

EXPLORING THE CAUSAL ROLE OF NEURAL OSCILLATIONS IN ENDOGENOUS
AND EXOGENOUS ATTENTION: DIFFERENT EFFECTS OF 40 HZ AND 10 HZ TACS
STIMULATION

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ABSTRACT

Jonathan Parsons: Exploring The Causal Role Of Neural Oscillations In Endogenous And Exogenous Attention: Different Effects Of 40 Hz And 10 Hz Tacs Stimulation
(Under the direction of Joseph B. Hopfinger)

Previous electrophysiological studies strongly implicate a role for both alpha (8 – 12 Hz) and gamma (30 – 120 Hz) oscillations in selective attention. However, establishing causality requires inducing these oscillations in the brain and observing the behavioral changes that result. To this end, we stimulated participants' right posterior parietal cortex at 10 Hz, 40 Hz or sham while they performed two separate cueing tasks—one endogenous and one exogenous. Stimulation at 40 Hz speeded responses to invalidly-cued targets, suggesting a facilitation of voluntary attentional shifting. There was also a marginal effect of 10 Hz stimulation, such that responses to invalidly-cued targets in the exogenous task were slowed. Possible reasons for a lack of lateralized effects are discussed. These results provide new information about the causal roles of different frequencies of neural oscillation in facilitating visuospatial attention, providing support for frequency-specific effects.

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CHAPTER 1: INTRODUCTION

Paying attention involves selecting some aspects of the current sensory environment for further processing while simultaneously suppressing others in order to minimize their interference with the selected stimulus. Understanding this process requires, on the one hand, the formation of abstract models that accurately predict the behavioral effects of attention. On the other, it involves elucidating the physical mechanisms by which attentional selection is accomplished.

Theories of attention typically divide the process of “attending” into several sub-categories. From early-on, theories distinguished between voluntary (endogenous) and reflexive (exogenous) forms of attention (Jonides, 1981). Posner and Petersen (1990) divided “the attention system” into three subsystems, one for orienting to sensory events, one for detecting environmental signals that may be behaviorally relevant, and one for maintaining an alert or vigilant state. These three subsystems have since been labeled as the Orienting, Alerting and Executive systems, and an enormous amount of research has been done on the basis of these constructs (Petersen & Posner, 2012).

Central to most theories of attention, and the ideas of selecting and suppressing mentioned above, are the concepts of neural excitation and inhibition (Houghton & Tipper, 1996; Knight, Staines, Swick, & Chao, 1999; Posner & Presti, 1987). These concepts, in turn, provide a critical link between abstract accounts of attention and descriptions of their neural underpinnings. Most of our knowledge of the physical mechanisms that may underlie attention comes from functional neuroimaging studies. Though many imaging techniques now exist and have been used to provide

much insight into attention, the two that are especially relevant to the proposed study are electroencephalography (EEG) and magnetoencephalography (MEG). Findings from these studies will be described in the following sections.

EEG/MEG frequency studies

It has been known since the advent of the electroencephalogram (Berger, 1929) that, in recording electrical potentials at the scalp, one may observe a pattern of very pronounced regularity. Such patterns of oscillating voltage have been attributed to the synchronous, periodic activation and inhibition of large groups of neurons (Whittington, Traub, Kopell, Ermentrout, & Buhl, 2000). These oscillations are typically subdivided into frequency ranges, each of which turns out to have particular functional associations. These are named delta (1-4 Hz), theta (4-8 Hz), alpha (8-14 Hz), beta (14-30 Hz) and gamma (30 – 120 Hz). Theta, alpha and gamma oscillations are all considered important for attention. Theta's most important role is thought to be in the coupling of distant brain areas (Clayton, Yeung, & Cohen Kadosh, 2015). However, as the current study is focused more on local, single area oscillations, the literature review will focus primarily on alpha and gamma.

Alpha-band oscillations (8 – 14 Hz)

As one of the most easily discernable features of the EEG, alpha oscillations have been a subject of study for roughly 80 years (Berger, 1929; Jasper & Cruickshank, 1937). And while the notion that they might be associated with attention is also longstanding (Martinius & Hoovey, 1972; Mulholland, 1969; Mulholland, Goodman, & Boudrot, 1983; Mulholland & Runnals, 1962), a more precise description of the relationship has only emerged in the last 15-20 years. This research has focused on, among other things, intra- and inter-individual differences in peak alpha frequency

(Haegens, Cousijn, Wallis, Harrison, & Nobre, 2014; Kelly, Dockree, Reilly, & Robertson, 2003; Klimesch, Doppelmayr, Russegger, Pachinger, & Schwaiger, 1998; MacLean, Arnell, & Cote, 2012) and its consequences for perceptual performance; the involvement of alpha oscillations in the relationship between attention and memory (Jiang, van Gerven, & Jensen, 2015; Klimesch, 1997, 1999; Myers, Walther, Wallis, Stokes, & Nobre, 2015); and the role of alpha oscillations in selectively attending to other sensory modalities (Frey et al., 2014; Haegens, Luther, & Jensen, 2012; Weisz, Müller, Jatzev, & Bertrand, 2013). However, most relevant to the proposed research are those studies that have focused on alpha and the allocation of visual attention. It is those studies that will be reviewed here.

Worden et al. (2000) demonstrated that alpha band power may be distributed over occipital cortex in a retinotopic fashion, specifically in a manner that reflects the current locus of visual attention. Participants completed a task in which a centrally-presented, non-predictive arrow directed them to covertly shift their attention to the left or right of the display. They were instructed to respond only to targets that appeared on the cued side, and only to one of four possible target types (they should withhold responding for the other three target types). Targets could appear in the upper left or right quadrants on half of the blocks, and in the lower quadrants on the other half. Worden et al. specifically focused on alpha activity in the period after cue onset but before target onset, so that differences in activity between cue directions could be specifically attributed to the allocation of attention, rather than stimulus processing. Increases in alpha power were observed contralateral to the *to-be-ignored* visual hemifield (ipsilateral to the *to-be-attended-field*). Moreover, the location of peak alpha-power was more dorsal in upper-quadrant blocks than in lower-quadrant blocks. Thus, alpha synchrony appears to be related to suppressing perceptual

processing in a specific, topographic manner. This finding was soon replicated across several different studies (Fu et al., 2001; Klimesch, Sauseng, & Gerloff, 2003; Sauseng et al., 2005).

Thut, Nietzel, Brandt, & Pascual-Leone (2006) added further evidence for the alpha-attention association by showing that probability of successful performance could be predicted by the relative balance of alpha power between hemispheres, prior to target onset. The researchers had participants perform a target localization task. Targets could appear to the left or right of fixation. An auditory cue that preceded the target correctly predicted its location on 66% of trials. Participants were required to respond by pressing one of two buttons to indicate which side of the display the target had appeared on. Thut et al. found that the relative intensity of alpha power between right and left hemispheres provided an index that could be used to predict both accuracy and reaction times. Specifically, more accurate and rapid responses were associated with a *relative* negativity of alpha power in the hemisphere contralateral to the upcoming target. They found that this difference was largely driven by desynchronization (i.e. – decrease in alpha power) in the contralateral hemisphere.

However, a subsequent study by Kelly et al. (2006) had contrasting findings. Kelly et al. noted that previous findings (e.g. - Thut et al., 2006) were made somewhat ambiguous by the fact that the mere appearance of a cue, as a stimulus onset, would cause alpha desynchronization. To address this issue, Kelly et al. administered a cueing task in which targets were presented on placeholders that flashed throughout the trial. In this way, onset-associated alpha desynchronizations could reasonably be said to be equated between the pre cue and post cue intervals. Under these conditions, Kelly et al. found that strong increases in alpha power were observed contralateral to the distracters. Another study by Thut and colleagues (Rihs, Michel, & Thut, 2007) also found evidence of considerable *increases* in alpha power over cortical areas

corresponding to to-be-ignored regions. While their task did not include distractors, per se, it did include an array of 8 placeholders, representing potential target locations, arranged in a circle. Rihs et al. speculated that participants may have needed to actively suppress these locations, which effectively gave them a “distracter-like” status.

Thus far, studies had either found evidence for attention related increases in alpha power, corresponding to distracter suppression, or decreases, corresponding to target facilitation, but not both. This would seem to suggest that the pattern of oscillation was task-dependent in some way. Rihs, Michel and Thut (2009) disambiguate the relationship by breaking down the distribution of anticipatory alpha into earlier and later periods, corresponding to the shifting and maintenance of attention, respectively. Rihs et al. had participants perform a cueing task in which they were required to discriminate between a + and a letter x. The centrally-presented arrow cue was either 75% or 95% valid (blocked), and the cue-target interval could be either 700ms or 1900ms (within a block). Only the long delay (1900ms) trials were analyzed, as these would contain both a period of initial preparation (0 – 700ms) and a period of sustained attention, once the participant realized that the target was not appearing right away (700 – 1900ms). Specifically, alpha power was analyzed for the intervals of 500 – 700ms and 1700-1900ms. Both periods were characterized by a relative imbalance of alpha power, such that more alpha power was observed over the target-ipsilateral hemisphere. Critically, in the early phase, this imbalance was found to be driven by a relative decrease in alpha power in the contralateral hemisphere, whereas in the late phase it was driven by a sustained increase in the ipsilateral hemisphere. Rihs et al. attributed these different phases to the initial *shift* of attention and the later *sustaining* of attention.

Gamma-band oscillations (30-120 Hz)

Owing to their smaller amplitude and higher frequency in the EEG, gamma-band oscillations (30-120 Hz) cannot typically be detected by visual inspection of the EEG. Research on gamma activity therefore began later, especially with regard to human populations. The earliest evidence of gamma's functional role came from intracranial recordings in animals (Eckhorn et al., 1988; Gray, Konig, Engel, & Singer, 1989; Gray & Singer, 1989; Singer, 1993). In both cats and monkeys, distinct areas of visual cortex were observed to oscillate synchronously at 30 Hz and above when the animal was presented with a visual stimulus. It was therefore suggested that this synchronization might represent an answer to the so-called "binding problem" (Roskies, 1999; Von Der Malsburg, 1994, 1999). In brief, the binding problem consists of an explanatory gap in our understanding of visual perception. If different features of a single object (e.g. - shape, movement, color, spatial location) are represented by distinct, distributed neural populations, how does the visual system determine which features belong to which object in a complex visual scene? It was suggested by the authors cited above that the features of a given object are "bound" together by the synchronous oscillation of the neural populations that underlie those features (Gray, 1999).

The first evidence for such a mechanism in humans came from Müller et al. (1996), who recorded subjects' EEG while they observed either a single moving bar (coherent motion condition) or two bars moving in opposite directions (incoherent motion condition). Compared to incoherent trials, neural responses to coherent trials consisted of increased power in the 40 – 96 Hz range over parieto-occipital sites contralateral to the moving bar. Müller et al. attributed this difference in gamma power to the fact that all active neurons were responding to a single stimulus, rather than two.

Given that selective attention had already been proposed as the *cognitive* mechanism by which an object's features are bound together (Treisman's 'Feature Integration Theory'; Treisman & Gelade, 1980; Treisman, 1996), Müller and colleagues (Gruber, Müller, Keil, & Elbert, 1999) proceeded to investigate the relationship between selective attention and gamma oscillations. In this experiment, subjects viewed displays containing many rectangles of different dimensions and colors. Following the presentation of a central arrow, which pointed to the left or right, the rectangles would change color several times. Subjects were required to attend to the side indicated by the arrow and to count the number of rectangles of a target color. In addition, as the rectangles changed color, one half of the display (left or right) would rotate horizontally. Gruber et al found that i) gamma power (35 – 51 Hz) was significantly higher over parieto-occipital sites contralateral to the rotating side ii) following the cue, the spatial distribution of gamma power was observed to shift from a general posterior distribution to a more focal peak over parieto-occipital sites in the hemisphere contralateral to the to-be-attended side, and that iii) the rotating side of the display elicited the highest intensity gamma oscillations when it was also the attended side. Thus, Gruber et al. replicated their previous finding that a moving stimulus elicits increased gamma synchrony generally and, critically, found evidence suggesting that the strongest gamma synchrony occurs when that stimulus is the focus of attention.

Thus it seems that selective attention is associated with increased gamma synchrony in the hemisphere corresponding to the attended hemifield. This characterization has since been further refined in several studies. Tallon-Baudry, Bertrand, Hénaff, Isnard and Fischer (2005), for example, found that attention-associated increases in gamma (30 – 130 Hz) power occur in both lateral-occipital cortex and the fusiform gyrus, but that these areas have distinct patterns of local synchronization. Fourteen patients with medically intractable epilepsy were implanted with depth

electrodes for pre-surgical localization of their seizure focus. Tallon-Baudry et al. had these patients perform a delayed matching to sample task in which they made judgments about abstract shapes that appeared at fixation. In the control task, the first stimulus would appear, but the second would not and, instead participants had to judge whether the fixation cross had changed luminance. Thus, in the main task, the first stimulus had to be attended, but in the control task it did not. Tallon-Baudry et al found that attention enhanced gamma synchrony in the fusiform gyrus *during* stimulus processing, whereas gamma in lateral occipital cortex was most pronounced in the period *anticipating* a to-be-attended stimulus and actually decreased during stimulus presentation. This may suggest that posterior gamma is especially associated with anticipatory attention.

In addition to playing different roles in different cortical areas, there is also evidence that gamma oscillations have different roles depending on the particular sub-band within the gamma range of frequencies. Vidal, Chaumon, O'Regan and Tallon-Baudry (2006) found evidence that visual grouping and selectively attending are associated with distinct gamma sub-ranges. Subjects' MEG was recorded while they performed a novel delayed-matching to sample task in which each trial presented 8 bars, each with a unique orientation, distributed in a circle around fixation. In the single group condition, each bar was half red, half green; in the other conditions, the bars were divided into two groups: 4 completely red, 4 completely green. In the single group condition, participants were always required to attend to and remember the whole display and, after a delay, indicate whether the test display contained a bar whose orientation had changed. In the two-group conditions, participants were either required to attend to and remember all 8 bars (indicated by a yellow fixation cross) or just one color of bar (indicated by a red or green cross). Vidal et al. compared the MEG frequency spectrum across conditions during the window 200 – 400 ms after the onset of the to-be-remembered display. They found a high gamma peak at central occipital

sensors, specifically in the 70 – 120 Hz range, which was significantly more pronounced in the single-group condition, as compared to the two-group conditions, which did not differ significantly from each other. Vidal et al. attributed this peak to a grouping process, which would explain why less synchrony was observed with two distinct groups. Furthermore, they found a low-gamma peak at right parietal sensors, specifically in the 44 – 66 Hz range, but only in those conditions where participants were required to attend selectively to a sub-group of bars (red or green). Vidal et al. associated this gamma activity with the process of attentional focusing.

In addition to binding and attentional selection, there is evidence that gamma activity may also be involved in voluntary attentional *shifting*. Landau, Esterman, Robertson, Bentin and Prinzmetal (2007) recorded participants' EEG while they performed a simple face discrimination cueing task in which the spatial cue, a peripheral flash, was either predictive (70% valid, 15% invalid, 15% no target) or non-predictive (40% valid, 40% invalid, 20% no target). Participants had to indicate which of two faces appeared as the target by pressing one of two keys; a third key was to be pressed if no target appeared. A time-frequency analysis of the EEG data revealed significantly more energy in the 30 – 70 Hz band during periods where voluntary orienting of attention would be expected, compared to conditions in which no reorienting would be expected. That is, increased gamma was observed following a predictive cue and following a target that appears in an unexpected location (thus requiring the participant to voluntarily reorient her attention), but not following a non-predictive cue (which would trigger an involuntary shift of attention) or following a target that appears in the expected location (which would not require an attention shift).

Further evidence for the involvement of *lateralized* gamma in orienting attention to one hemifield came from Doesburg, Roggeveen, Kitajo and Ward (2008), who recorded participants'

EEG while they performed a simple spatial cueing task (similar to that of Worden et al. (2000), reported in this paper's section on alpha oscillations). A non-predictive, central arrow directed participants to shift their attention to the left or right side of a display where, after a brief delay, a target would appear. Participants were to respond only to targets that appeared on the cued side, and only for one of two possible target identities. In the period roughly 240ms – 380ms after cue onset, Doesburg et al observed a prominent increase in gamma (36 – 43 Hz) synchrony within parietal cortex on the side *contralateral* to the cued hemifield (electrode P7 or P8) and multiple other cortical areas.

Neurostimulation

While neuroimaging techniques have provided unprecedented insight into the links between brain and behavior, they are not without their limitations. Boundaries of spatial and temporal resolution aside, the evidence obtained using these methods is ultimately correlational, showing that a given behavior is *associated* with a particular change in neural activity. Demonstrating causality would require directly influencing a given brain region and then observing the behavioral consequences.

In the past, human lesion studies have provided valuable insight in this regard, insofar as a loss of function following damage to a particular brain area implies the causal involvement of that brain area in facilitating that function. The most well-known example of this type of inference involving attention is that of hemispatial neglect (Heilman & Van Den Abell, 1980). A neglect patient, despite having apparently normal vision, chronically fails to acknowledge one side of space, typically the left (e.g. - Mesulam, 1981; Ro & Rafal, 1996). Post-mortem inspection and/or structural MRI of the patient's brain typically reveals a lesion over parietal cortex, contralateral to

the neglected side. While often insightful and thought provoking, such studies necessarily suffer from a substantial lack of experimental control. For one thing, patients tend to have fairly widespread lesions that are rarely fully the same between two individuals, which makes it difficult to relate lesion to symptom beyond a rather general level of description (e.g. - Vallar, 1998). Moreover, since subjects are typically recruited post-lesion, it is impossible to determine the extent of a subject's impairment compared to their pre-lesion ability. That is, a particular patient typically becomes known to a researcher *because* of their impairment, and there is likely little to no documentation of their prior abilities for comparison.

In recent decades, neurostimulation has emerged as a potential solution to the above-mentioned problems (e.g. - Peterson & Deer, 2013). By directly influencing (enhancing or impairing) brain activity via the application or induction of an electric current, neurostimulation offers the possibility of establishing a causal relationship between particular brain structures and their associated functions (Hallett & Hallett, 2007; Parkin, Ekhtiari, & Walsh, 2015). Since stimulation is controlled by the experimenter, it can be applied at a consistent (and relatively precise) location, and performance can be measured before, during and after stimulation.

The earliest such technique, transcranial magnetic stimulation (TMS; Barker, Jalinous, & Freeston, 1985), stimulates a brain region by delivering magnetic pulses very close to the scalp, which, in turn, induce transient currents in the underlying neural tissue. This stimulation is thought to temporarily inhibit activation of the stimulated region, which may then disrupt performance (though a recent review by Luber and Lisanby [2014] has shown that there are many instances in which performance is actually enhanced). If performance is disrupted, the inhibited neural region is inferred to be necessary in producing the goal behavior, and not necessary if performance is not disrupted (Hallett & Hallett, 2007). Furthermore, stimulation may be delivered in single pulses, or

in trains of pulses. The latter technique is typically referred to as repetitive TMS (rTMS). This technique may be used to produce longer-lasting disruptions or facilitations of neural function and, as will be discussed, may even be able to induce endogenous oscillations with the same frequency as the stimulator's pulse rate. This technique allows for more complex experiment designs that may be used to answer more sophisticated causal questions (Fitzgerald, Fountain, & Daskalakis, 2006; Pascual-Leone, Walsh, & Rothwell, 2000).

Somewhat more recently, a group of techniques have been developed in which electrical current is passed through the cortex via rubber electrodes applied to the scalp. These include transcranial direct current stimulation (tDCS), transcranial alternating current stimulation (tACS), oscillatory tDCS (o-tDCS), and transcranial random noise stimulation (tRNS). Now collectively referred to as transcranial electrical stimulation (tES), these techniques differ primarily in the parameters of the applied current (Paulus, 2011). As its name implies, tDCS involves delivering direct current, that is, current of a constant intensity and direction. Thus, there is a positive, or anodal, electrode, and a negative, or cathodal, electrode (Gandiga, Hummel, & Cohen, 2006). Facilitatory effects tend to be observed at the anodal site, while inhibitory effects are more commonly observed at the cathodal site (Coffman, Clark, & Parasuraman, 2014). tDCS is most clearly contrasted with tACS, in which the current direction and intensity vary in a periodic fashion. O-tDCS delivers an alternating current with a constant DC offset, whereas tRNS delivers an alternating current that varies randomly (i.e. – noise). As this study employed tACS, this technique will be explained in further detail (but see Herrmann, Rach, Neuling, & Strüber, 2013, and Paulus, 2011 for further description of all the techniques).

In tACS, two electrode pads are typically used. The reference electrode is typically larger and placed over midline so as to minimize effects of current at that location. The stimulating

electrode is typically smaller and placed over the brain area of interest. “Alternating” refers to the fact that the strength and direction of the applied current varies in a sinusoidal pattern around a neutral current of 0 mA. The usefulness of this particular technique lies in the fact that the frequency of stimulation can be precisely controlled, which induces the effects of endogenous oscillations of that frequency at that location (e.g. - Kanai, Chaieb, Antal, Walsh, & Paulus, 2008). Thus, tACS holds potential for determining causality in the correlational associations that have been demonstrated in previous EEG frequency research. This is the goal of the proposed study.

Rhythmic neurostimulation studies: rTMS and tACS

As previously discussed, the neuroimaging literature has provided compelling evidence that alpha and gamma neural synchrony are strongly *associated* with preparatory attention, in a spatially-specific fashion. However, this technique cannot absolutely confirm that such activity *causes* changes in attention. It could be the case that these oscillations are simply so-called *epiphenomena* (Clayton et al., 2015), or that they are necessary, but not sufficient to cause shifts of attention. In attempts to demonstrate that it does have a causal role, neurostimulation techniques that can deliver *rhythmic* stimulation, brief or continuous, should be valuable, as these may have the potential to simulate and/or induce oscillatory activity in the target band (Thut, Schyns, & Gross, 2011). The following section will discuss studies that have used repetitive transcranial magnetic stimulation (rTMS) and tACS.

Klimesch et al. (2003) provided early indications that rTMS could be used to modulate attention performance. Participants performed a mental rotation task that is part of a standard German IQ test, in which they had to say which of 6 rotated cubes matched the target cube (cube faces were differentiated by each face having a different symbol on it). Prior to each trial, a train

of 24 TMS pulses was delivered at the participant's upper individual alpha frequency (IAF+1) over mid-frontal (Fz) and right-parietal (P6) cortex. Control conditions included sham IAF+1 stimulation (stimulator rotated 90 degrees) over parietal cortex, as well as lower-alpha (IAF-3) and beta (20 Hz) stimulation. IAF+1 stimulation led to improved task performance, whereas the control conditions did not differ from one another. Thus, it seemed that alpha stimulation could improve performance in a general way, though this could not be attributed to modulated spatial orienting, specifically, so much as overall increased focus.

Romei, Gross, and Thut (2010) did investigate the effects of alpha rTMS on the spatial distribution of attention. Participants performed a simple detection task in which targets appeared on the left or right side of a display after the appearance of a fixation cross. There was no spatial cue. Prior to target appearance, rTMS was applied over left or right parietal or occipital cortex. The stimulation frequency of interest was 10 Hz. This was contrasted with sham stimulation, but also 5 Hz and 20 Hz stimulation as higher- and lower-frequency active controls. With 10 Hz stimulation, Romei et al. found that target detection was impaired in the hemifield opposite the side of stimulation and enhanced in the ipsilateral hemifield. However, neither of these effects was observed with 5 or 20 Hz stimulation. These results suggest that 10 Hz (alpha) oscillations play a unique role in selective attention.

The results of Romei et al. (2010) certainly add considerable support to the notion that alpha oscillations are causally involved in the allocation of attention. However, rTMS has some technical limitations that may warrant caution in the interpretation of their results. First, the stimulation delivered was sudden and brief, as is necessarily the case with rTMS. Moreover, Romei et al. note that the effects did not last longer than roughly 3 seconds after the end of the rTMS pulse. While this has the benefit of demonstrating how brief changes in alpha activity may

influence attention, rTMS cannot inform us as to how more sustained alpha activity may play a role. As Rihs et al. (2009) demonstrated that brief and sustained changes in alpha may have different effects, understanding the role of sustained alpha is critical. Second, and perhaps more problematic, is the fact that rTMS pulses only very roughly approximate the sinusoidal form of an endogenous alpha oscillation (Herrmann et al., 2013). While the TMS pulses are evenly spaced in time at the appropriate frequency (e.g. – 10 Hz for alpha), simulating the peaks of a sine wave, the pulses themselves essentially produce a very brief burst of noise (i.e. – delivering power across a broad range of frequencies). This makes it more difficult to attribute the results of such stimulation to modulation in the alpha-band, specifically, since other frequencies are produced, albeit less strongly. tACS, by contrast, delivers a single frequency of stimulation, and can do so for prolonged periods (again, see Herrmann et al., 2013). This may make it better suited, or at least complementary to rTMS, as a method for causal testing of neural oscillations.

To my knowledge, tACS has so far been used in only one study to examine the effects of alpha power on the spatial distribution of attention (Brignani, Ruzzoli, Mauri, & Miniussi, 2013). This study applied lateralized tACS at frequencies in the theta, alpha and beta ranges, but failed to produce hemisphere-specific effects. Based on their results, Brignani et al. speculated that tACS may not be as effective as hoped in modulating endogenous oscillations. There are, however, several reasons, which I will outline below, that I believed this to be a premature conclusion. Brignani et al. had participants perform a detection and discrimination task while receiving tACS stimulation over electrode sites PO7 or PO8 of the 10/10 electrode placement system (Jurcak, Tsuzuki, & Dan, 2007). Participants were required to indicate the presence/absence and orientation of a Gabor patch that could appear to the left or right of fixation. The target was preceded on all trials by a brief warning signal, presented at fixation. The experimenters wished to add causal

evidence to the association between alpha (10 Hz) oscillations and lateralized attention. In addition to 10 Hz stimulation and sham conditions, they included one lower-frequency (6 Hz) and one higher-frequency (25 Hz) condition as active controls. Brignani et al. found that both 6 Hz **and** 10 Hz stimulation impaired detection performance, compared to baseline, but no other effects of stimulation were found. Critically, Brignani et al. reported that the observed impairment did not show retinotopic specificity. That is, impairment was observed regardless of which hemisphere was stimulated. Based on the observed effects, which were not as specific as hypothesized, Brignani et al. questioned whether tACS was effective at modulating brain oscillations. While the researchers' concern is understandable, it may be premature, considering the limitations of their study design. The task itself may not have been optimal for finding effects of the tACS. There was no spatial cue, but at the same time the detection/discrimination task was quite difficult, which likely would have led participants to adopt an alert but diffuse attentional state in the period between the warning signal and the target. This could partly explain Brignani et al.'s failure to find the expected effects of alpha oscillations, as such an alert state would likely be reflected in overall low alpha activity, whereas (Rihs et al., 2009) only found alpha effects in those participants that had higher baseline levels of alpha activity. Moreover, the task instructions emphasized that participants should prioritize accuracy over speed, and participants were given 1500ms to make their presence/absence judgements and another 1500 to make the orientation judgement. This allows for considerable post-target processing and opportunities for the stimulation to interfere in ways that were not germane to the researchers' hypotheses. Relatedly, Brignani et al. only measured accuracy, whereas EEG studies have found associations of alpha power with both accuracy and reaction time (Rihs et al., 2007, 2009; Thut et al., 2006). Also, increased alpha power has been associated with active suppression of irrelevant information (Rihs et al., 2007; Worden

et al., 2000), so it is less clear what should be expected to happen when alpha stimulation is applied in a task with only targets and no distracters.

Researchers have also utilized tACS in hopes of influencing attention via stimulation in the gamma band. Laczó, Antal, Niebergall, Treue, and Paulus (2012) had participants detect random dot patterns (RDPs) that would appear randomly at one of eight positions (4 were to the left or right of fixation, just above or below the horizontal meridian; the other 4 were above or below fixation, just to the left or right of the vertical meridian). Prior to the appearance of the RDP, a noninformative peripheral cue could appear to the left or right of fixation, capturing the participant's attention to that side of the display. During the task, 40, 60 or 80 Hz stimulation or sham stimulation was administered over primary visual cortex (area V1). Compared to sham stimulation, Laczó et al. found that 60 Hz stimulation led to increased contrast sensitivity, but no other effects, perceptual or attentional, were found. The positive result seems consistent with other studies that report an association of posterior gamma with perceptual grouping and/or binding (Tallon-Baudry et al., 2005; Vidal et al., 2006). Moreover, the lack of attention effect also seems consistent with studies that report *lateralized* gamma being associated with attention (Doesburg et al., 2008; Gruber et al., 1999; Vidal et al., 2006). Since Laczó et al. only stimulated at the occipital pole, one would not expect them to find effects on attentional orienting.

Multiple studies have demonstrated that both alpha and gamma power over parieto-occipital cortex varies as a function of recorded hemisphere and attended visual hemifield, such that alpha decreases contralateral to the to-be-attended hemifield and increases in the to-be-ignored hemifield (Sauseng et al., 2005; Worden et al., 2000), and the opposite pattern holds true for gamma (Doesburg et al., 2008; Gruber et al., 1999; Vidal et al., 2006). However, it has been less conclusively demonstrated that these modulations are *causally involved* in the increased processing

of some stimuli and increased inhibition of others, that is, attentional selection. It is therefore the aim of the proposed study to modulate neural oscillations in the alpha and gamma bands, using tACS, and observe the consequences of these modulations for behavior.

CHAPTER 2: METHODS

Participants

Twenty-three healthy young adults (ages 18-27; 14 female) participated in all conditions and were included in the analyses. Participants were all right-handed, with 20-20 or corrected to 20-20 vision and no history of psychiatric illness, neurological disorder or incident (such as concussion). The original sample contained 28 participants, but five subjects were excluded because it was unclear if they understood and followed the instructions; their behavioral results in the no-stimulation ('sham') condition showed an inverted validity effect in the endogenous condition, with faster and more accurate responses at the to-be-ignored location. Since the purpose of this experiment was to investigate how neural stimulation may modulate the standard attention cuing effect (i.e., improved performance at the attended location versus the to-be-ignored location in the endogenous condition), we excluded subjects who showed the opposite pattern in the baseline (i.e., sham/no-stimulation) condition.

Design

A within-subject experimental design was used. There were three stimulation conditions and, during each stimulation session, participants completed two spatial cueing tasks—one to assess voluntary attention and one to assess reflexive attention.

In previous rTMS and tACS studies, 10 Hz has been the most commonly used frequency to represent the alpha band (Brignani et al., 2013; Kanai et al., 2008; Romei et al., 2010). This

choice is justified not only because it falls in the middle of the alpha range, but because, barring the concurrent use of EEG (which is not practicable for this study), 10 Hz is likely the best approximation of individual peak alpha (Haegens et al., 2014). Thus, 10 Hz was used in the proposed study to approximate alpha.

The choice of frequency to approximate gamma was made more difficult by the fact that the band is very wide (30 – 120 Hz) and attention has been associated with oscillatory activity in a number of sub-bands within this range. However, those studies that looked specifically at focused attention (Doesburg et al., 2008; Gruber et al., 1999; Vidal et al., 2006) found that synchrony was most prominent in the lower part of the gamma range, around 40 Hz. Since we were interested in selective attention, specifically, 40 Hz was chosen as the representative gamma frequency.

In addition to these two conditions, which served as active controls for one another, a sham condition was used. Sham conditions are typical in tACS studies (Brignani et al., 2013; Laczó et al., 2012) and involve turning on stimulation for a brief period (no more than 30 seconds) before gradually ramping the intensity down to zero. This allows for the mild tingling sensation that some participants feel at the onset of stimulation (e.g. - Kanai et al., 2008), which gives the participant the impression that they are being stimulated, but is brief enough as to not have a lasting effect. In this experiment a 25 Hz sham was used, chosen because it is midway between the two experimental stimulations and to ensure that neither of the active stimulation frequencies occurred more often in the experiment.

Both cueing tasks required participants to discriminate between two target types: a circle with a small (45 degree) gap at its bottom and a circle with a large (90 degree or 135 degree) gap

at its bottom. Practice always began with 90 degrees for the large gap. If, after several practice blocks, a participant's accuracy remained below 75%, the large gap was changed to 135 degrees.

In the voluntary task, rather than directing attention with a central symbolic cue on every trial, the target appeared on one side of the display (right or left) on 80% of all trials. The more likely side changed every 20 trials, alternating between left and right. This change was indicated by an arrow that appeared at the center of the screen before each chunk of 20 trials. Note that most studies of voluntary orienting cue the subject to shift their attention on every trial (e.g. - Jonides, 1981). We chose to manipulate voluntary attention in a blocked fashion because changes in alpha power during a shift of attention (decrease in power over the contralateral hemisphere) are opposite those observed during the sustaining of attention (increase in power over the ipsilateral hemisphere) (Rihs et al., 2009). As the hemisphere of stimulation would by necessity stay the same throughout a block, clearer conclusions could be drawn from a paradigm that engaged only one part of this process (sustaining attention). Targets that appeared on the predicted side were termed valid, while targets that appear on the opposite side were termed invalid. Thus, the voluntary task followed a 2 (validity: valid, invalid) x 2 (target side: left, right) x 3 (stimulation condition: 10 Hz, 40 Hz and sham) within-subjects factorial design.

The reflexive task employed non-predictive, peripheral onset cues, similar to those that have been used in previous studies of reflexive attention (Jonides, 1981; H. J. Müller & Rabbitt, 1989; Posner, 1980). The goal here was to assess the effect of alpha and gamma oscillations on resistance/susceptibility to distraction. To assess how response to the peripheral cue changes with time, two cue-target stimulus onset asynchronies (150ms and 300ms) were used, to assess the time-course of this process. These times were selected to evenly divide the post-cue interval between 0 and 300ms after which a reversal of the typical cueing effect is known to emerge

(Klein, 2000), which was not of interest in this study. Targets that appear on the same side as the preceding cue were termed cued, while targets that appear on the opposite side were termed uncued. Thus, the design of the reflexive task was 2 (target cuedness: cued, uncued) x 2 (target side: left, right) x 3 (stimulation condition: 10 Hz, 40 Hz and sham), within subjects.

After practice, the experiment consisted of 6 blocks: 1 reflexive and 1 voluntary for each stimulation condition. Which task comes first was counterbalanced between participants. The order of the stimulation conditions was counterbalanced as follows (with A=10 Hz, B=40 Hz, and C=Sham): ABC, BCA, CAB, CBA, BAC, ACB. Subjects were assigned in that order as they are enrolled (and after every 6th subject, the sequence repeated).

The dependent measures were the continuous variables reaction time and accuracy. Reaction times were measured in milliseconds and refer to the manual response time (button press) that the subject makes upon discriminating the target, measured from time of target onset. Accuracy refers to the percentage of targets accurately discriminated by the subject.

Materials & Procedure

Experiment sessions were conducted in an electrically shielded room. Visual stimuli were presented on a CRT monitor positioned 75cm from the participant. Participants received, at a minimum, 2 practice blocks: one for each task (voluntary and reflexive). This was to allow them to get used to the task and to covertly orienting their attention (with eyes fixed on the central cross). If the participant's accuracy on the practice for either condition is less than 75%, the task instructions were either clarified or the large gap changed from 90 to 135 degrees, depending on what was needed. The practice block for that condition was then repeated to ensure that the

participant was able to perform at an acceptable level before beginning the experiment proper. Practice trials were not analyzed.

The experimental blocks of the voluntary task consisted of 80 trials each, yielding 8 left invalid, 8 right invalid, 32 left valid and 32 right valid trials. The experimental blocks of the reflexive task consisted of 64 trials, yielding 16 left uncued, 16 right uncued, 16 left cued and 16 right cued targets.

Stimuli were presented and responses recorded using Presentation software (v.18.1; www.neurobs.com). The trial sequence for reflexive task (Figure 1) took place on a static, gray background (RGB = 75, 75, 75) with a white fixation cross and two white peripheral boxes. Trials began with a 1000ms inter-trial interval (ITI), followed by a 500ms fixation period, after which the cue (four dots centered on the outer edges of one box) appeared for 34ms, followed by an inter-stimulus-interval (ISI) of either 116ms or 266ms, resulting in a stimulus onset asynchrony (SOA) of either 150ms or 300ms. The target was then presented for 50ms. Participants were required to indicate whether the gap was large or small as quickly as possible. Trials timed out after 1500ms. The voluntary task was much like the reflexive task, with the following exceptions. There was no peripheral cue: an added delay of 150ms or 300ms still occurred, but without a cue. The target appeared on one side of the screen on 16 out of every 20 trials (80%) and this side changed every 20 trials. The change was indicated by an arrow that appeared above fixation for 1500ms before the start of the trial, pointing left or right, with the corresponding word inscribed.

Stimulation was delivered using the NeuroConn DC-Stimulator Plus. Electrode pads were affixed to the scalp using Ten20 conductive paste. The smaller (5 x 5 cm), stimulating

electrode was placed over location P6 of the 10-20 standard system for electrode placement, corresponding roughly to the right angular gyrus (Herwig, Satrapi, & Schönfeldt-Lecuona, 2003). The larger (5 x 7 cm), reference electrode was placed over Cz, at the intersection of sagittal and coronal midlines. The pads were placed at the beginning of the experiment session, but stimulation was not applied during practice. In all three stimulation conditions, the current had a maximum amplitude of 1mA (2mA peak-to-peak). In the sham condition, 25 Hz stimulation was applied for 30 seconds and then ramped down to achieve the light itching sensation that some individuals feel at the beginning of stimulation. In all cases the block was only started 45 seconds to one minute after the beginning of stimulation so that the sham condition had no ongoing stimulation during the block.

CHAPTER 3: RESULTS

Manual reaction times for correct trials were first submitted to a $2 \times 3 \times 2 \times 2$ analysis of variance (ANOVA), with factors of attention condition (endogenous, exogenous), stimulation (alpha, gamma, sham), visual field of target (left, right), and validity (valid, invalid). All results here are reported with Greenhouse–Geisser correction for non-sphericity, where applicable. The omnibus analysis resulted in significant main effects of attention condition ($F(1,22) = 7.67, p = .011$) and validity ($F(1,22) = 20.78, p < .001$). The main effect of visual field did not approach significance ($F(1,22) = 0.05, p = .827$), and the main effect of stimulation condition was not significant ($F(1.62,35.65) = 2.04, p = .142$). Critically, however, there was a significant three-way interaction between attention condition, stimulation condition, and validity ($F(1.67,36.83) = 3.53, p = .047$). The only other significant interaction was between attention condition and validity ($F(1,22) = 5.17, p = .033$). To further analyze the three-way interaction, we performed separate analyses for each of the stimulation conditions versus the sham condition (note, these following analyses would be most comparable to previous stimulation studies that only used one stimulation frequency along with sham stimulation).

In the analysis of just the 40 Hz (gamma) stimulation versus sham, the $2 \times 2 \times 2 \times 2$ ANOVA consisted of the factors attention condition (endogenous, exogenous), stimulation (gamma, sham), visual field of target (left, right), and validity (valid, invalid). This analysis revealed significant main effects of attention condition ($F(1,22) = 8.38, p = .008$), validity ($F(1,22) = 10.60, p = .004$), and stimulation ($F(1,22) = 4.40, p = .047$). The main effect of visual field again did not approach significance ($F(1,22) = 0.02, p = .888$). Again, however, there was a

significant three-way interaction between attention condition, stimulation condition, and validity ($F(1,22) = 5.14, p = .034$). There were no other significant main effects or interactions, although the two-way interaction of attention condition by validity was near significant ($F(1,22) = 4.26, p = .051$). As illustrated in Figure 2 (top), the three-way interaction was driven predominantly by the effect of gamma stimulation on invalid trials in the endogenous condition. Paired t-tests confirm this, as the only significant difference was that the responses to invalid trials in the endogenous condition were faster in the gamma stimulation condition, relative to that same type of trial in the sham condition ($t(1,22) = -2.179, p = .040$).

In the analysis of just the 10- Hz (Alpha) stimulation versus sham, the $2 \times 2 \times 2 \times 2$ ANOVA consisted of the factors attention condition (endogenous, exogenous), stimulation (10 Hz, sham), visual field of target (left, right), and validity (valid, invalid). This analysis revealed significant main effects of attention condition ($F(1,22) = 5.97, p = .023$) and validity ($F(1,22) = 19.65, p < .001$). The main effects of stimulation ($F(1,22) = 0.004, p = .95$) and visual field did not approach significance ($F(1,22) = 0.001, p = .98$). There was a significant attention condition by validity interaction ($F(1,22) = 6.99, p = .015$), and interestingly, there was a marginal three-way interaction between attention condition, stimulation condition, and validity ($F(1,22) = 3.23, p = .086$). There were no other significant main effects or interactions. As illustrated in Figure 2 (bottom), the marginal three-way interaction was driven predominantly by the effect of alpha stimulation on invalid/uncued trials in the exogenous condition. Paired t-tests confirm this, as the only difference approaching significance was that the responses to invalid trials in the exogenous condition was slower in the alpha stimulation condition, relative to that same type of trial in the sham condition ($t(1,22) = 1.87, p = .074$). Although any interpretation of these marginal effects must proceed with caution, it is potentially interesting that the only effect approaching

significance following alpha stimulation was in the uncued location target trials in the exogenous attention condition, whereas the only significant effect of gamma stimulation was for the invalid trials in the endogenous attention condition.

Analyses of the accuracy of responses was also performed, using the same omnibus ANOVA as described above, a $2 \times 3 \times 2 \times 2$ ANOVA, with factors of attention condition (endogenous, exogenous), stimulation (alpha, gamma, sham), visual field of target (left, right), and validity (valid, invalid). This analysis revealed no significant main effects (attention condition: $F(1,22) = 2.124$, $p = .159$; validity: $F(1,22) = 0.006$, $p = .939$; visual field: $F(1,22) = 0.622$, $p = .439$; stimulation condition: $F(2,44) = 1.098$, $p = .335$). There were also no significant interactions (all p values $>.08$), as accuracy was consistently high across all conditions (mean percent correct = 94.1%; range across conditions = 91.9–96.5%). The critical three-way interaction between attention, stimulation, and validity did not approach significance ($F(1.65,36.26) = 0.864$, $p = .411$). Therefore, there was no evidence for a speed–accuracy tradeoff that may have affected the reaction time results.

CHAPTER 4: DISCUSSION

Different frequencies of neural oscillation are thought to play distinct roles in facilitating visuospatial attention, but support for such a causal relationship must include experiments that directly manipulate those oscillations. Here we have found support for a causal role of 40 Hz oscillations in posterior parietal cortex. Stimulation at this frequency in the gamma band led to faster reaction times to invalidly cued targets than did sham stimulation. Further specificity of this effect was seen in that it only affected reaction times in the voluntary attention task. Critically, we did not find any differences in reaction times between 10 Hz and sham stimulation during the voluntary attention task, suggesting that the 40 Hz effect was truly frequency-specific not just a general effect of stimulation vs. sham.

This effect of 40 Hz stimulation that we observed complements Landau et al. (2007), who found that voluntary shifts of attention, including voluntarily reorienting from an invalidly cued location, were associated with an increase in gamma-band power. Landau et al. found that this pattern was associated with both orienting in a voluntary task and reorienting from an invalidly cued location in both voluntary and reflexive tasks. Our voluntary task involved maintaining attention at one location on most trials, and only required an attentional shift on invalid trials, so we cannot speak to how 40 Hz stimulation might influence cued voluntary orienting. Moreover, during 40 Hz stimulation, we might expect an improvement on the reflexive task in shifting attention following an invalid exogenous cue, as this is arguably a voluntary shift, and Landau et al. found increased gamma-band activity in this condition as well. However, for reasons that are not clear, our exogenous task failed to produce the normal cueing effect in the sham condition,

such that reaction times were no slower on uncued trials than cued trials (whereas we did get the normal cueing effect during no-stimulation pilot testing). Since participants' attention was apparently not captured to the invalid location, we could not observe how 40 Hz stimulation might have influenced reorienting to the target. Finally, although gamma oscillations have previously been associated with perceptual grouping and/or feature binding (Tallon-Baudry et al., 2005; Vidal et al., 2006), we did not observe evidence of any enhancement in this regard. That is, if feature binding had been induced by gamma stimulation, we might expect target discriminability to improve, which would lead to overall faster reaction times during 40 Hz stimulation, as compared to sham. The fact that we did not find such an effect is in line with Vidal et al. (2006), who found that attentional focusing was associated with lower gamma over PPC, but that visual grouping was associated with higher gamma at occipital sites. It also agrees with the findings of Laczó et al. (2012) that 60 Hz stimulation over the occipital pole, but not 40 Hz, improved contrast sensitivity without having any effect on orienting. Laczó et al. also found no effect of 80 Hz stimulation, suggesting an upper limit for the frequencies involved in perceptual feature processing. Our understanding of the role of gamma oscillations in visual processing would benefit from a design that fully crosses gamma frequencies (40, 60 and 80 Hz) with stimulation site (occipital, parietal).

While we found no significant effects of 10 Hz stimulation, as compared to sham, there was a marginal effect, such that invalidly cued targets in the reflexive task were, on average, responded to more slowly during 10 Hz stimulation than during sham. Acknowledging the tenuousness of interpreting marginal effects, possible interpretations of these mean differences will be briefly considered here. Alpha oscillations are frequently associated with active suppression of perceptual input (Haegens et al., 2012; Mathewson et al., 2011; Mathewson,

Gratton, Fabiani, Beck, & Ro, 2009). It may therefore be plausible that the 10 Hz stimulation condition made target discrimination more difficult, making the (apparently weak) effects of the exogenous cue noticeable. This account is in line with Brignani et al. (2013), who found that 10 Hz, but not 25 Hz, stimulation impaired detection performance. Brignani et al. also found that 6 Hz stimulation worsened performance; the reason for this is less clear, as theta oscillations are more typically associated with frontal contributions to attention (Aftanas & Golocheikine, 2001), alertness (Braboszcz & Delorme, 2011) and cross-frequency coupling (Landau, Schreyer, Van Pelt, & Fries, 2015).

It is somewhat surprising that our manipulations did not yield any significant effect of visual hemifield. Previous studies, already described in this paper, have found that stronger alpha power in one hemisphere is associated with enhanced processing in the ipsilateral hemifield (Kelly et al., 2006; Rihs et al., 2009; Thut et al., 2006). Conversely, stronger gamma in one hemisphere has been associated with enhanced processing in the contralateral visual hemifield (Bosman, Lansink, & Pennartz, 2014). One might therefore expect that applying stimulation over right parietal cortex would cause faster reaction times ipsilateral to alpha stimulation and faster reaction times contralateral to gamma stimulation. While our results agree with the overall associations of gamma facilitating and alpha inhibiting, these effects appear to have manifested uniformly throughout the visual field in the present study. Reasons that this may be the case are explored below.

One fact that might explain the lack of lateralized effects is that, while both hemispheres make contributions to attention, more attentional processing is thought to be done in right parietal cortex than left (Heilman & Van Den Abell, 1980; Shulman et al., 2010). Stroke patients with lesions that include right PPC tend to suffer severe neglect of the left side of space. While

patients with left PPC lesions may have some initial difficulty in attending to the right side of space, they are far more likely to recover the capacity to attend to the whole visual field (Mesulam, 1981; Vallar, 1998). This difference has been attributed to the idea that, whereas left PPC facilitates attending to the right side of space only, right PPC is involved in attending to both hemifields. It is therefore plausible that our choice of right-hemisphere stimulation had an effect on both hemifields. This interpretation would seem to be contradicted by Romei et al. (2010) who found that 10 Hz rTMS to PPC, but not 5 Hz or 20 Hz, slowed responses to targets appearing in the hemifield contralateral to stimulation, whether stimulation was applied over left or right PPC. However, it may point to important differences between rTMS and tACS. The pattern of stimulation is much different in rTMS, both in that it is not sinusoidal (as argued before) and in that it must be applied in short trains of pulses, separated by periods of no-stimulation. Though Romei et al. did find frequency-specific effects, and rTMS has been shown to entrain neural oscillations at the stimulation frequency (Thut, Veniero, et al., 2011), the short-lived nature of each stimulation burst may cause entrainment that isn't as strong (and thus doesn't affect both hemifields in right PPC stimulation), or leads to less propagation of stimulation effects than in tACS.

Much research supports the idea that the effects of neural stimulation propagate to influence regions beyond the site of stimulation. For example, applying sub-threshold 1 Hz rTMS for 1500 pulses has been shown to increase interhemispheric EEG-EEG coherence (Strens et al., 2002) and 20 minutes of tDCS to the left DLPFC can increase functional resting-state connectivity between hemispheres. In the case of both techniques, stimulation is applied in a relatively continuous fashion (the rTMS is applied at a rate of 1 pulse per second, rather than in pulse trains) for an extended duration, as was our tACS. Although to my knowledge the effects of

unilateral tACS on hemispheric coherence have yet to be studied, it seems plausible that stimulation of only the right PPC may have affected both hemispheres similarly.

Another possibility is that, rather than stimulation propagating to the contralateral hemisphere, the contralateral hemisphere had sufficient time to habituate and “rebalance” to the stimulation. Models have been proposed that emphasize inhibitory (Kinsbourne, 1977) or excitatory (Bloom & Hynd, 2005) connections in describing callosal interhemispheric communication. A recent study by Chechlacz, Humphreys, Sotiropoulos, Kennard and Cazzoli (2015) proposed a hybrid excitatory-inhibitory model and showed that the individual variation in effects of 10 Hz rTMS to right- and left-PPC can be predicted from the macrostructure and microstructure of the corpus callosum. The total volume (macrostructure) and anisotropic properties (microstructure) could be used to predict, respectively, the degree of excitatory and inhibitory connections between hemispheres, which, in turn, could predict how well the unstimulated hemisphere is able to rebalance. The extended duration of tACS, by contrast, might allow the rebalancing process to occur regardless of the structural properties of each individual’s corpus callosum.

Our results make a novel contribution to the attention literature in demonstrating support for the causal involvement of low-gamma, but not alpha, PPC oscillations in the voluntary shifting of visual attention. The 40 Hz stimulation condition facilitated responses to invalidly cued targets in the voluntary task. However, due to limitations of the voluntary attention task, we cannot distinguish whether this effect was due to improved disengagement, reorienting or some combination of both. Future studies could make this distinction by employing a voluntary cueing task, rather than a voluntary sustained attention task. If 40Hz stimulation facilitates reorienting, we would expect to see faster response times to both validly and invalidly cued targets. If,

however, the benefit was mostly an improvement of disengaging, we would expect to see benefits only on invalid trials. As mentioned earlier, in this experiment we would have expected 40 Hz stimulation to speed responses to invalidly cued targets in the *reflexive* task, as well, but were unable to test this prediction because our exogenous cue was not effective, and reaction times may have been at floor. Although it isn't clear why the task didn't work as it did during pilot testing, for future studies we will have to revisit the design of this task to ensure a stronger exogenous cueing effect.

Future studies should also explore different stimulation parameters. Due to practical constraints, we were only able to stimulate the right PPC, but not the left. Given that the right hemisphere is more strongly implicated in attention, we might expect to see different effects of stimulation over left PPC, including, potentially, hemifield-specific effects. Moreover, paradigms that stimulate both hemispheres and/or different regions of one hemisphere simultaneously will be critical in advancing our understanding of neural oscillations in attention. Theta (4 - 8 Hz) oscillations, in particular, are thought to facilitate communication between different regions which give rise to attention by increasing phase coherence between different prefrontal regions (van de Vijver, Ridderinkhof, & Cohen, 2011) as well facilitating longer-range communication (Von Stein & Sarnthein, 2000; Wang, Viswanathan, Lee, & Grafton, 2016). Future studies may investigate the causal involvement of theta oscillations by stimulating multiple areas in- or out-of-phase with one another.

More complex techniques of tACS should be also considered in the longer-term. Future studies may aim to explore the role of cross-frequency coupling in attention (Szczepanski et al., 2014) by employing more complex patterns of stimulation. Ideally, future studies should employ simultaneous EEG-tACS in order to monitor the effects of stimulation in real-time, as well as to

tailor stimulation to each participant's characteristic frequencies of oscillation. Imaging the effects of neurostimulation, using electrophysiological measures or fMRI and related measures, will be critical in helping us understand exactly what tACS and other neurostimulation techniques do, and ultimately interpreting the resulting changes in behavior. Although for the most part the use of these techniques is largely limited to theoretical research, a deeper understanding of the mechanisms by which they act will allow for practical applications with clear theoretical motivations and expected outcomes.

APPENDIX A: FIGURES

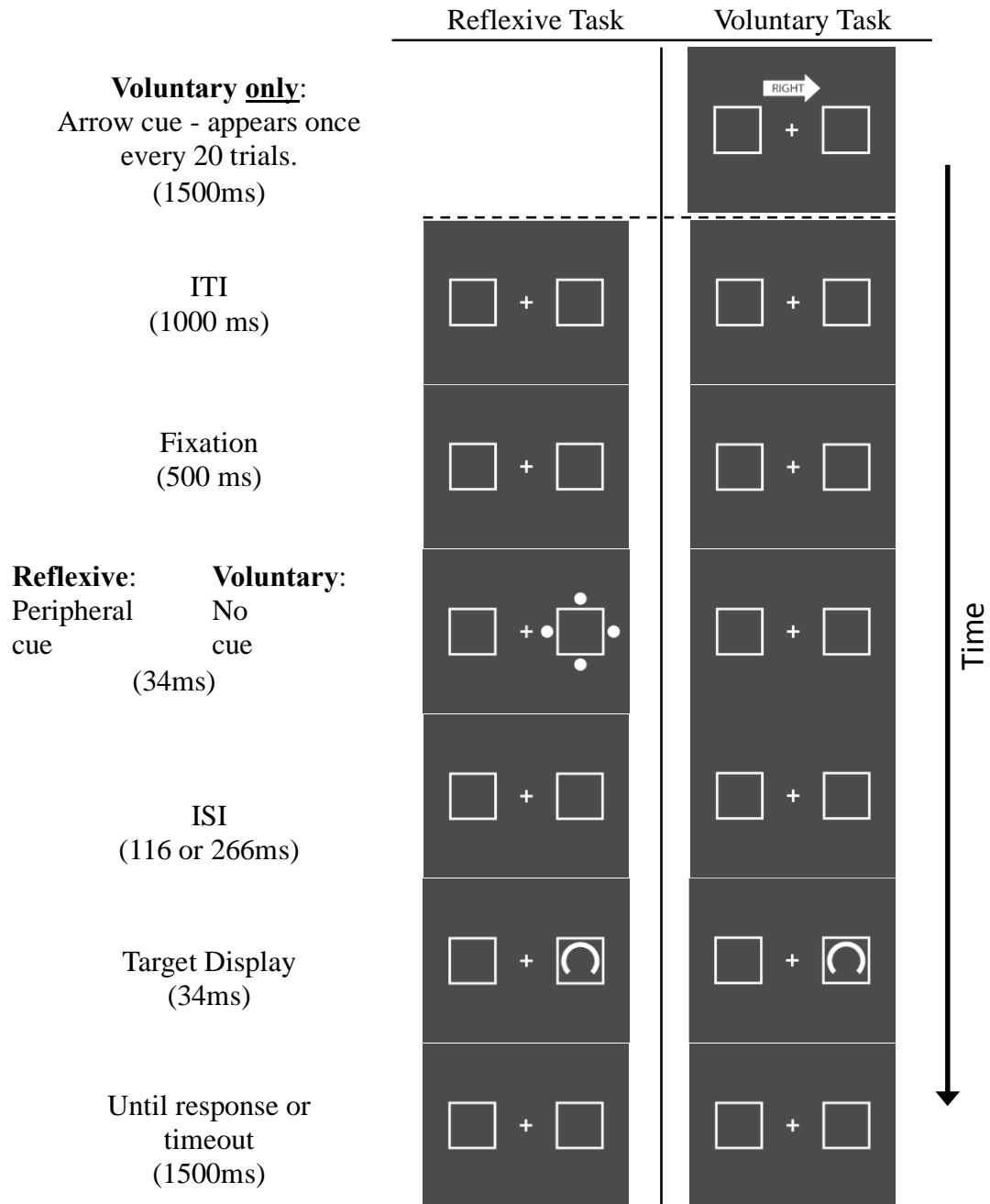


Figure 1. Example trial sequences for the reflexive and voluntary tasks. Note that the stimuli have been enlarged for ease of viewing.

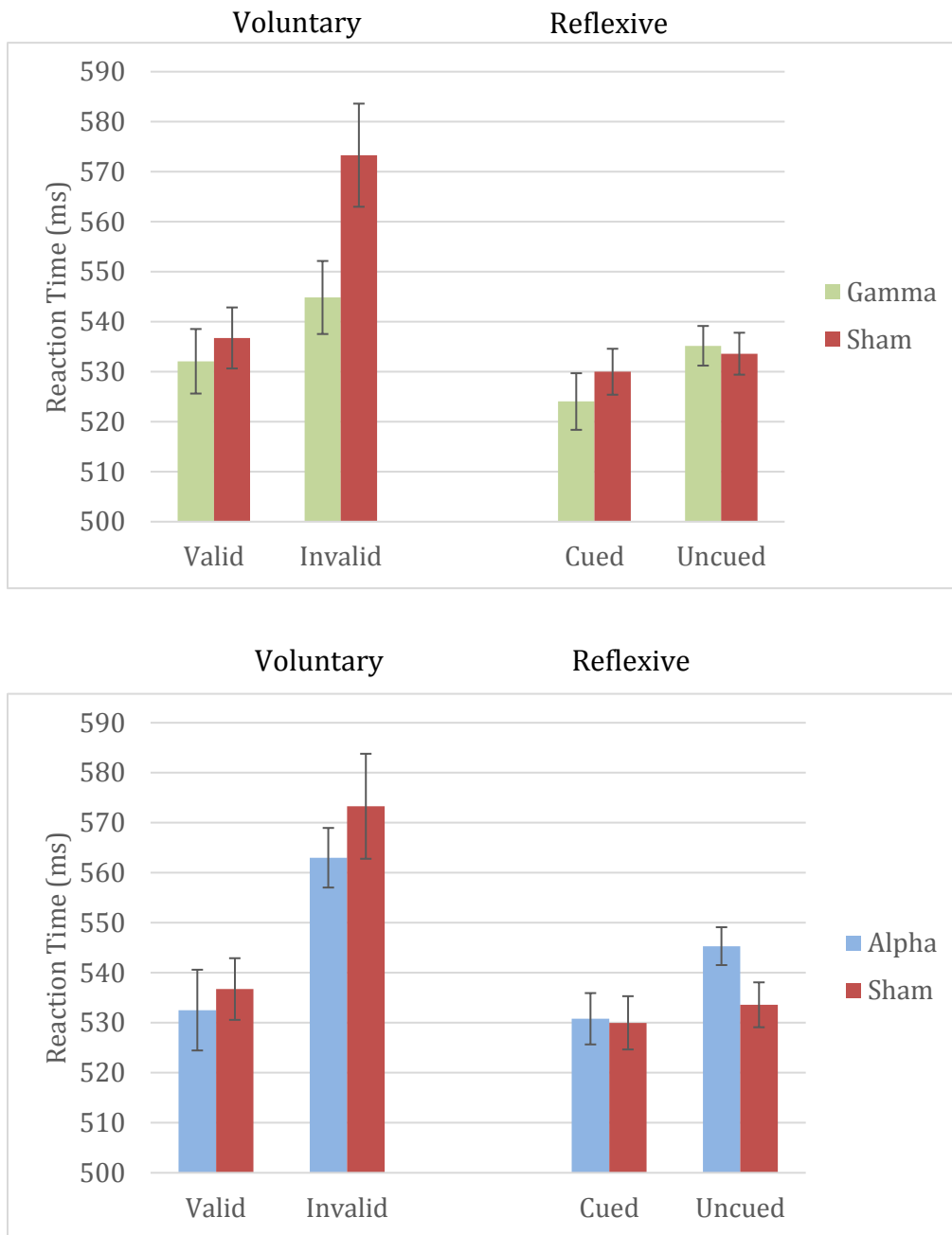


Figure 2. Mean reaction times for all conditions in the voluntary (left) and reflexive (right) tasks. Top: Gamma vs Sham Bottom: Alpha vs Sham

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