

University of Tartu
Institute of Psychology

Henri Ingelman

Using motion aftereffects to contrast conscious perception and attention in an EEG
experiment
Seminary work

Supervisor: Talis Bachmann

Co-supervisor: Jaan Aru

Running head: An EEG experiment of consciousness and attention

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Abstract

The search for neuronal correlates of attention and consciousness has lasted for years, but still, the results are mixed. By using the method derived from Murd and Bachmann (2011) and adding electroencephalographic (EEG) measuring, we tried to find and confirm the correlates of consciousness and attention found by other authors. We hypothesized that a) consciousness is associated with lower frequency local gamma band activity, and b) attention is related to local gamma band activity of 60-80 Hz on the posterior EEG electrodes. Unfortunately, the results did not confirm the hypotheses. The main reasons could be insufficient number of total trials in the experiment and low sensitivity of the EEG recordings to the high gamma band activity.

Liikumise järeleefekti abil teadvuse ja tähelepanu vastandamine EEG katses

Kokkuvõte

Tähelepanu ja teadvuse neuraalsete korrelaatide leidmine ja eristamine on kestnud aastaid, kuid siiani leidub vastandikke tulemusi. Kasutades Murd ja Bachmann (2011) tööst tuletatud metoodikat ning lisades sellele elektroentsefalograafia (EEG), prooviti käesolevas töös leida ja kinnitada eelnevalt leitud korrelaate nii teadvuse kui ka tähelepanu kohta. Püstitasime hüpoteesid, et a) teadvus on seotud madalama sagedusega lokaalse gammaaktiivsusega, ning b) tähelepanu on seotud lokaalse gammasagedusega vahemikus 60-80 Hz tagumistel EEG elektroodidel. Tulemused paraku püstitatud hüpoteese ei kinnitanud. Peamisteks põhjusteks võisid olla liiga vähe katsekordi üle terve eksperimendi ning EEG aparatuuri liiga väike tundlikkus kõrge gammasageduse suhtes.

Introduction

Consciousness and (selective) attention are closely related neural processes and because of that, clearly segregating them from each other is important for a better understanding of both attention and consciousness (Koch & Tsuchiya, 2007). Although most researchers agree that consciousness and attention are entirely independent, but interacting processes (Aru & Bachmann, 2013), some still think that attention is needed for conscious experience and events or stimuli that are not attended to, remain hidden from the conscious experience. The truth is that, interactions between attention and consciousness are far more complicated: in addition to processes that need both of them (e.g., working memory, detection and discrimination of unexpected and novel stimuli), there are processes that need only one or neither of them. For example, one can be aware of something without selectively attending to it - that is the case for rapid vision (Mack & Rock, 1998). Moreover, there are processes that need selective attention but where no conscious experience emerges. For example consider visual search - one's attention is tuned to the qualities of the item that one is searching for but there is no conscious percept of the item in one's mind (Melcher, Papathomas, & Vidnyánszky, 2005).

Experiments with afterimages and bistable figures show that selective attention and consciousness can sometimes have mutually adverse effects. Murd and Bachmann (2011) showed that when subjects selectively attend to motion aftereffect, the aftereffect disappears faster from consciousness. Attending to aftereffect reduces its conscious perception and this phenomenon allows us to explore attention and consciousness in a very interesting way. By modifying the aforementioned experiment and adding EEG measurement, one can contrast attention and consciousness and thus perhaps study the differences between them and also test the neuronal correlates proposed previously by other authors (Wyart & Tallon-Baudry, 2008). There is some controversy around the correlates of attention and consciousness also on the neural level, as for example, local gamma-band activity has been suggested to be neural correlate for both attention and consciousness. Local gamma-band activity was the neuronal correlate of conscious perception in the works of Aru and Bachmann (2009). But Womelsdorf and Fries (2007) proposed earlier that local gamma-band activity could be a correlate for attention. Interestingly, Wyart and Tallon-Baudry (2008) showed that local gamma-band activity correlates with attention as well as consciousness, but in different frequency ranges.

The purpose of this study is to try and disentangle the relationship between local gamma-band activity, consciousness and (selective) attention. Based on Wyart and Tallon-Baudry's work (2008) our hypothesis is that attention is related to higher frequency gamma band activity and consciousness to lower frequency gamma band activity. Specifically, we expect attention to be related to 60-80 Hz gamma activity in the posterior EEG electrodes (Koelewijn et al., 2013).

Methods

Subjects

Ten subjects (2 females, 8 males, age 18-25) with normal or corrected-to-normal visual acuity participated in the experiment. Each subject read and signed informed consent form and was paid for participation. The study received ethical approval from the University of Tartu Research Ethics Committee.

Stimuli and procedure

In every trial, two disc-shaped areas, equidistant and horizontally in line with a small central fixation cross were used for presenting the adapting and test stimuli. In these areas, achromatic sine-wave gratings were showed - in the adapting phase (of each trial) the grating moved vertically either upward or downward and thus the movement directions of two stimuli were opposite to each other. Movement directions were assigned randomly for disc-shaped motion areas: up or down for one grating and the opposite for the other. The diameter size of both areas was about 6° as estimated from the viewer's point of view, the distance of the center of both areas from the fixation cross was about 4° of the visual angle. Gratings had spatial frequency equal to 1.4 cycles/deg and a temporal frequency of 2 Hz. The space-average luminance of the background was set to 63 cd/m². The adapting stimuli appeared in combinations of two different motion directions (left – up, right – down or vice versa) and, when switched off, were followed by opposite direction motion aftereffects spatially projected onto two static testing gratings presented in the same disc-shaped areas where the adapting stimuli were previously shown. The contrast of the adapting stimuli was set to 0.9 and for the static stimuli it was set to 0.4. The stimuli were presented on Sun Microsystems CM751U monitor (100 Hz refresh rate). Participants sat in the subject chair of Nextim Eximia EEG/TMS set, with a distance of 80 cm to the monitor.

Each trial consisted of presentation of two simultaneously displayed discs filled with moving gratings for 15 s, after which, upon motion offset, static gratings were presented in the discs (Figure 1). The experiment was carried out in sessions consisting of 20 trials each. The subjects were instructed to keep their gaze fixated at the central fixation cross during the whole session. The participants were asked not to move their eyes in order to prevent artifacts in the EEG recording. In addition they were instructed not to blink during the static gratings. The subjects were asked to focus their covert attention to one static grating indicated by an arrow presented instead of the fixation cross on testing phase and to report, which of the aftereffects faded first. Subjects were instructed to respond only about the first fading, in case the aftereffect should reappear in some of the trials. Subjects used computer keyboard for answering. In addition to normal “left” or “right” answers, subjects had an option for third answer, which they were instructed to use only when no aftereffect appeared, or when they could not distinguish which aftereffect faded first or for other various reasons which could ruin the results (e.g. subject sneezed or did not focus on the central fixation cross during the adapting phase).

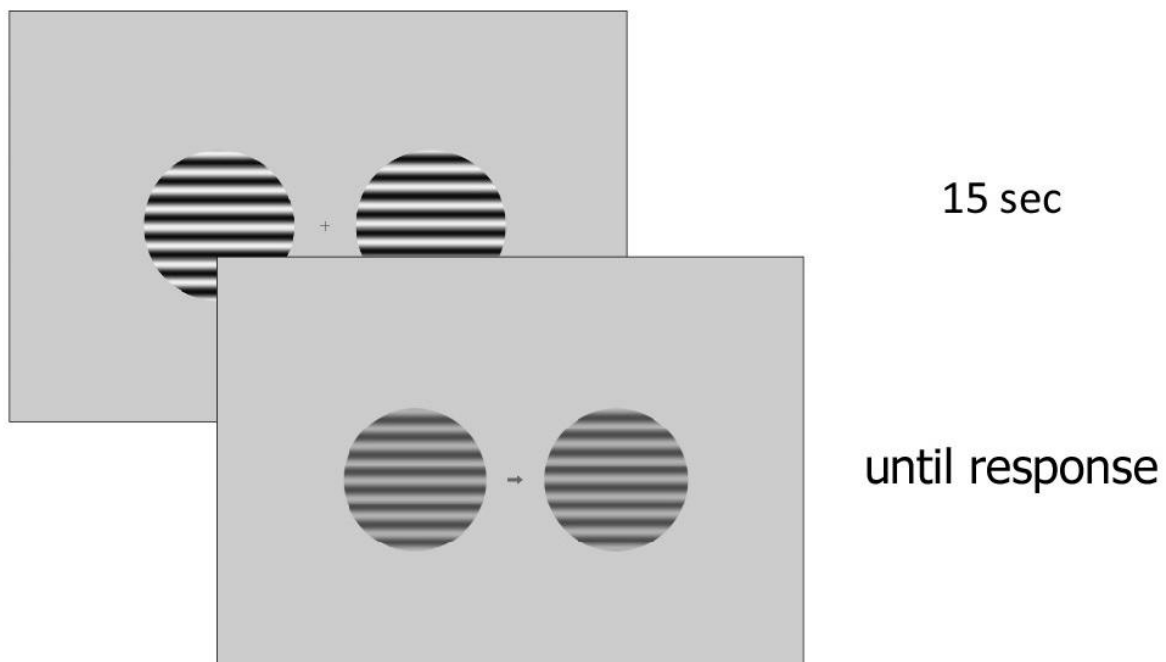


Figure 1: Illustration of the structure of the experiment. Adapting phase (top frame) consisted of two vertically, oppositely moving stimuli presented for 15 seconds. Subsequent to this, the testing phase followed (bottom frame), where indication arrow and static stimuli substituted the central fixation cross and the moving stimuli. The testing phase lasted until subjects gave a response on the keyboard.

Before starting the experiment, each subject performed 3-10 training trials in order to familiarize them with the procedure and aftereffect. Between each session, a resting pause of few minutes was administered. Subjects performed 140-200 trials (one 140, five 200, four subjects 180 trials).

EEG recording

For EEG recording we used Nexstim Eximia EEG system with 60-electrode cap. Reference electrode for EEGs was placed on the forehead. The impedances were kept below 10 k Ω . The sampling rate was 1450 Hz, all signals were amplified with a gain of 2000 and a hardware based bandpass filter of 0.1–350 Hz. EEG was segmented into epochs –3000 to 1000 ms relative to the moment when the subjects answered which aftereffect faded first. Vertical electrooculogram (VEOG) was also recorded to control for blinks. All data was visually inspected for EMG artefacts.

EEG data analysis

EEG data was analyzed in the frequency domain with wavelets. Analyzed frequencies ranged from 3 to 84 Hz in steps of 3 Hz and the wavelet width increased from 3 cycles at 3 Hz to 8 at 84 Hz. However, further analysis focused only on the gamma frequency band (30-80 Hz). For figure 3 the result of the wavelet transform was provided with full time-resolution. For figures 4 and 5 and the corresponding analysis we created a wavelet power spectrum by averaging over the time dimension. As attention is deployed over the whole time-interval, we analyzed the attentional effect over the time window -2.6 to -0.4 seconds before the response. The fading effect (effect of consciousness) only manifests itself at the end of the response window, thus for figure 5 and for the corresponding analysis we assessed the time window -1.0 to -0.4 seconds before the response. We analyzed single-electrode responses at the sites O1 and O2, which are closest to the primary visual cortex which is known to be the neural source of the processing of the gratings (Koelewijn et al., 2013). We also analyzed regions of interest which included electrodes in the posterior-occipital areas separately for both hemispheres (O1, PO3, P1, P3 and P7 for the left hemisphere, O2, PO4, P2, P4 and P8 for the right hemisphere). Finally we assessed the experimental effects in an unconstrained manner over the whole

electrode space with the cluster-permutation method (over dimensions channels and frequencies, 2000 permutations, see Maris & Oostenveld, 2007).

Results

Behavioral results

We first wanted to see whether attention influences the duration of the afterimage. As stated in the introduction, the prediction based on the work of Bachmann and Murd (2011) is that afterimage fades quicker on the side where attention is deployed. To analyse that we conducted a repeated measures ANOVA on the proportion of trials with quicker fading with the following factors: side of attention (left, right) and side of quicker fading (left, right). The interesting part of this analysis is the interaction term, because the prediction says that when attention is directed to the right side, the right stimulus should fade first, while leftward directed attention should lead to quicker fading on the left side. This interaction term, however, was not significant ($F = 3.264$; $p = 0.104$). The main effects confirmed that it did not matter to which side attention was directed to ($p > 0.7$), but it turned out that in general subjects reported more often that the leftward stimulus faded first (i.e. irrespective of where attention was directed to) ($F = 5.363$, $p = 0.046$). These results are illustrated on Figure 2.

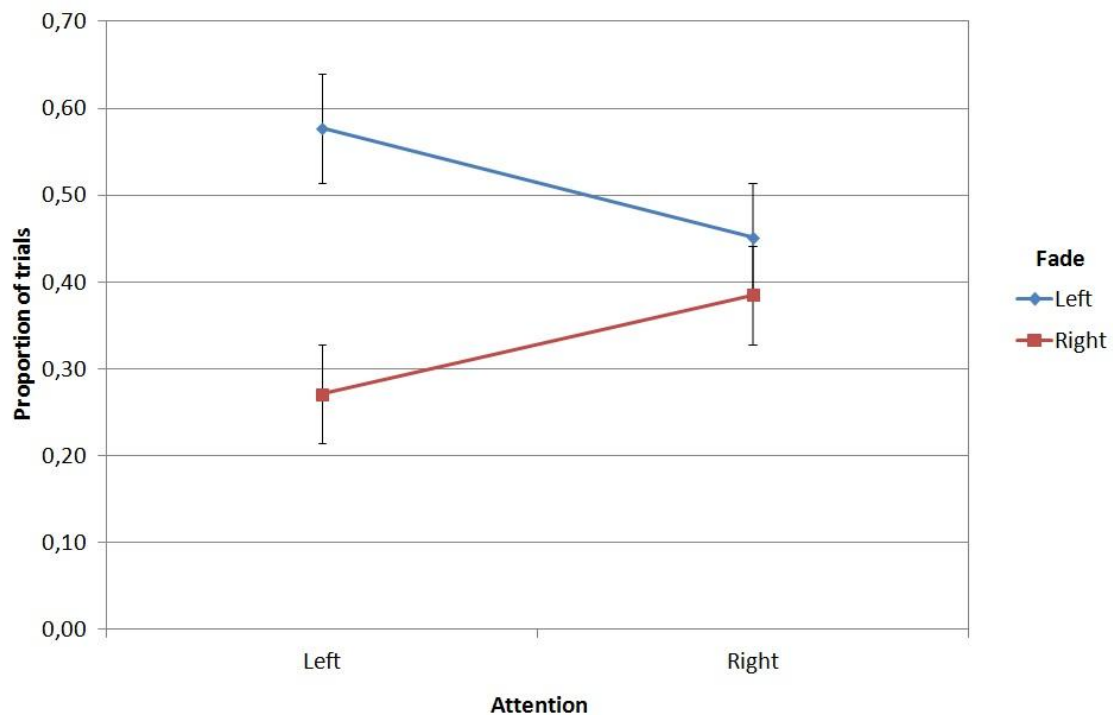


Figure 2: Diagram showing the relationship between attentional direction and the aftereffect that faded first. The previous results would predict a cross-over so that when attention is directed to the right side subjects report that the right stimulus fades first. However, we obtained such an attentional effect only in the case when attention was directed to the left.

As can be seen from the figure, when attention is directed left there seems to be an attentional effect on afterimage disappearance and this is indeed confirmed with the direct t-test between conditions <attention left, fading left> versus <attention left, fading right>: when attention is directed to the left side, leftward afterimage fades quicker ($T = 4.262$, $p = 0.002$). There is no effect when attention is directed to the right side ($p > 0.6$). Taken together, the behavioral results did not support the prediction to its full extent but rather showed that attention leads to quicker fading of the afterimage only in the left visual field.

EEG results

We next sought to exploit our experimental paradigm to study the neural mechanisms behind attention and consciousness. We first contrasted the two attentional conditions (attention left vs. attention right). Based on previous results with similar stimuli (Koelewijn et al., 2013) we expected the attentional effect around 60-80 Hz at the posterior electrodes. In particular, when attention is directed to the left visual field, at the right-hemisphere electrodes gamma power

should be higher as compared to the condition where attention is directed to the right visual field (and vice versa for the left-hemisphere electrodes). This should be manifested as a narrow-band increase around 70 Hz. However, when inspecting single electrodes and electrode combinations, no such effects were visible. It rather seemed that attention to the left condition elicits stronger gamma power in both right and the left hemisphere than the attention to the right condition. Figure 3 depicts an electrode from the left hemisphere (O1) and another from the right hemisphere (O2). We should find that when attention is directed to the right visual field there is more power at O1 than in the condition where attention is directed left. However, at least numerically leftward attention leads to stronger power in both conditions.

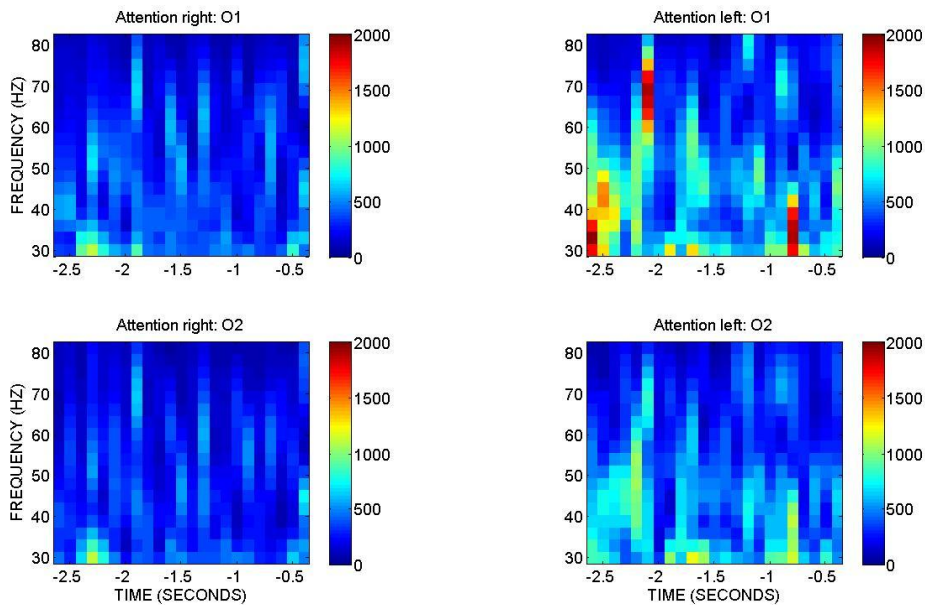


Figure 3: Time-frequency representations of the two attentional conditions averaged over subjects. It can be seen that there is no clear oscillatory structure present and that overall, power seems to be higher for the leftward attention condition. Time is relative to the response onset.

However, this effect is not statistically significant, not on the single electrode level, on the level of electrode groups or over all the electrodes (all $p > 0.1$). We next inspected individual power spectra averaged over 5 electrodes on the left and right hemisphere to understand the effect of our attentional manipulation. To remind the prediction we started out with: when attention is directed to the right visual field, gamma power on the left-hemisphere electrodes should be higher; when attention is directed to the left visual field, gamma power on the right-

hemisphere electrodes should be higher. However, this prediction is not in any sense consistent with our data (Figure 4).

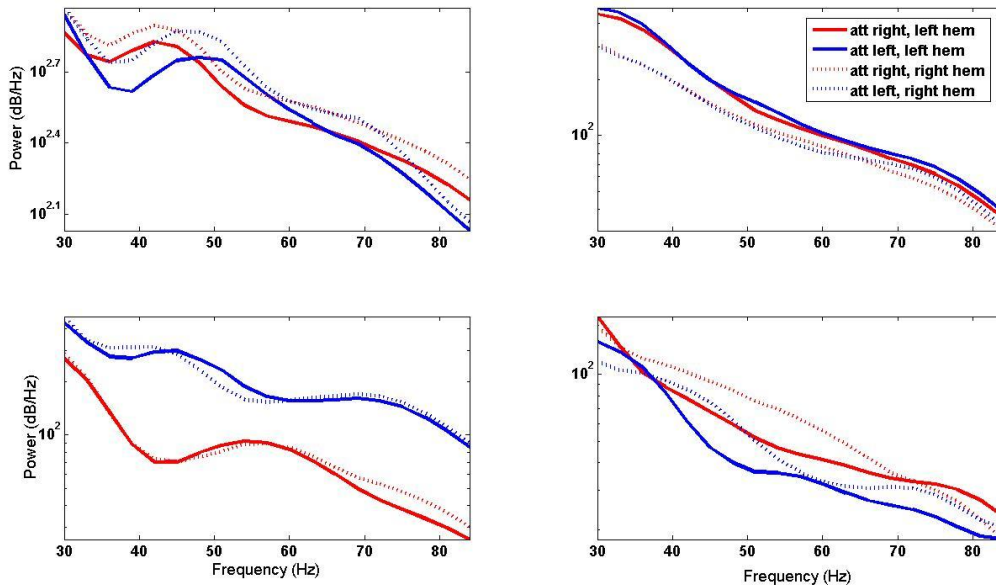


Figure 4: Power spectra from 4 example subjects. Although attention to the right visual field should lead to higher power on the left-hemisphere electrodes and the other way around attention to the left should increase power on the right hemisphere electrodes, this is not evident in the data. On the figure attention to the left is represented by blue lines, attention to the right by red lines; the solid lines represent left-hemisphere electrodes, dashed lines right-hemisphere ones. Based on previous results one would predict that in the frequency range where attention has its effect (e.g. 60-80 Hz), for the red lines the solid line should be higher than the dashed line and for the blue lines the dashed line should be higher than the solid line. This is only somewhat the case for the bottom left plot around 45-55 Hz and bottom right plot around 75-85 Hz, but in general, no consistent pattern emerges. Att – attention; hem – hemisphere.

Next we ran the same analysis for the consciousness contrast by comparing trials where subjects reported that the leftward stimulus disappeared first with those trials where subjects reported that the rightward stimulus disappeared first. Initially we did not have a clear hypothesis here regarding the frequency band, but after failing to find the predicted attentional effect around 60-80 Hz, we considered the possibility that the 60-80 Hz effect could be attributed to consciousness. However, when comparing the different trials with different fading we were not able to find any statistically significant effects when comparing single electrodes, electrode groups or all electrodes (all $p > 0.1$). Figure 5 is analogous to Figure 4 and illustrates that the results from the consciousness contrast are as heterogeneous and non-consistent as with the attentional contrast.

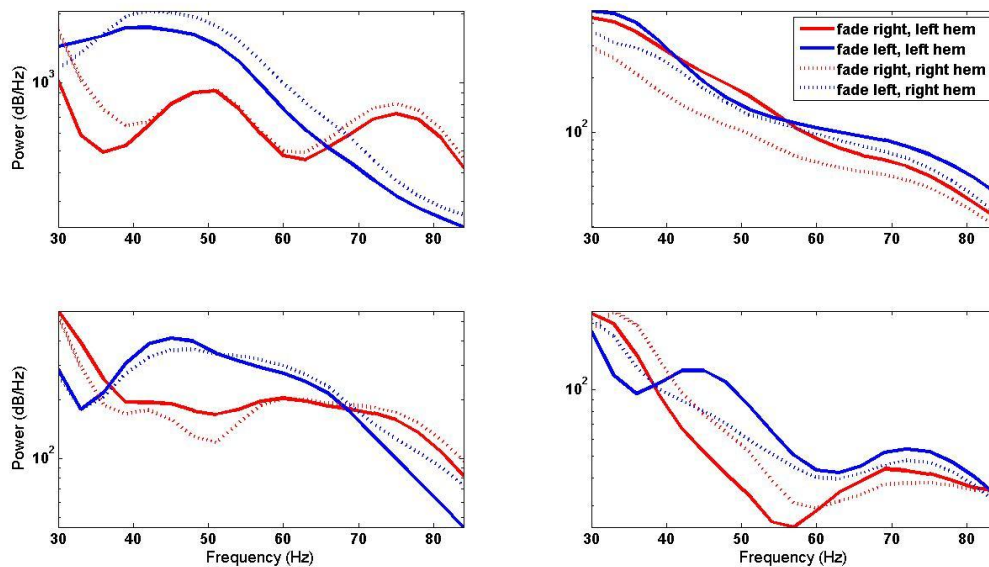


Figure 5: Power spectra from the same 4 subjects as on figure 4 but illustrating the consciousness effect. On the figure fading first on the left is represented by blue lines, fading first on the right by red lines; the solid lines represent left-hemisphere electrodes, dashed lines right-hemisphere ones. If local gamma signal is important for conscious perception, for the red lines the solid line should be higher than the dashed line and for the blue lines the dashed line should be higher than the solid line. As can be seen, subjects and their effects as measured in the power spectra are very different and in general, no consistent pattern emerges. Fade – fading; hem – hemisphere.

Discussion and conclusions

In the present experiment, we tried to clarify the relationship between consciousness, (selective) attention and local gamma-band activity. Our hypothesis was that attention is related to higher and consciousness to lower frequency gamma band activity. We expected attention to be related to 60-80 Hz gamma band activity in the posterior EEG electrodes. (Wyart & Tallon-Baudry, 2008, Koelewijn et al., 2013). Unfortunately, the results did not confirm our expectations. In addition to EEG findings, even the behavioral results did not comply with the findings of Murd and Bachmann (2011) in a similar experiment.

Problems with behavioral results

Murd and Bachmann (2011) had 6 subjects with 45 trials and a total of 270 trials (counting trials from the part of the experiment that measured fading of consciousness under attention), while we had 10 subjects with a average of 186 trials per subject. There is a possibility that we had too many trials per subject and that might have tired the participants too much.

However, from the pure length of the experiment ours was not longer than that of Murd and Bachmann (2011) because they also had a second condition and each of their trials was longer than ours because of the longer presentation of the adapting stimulus. Although the duration of adapting stimulus in our study was much shorter than in their experiment (15 sec vs 25 sec), this time was not too short for the aftereffect to appear - in the training trials, every subject reported having perceived clear aftereffects. Interestingly, most of the subjects reported perceiving less aftereffects in the last 2-3 blocks. Maybe the experiment was too long and exhausting and this attenuated the aftereffect in late blocks. It would be interesting to run the same experiment again, with, for example 20 participants with 100 trials per subject and see the results. Also we could potentially find better results when we would only analyze the first 140 trials of each subject's data. In addition, it would be interesting and necessary to analyze the behavioral results of Murd and Bachmann (2011) in the same way as in this experiment – to analyze attentional effects between attentional direction in terms of position on the visual field (not aftereffect moving direction as in their case) and percentage of fading first of the particular stimulus. It might also be that the type of attentional task – search according to feature or spatial cuing – has definite differences in terms of the effects. Furthermore, in Murd and Bachmann (2011) there were four spatial alternatives while we had only two. This also may have brought in differences.

One more possible confounding factor could be the distance between stimuli. Since our stimuli were bigger than in their experiment (diameter size of stimuli - 6° vs 3.5°), but the distance from the central fixation cross to the center of stimuli was similar (4° vs 3.5°), there is a possibility that the stimuli in our experiment were too close together and therefore may have caused lateral inhibitory effects and/or confounding effects on the focus of subject's attention, i.e. that it was too hard to focus on solely one target. However, in the training trials all subjects reported that they could do the task. An additional difference between our experiments is spatial frequency of the stimulus – they had it at 2.86 cycles/degree, in our experiment it was 1.4 cycles/degree. This may have influenced both the behavioral and EEG results in unforeseen ways.

Problems with EEG results

As mentioned before, there is a possibility that we had too few subjects and too many trials per one participant. In terms of EEG results, additional problem may be that we should have

had more total trials in our experiment (we had a total of 1860 trials in our experiment). For example, Wyart & Tallon-Baudry (2008) had twelve subjects. Each subject performed 8 blocks with a total of 736 trials, total 8832 trials over 12 subjects. On the other hand, Aru and Bachmann (2009) had 7 subjects, each subject performed 240 trials over 6 blocks, summing up total of 1680 trials for the whole experiment, but still obtained valid results. However, their results are stimulus-locked: their gamma-band results are induced by stimuli, whereas we were trying to find signatures of purely internal processes.

Also, Koelewijn et al. (2013) used 18 subjects, where each subject performed 40 trials, total of 720 trials per experiment. But their experiment was different – it may be that their experimental design minimized the probability of boring the subjects. In their experiment, the subject had to actively match the parafoveal grating with the central line or vice versa. In addition to keeping the subject actively participating, this design may also need more attention from the subject, thus providing bigger gamma response. Another reason why we have failed to confirm our hypotheses is that the EEG gamma band signal may have been too noisy or weak. For example, Muthukumaraswamy and Singh (2013) found that annular stimuli produced larger gamma-band power than square wave stimuli. The stimuli in our experiment were moving uni-directionally rather than annularly. Also, based on their work, one would expect that bigger stimuli create larger gamma-band power, but most likely stimuli in our experiment were within an adequate size range. As mentioned earlier, spatial frequency of the stimulus may also caused problems in the EEG results. Some authors have found that the optimum spatial frequency of the stimuli for creating maximum-contrast gratings that extend across several degrees of visual field delivering the maximal gamma response is about 3 cycles/degree (Adjamian et al., 2004). In our experiment, it was suboptimal - 1.4 cycles/degree. It may have caused a weaker gamma response. Muthukumaraswamy and Singh (2013) also found that occipital EEG sensors tend to have lower signal to noise ratio for induced visual gamma compared to MEG system. Based on this finding, we think that this may have been a major setback – our hypotheses based on the results that were found by using MEG systems (Wyart & Tallon-Baudry, 2008, Koelewijn et al., 2013), but we used EEG system. Hence weak gamma response may have been a reason, why we could not successfully test our hypotheses. Taken together, our experiment might have yielded mixed results mostly because of insufficient number of total trials and low sensitivity of the EEG recordings to the high gamma band activity.

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Henri Ingelman