The effect of alpha stimulation of the visual cortex on visual search efficiency.

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Submitted: July 15th 2013

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Top-down attention seems to facilitate visual processing at the attended area but inhibit it at unattended locations. Oscillations in the alpha band (8-12 Hz) seem to correlate with the suppression of irrelevant information as a result of attention. To investigate the hypothesis of alpha suppression, oscillations were actively manipulated using transcranial alternating current stimulation (tACS). Attention was measured using a conjunction search task while participants received tACS at alpha, theta or sham frequency. The visual search task was lateralised and the occipital cortex was stimulated either left or right. Stimulation affecting the target was compared with stimulation affecting the irrelevant distractors. No effect of stimulation hemisphere or stimulation frequency on search efficiency was found. These results fail to verify the hypothesis of alpha suppression. Further research is needed to investigate the tACS induced manipulations and the role of alpha in attention.

INTRODUCTION

Imagine you drive a red car and parked it amidst a parking lot in front of an office. As the car is surrounded by black ones, your car is very easy to spot, and will seem to pop out the scene for people passing by. Now imagine that when you return to your car, most black cars have disappeared and the parking lot is now full of colored cars. You will have to put more effort into searching for your car and it will take you some time to check out which of the red cars is yours.

The example above illustrates how we can voluntarily guide our attention by actively looking for something, and how sometimes our attention is automatically drawn to saliencies in our environment. The capture of attention by stimuli is referred to as bottom-up attention and is thought to happen at an early sensory stage, as it happens automatically and irrespective of our intentions and goals. In contrast, the active direction of attention is called top-down attention and is seen as an active voluntary process. Top down attention is dependent on our intentions, goals and strategies and is therefore thought to be a higher cognitive function.

The visual search task is used to investigate the different dynamics of top-down and bottom-up attention (Treisman & Gelade, 1980). In this task, participants were instructed to find a specific stimulus, the target. An array that might contain the target and a number of distracting stimuli was presented. Participants had to make a button response to report presence or absence of the target and reaction times were measured. The effect of different distractors on search time revealed involvement of different forms of attention. When all the distractors had the same appearance and differed only from the target on basis of a single feature, the target seemed to pop out (look for a red L surrounded by green L's) and was found almost instantly. During this pop-out search, reaction times were not only very low, but also independent of the number of distractors (Treisman & Gelade, 1980). This constant reaction time suggests parallel bottom-up attention processes are used in pop-out search.

Conjunction search is used to investigate top-down attention. When the distractors were different from each other, the target was defined by a conjunction of features (look for a red L surrounded by green L's and red T's) and could not be found by looking only to one single feature. During this type of search reaction times were high and increased with the number of distractors (Treisman & Gelade, 1980). This suggests attention is deployed to each item in the search display separately in order to find the target, and thus indicates involvement of top-down attention. A quantative measure for this deployment of attention is the search efficiency, or search slope measured in ms per item. The search slope is calculated by dividing the reaction time by the number of items on screen and increases as the task gets harder (Wolfe, 1998). The search slope in conjunction search is a measure for efficiency of top-down attention.

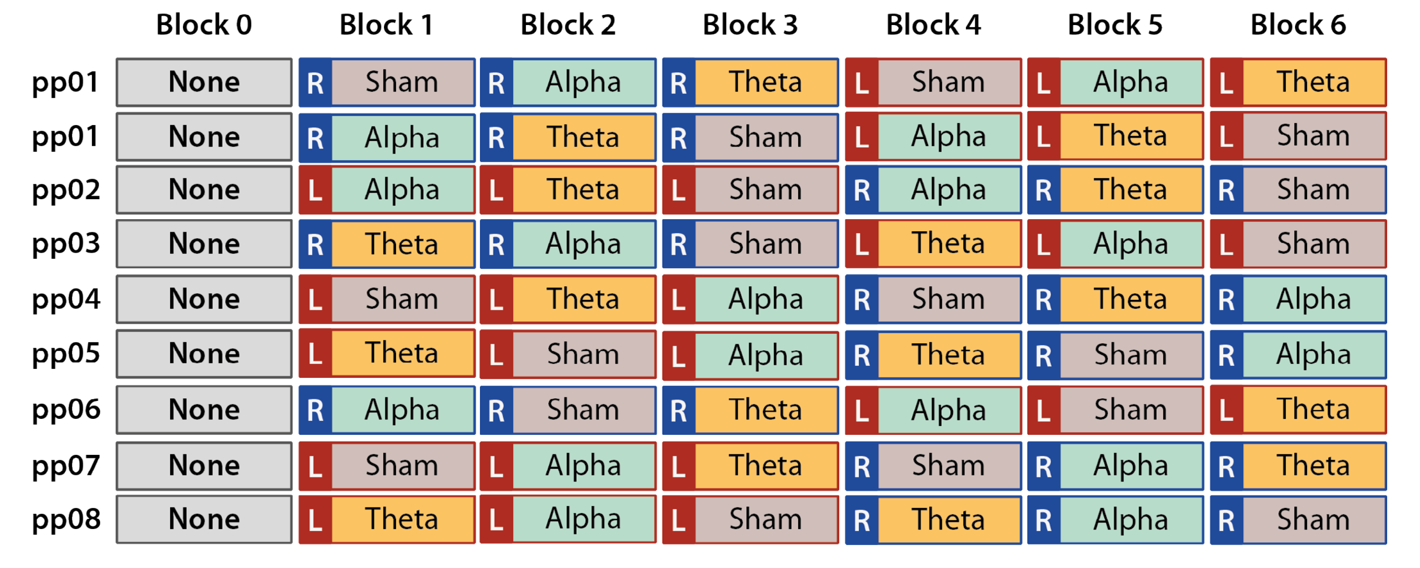
Top-down attention selectively enhances perception at the attended location. Eriksen and Hofmann (1972) showed participants an array of letters, of which one was the target (indicated by a cue). Participants had to report which letter this was. When the cue was presented before onset of the letter array, participants responded faster to the target as they were already attending the correct location. Posner et al. (1978) used a cue to direct participants' attention to either the left of the right side of the visual hemifields, or nowhere specifically and asked them to react to a target stimulus. When the cue correctly indicated the location of the target, participants responded faster and more accurate compared with a neutral cue. On the other hand, when the cue was incorrect, and the target appeared in the uncued hemifield, reaction times were lower than with a neutral cue. Attention thus facilitates visual perception locally and inhibits perception at unattended areas.

The selective enhancement of top-down attention is likely the result of modified early visual processing. The fact that attending to a location is able to affect the most basic visual operations, such as responding to a stimulus (Eriksen & Hoffman, 1972) or detecting a target (Treisman & Gelade, 1980), suggests that attention affects visual processing at a very early stage. The Event Related Potential (ERP) during a visual search task provides electrophysiological support for this hypothesis. An occipital ERP component was found, just before target detection during conjunction search (Luck, 1994). Since the occipital cortex compromises mostly of primary visual areas (Clarke & Miklossy, 1990), this component may well reflect modifications of early visual processing. Moreover, this occipital ERP component was preceded by a component originating from the parietal cortex (Luck, 1994). The parietal cortex has often been associated with directing attention (Hopfinger et al., 2000; Colby et al., 1999; Bressler et al., 2008) and this signal may thus reflect the source of the visual modulation. Taken altogether, the parietal cortex seems to modulate processing in early visual areas during top-down attention.

Another electrophysiological signal often associated with attention is the power or amplitude of oscillations in the alpha band (8-12 Hz). When participants were instructed to attend to one side of the visual hemifield, alpha power was elevated in the occipital hemisphere ipsilateral to the attended hemifield (representing the unattended hemifield) (Kelly et al., 2006; Sauseng et al., 2009). Furthermore, this increase in alpha power was dependent of the number of items to ignore (Sauseng et al., 2009). As alpha power increases when information becomes irrelevant, elevated alpha power may indicate suppression of visual information. Correspondingly, alpha amplitude has earlier been associated with inhibition of irrelevant brain areas in working memory tasks (Klimesch, 1999). Alpha oscillations are associated with attention and alpha suppression may be an important mechanism of attentional top-down modulation.

Current evidence for alpha suppression is observational and is therefore unable to prove a causal relationship between alpha oscillations and attention. It remains unclear whether attention-induced changes in alpha power are the cause of behavioral findings or just an artifact. A technique to actively manipulate brain oscillations is transcranial Alternating Current Stimulation (tACS). During tACS, an alternating current is applied over the scalp and brain areas in between the electrodes are supposed to pick up the injected frequency (Neuling et al., 2012). Proof of principle was demonstrated by Zahele et al. (2010). After 10 minutes of tACS at alpha frequency, alpha power in the EEG was significantly elevated. In addition to this, Laczo et al. (2012) demonstrated that tACS is able to affect visual processing. tACS at occipital cortex resulted in the perception of phosphenes, but only at specific frequencies (Laczo et al., 2012). Using tACS, alpha rhythms can be manipulated to obtain causal evidence for their role in top-down attention.

To test the hypothesis of alpha-suppression as a mechanism of top-down modulation, this study investigated the effect of alpha stimulation on the performance on a visual search task. A lateralized search display was used and hence the target was always located in either the left or right visual hemifield. To investigate the effect of alpha stimulation on irrelevant and relevant representations, the left and right occipital cortex were stimulated separately. Target present trials were stimulation affected the target representation were compared with trials were stimulation affected the representation of irrelevant distractors. Stimulation was expected to affects representation of the target on trials where the target appeared contralateral to the stimulated hemisphere. When, on the other hand, the target appeared ipsilateral to stimulation, the representation of irrelevant distractors was influenced by stimulation. The effect of stimulation on search efficiency during conjunction search was examined to investigate the dynamics of top-down attention. Since alpha is thought to suppress information, it is expected that search efficiency will decrease for contralateral alpha stimulation but increase for ipsilateral stimulation, as irrelevant information is suppressed. Theta and sham are used as a control, and



	Block 0	Block 1	Block 2	Block 3	Block 4	Block 5	Block 6
pp01	None	R Sham	R Alpha	R Theta	L Sham	L Alpha	L Theta
pp01	None	R Alpha	R Theta	R Sham	L Alpha	L Theta	L Sham
pp02	None	L Alpha	L Theta	L Sham	R Alpha	R Theta	R Sham
pp03	None	R Theta	R Alpha	R Sham	L Theta	L Alpha	L Sham
pp04	None	L Sham	L Theta	L Alpha	R Sham	R Theta	R Alpha
pp05	None	L Theta	L Sham	L Alpha	R Theta	R Sham	R Alpha
pp06	None	R Alpha	R Sham	R Theta	L Alpha	L Sham	L Theta
pp07	None	L Sham	L Alpha	L Theta	R Sham	R Alpha	R Theta
pp08	None	L Theta	L Alpha	L Sham	R Theta	R Alpha	R Sham

Figure 1.1 Stimulation counterbalancing scheme. All subjects started the second session with a training session (Block 0). Next, one of the two hemispheres was stimulated for the first three blocks, the other one was stimulated the next three blocks. The order of the three stimulation frequencies (sham/theta/ alpha) was the same for both hemispheres.

no differences are expected between contra- and ipsilateral stimulation at theta or sham frequency.

Methods and Materials

Participants

Eighteen people participated in this study (5 male, 13 female). Participants were 19-24 years of age (mean=21,6). Only right-handed adults with normal or corrected-to-normal vision were allowed to participate in this experiment. Participants were screened for potential risk factors (such as epileptical history, skin problems or pregnancy) by means of a questionnaire, and were excluded if any of the factors was reported. Participants signed a written consent and were paid for their efforts. The experiment was approved by the ethics committee of the department of Psychology of the University of Amsterdam.

Procedure (& Design)

Participants were invited for two 2-hour sessions, separated by at least a week. The first session was a training session, in which participants were trained on the visual search task (2 blocks; 8 minutes each) and introduced to transcranial Alternating Current Stimulation (tACS). Participants received tACS at 16 Hz for 30 seconds using the electrode configuration Cz - Oz. Perception of phosphenes was noted and participants were able to make a well informed decision of participation.

The real experiment was conducted during the second session. Participants first performed a training block without stimulation followed by six blocks with stimulation.

Next to alpha stimulation, sham and theta were used to control for frequency-unspecific effects. Each type of stimulation was applied two out of six blocks for every participant. The exact order of the three stimulation frequencies was varied by counterbalancing all possible combinations of these three stimulation types across participants.

The determined order of alpha, theta and sham was repeated two times for each participant. During the first three blocks, one hemisphere was stimulated, and the other one was stimulated during the last three blocks, the frequencies in the same order. To distinguish the temporal effect from hemispheric effects, the hemisphere used in the first block was counterbalanced across participants (figure 1.1). After completion of the six blocks, participants were debriefed and filled out a questionnaire to test whether they experiences stimulation after-effects.

Experimental Paradigm

Each block consisted of four search tasks (of 96 trials each), one for each possible target (2 colors x 2 shapes). The order of those 4 search task was randomly determined at the beginning of each block. At the beginning of each search task, a brief target instruction was shown for 15 seconds. Each trial started with a fixation cross and after a variable delay of 500 - 900 ms, the search display appeared. Subjects had to make a response using the left and right shift keys (target present/target absent) but the next trial automatically started after a delay of 2800 ms. The exact allocation of the keys (left/right) to the responses (target present/absent) was randomly determined for each participant. A full factorial design of search type (shape:color:conjunction = 1:1:2) x target presence (target:blank = 2:1) x target hemifield (left/right) x setsize (6/12/18/24) resulted in 48 unique trials. Every unique trial was presented twice during each search task; the 96 trials of each search task were presented in a random order. (Figure 1.2)

Stimuli

Stimuli were horizontal and vertical (1.46° x 0.58°) rectangles in red (R=200, G=0, B=0) or green (R=0, G=139 B=0) presented on a grey (R=113 G=113 B=113) background. Each search display consisted of 6, 12, 18 or 24 items evenly distributed over an imaginary left and right grid. Both grids were 8.74° x 17.38° and separated by 4.38° in the center. Stimuli were randomly placed on one of the two grids, with a minimum distance of 1.46°

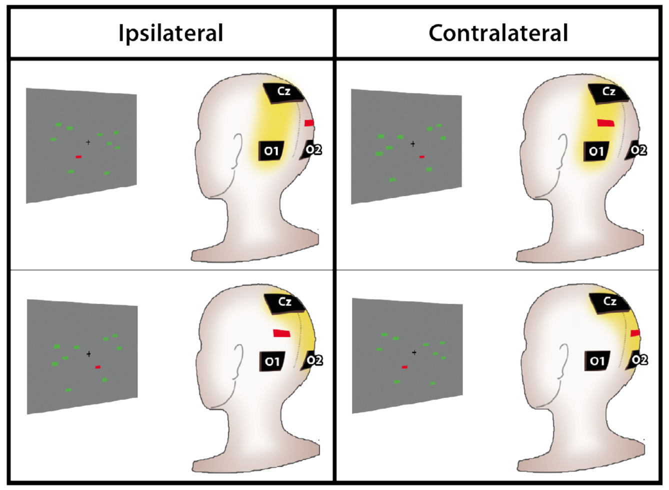


Figure 1.3 Electrode positions and the two conditions for target position with respect to stimulation. The electrode setup Cz – O1 was used for left hemispheric stimulation and Cz – O2 for right. In the contralateral condition, the target was represented by the hemisphere affected by stimulation. In the ipsilateral condition, irrelevant distractors were represented by the stimulated hemisphere.

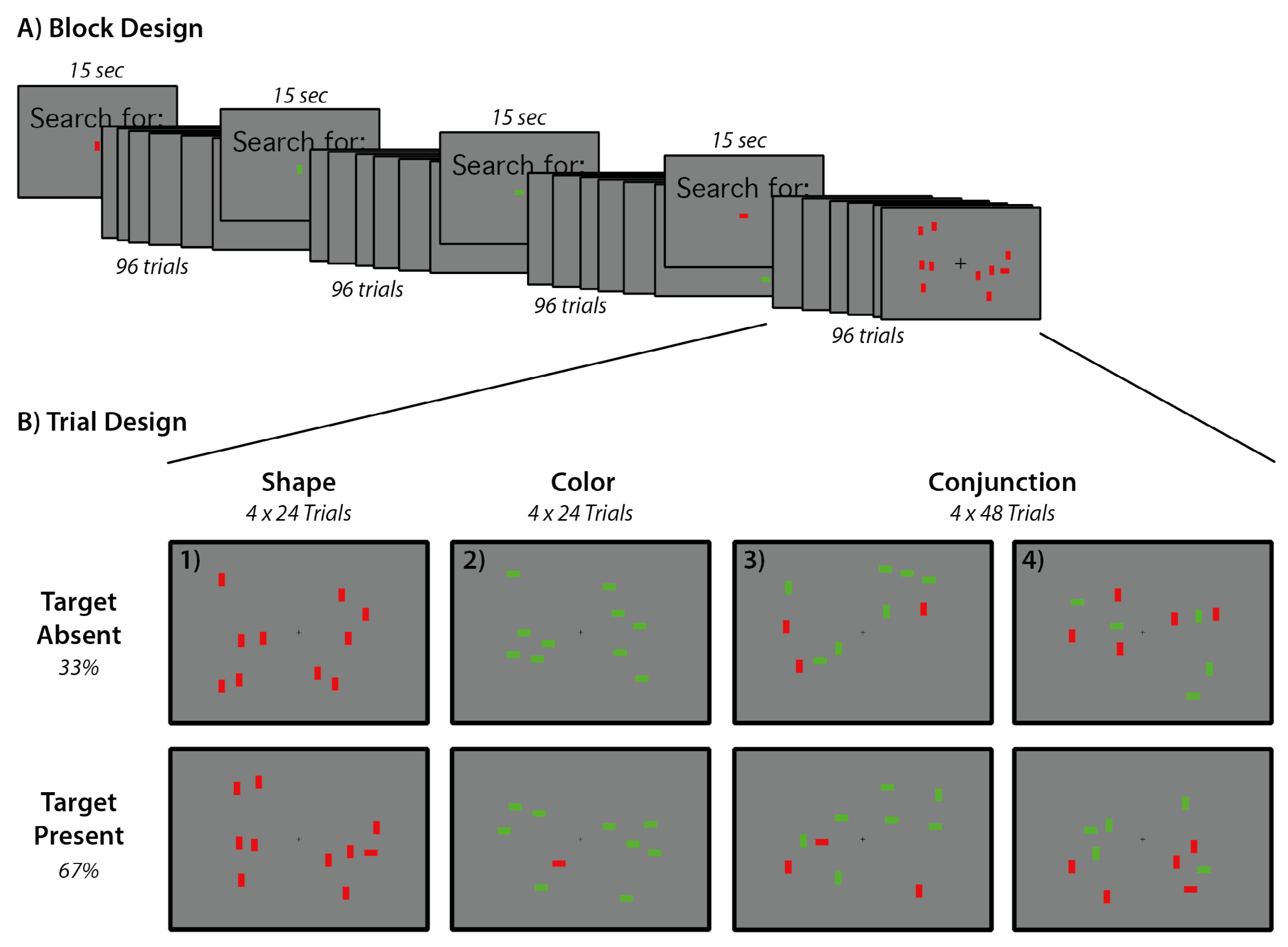


Figure 1.2 A) Study Design. Each block consisted of smaller blocks of 96 trials for all possible targets presented in a random order. Target instructions were presented for 15 seconds in order to avoid fatigue. The order of the targets for the four trial sequences was determined randomly each block

Figure 1.2 B) Search displays for each search task. The target is a red vertical rectangle for all the 96 trials.

with respect to other stimuli. For both feature searches (shape and color), all distractors were equal to the target for the irrelevant feature, and differed from the target on the irrelevant feature. When the target would be vertical and red, for example, distractors on shape trials would be horizontal and red, whereas distractors on the color trials would be vertical and green (Figure 1.2B 1 , 2). For conjunction trials, all three distractors were presented. It was randomly determined whether the shapes (Figure 1.2 B, 3) of the colors (Figure 1.2 B, 4) would be evenly represented for each trial.

Stimulation

A 7x5cm reference electrode at Cz was always used. Electrodes of 3x3 cm for stimulation of either the left or right hemisphere were placed between O2 and PO8 or between O1 and PO7 respectively. (Figure 1.3)

A frequency of 10.0 Hz was used for alpha stimulation, whereas 6.5 Hz was used for theta-stimulation. A ramp-up/ramp-down period of 100 cycles was used and stimulation intensity was 1000 µA (current density: 62,5 µA/cm2) Sham stimulation consisted of a 8 seconds ramp up, followed by a 5 second ramp down. During the stimulation impedance was checked at very low current intensities.

Equipment

Electrical stimulation was controlled by a Neuroconn DC-PLUS Stimulator. Experiments were conducted using customized software compiled on Matlab 7.11.0.584 (Mathworks inc.) using Psychtoolbox 3.0.10. Software was running on a 32-bits computer running Windows 7 (version 6.1) and stimuli were presented on a 23" Asus VG-236H monitor running at 120 Hz. Responses were collected using a Dell SK-8135 USB keyboard.

Data Analysis

Only trials with a reaction time between 200-2800 ms were included for data analysis. For each participant, trials with a reaction time differing more than 2,5 standard deviations from the mean were excluded from analysis. Due to unexpectedly high reaction times, stimulation sometimes ended before completion of the search task. To avoid a loss of power, all trials conducted after offset of stimulation were excluded.

First, the relationship between set size and reaction times was examined for target present / target absent and color / shape / conjunction search separately. During feature search no slope was expected and when this assumption was met, only conjunction trials with a target present were examined.

As a measure of top-down attention, search efficiency was calculated for all experimental conditions during conjunction search. Search efficiency was calculated for all unique combinations of participant, stimulation frequency, stimulation hemisphere separately and will be determined by linear regression of reaction time and set size for relevant trials. Next, a repeated-measures ANOVA was conducted for stimulation frequency x stimulated hemisphere x target position.

In order to explore possible post-stimulation effects, search slopes were calculated during sham-blocks following stimulation of the frequency of interested (theta or alpha). Post-alpha search slopes were calculated during sham-blocks following alpha stimulation and post-theta search slopes are calculated during sham-blocks after theta blocks.

RESULTS

Inclusion

All 18 participants finished the study. One participant failed to receive right-hemispheric due to a too low skin conductance. However, the results obtained during left hemispheric stimulation were included since search efficiency was calculated for each block independently. Performance was high (94,5%) and did not vary across different types of stimulation (see supp fig1. for performances under different stimulation conditions). Figure 2.1 shows the distribution of reaction times for correct and incorrect trials. Of the 40386 trials, only the 38918 correct trials were included in the data analysis. After exclusion of reactions times 2,5 standard deviations away from the mean, 38918 trials remained. Trials conducted after offset of stimulation were removed leaving 81,7% of the initial data for data analysis (31439 trials).

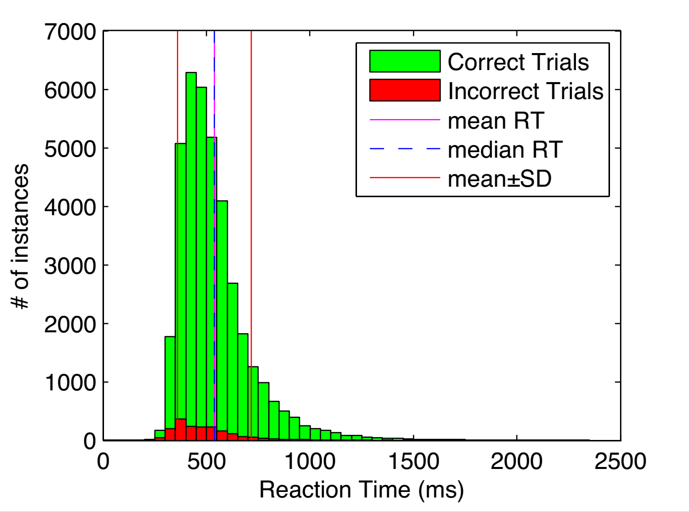


Fig 2.1 Distribution of reaction times. n = 40386. Overall proportion of correct trials was 94,5%. Mean, median and SD are depicted for the subset of correct trials.

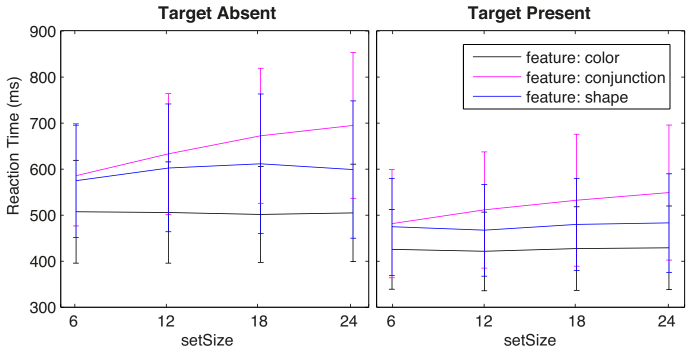


Figure 2.2 Mean Reaction times as a function of setsize. Pooled average of all participants and stimulation settings. Bars indicate standard deviation.

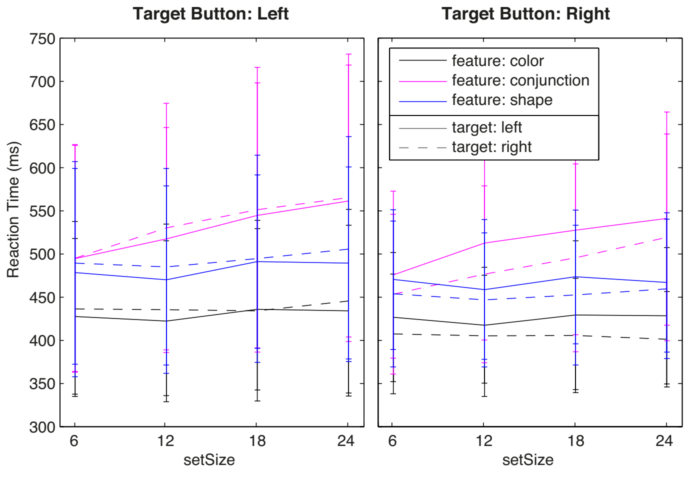


Fig 2.3 Effect of target position (left/right) and button position (left/right). Participants respond faster when the target was on the same side as the button they have to press to indicate it's presence. Eight participants were assigned to the right button and for the left button n =10. Reaction times are the average of all particpants in each condition and bars indicate standard deviation.

General Search Performance

Figure 2.2 shows the mean reaction times as a function of set size for conjunction-, shape- and color–search trials, target present and target absent. For all search-types, reaction times were higher in the target absent trials compared with target present trials. As expected, reaction time increased with set size in conjunction search but were independent of set size for feature search.

Button Position

Figure 2.3 shows the effect of button position and target hemifield. Participants responded faster when the target appeared at the same side as the button the had to press to indicate it's presence. This trend was visible for almost all individual subjects (See supp fig 2 for individual results). The decrease in reaction time for targets at the side of the button was larger for participant which had to press a right button compared to participants pressing the left button.

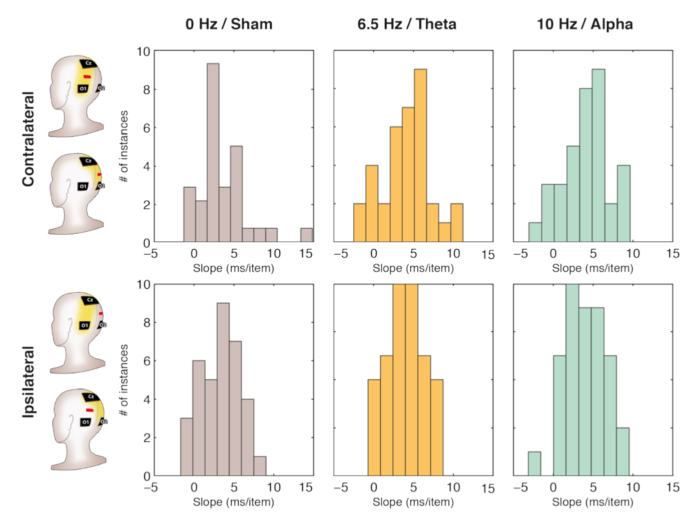


Fig 2.4 Distribution of search slopes. For each subplot n=36.

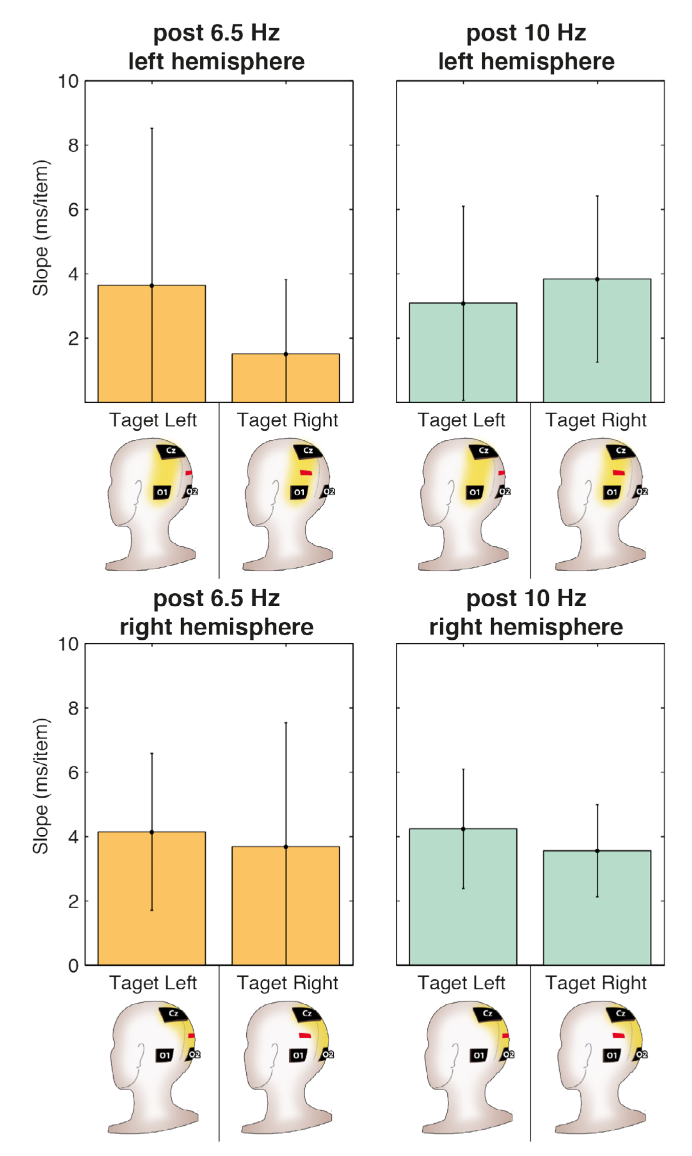


Figure 2.6 Post Stimulation effects. Search slopes were calculated over de sham blocks after stimulation. For each bar, n = 8. Bars indicate standard deviation.

Search Slopes

Search slopes were calculated by linear regression of set size and reaction time. See supplementary figure 3 for individual scatterplots and fitted slopes. Figure 2.4 shows the distribution of search slopes for all participants and stimulation settings. The range -2 – 10 ms is consistent with previous research (Wolfe et al., 1998).

Stimulation Effects

Figure 2.5 shows the effects of stimulation on search slope. Although ANOVA showed no significant effect of stimulation frequency (F(2,32)=0,887 p=0,442), there seemed to be a trend of stimulation frequency. Search slopes for alpha seemed higher (mean 4,027±408) compared with sham (mean = 3,502±500) and theta (mean = 3,882±328). Contra- and ipsilateral stimulation effects were examined by the interaction target hemifield * stimulation hemisphere which showed no effect (F(1,16)=0,224 p=0,643). The interaction of this effect and stimulation frequency was neither significant (F(2,32)=0,39 p=0,962).

Search slopes did not differ significantly between targets contra- and ipsilateral to stimulation. Search slopes seemed to increase for ipsilateral targets compared with contralateral targets in the theta and sham condition, but this trend was not visible in the alpha condition.

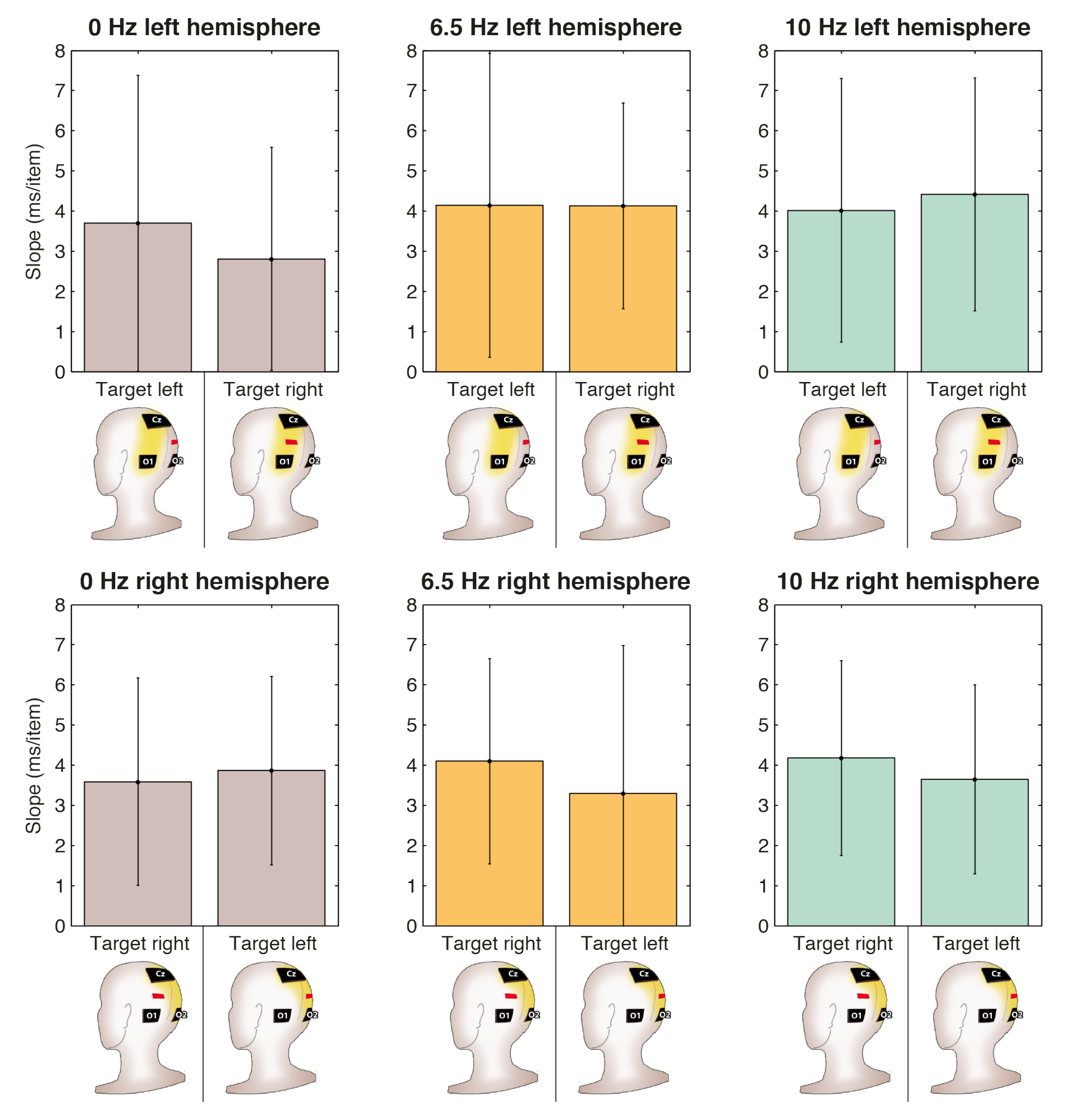


Figure 2.5 Exploration of the effects. For each bar n=18. Bars indicate standard deviation.

Post-Stimulation Effects

Figure 2.6 shows the post stimulation effects. Search slopes during sham were calculated, and the preceding stimulation frequency was used for analysis. During alpha stimulation, search slopes were higher for contralateral targets compared with ipsilateral targets. This effect was consistent across the two stimulated hemispheres. During theta stimulation, search slopes differed between contra- and ipsilateral targets as well. These effects were inconsistent across the stimulated hemispheres but big in magnitude.

Discussion

To investigate the hypothesis that attention influences early visual processing by controlling alpha oscillations, search efficiency was measured during alpha, theta and sham stimulation. Search efficiency was compared between contralateral stimulation, where the hemifield containing the target was affected, and contralateral stimulation, affecting the irrelevant hemifield. During alpha stimulation, search efficiency did not differ between contra- and ipsilateral stimulation. There thus seems to be no functional difference between alpha stimulation of relevant of irrelevant visual areas in this task. Furthermore search performance during alpha and theta stimulation did not differ from sham stimulation. Oscillations in the occipital cortex thus do not seem to play a role in attention during this task.

The tACS used in this experiment may have failed to affect the desired areas. Due to the complex anatomy of the brain and its surrounding tissues, it is hard to predict the current flow between two tACS electrodes. Computer models revealed that brain areas spatially in between the electrodes are not always the ones most affected, and are sometimes barely affected at all (Neuling et al. 2012, Wagner et al. 2007). So far, no information about the effectiveness of the used electrode setup exists yet. Since the electrodes at O1 and O2 are located almost directly on top of the visual cortex, the tACS current may not have affected it. A more lateralized setup using PO7 and PO8 may have been more effective. However, the electrode configuration Oz – Cz is known produce tACS effects (Laczo et al., 2012, Zaehle et al., 2012) and this electrode setup is very similar to the O1 / O2 – Cz setup. The Oz – Cz setup could not be used in this study since it does not allow for separate stimulation of the left and right hemisphere. Further research combining tACS and EEG is needed to examine the effect of a lateralized electrode setup.

The distinction between stimulation of the left and right hemisphere may not have been as accurate as expected. Oscillations in one hemisphere may have influenced oscillations in the other hemisphere. Therefore, oscillation injection in one hemisphere might have resulted in enhancement of that oscillation in both hemispheres. If so, a general effect of alpha stimulation on search performance is expected compared with sham and theta. Although this effect was not significant, there seemed to be a trend of alpha slowing supporting the idea that lateral alpha injection lead to enhanced alpha power in the entire visual cortex. This trend is thus consistent with the theory of alpha suppression but should be reproduces. To confirm the hypothesis of alpha suppression, the effect of occipital alpha stimulation on a normal (not lateralized) visual search task should be examined.

In addition, parietal alpha may have been equally affected during left and right stimulation. In both stimulation conditions, a reference electrode at Cz was used. This electrode extended 3,5 centimetres to both sides and since this electrode was used for both left and right hemispheric stimulation, the underlying parietal cortex may have been equally stimulated in both conditions. As the parietal cortex is thought to be the source of top-down modulation (Hopfinger et al. 2000, Colby et al., 1999, Bressler et al., 2008), alpha suppression may have occurred equally during left and right stimulation. To investigate the role of parietal alpha oscillations on attention, a P3 – P4 electrode setup should be used to stimulate the parietal cortex (Neuling et al., 2012). If alpha suppression facilitates attention, parietal alpha stimulation should result in increased search efficiency (or decreased search slopes) as the distractors will be better suppressed. These results should be confirmed using a cued response task. It is expected that performance will be more independent of irrelevant (non-target) stimuli during alpha stimulation. By examining the effect of parietal alpha stimulation on attention, the hypothesis of alpha-inhibition can be investigated.

tACS at alpha frequency may not have been able to enhance on going alpha oscillations during the task. The alpha frequency ranges from 8 to 12 Hz and is different for every individual (Berger, 1929). A participant's individual alpha frequency (IAF) is obtained by measuring the EEG signal with the eyes closed (Posthuma et al., 2001; Klimesch, 1999). The tACS induced enhancement in alpha power was measured at individual alpha frequency. (Zaehle et al., 2012) In the current study, a frequency of 10 Hz was used for all participants and due to differences in IAF, this may not have affected all participants equally. Repeating this study with stimulation at IAF will result in a stronger manipulation and may result in significant differences.

Another problem may be that endogenous alpha power might have been to high to be increased any further. Neuling et al (2013) found that tACS could only elevate alpha power when alpha was already low. When subjects had their eyes closed, alpha power increased, and tACS failed to enhance IAF. If alpha suppression is important in visual search, endogenous alpha may have been elevated already and tACS may not have had any effect. Finally, different frequencies within the alpha range may affect different aspects of attention or have no effect at all. Klimesch et al (1998) found that in a cued target task, frequencies below 10 Hz correlated with expectance and alertness, whereas frequencies above 10 Hz did not. Further investigation of the hypothesis of alpha suppression should therefore focus on the individual alpha frequency and the spontaneous alpha levels should be kept low.

It remains unclear whether effects of tACS are optimal during, or after stimulation. The perception of phosphenes by Laczo et al., (2012) was measured during stimulation and stopped right after offset of stimulation. This suggests that effects are only found during stimulation. However, Zaehle et al. (2012) found that IAF was increased post-stimulation; EEG was measured during 3 minutes following ten minutes of tACS (at IAF). This study focused on effects during stimulation but post-stimulation effects were also explored. Although neither stimulation nor post-stimulation effects were found, the post alpha-stimulation trends seemed to be consistent with the hypothesis of alpha stimulation. Nonetheless, this study design was not optimized for examination of post-stimulation effects. Further research is needed to examine the exact timescale of tACS effects. To examine the effect on of tACS on alpha power, EEG could be measured every 2 minutes after on- and off-set of alpha tACS. Similarly, short visual search blocks could be conducted during and after tACS. Investigating the exact timescale of tACS will result in better study design and more accurate interpretation of study results.

Differences in performance between left and right targets, and left and right button presses may reveal a hemispherical dominance for attention systems. Participants who were (randomly) assigned to press the right button were faster than participants who had to press the left button. Furthermore, the decrease in reaction time for targets that appeared on the same side as the button was a lot larger for right-button responders. This result is strikingly similar to Heilman et al (1980) who measured the differences in left and right parietal alpha power as a response to lateralised stimuli. Alpha desynchronisation was largest in the left parietal lobe and the desynchronisation in the right parietal lobe was equal for left and right stimuli. Correspondingly, the areas associated with attention using fMRI were mainly present throughout the left cortex (Hopfinder et al., 2000). Although this evidence suggested lateralisation of attention, tracking of targets seems to happen independent in for the left and right hemifield (Alvarez and Cavanagh, 2004). Further research is needed to examine the exact amount of hemispheric dominance of attention and its electrophysiology.

It is not certain how and if top-down attention was deployed during this task. Contrary to cueing, attention is not directed to a specific spatial location during visual search. Although it is generally accepted that pop-out search is mediated by bottom-up attention, there still is controversy about the deployment of attention during conjunction search. Some experiments suggest conjunction search is a serial, self-terminating process, where each item is checked out independently (Donders, 1968; Treisman & Gelade, 1980) whereas others suggest a combination of different bottom-up mechanisms where top-down attention only guides this process (Wolfe et al., 1980; Bundesen & Petersen, 1983). Discussed evidence of alpha suppression was mainly found during cueing tasks and if this reflects a different process than present in conjunction search, alpha suppression may not be relevant. However, Luck et al. (1994) discovered that the ERP during conjunction search was similar to the ERP during cueing tasks indicating similar neural mechanisms. To confirm this, the role of oscillations in visual search should be measured using EEG. If the role of attention is similar as in cueing tasks, it is expected that alpha is only elevated during conjunction search, but not in pop-out search. The role of alpha tACS on performance during cueing task should also be examined.

tACS stimulation may not only enhance oscillations, but also cause confounding artefacts. Alpha power increase is usually called event related synchronisation (ERS) as it is thought that neurons firing at the alpha rate synchronise resulting in a net increase in amplitude. As most interneurons in the brain are GABA-ergic (Braitenberg & Schuz, 1991), this increased activity may result in increased release of inhibitory GABA leading to alpha suppression. Transcranial Direct Current Stimulation (tDCS) is stimulation like tACS using a constant rather then an alternating current. tDCS is known to affect GABA concentrations in humans (Stagg et al., 2009) and it is therefore very likely that tACS also affects GABA concentrations. This would result in increasing GABA during the conduction of the experiment. Furthermore, it is not clear whether different frequencies have different effects on neurotransmitter concentrations. To examine the exact role of GABA in alpha suppression magnetic resonance spectroscopy (MRS) and magnetoencephalography (MEG) should be used during attentional tasks. Using this approach (Suresh et al., 2009) found that stimulus evoked theta oscillations were correlated with GABA in V1. However, the role of GABA in alpha suppression should still be investigated in humans.

This study failed to demonstrate effects of alpha stimulation on attention. Further research should investigate whether alpha oscillations were not manipulated as expected, or if the manipulations did not have the expected result on attention. Further research should combine attention paradigms with techniques as MRS, MEG and tACS to answer the many questions about the mechanism of attention.

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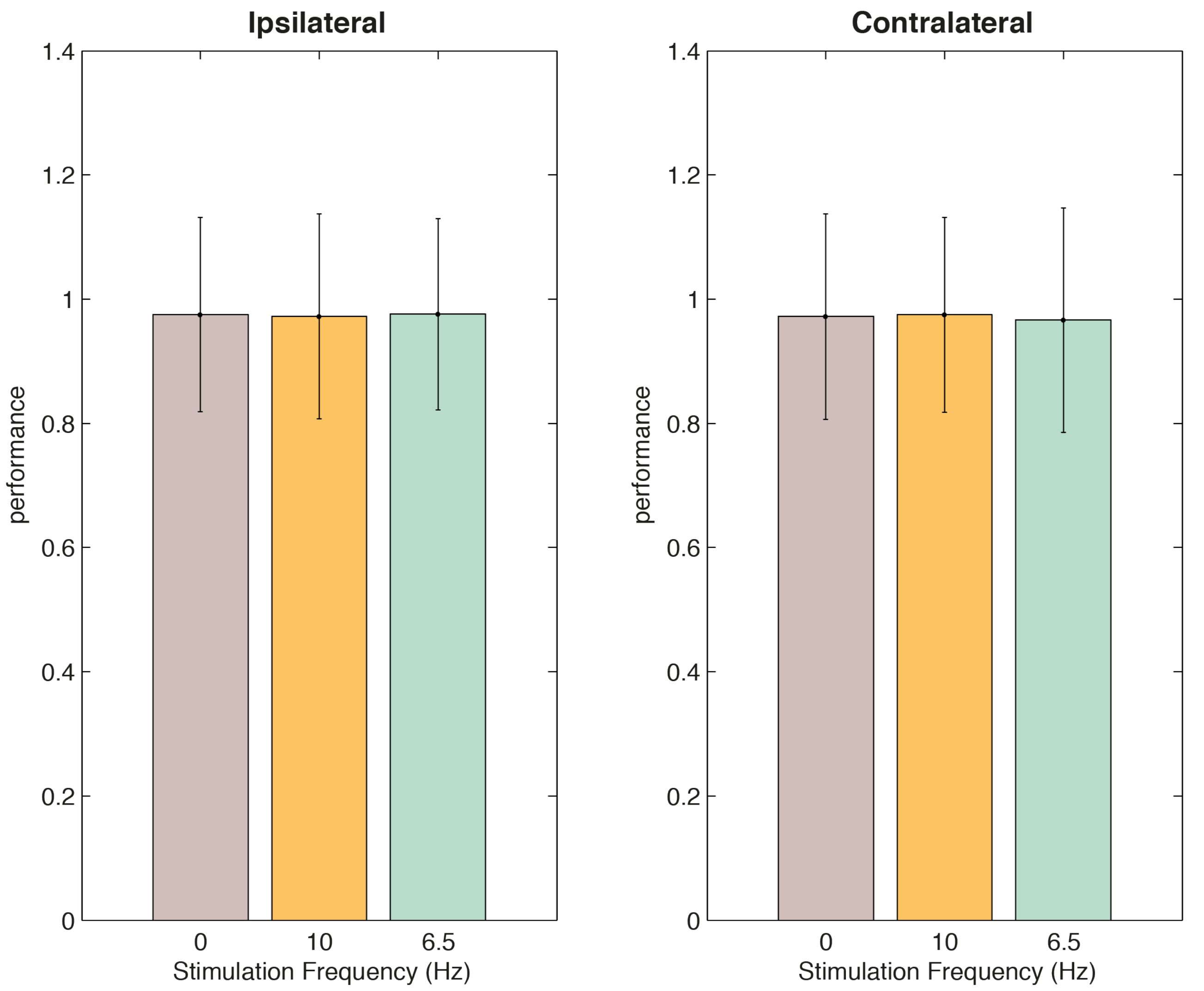
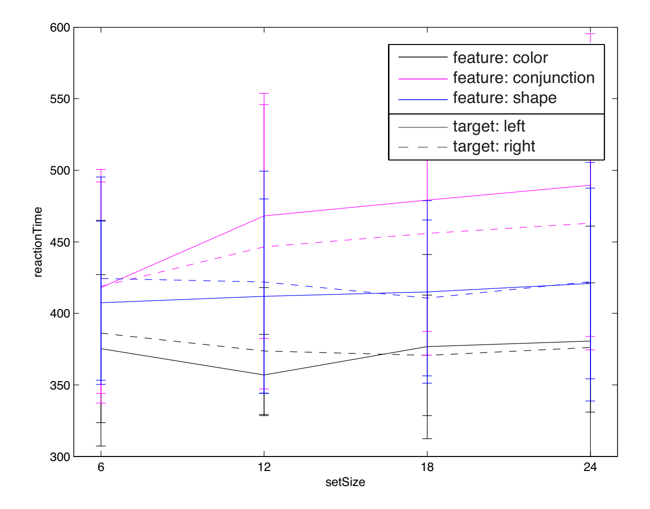
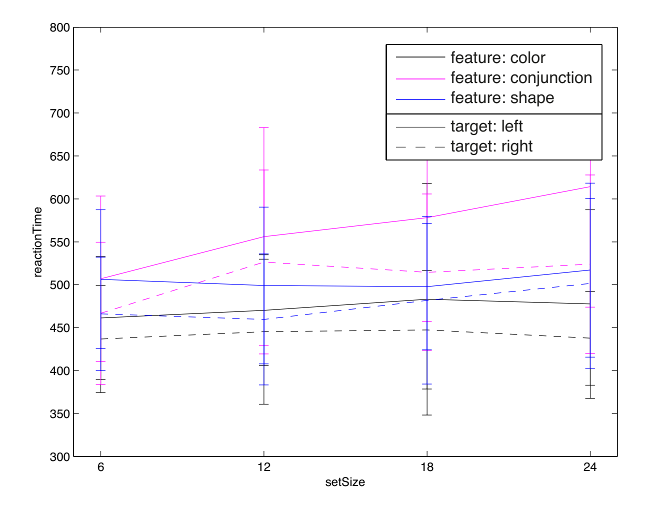


Supp Fig1 Mean performance across conditions. Error bars indicate standard deviation, n=31439



Supp Fig2.01 Effect of target position (left/right) for particpant 01. The targetbutton was located left



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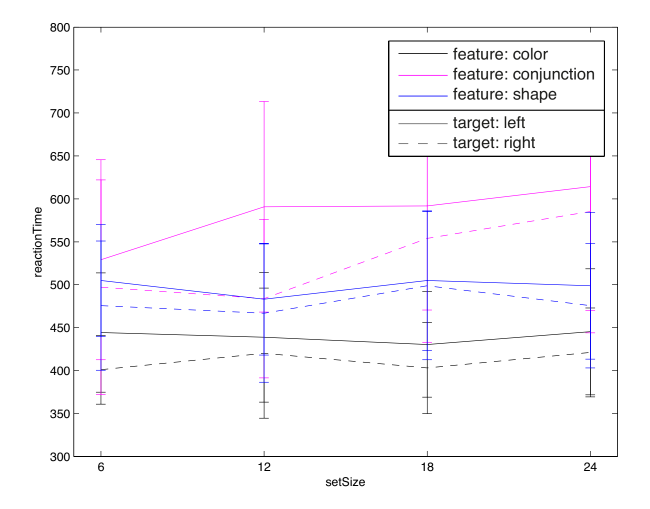
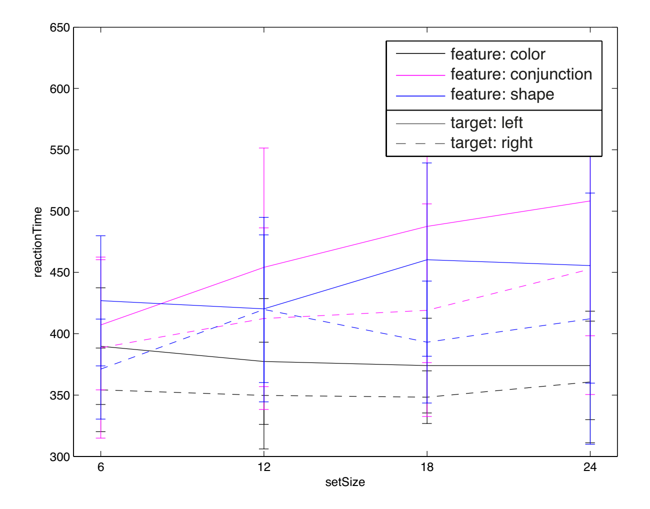
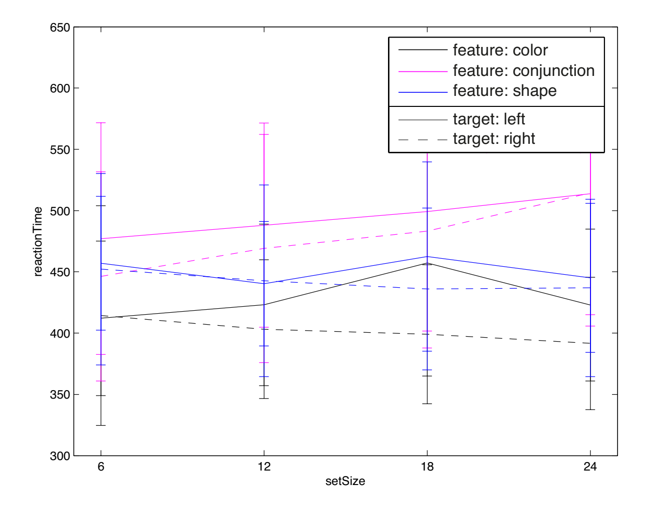


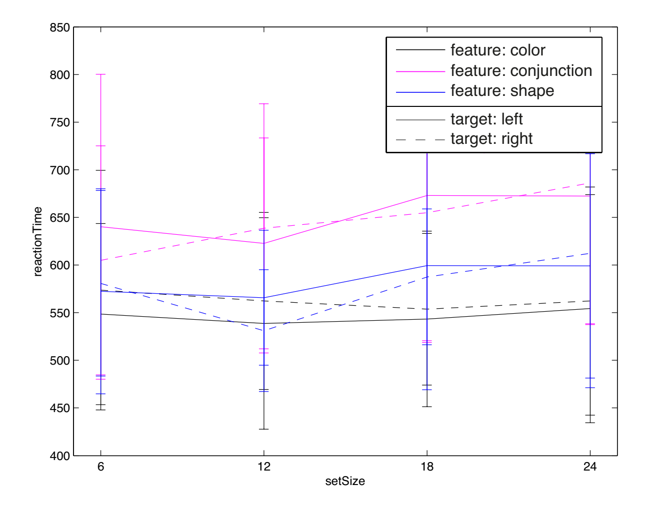
Supp Fig2.03 Effect of target position (left/right) for particpant 03. The targetbutton was located right



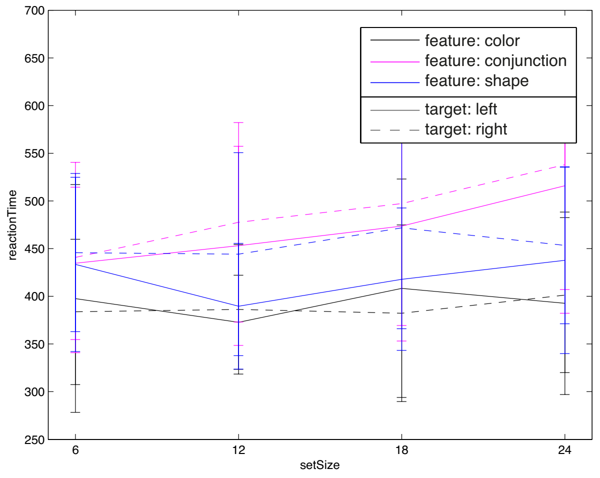
Supp Fig2.04 Effect of target position (left/right) for particpant 04. The targetbutton was located right



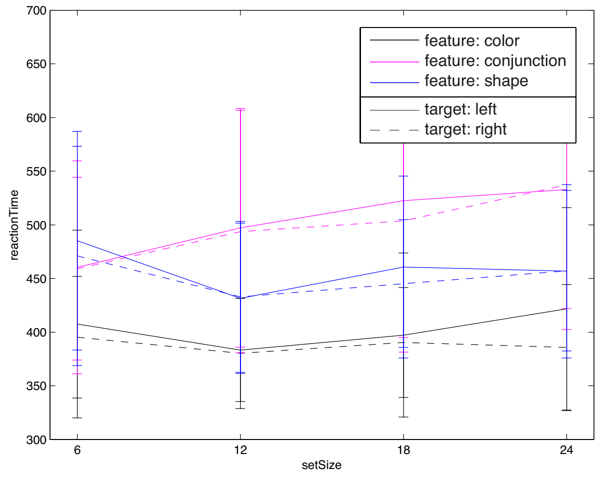
Supp Fig2.05 Effect of target position (left/right) for particpant 05. The targetbutton was located right



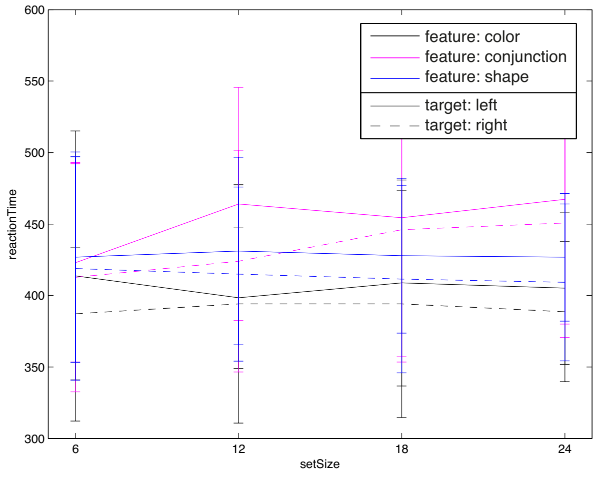
Supp Fig2.06 Effect of target position (left/right) for particpant 06. The targetbutton was located left



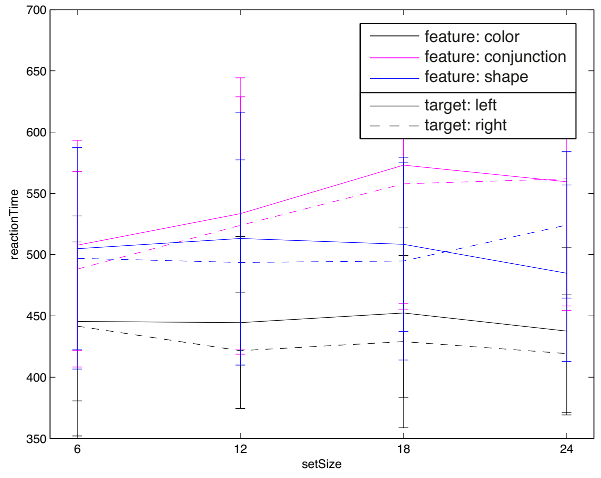
Supp Fig2.07 Effect of target position (left/right) for particpant 07. The targetbutton was located left



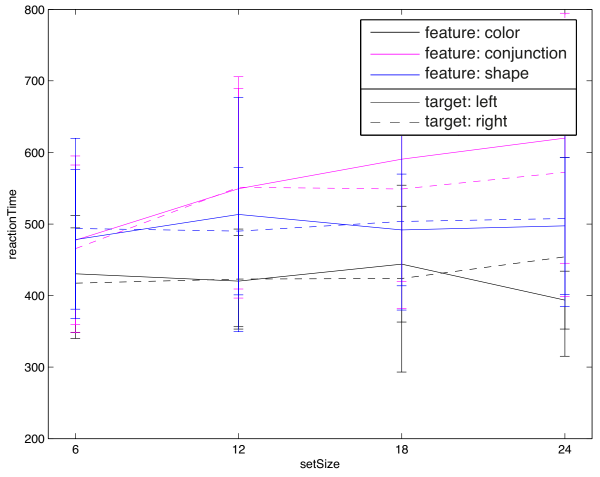
Supp Fig2.08 Effect of target position (left/right) for particpant 08. The targetbutton was located right



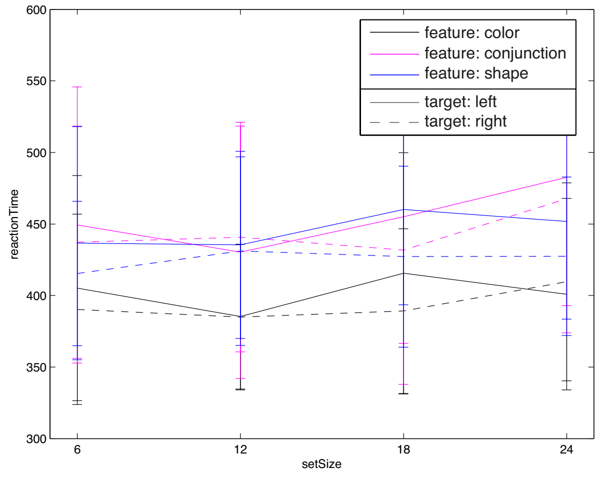
Supp Fig2.09 Effect of target position (left/right) for particpant 09. The targetbutton was located right



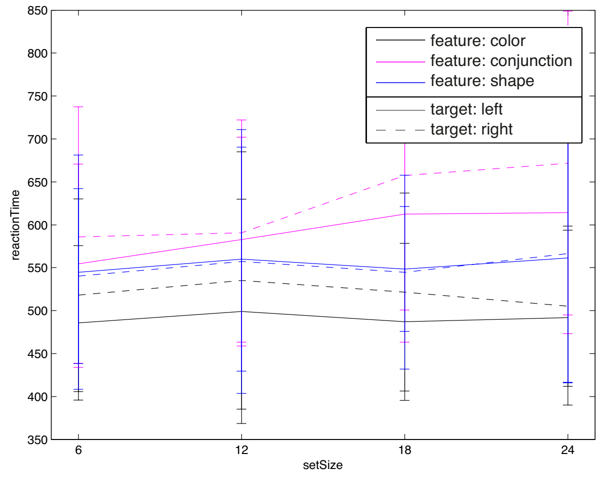
Supp Fig2.10 Effect of target position (left/right) for particpant 10. The targetbutton was located right



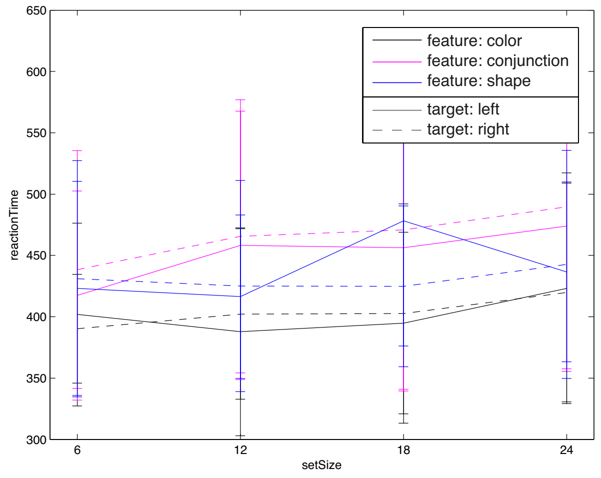
Supp Fig2.11 Effect of target position (left/right) for particpant 11. The targetbutton was located left



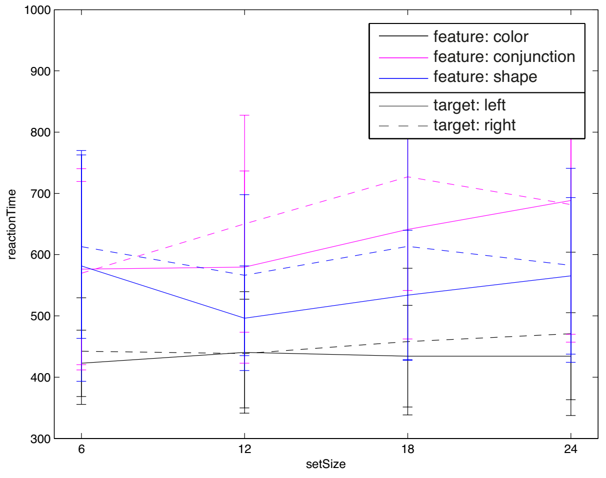
Supp Fig2.12 Effect of target position (left/right) for particpant 12. The targetbutton was located left



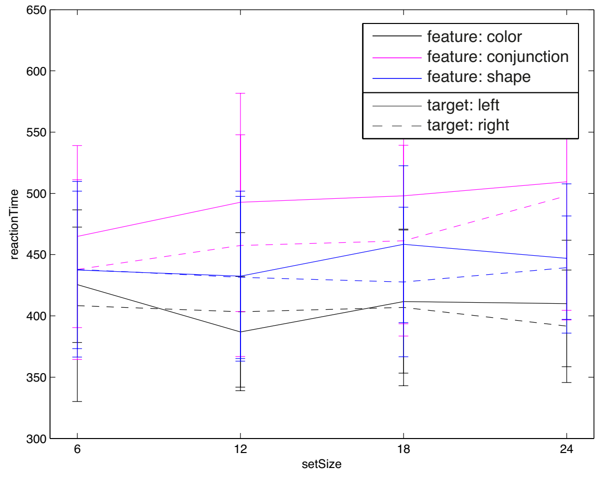
Supp Fig2.13 Effect of target position (left/right) for particpant 13. The targetbutton was located left



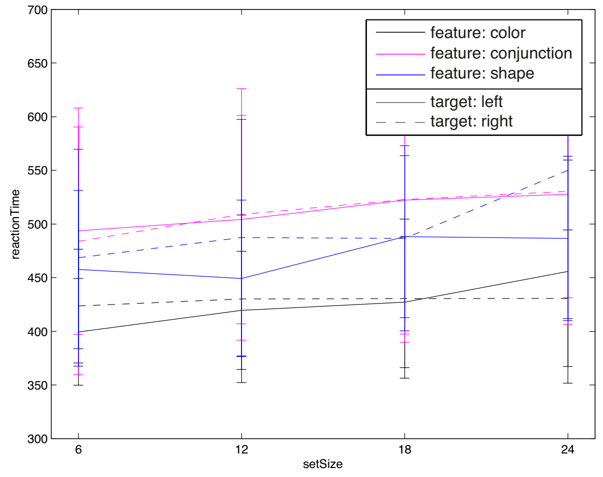
Supp Fig2.14 Effect of target position (left/right) for particpant 14. The targetbutton was located left



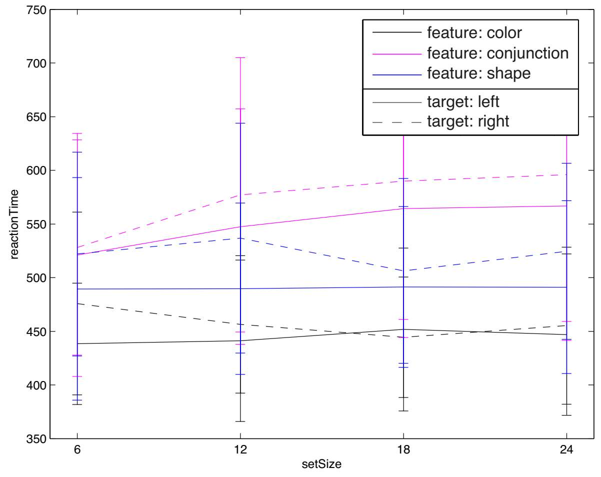
Supp Fig2.15 Effect of target position (left/right) for particpant 15. The targetbutton was located left



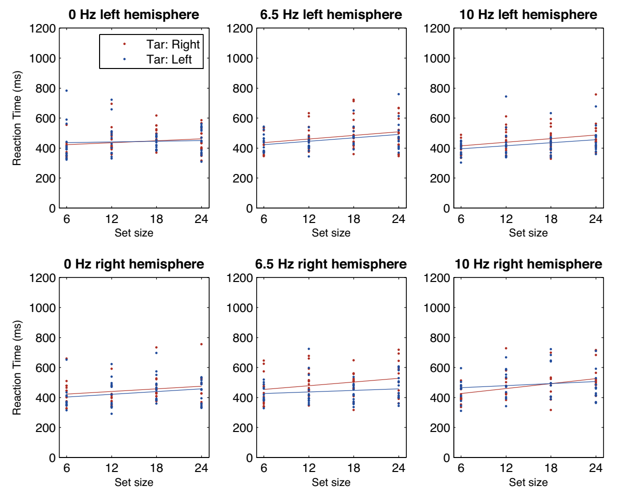
Supp Fig2.16 Effect of target position (left/right) for particpant 16. The targetbutton was located right



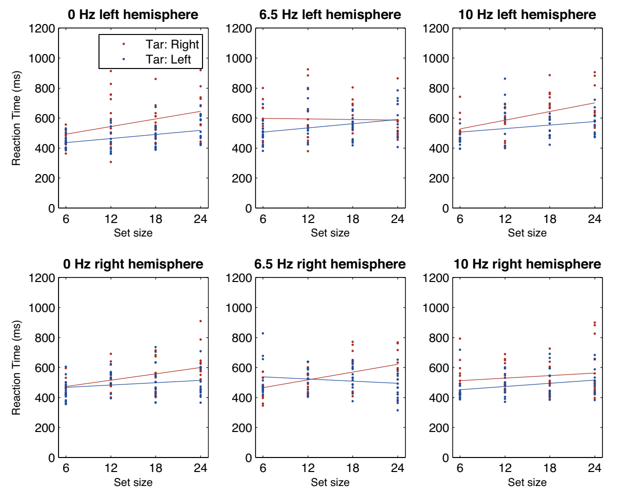
Supp Fig2.17 Effect of target position (left/right) for particpant 17. The targetbutton was located left



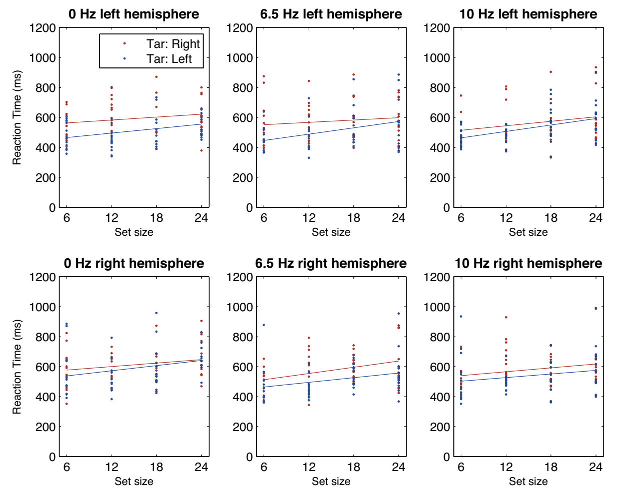
Supp Fig2.18 Effect of target position (left/right) for particpant 18. The targetbutton was located left



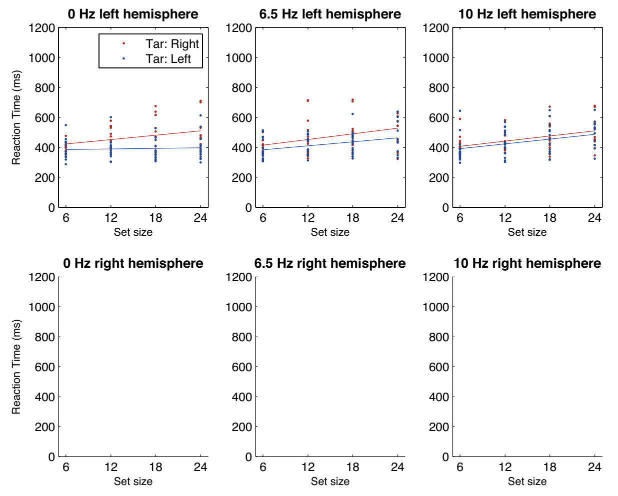
Supp Fig3.01 Set size / Reaction time scatterplot for particpant 01. The search slope is plotted as a line



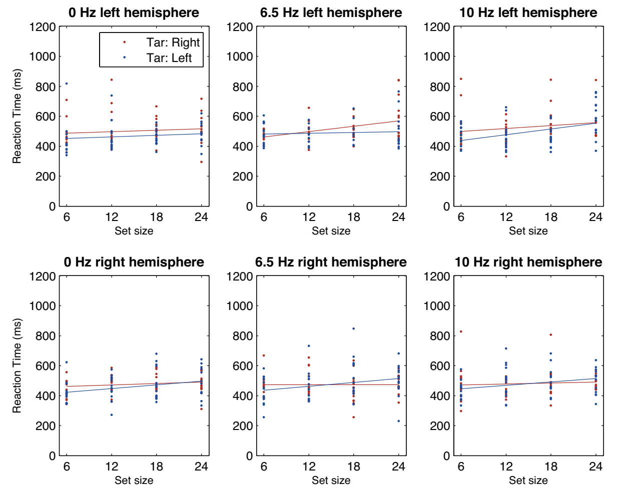
Supp Fig3.02 Set size / Reaction time scatterplot for particpant 02. The search slope is plotted as a line



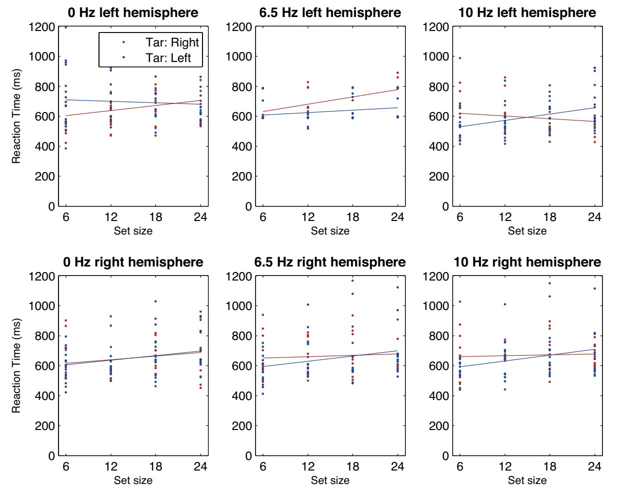
Supp Fig3.03 Set size / Reaction time scatterplot for particpant 03. The search slope is plotted as a line



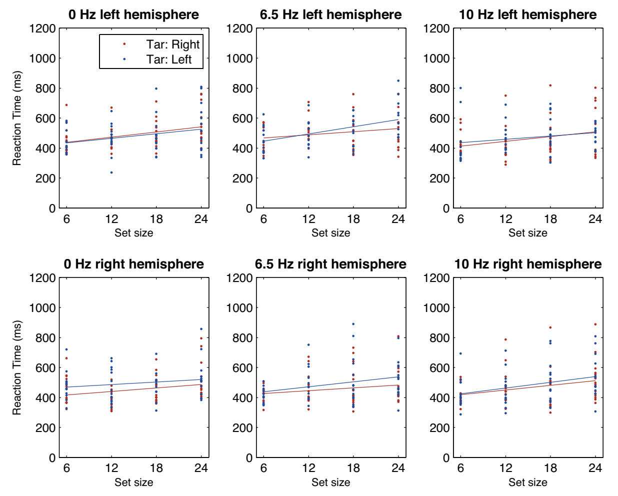
Supp Fig3.04 Set size / Reaction time scatterplot for particpant 04. The search slope is plotted as a line



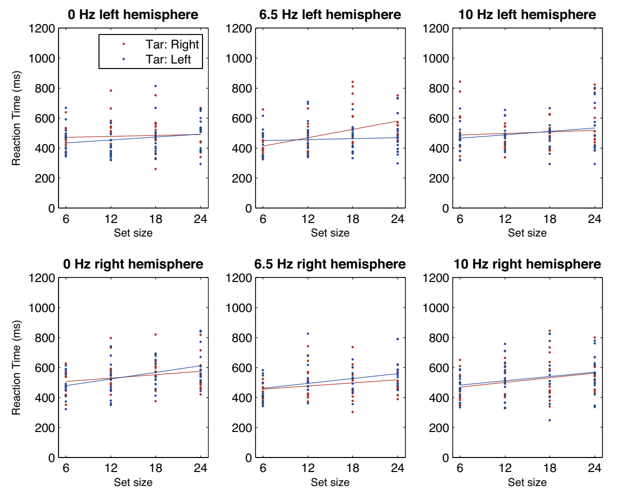
Supp Fig3.05 Set size / Reaction time scatterplot for particpant 05. The search slope is plotted as a line



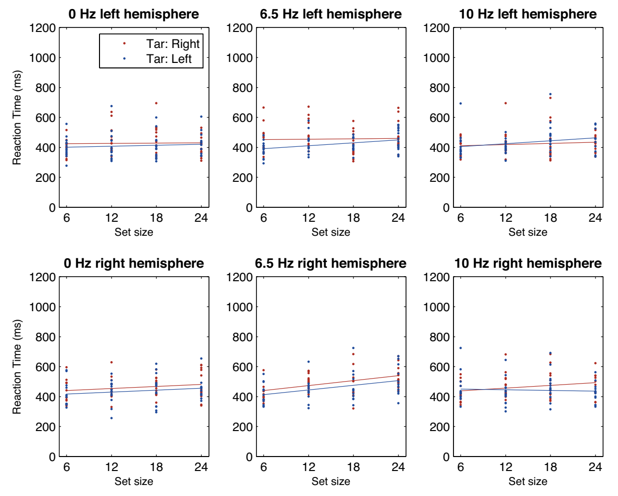
Supp Fig3.06 Set size / Reaction time scatterplot for particpant 06. The search slope is plotted as a line



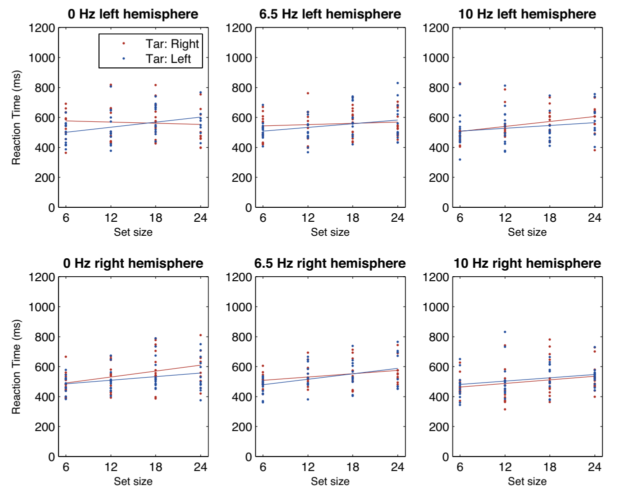
Supp Fig3.07 Set size / Reaction time scatterplot for particpant 07. The search slope is plotted as a line



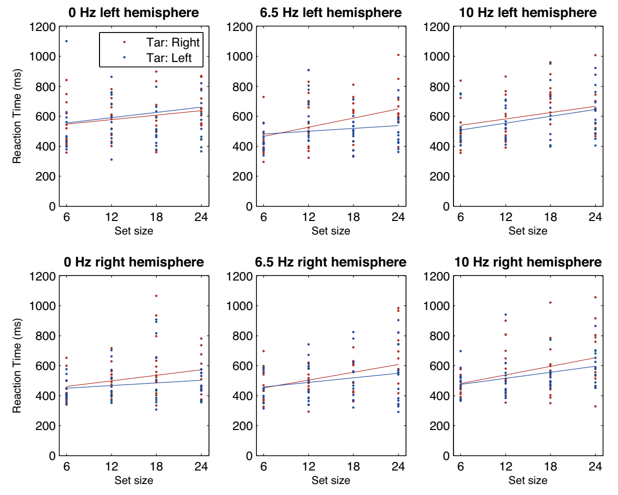
Supp Fig3.08 Set size / Reaction time scatterplot for particpant 08. The search slope is plotted as a line



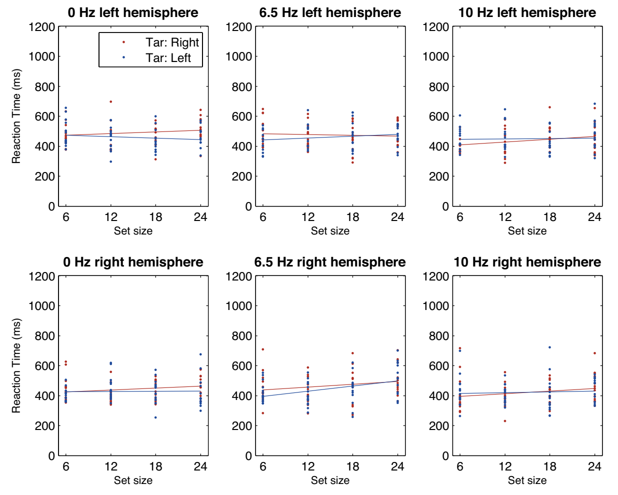
Supp Fig3.09 Set size / Reaction time scatterplot for particpant 09. The search slope is plotted as a line



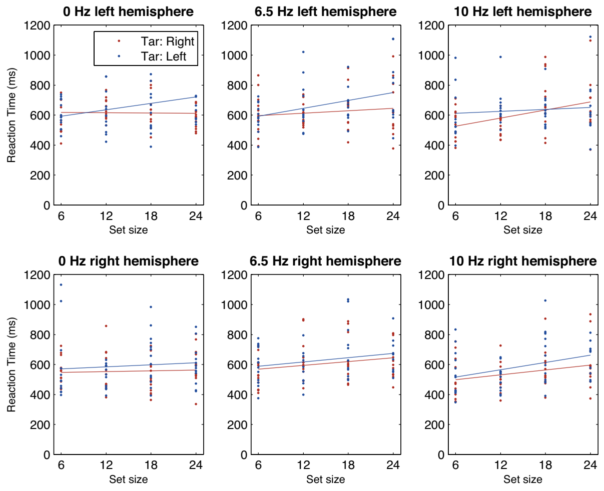
Supp Fig3.10 Set size / Reaction time scatterplot for particpant 10. The search slope is plotted as a line



Supp Fig3.11 Set size / Reaction time scatterplot for particpant 11. The search slope is plotted as a line



Supp Fig3.12 Set size / Reaction time scatterplot for particpant 12. The search slope is plotted as a line



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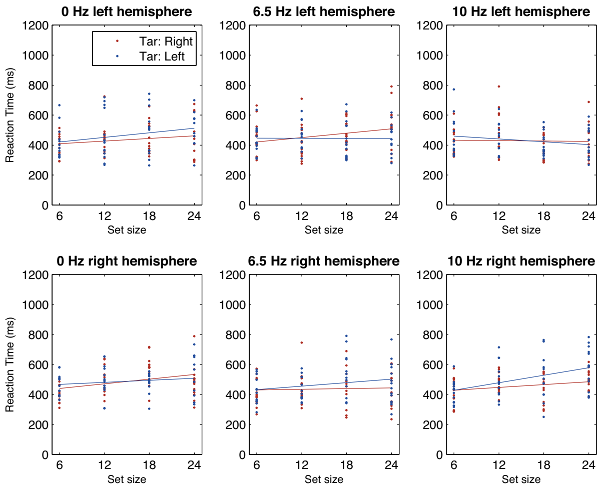
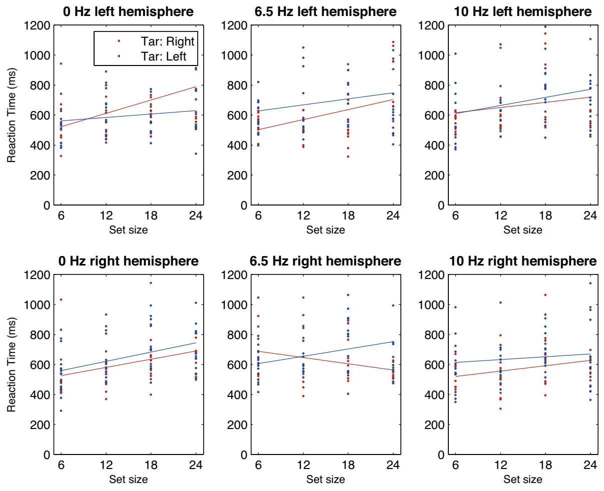
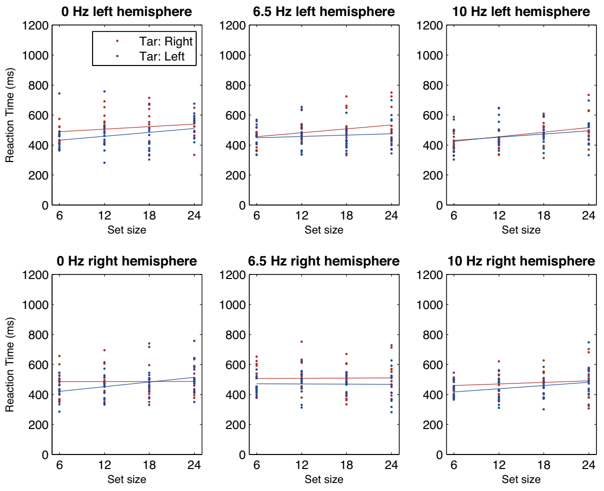


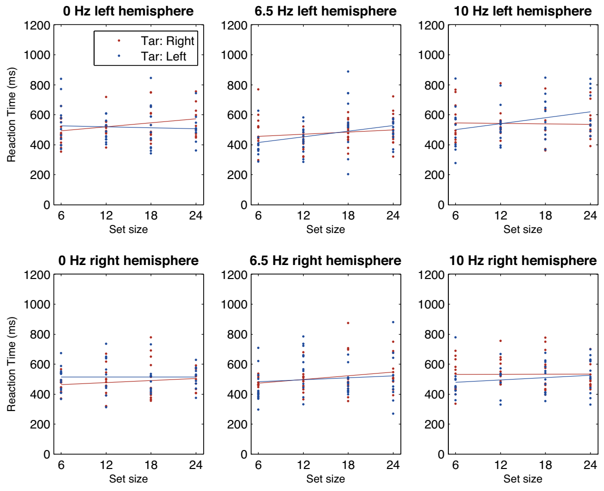
Supp Fig3.14 Set size / Reaction time scatterplot for particpant 14. The search slope is plotted as a line



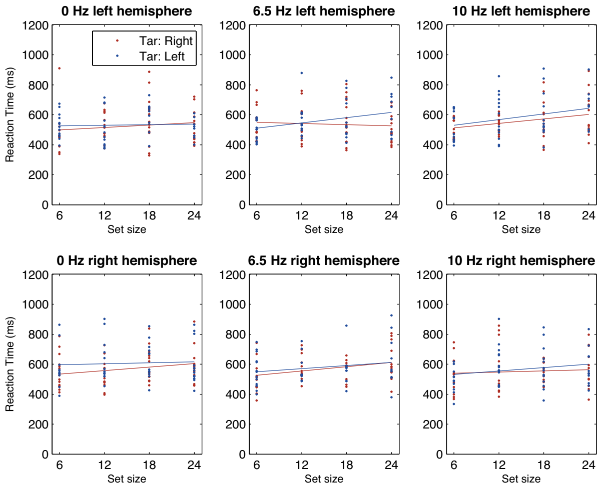
Supp Fig3.15 Set size / Reaction time scatterplot for particpant 15. The search slope is plotted as a line



Supp Fig3.16 Set size / Reaction time scatterplot for particpant 16. The search slope is plotted as a line



Supp Fig3.17 Set size / Reaction time scatterplot for particpant 17. The search slope is plotted as a line



Supp Fig3.18 Set size / Reaction time scatterplot for particpant 18. The search slope is plotted as a line