, or by a combination of the two.

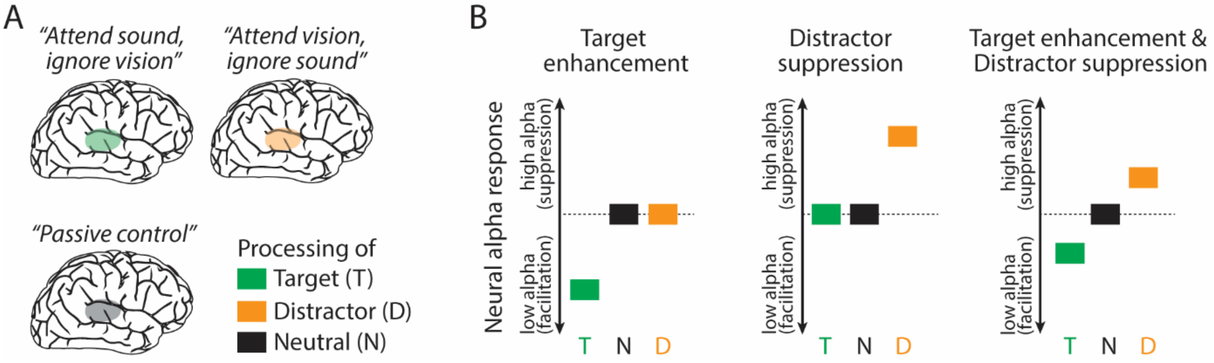

Figure 1. Neurophysiological responses distinguish target enhancement from distractor suppression. (**A**) Example for one possible operationalization of brain regions hosting neural oscillators related to processing target, distractor, and neutral stimuli. In a cross-modal attention paradigm, auditory cortical regions process the target stimulus in case the task requires attention to the auditory modality. Vice versa, auditory regions process the distractor stimulus in case the task requires attention to the visual modality. In a passive control condition, auditory regions can be considered processing neutral stimuli. (**B**) In all three panels, the difference in the alpha power response to the target (T) versus the distractor (D) is identical. A neutral (N) control condition is required to differentiate target enhancement versus distractor suppression (see main text for details).

As we illustrate in Figure 1, recording the neurophysiological response to an appropriate neutral control condition is a potential approach to quantify distractor suppression in a narrow sense in order to distinguish between target enhancement and veridical distractor suppression: *Target enhancement* refers to a case where the target is enhanced relative to the distractor, and crucially also relative to a neutral control. *Distractor suppression* refers to a case where the distractor is suppressed more than the target, and more than the neutral control stimulus. This can occur either independently of or in concert with target enhancement.

Interestingly, the recent literature on the role of alpha oscillations for selective attention abundantly refers to the concept of *active* distractor suppression without a clear conceptualization of the opposite, i.e. *automatic* distractor suppression. In its simplest case, active distractor suppression is a suppressive mechanism independent of target enhancement. To the contrary, automatic distractor suppression is a side effect of target enhancement (also referred to as secondary inhibition; Noonan et al., 2018). In the following, we focus on the hemispheric lateralization of alpha power as prominent neural signature of spatial attention to demonstrate promising recent advances in differentiating active from automatic distractor suppression.

Hemispheric alpha power asymmetries in response to cues indicating the relevance or irrelevance of lateralized stimuli have been interpreted as evidence for an active attentional suppression mechanism (e.g., Händel et al., 2011; Kelly et al., 2006). In essence, alpha power relatively increases over the hemisphere that is biased towards processing the distractor, and relatively decreases over the hemisphere that is biased towards processing the target. It is compelling to interpret these two alpha responses as evidence in favor of active distractor suppression and target enhancement, respectively. However, it might be the case that distractor suppression is secondary to target enhancement and thus, automatic. In this sense, the neuro-cognitive system might actively implement target enhancement, by decreasing alpha power in the hemisphere processing the target. The observed concurrent alpha power increase over the other hemisphere, however, might be driven by lateral inhibitory connections between the two hemispheres. Note that such a secondary or automatic alpha power modulation in the opposite hemisphere should surface in a negative correlation of target-related and distractor-related alpha responses, and in theory it should show up even in case no distractor is present.

A recent study was designed to separate independent contributions of lateralized alpha power for target enhancement versus distractor suppression (Wöstmann, Alavash, et al., 2019). Instead of pairing a target stimulus in one hemifield with a distractor in the other hemifield, either the target or the distractor was presented centrally in front of participants and the other stimulus varied systematically between the left and right side (Fig. 2). Active target enhancement independent of distractor suppression was evidenced by hemispheric lateralization of alpha power when anticipatory attention was directed to the left versus right side under fixed distraction from the front. Active distractor suppression independent of target enhancement was evidenced by hemispheric lateralization of alpha power when distraction was expected to occur on the left versus right side under fixed attention to the front. Critically, the neural sources of these two lateralized alpha responses, associated with target enhancement and distractor suppression, respectively, were partially non-overlapping on the source level. In addition, the two alpha responses were not correlated. Together these results support the notion that anatomically and functionally distinct alpha oscillatory responses independently signify target enhancement and distractor suppression.

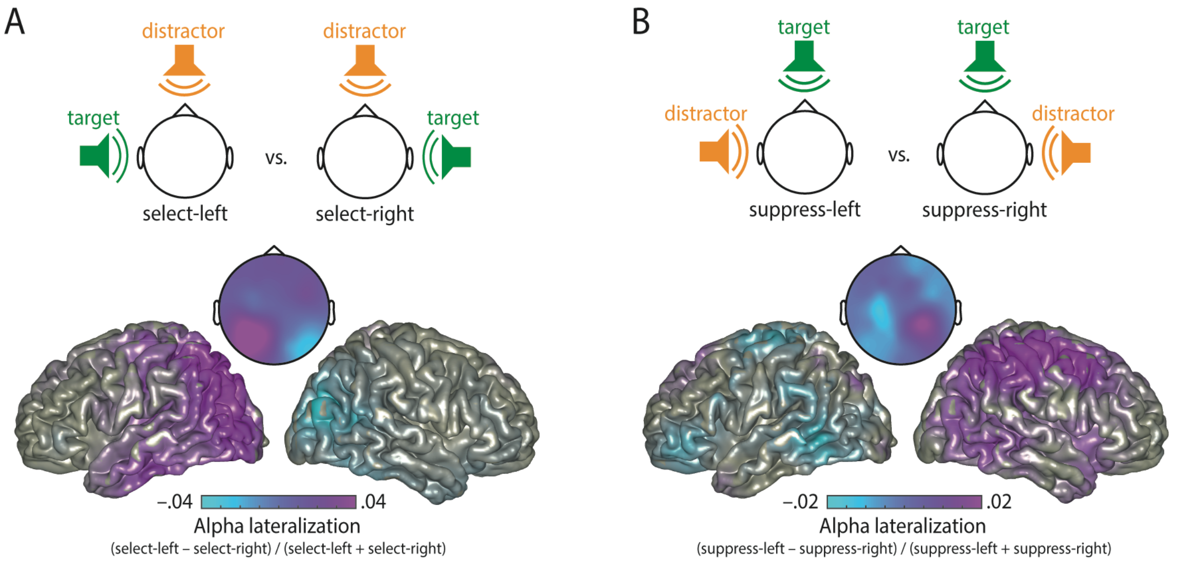

Figure 2. Alpha power modulations reflect independence of target enhancement and distractor suppression. In an auditory spatial attention paradigm, participants had the task to report the direction of a pitch-varying tone sequence at a target location. A distracting tone sequence was presented concurrently at another location. To this end, the position of two loudspeakers changed between front-and-left and front-and-right in a blockwise fashion. Each trial started with an auditory cue to indicate the to-be-attended loudspeaker location; the non-cued loudspeaker location was supposed to be ignored. The hemispheric lateralization of alpha power (8–12 Hz) was assessed in the EEG in-between spatial cue onset and onset of competing tone sequences. Visualizations show grand-average topographic maps and source localizations of lateralized alpha power. (**A**) When the distractor was fixed in the front, alpha power increased in the hemisphere ipsilateral to the upcoming target and decreased in the contralateral hemisphere. Since the distractor position was fixed, this lateralized alpha response can be ascribed to target enhancement independent of distractor suppression. (**B**) When the target was fixed in the front, alpha lateralization reversed such that alpha power decreased in the hemisphere ipsilateral to the upcoming distractor and increased in the contralateral hemisphere. Since the target position was fixed, this lateralized alpha response can be ascribed to distractor suppression independent of target enhancement. Adapted from (Wöstmann, Alavash, et al., 2019).

In other words, if one component of selective attention is kept constant by experimental design, and if systematic variation of another component of selective attention modulates neural responses, the latter can be considered largely independent of the former and thus, *active*. Converging findings in the visual domain have been found in experiments that required selection of lateralized versus non-lateralized information stored in working memory (Rösner et al., 2020; Schneider et al., 2019).

4. Linking Neural to Behavioral Signatures of Attention

An important test for the behavioral relevance of an observed neural signal is whether the modulation of the neural signal, e.g. alpha power, relates to a modulation of behavior in a selective attention task, e.g. accuracy of target detection. Here, we emphasize that only once the anatomical location and the temporal response profile (see section 2), as well as the functional role of an alpha oscillator (see section 3) for attention have been established, the veridical causal influence of the alpha oscillator on behavior can be tested (Fig. 3).

Although an increasing number of neurostimulation studies supports causal links between stimulated alpha oscillations and behavior in attention tasks, the insights that can be gained from such causal evidence remain somewhat limited, unless the above-established prerequisites are met. To illustrate this, a study that aimed to stimulate alpha oscillations in left temporo-parietal cortex regions via transcranial alternating current stimulation (tACS) found improved auditory target recall when the stimulated hemisphere was mainly engaged with processing distractors compared to targets (Wöstmann et al., 2018). Although this result in principle supports the functional relevance of alpha oscillations in attentional selection (for recent studies with converging results, see Deng et al., 2019; Kasten et al., 2020; Schuhmann et al., 2019), its insights are limited for three reasons. First, since the stimulation targeted auditory sensory as well as supramodal parietal areas, it remains unclear which of these areas host behaviorally relevant alpha oscillators. Second, since stimulation was delivered throughout the task, it remains unclear at which point(s) in time modulation of alpha oscillators exerts an influence on behavioral indices of attention. Third, since the experimental paradigm did not allow to quantify independent contributions of processing targets versus distractors on behavior, it remains unclear whether stimulation modulated alpha responses related to target enhancement, distractor suppression, or both.

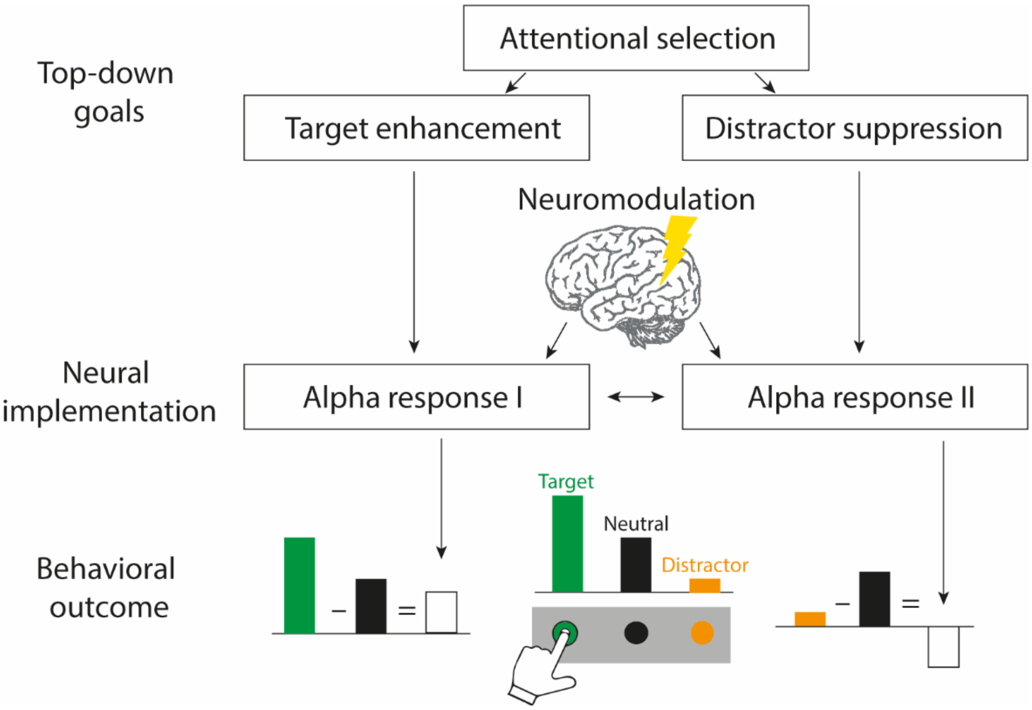

Figure 3. Possible relations between top-down goals, neural alpha responses, neuromodulatory influences, and behavior. The top-down goal to attend selectively can be realized by target enhancement or distractor suppression (or both; although the observer is not necessarily consciously aware of both of these mechanisms). On the neural level, different alpha oscillatory responses (denoted here arbitrarily as I & II) can be associated with target enhancement versus distractor suppression (Fig. 2 demonstrates one possible paradigm to test whether these alpha responses are independent). If anatomical location, temporal response profile, and functional role of an alpha oscillator for attention are known, it can be perturbed through neuromodulation to test its causal effect on behavior in selective attention tasks. In order to unanimously reveal causal relevance of a neural alpha oscillator for a particular component of attention (e.g. target enhancement or distractor suppression), behavioral outcome measures need to quantify processing of target, distractor, and neutral control stimuli. This, however, is rarely the case in conventional selective attention tasks, which often do not include a direct behavioral response to the distractor. Neuromodulation studies should carefully reconsider which of the hypothesized links (indicated by arrows) they test.

That said, to draw cogent conclusions regarding the functional relevance of a neural signature, it is essential to examine which dependencies in an experiment actually allow for causal inferences (see Fig. 3). This is emphasized by two recent studies, challenging the mechanistic role of alpha oscillations in sensory gain control and active inhibition (Antonov et al., 2020; Gundlach et al., 2020). Both used steady-state visual evoked potentials (SSVEPs) as a direct measure of sensory target or distractor processing. Neither were changes in SSVEPs preceded by modulations of alpha-band oscillations, nor was there any systematic relation between trial-by-trial changes in SSVEP amplitudes and fluctuations of alpha lateralization. Importantly, while these findings question previous interpretations of alpha oscillations as an active inhibitory or facilitatory mechanism, they do not per se rule out their causal role for behavior. That is, stimulation-induced changes in alpha-band amplitude in selective attention paradigms (e.g. Romei et al., 2010) do very well establish a causal relationship between alpha oscillations and behavior; but alpha oscillations may simply exert their influence at a later point in the processing cascade rather than reflecting a sensory gating mechanism that directly affects early neural responses to targets and distractors.

This recent debate illustrates the need to (a) carefully consider which neural processes are affected by neuromodulation, and (b) to acknowledge that the relationship between any non-modulated neural process and behavior remains correlational (Jazayeri & Afraz, 2017). A related challenge lies in the identification of off-target and secondary effects of neuromodulation that may complicate the interpretation of results. For instance, Wöstmann et al. (2018) acknowledge that the observed opposite effects of transcranial alpha and gamma stimulation do not necessarily render both types of oscillations causally effective. That is, it remains possible that externally stimulated gamma oscillations do not directly affect behavior but rather indirectly via a decrease of causally effective alpha oscillations.

Finally, the successful characterization of brain-behavior relationships via neural stimulation also depends on a prudent selection of behavioral measures that are suitable for capturing the mental representation of either target or distractor stimuli (see Fig. 3). Ensuring that behavioral outcome measures specifically quantify the processing of the target, the distractor and a neutral control stimulus is not trivial and requires a solid theoretical framework of the assumed underlying processes. A recent review, considering the relationship between spontaneous alpha power fluctuations and visual task performance (Samaha et al., 2020), illustrates the intricacy of high-dimensional behavioral constructs such as perceptual decision-making: While pre-stimulus alpha power affects hit rates, false alarm rates as well as subjective confidence and visibility ratings, it has no effect on discrimination accuracy or sensitivity.

5. Conclusion

In the present opinion article, we define a testable framework of alpha power for target enhancement versus distractor suppression in general (Fig. 1), for active versus automatic distractor suppression specifically (Fig. 2), and for the establishment of meaningful causal relations of alpha oscillations to selective attention performance (Fig. 3). There are two essential criteria to be fulfilled in studies that adopt the goal to test this framework. First, the proposed mechanism must be directly *testable*, and not be inferred solely form an observed relative difference. This means that experiments have to be designed in such a way, that the empirical evidence can separate active from automatic distractor suppression. This criterion is not always fulfilled: While it is easy to find studies in the literature that interpret their results in support of an active mechanism of distractor suppression, it often remains unclear which alternative patterns of results, if any, might have given evidence for automatic suppression. Thus, if the goal of a study is to test active versus automatic distractor suppression or, more generally, target enhancement versus distractor suppression, there must be possible patterns of empirical data that can be assigned to either of the two (for a paramount example, see Seidl et al., 2012).

Second, evidence for the framework must be *mutually exclusive*. The experimental design should make sure that a single empirical finding cannot support both mechanisms (e.g. target enhancement and distractor suppression) at the same time. Note however, that it is well conceivable in a dual mechanism framework that two separate neuro-cognitive mechanisms, target enhancement and distractor suppression, operate in parallel (see Figure 1B, right panel). In such a case there is one mechanism at play that increases the neural response to the target stimulus (relative to neutral and distractor stimuli) and another one that suppresses the neural response to the distractor (relative to target and distractor stimuli).

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