Which parameters of pre-stimulus EEG activity best predict conscious perception?
Contents
1 Introduction ......................................................................................................................... 3
2 The experiment .................................................................................................................. 3
3 The method ....................................................................................................................... 4
4 Preliminary analysis of the data ....................................................................................... 5
5 Alpha waves and slow negativity as predictors of conscious perception ....................... 7
   5.1 Alpha waves ............................................................................................................... 7
   5.2 Slow negativity .......................................................................................................... 8
6 Results ............................................................................................................................... 9
   6.1 Linear discriminant analysis .................................................................................... 9
   6.2 Permutation test ....................................................................................................... 11
7 Discussion ......................................................................................................................... 12
8 Conclusion ......................................................................................................................... 13
References ............................................................................................................................ 13
1 Introduction

It has been shown that barring any significant changes in the visual stimulus, conscious perception of it may at times succeed and at others fail, even in the context of largely static external conditions. This implies that some internal neuronal activity or activities other than the expected spiking activity of the relevant neurons can effectively interfere with or facilitate conscious visual perception and delineating such activity could shed light on the process of perception in general.

It has been proposed (e.g., Lange et al. 2013) that high level alpha oscillations may inhibit occipital neuronal activity, and thus contribute to not consciously perceiving a stimulus. This can be explained by the link between alpha oscillations and temporal attention, the latter of which is reduced with higher level alpha activity. Furthermore, Mathewson et al. (2009) have shown that visual awareness also turns on alpha phase. Lastly, pronounced levels of slow negative cortical potential (which I will further on refer to as simply slow negativity), which has been linked to attention and anticipation (cf. Bladin 2006), is hypothesized to also facilitate the formation of conscious percepts. Our aim in this study was to evaluate the extent to which each of the three phenomena might contribute to conscious perception within the context of a single experiment conducted upon 22 test subjects. What we were looking for is a clear pre-stimulus EEG signature that could be used to reliably predict the presence of conscious visual perception.

Due to complications pertaining to the analysis of alpha phase (e.g., the problem of dividing up the phase, difficulties in doing statistical analysis of angular data) and the limited time frame of the project, the goal of analyzing alpha phase was not met. However, we were able to produce some statistically significant data for both alpha power and slow negativity, even though the results were far from conclusive.

2 The experiment

The experiment was done with 22 test subjects, with reliable data being produced from 18 of them. Each of those 18 were seated behind a computer screen and presented with a sequence of around 700 low contrast images. They were asked to indicate with a button press whether they saw an image or not. The test was fine-tuned for each participant in a way that would elicit a roughly equal distribution of positive and negative trials. Throughout the experiment,
EEG activity of the subjects was recorded from all 60 channels of the 10-20 system (Nexstim Ltd, Helsinki, Finland).

3 The method

The experimental data was preprocessed with the help of the fieldtrip toolbox for Matlab (http://www.fieldtriptoolbox.org/; version 2015.04.24). All trials with artifacts (e.g. blinks or eye movements) had already been removed from the data. For initial analysis, baseline correction at the interval of 500 ms to 400 ms before the stimulus onset was done, and a low-pass zero phase shift Butterworth filter at 30 Hz was used. Plotting the datasets after the initial preprocessing revealed clear and distinct EEG signatures for trials wherein the stimulus was seen by the subjects and those wherein it was not (the P300 component).

Information about alpha power and slow negativity were then extracted again with the help of fieldtrip. For slow negativity the baseline correction was done as before, and the data was filtered through a low-pass zero phase shift Butterworth filter at 5 Hz. Slow negativity was averaged over the EEG channels Cz, CPz, and Pz, using 0 ms (the stimulus onset) as the relevant time window. Data on alpha power was extracted from the channel Pz only, which is typical for such alpha wave studies. For alpha power we did a Fourier spectra analysis, and implemented a multitaper time-frequency transformation using a Hanning window function. The frequencies of interest were set to range from 6 Hz to 12 Hz, depending on the data produced by specific test subjects (i.e. peak alpha). Information about alpha power was again extracted from the time point 0 ms.

In order to evaluate the acquired data in terms of conscious perception being mediated by slow negativity and alpha power, we performed a linear discriminant analysis, using Matlab resources for Fisher discriminant analysis created by Quan Wang (2013). This allowed us to train classification models that operated on the data on slow negativity and alpha power in order to predict whether a stimulus was seen in each trial based on that.

In order to evaluate the results that emerged from the linear discriminant analysis, we performed a permutation test. We compared the classification models trained on the actual preprocessed datasets with those trained on randomly permuted ones, where the column storing information about whether the stimulus was seen or not was shuffled. For each of the test subjects, we created 10000 of such alternative models and compared their classification performance rate with models trained on the actual data. Analysis revealed statistically
significant higher success rates in some of the test subjects, implying a correlation between the studied neuronal activities and the presence of conscious visual perception in these cases, which is what we were looking for.

4 Preliminary analysis of the data

Data from the experiment revealed a clear and expected difference in the EEG activity of the analyzed channels of the subjects between trials wherein they reported conscious perception and trials wherein they reported none (Figures 1 and 2).

Figure 1. Averaged positive trials for test subject 1. Upon averaging over the trials where the test subject reported that they saw the stimulus, an expected peak in neuronal activity of the relevant channels can be seen at around 400 ms after the stimulus onset. This is the P300 component which constitutes one of the most prominent correlates of conscious perception (Dehaene and Changeux 2011).
Figure 2. Averaged negative trials for test subject 2. Averaging over the trials where the test subject reported that they saw no stimulus shows no peak in the activity of the relevant EEG channels.

EEG recordings from the trials wherein no image was actually shown were similar to those wherein an image was shown, but no perception of it was reported (Figure 3). This is important for establishing the significance of conscious perception for the purposes of our study, as it was not the actual presence of a stimulus, but perception of it, that interested us.

Figure 3. Averaged catch trials for test subject 1. As with the data averaged over all negative trials, no peak is present when averaging over catch trials (where there was no actual stimulus). Noisier graph is attributed to a smaller sample size (around 60 trials for TS1).
While the possible inputs from the subjects were discreet (i.e. 'yes' or 'no' to whether an image was seen), the experiences reported by the subjects were not always so clear. Since the experiment was purposefully conducted with very low contrast images, some ambiguity in this regard was to be expected. This ambiguity would naturally also be reflected in the collected data, which might be partly responsible for the fact that a correlation between the studied neuronal activity and conscious perception was not established for all test subjects.

5 Alpha waves and slow negativity as predictors of conscious perception

In order to explain why people sometimes fail and sometimes succeed in perceiving some visual stimulus despite no significant changes in the viewing conditions, it has been proposed that both alpha oscillations and slow negativity may play a role in modulating visual perception. Both phenomena have been linked to attention and are thus known to be consciously alterable by the agent to some degree. In our researched we looked at both of the phenomena in an attempt to establish that low alpha power and high rates of slow negativity could serve as predictors of conscious visual perception of near-threshold stimuli.

5.1 Alpha waves

Alpha waves are neural oscillations with the frequency of around 7.5-12-5 Hz. Being most prevalent in relaxed wakeful states, they are known to be modulated by top-down attention, where heightened visual attention is correlated with lower levels of alpha activity. Furthermore, alpha waves are known to have an inhibitory function on the unused areas of the cortex, as well as playing an active role in information processing (by timing neuronal activity; c.f. Klimesch 2012).

Numerous studies have found that alpha-band activity in the parieto-occipital areas are negatively correlated with subjective perception in visual detection and discrimination tasks (Worden et al. 2000, Hanslmayr et al. 2007, van Dijk et al. 2008, Wyart and TallonBaudry 2009, Romei et al. 2010). However, Lange et al. (2012) found that this does not establish a correlation between low levels of alpha activity and subjects’ performance in visual detection and discrimination tasks. Their near-threshold masked visual stimuli study established that low levels of alpha power can predict enhanced neuronal excitability, rather than improved visual perception. While subjects were more likely to report the presence of a stimuli when
their alpha levels were low, they were likely to do so even when no actual stimuli were present, and what they perceived was an illusion. This was the result of a complex masked stimuli experiment that our simple low contrast stimuli experiment couldn’t possibly replicate (subjects were in fact not inclined to report the presence of a stimuli when it was not there, even in favorable neuronal conditions), and is consistent with the way we framed the goal of our project – we were not concerned with the task of veridical detection, but rather conscious visual perception, which concerns whether a subject is consciously aware of some stimulus or not, be it illusory or otherwise. Even though our experiment didn’t necessitate such a distinction, it is important to keep this in mind, as it illustrates the fact that neuronal activity ought to be, first and foremost, correlated with a person’s subjective experience of the world, and not with a veridical representation of it.

5.2 Slow negativity

Slow negative cortical potentials are gradual changes in the membrane potentials of cortical dendrites, which translate to negative polarizations in EEG that last from 300 ms to several seconds. They function as a threshold regulation mechanism for local excitatory mobilization of cortical networks. By redistributing one’s attentional resources, one can learn to voluntarily regulate these potentials, thus facilitating higher performance levels of various motor and cognitive tasks. (Birbaumer 1999)

Several studies have suggested a correlation between slow negativity and the detection of visual stimuli at sensory threshold level (Elbert 1990, Devrim et al. 1999, He and Raichle 2010), with slow cortical potentials preceding the detected stimuli tend to be more negative than those preceding the missed stimuli. Since slow cortical potentials are known to regulate the threshold of neuronal excitability, this phenomenon can be explained in terms of higher slow negativity lowering the threshold for visual detection. Negative slow waves also indicate anticipation (Brunia et al. 2010) and as they can be regulated by attentional means (a skill that improves by training), it is fair to expect that the results one could get from the experiment such as ours turn heavily on the strategies that the individual test subjects employed throughout all of their trials.
6 Results

Sadly, the results of our study weren’t conclusive. For some of the test subjects, correlation between the analyzed neuronal phenomena and conscious visual perception was established, while for others, it was not. Furthermore, the correlation didn’t always seem to go in the same direction. The reasons for this are unclear, but I will provide a few suggestions in section 7.

6.1 Linear discriminant analysis

In order to establish the relevance of slow negativity and alpha power to consciously perceiving a stimulus, we performed a Fisher linear discriminant analysis on the data acquired from all of the test subjects. By training a classification model on the dataset corresponding to a specific test subject and testing it, we acquired the rate of success for such a model. The model takes the slow negativity and alpha power information for each of the trials as predictors for classifying each of the trials as either one wherein the stimulus was seen, or one wherein it was not. Comparing the results to the actual class values (1 or 0 for each trial) gives the success rate of the model. For visualization we created a two-dimensional space with each of the dimensions corresponding to one of the analyzed phenomena and placed each trial as a vector in this space, before drawing the best linear classification border available to the model (Figures 4 and 5).

Since the ‘seen’ and ‘not seen’ trials were somewhat uneven for each of the test subjects, we took whichever of the sets that had a lower number of trials and then took the same number of trials from the other set, in order to avoid statistical errors. For the purposes of the analysis, we also removed the catch trials since, as there were no reports of illusory perception, these would have distorted the data.
Figure 4. Classification border for test subject 1. A correlation between slow negativity and positive trials can be seen. However, the correlation seems to strangely go the wrong way, as positive trials seem to crowd more to the right side of the graph where negativity isn’t as pronounced, but it should be the other way around. Correlation with alpha power isn’t as easy to see with the eye, however, the slanted the classification border suggests a correlation.

Figure 5. Classification border for test subject 19. A decidedly more vertical classification border is present for test subject 19. More negative slow waves are this time rightly correlated with perceived stimulus, while a correlation with alpha power is less apparent.
6.2 Permutation test

In order to evaluate the classification models attained by linear discriminant analysis, it is useful to do a permutation test on each of them. For each of the test subjects, we randomly shuffled the information about whether a stimulus was seen or not over all the trials. Then we trained a classification model on the permuted data. We repeated this 10,000 times for each of the test subjects and compared the resulting empirical distribution of classification scores under the null-hypothesis with the original models that were trained on the actual data. If the classification score of the original model was no better than 95% of the permuted ones, then its success could be rightfully attributed to chance. Otherwise, there’s something more to it, and the predictors used for training (i.e. alpha phase and slow negativity information) prove to be at least somewhat meaningfully correlated with conscious visual perception. Figure 6a shows the results of the permutation test for each of the test subjects, while 6b is a histogram of the process for one of the more successful models.

Figure 6. Permutation test. a) The numbers represent how often the randomly permuted models attained better classification scores than the original models, each line standing for one of the test subjects. Numbers under 0.05 mean that less than 5% of the permuted models did a better job than the original model; b) histogram for test subject 1 shows an even distribution of classification scores for the models trained on the permuted data of TS1. The classification score of the actual model, at nearly 60% success rate (dotted line), stands out, implying better-than-chance classification and a meaningful correlation between the predictors and classes.
7 Discussion

Even though some statistically meaningful correlations between the analyzed phenomena and conscious perception were established, these were not present across the board. It is of course possible that the data itself or the processing and analysis of it is at fault, in which case little can be done at this point. Assuming, however, that this is not the case, a few other explanations for the variance can be thought of.

An immediately obvious explanation would be that some other untested neuronal phenomenon might be at play, which is effectively interfering with low alpha amplitude and slow negativity in a way that prevents them from facilitating conscious perception in the expected manner. Due to any unseen reasons this could have been more prevalent in a subset of the test subjects whose datasets didn’t allow for the training of a reliable classification model.

Both slow negativity and alpha power are known to be susceptible to voluntary modulation by the subject, and both are closely linked to attention. However, the mechanisms for controlling either of the phenomena are decidedly different – alpha activity can easily be inhibited by exercising one’s visual attention or cognitive capacities, whereas regulating slow cortical potential is more of a learned skill, often requiring some form of biofeedback training in order to achieve significant results (Elbert et al. 1980). Individual differences across subjects are also to be expected, as well as that individual subjects have a varying degree of control over these mechanisms and would accordingly use different strategies for stimulus detection tasks.

I think crucial here is the experimental setup, where the near-threshold level contrast for the shown images is determined. Inconsistencies between the setup phase and the testing phase could translate into inconsistencies in the acquired data. Also, since the two phenomena facilitate perception in different ways, it could be that in some trials the bulk of the work is done by one and not the other, and vice versa. If in some cases the slow negative potentials successfully lower the excitability threshold for occipital neurons by a significant degree, then conscious perception naturally turns less on alpha amplitude in those instances (a large variance in alpha amplitude could easily produce the same results). Similarly, overly active alpha band oscillations could well inhibit the formation of conscious perception, even when conditions pertaining to slow negativity are favorable.

Finally, a case could potentially be made about how the actual content of the presented images could determine the success rate of their detection. Even though in the experiment at
hand the images shown were quite similar, and in fact identical in regards to the feature taken to be the most relevant – their contrast – it is still possible that different images could have been more likely to elicit a neuronal response in different test subjects.

8 Conclusion

A number of studies have shown that both alpha wave activity and slow negative cortical potentials could inhibit or facilitate the formation of conscious visual percepts in conditions where the stimulus stays the same (to any relevant degree) and viewing conditions are kept static. More specifically, lower amplitude alpha band activity and more negative slow cortical potentials seem to be correlated with a higher likelihood of conscious perception.

Our attempts to replicate these results were met with only partial success. By processing and analyzing experimental data from a near-threshold low-contrast visual detection experiment, a link between the aforementioned neuronal phenomena and conscious visual perception was established for some of the test subject. This was illustrated by the fact that based on the data of those few test subjects, models that could somewhat predict whether the stimulus was seen or not based on information about alpha power and slow negativity, could be trained. While the classification score of these models wasn’t great (peaking at around 60% success rate at best), it is still a statistically meaningful step up from random classification.

Barring concerns about the data itself or its processing (which might well be justified), some of the inconsistency in the results could be attributed to neuronal phenomena that weren’t accounted for, differences in the subjects’ strategies for the task which turn on the intricate nature of both of the phenomena that were accounted for, or perhaps to neuronal selectivity in regards to the types of stimuli that were presented to the subjects.

References


