

# Alpha waves: a neural signature of visual suppression

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**Abstract** Alpha waves are traditionally considered a passive consequence of the lack of stimulation of sensory areas. However, recent results have challenged this view by showing a modulation of alpha activity in cortical areas representing unattended information during active tasks. These data have led us to think that alpha waves would support a ‘gating function’ on sensorial stimulation that actively inhibits unattended information in attentional tasks. Visual suppression occurring during a saccade and blink entails an inhibition of incoming visual information, and it seems to occur at an early processing stage. In this study, we hypothesized that the neural mechanism through which the visual system exerts this inhibition is the active imposition of alpha oscillations in the occipital cortex, which in turn predicts an increment of alpha amplitude during a visual suppression phenomena. We measured visual suppression occurring during short closures of the eyelids, a situation well suited for EEG recordings and stimulated the retinae with an intra-oral light administered through the palate. In the behavioral experiment, detection thresholds were measured with eyes steady open and steady closed, showing a reduction of sensitivity in the latter case. In the EEG recordings performed under identical conditions we found stronger alpha activity with closed eyes. Since the stimulation does not depend on whether the eyes were open or closed, we reasoned that this should be a central effect,

probably due to a functional role of alpha oscillation in agreement with the ‘gating function’ theory.

**Keywords** Alpha oscillations · Visual suppression · Attention · EEG

## Introduction

Alpha waves constitute oscillatory activity of the EEG recorded primarily on occipital regions and typically show a frequency range between 8 and 12 Hz (Horne 1988). Since their discovery (Berger 1929) they have been assumed to reflect lack of activity in the visual occipital cortex. Berger (1929) recorded brain activity from the scalp, expecting an increased activity while the subject was alert and active, but he found the opposite effect: when subjects had their eyes closed, electrical activity became slower and had greater amplitude. This was interpreted as a synchronization of brain activity due to a lack of desynchronizing visual stimulation. In fact, stimulating primary sensory area generates low-amplitude, desynchronized EEG patterns in which the alpha rhythm is attenuated or blocked (Pfurtscheller et al. 1996), while a more synchronized pattern in the alpha band seems to be a correlate of a brain area that ‘has nothing to do’ (Adrian and Matthews 1934). Some authors have challenged this view on the basis of data inconsistent with this theory. In particular when subjects are involved in a reading task and occipital areas are activated, the somatosensory cortex shows an increment of alpha rhythm without changes of the input. Similar data do not fit with the classical view on the role of alpha oscillations (Pfurtscheller et al. 1996). Further, many studies have shown an attentive modulation of alpha oscillations (Kelly et al. 2006; Rihs et al. 2007; Thut et al. 2006;

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Worden et al. 2000). When subjects were involved in a variation of the Posner cueing paradigm (Posner et al. 1980), there was an inter-hemispheric difference in the amplitude of the alpha rhythm consisting in an increase in the unattended side (Kelly et al. 2006). This has led to an interpretation of the alpha rhythm in terms of ‘gating function’ of these oscillations (Pfurtscheller and Lopes da Silva 1999), a functional approach that is linked to the idea that neuroelectric oscillations reflect variations in neuronal excitability (Bishop 1933). In the ‘40s, Wiener (1948) proposed that the alpha waves may embody the mutual entrainment of an ensemble oscillations generator such that the frequencies of individual members would be pulled synchronously toward a central frequency, in a way to block the sensorial processing. A similar proposal has been made by Lopes da Silva (1991), who noticed that EEG activity occurs in a rather synchronized form over a large neuronal population and imply a consequent change in the mean neural membrane potential level. For this reason, he proposed that these synchronized long lasting changes in neuronal network potential could behave like the thalamic cells generating sleep spindles.

In this framework, alpha waves behave like sleep spindles, inhibiting incoming information from sensory systems at the thalamic and early cortical level. Indeed, alpha waves from visual areas are generated in the thalamus and in the striate cortex, where the signal cannot be predicted by the thalamic signal (Lopes da Silva et al. 1980), and the alpha spectrum is very similar to the spectrum of the spindles (7–14 Hz, according to Lopes da Silva 1991). Recordings from single thalamo-cortical relay cells, that are responsible of spindles generation, have evidenced an oscillation in the alpha range during (and probably due to) the hyperpolarization of the membrane potential produced when these cells are less receptive (see Lopes da Silva 1991 for a review). Therefore, these kinds of oscillations in the primary visual areas may represent a mechanism to stop incoming information. The ‘gating function’ theory, along with the classical alpha desynchronization, predicts higher alpha activity in inhibited cortical areas and lower activity in areas engaged in information processing.

A well-known psychophysical phenomenon in which the visual system inhibits the processing of incoming information is defined as ‘visual suppression’ (Volkman 1986). It consists of a decrease in sensitivity during visual tasks involving transient changes, such a saccades or blinks, in order to maintain the stability of visual scenes (Burr 2004, 2005), and it seems to depend on central, active neural mechanisms rather than being an epiphenomenon of the speed of the image on the retina or of masking (Burr 2004). Indeed, simulated saccades on a white screen do not increase visual thresholds (Diamond et al. 2000), and the saccadic reduction of sensitivity is independent on the

contrast of both forward and backward masks, as if saccadic suppression occurred before the masking effect (Burr et al. 1994), suggesting suppression occurs at the level of the primary visual cortex or earlier (Bonds 1992; Morrone et al. 1982). Further evidence has come from a study (Thilo et al. 2004) in which it was shown that phosphene evocation thresholds rise during saccadic movement, when phosphenes are generated by retinal and not by cortical TMS stimulation. This implies that the saccadic suppression has occurred at a cortical or thalamic stage rather than at the retinal level.

Visual suppression occurs also during eye blinks. Volkman et al. (1980) found increased visual thresholds during blinks that were not due to the effect of the eyelids. They bypassed the standard light path through the pupil, stimulating the retina from the oral cavity through the palate. Subjects had to detect a brief light decrement occurring in one of two voluntary blinks. They compared visual threshold in normal and blink conditions and showed a reduction of sensitivity that was largest at the beginning of the blink. Saccadic and blink suppression share several properties, including the temporal dynamics, the fact that the magnitude of the effect increases with the amplitude of the movement and that both phenomena do not occur at high spatial frequencies and with chromatic stimuli. This may imply a single, magnocellular mechanism underlying both phenomena (see Ridder and Tomlinson 1997 for a review). Furthermore, fMRI studies show a reduction of BOLD signal during blinks in V3 but also in earlier stages such as the NGL (see Burr 2005 for a review). If the visual suppression is early and, as suggested by the ‘gating function’ theory, alpha waves are generated in the thalamus and in the primary visual cortex to inhibit the incoming information, then it is possible that the visual system uses the same mechanism to block potentially disruptive information.

The above findings lead to the prediction that visual suppression phenomena are correlated with an increase in activity in the alpha range. A difficulty in testing this prediction is that EEG recordings are spoiled by blinks and saccades, as they yield signal artifacts due to the dipolar nature of the eyeball and are too quick to yield an oscillatory activity in the alpha band. However, a small but measurable effect has been found also during the closing and opening of the eyes, as well as during steady closed eye positions (Volkman et al. 1982). The experimental conditions used by Volkman et al. (1980) constitute a very good platform for recording EEG without the artifacts arising from saccades and blinks. We reasoned that if the closed eye suppression of visual thresholds could be replicated, then we could expect stronger energy in the alpha range of the EEG during visual suppression. Even though this would not guarantee that this kind of suppression is the same as the saccadic and the blink suppression, it would strongly support the possibility of a common system for inhibiting

visual information processing whose signature would be the presence of oscillations in the alpha range.

The purpose of this study is hence to measure the visual suppression effect with the eyes closed (Volkman et al. 1980) and to search for a time-locked increase in alpha spectral contribution in the same condition, as predicted by the ‘gating function theory’. In two separate experiments comparing eyes closed and with eyes opened, we measured psychophysical luminance detection thresholds from intra-oral visual stimuli of controlled intensity and measured the EEG under identical conditions in order to compare the frequency spectrum obtained with closed and opened eyes. We found higher visual thresholds in the closed eyes condition, which is a signature of visual suppression, and a higher spectral power in the alpha band, which suggests a correlation between visual suppression and alpha oscillations.

## Methods

### Subjects

Three volunteers were used in the psychophysical experiment, two of them naive to the purpose of the experiment, the other one of the authors. They were all university students aged 19 (RB), 22 (MP) and 24 years old (MT). In the EEG experiment, two of the three subjects of the psychophysical experiment (MT & RB) and an additional subject (AM, 19 years old) participated. All the subjects signed an informed consent approved by the ethical committee of the ERC project STANIB.

### Intra-oral stimulation

Both experiments were performed with intra-oral stimulation of the retina. In order to prevent any light stimulation from the normal light path reaching the retina through the optical structures of the eye, subjects performed the measures in a fully dark environment and wore obscured glasses. Plastic glasses were obscured with a liquid zinc spray and tested with the photographic exposimeter Gossen Labosix, which could not reveal any light throughout the glasses. Participants were not able to state if they stood in a dark or lighted environment. This ensured that all the light that stimulated the retinal cells came from the oral cavity passing through the palatine bone. Subjects were asked to bite an endoscopic mouthpiece in which we inserted a 5 W high power led, EN STAR MCE model.

### Stimulation device

The electronic board used to administer the stimuli was implemented with a PIC16F84 chip that allowed light to be

driven at 167 kHz through the serial port using Matlab. The led was controlled by the pulse width modulation (PWM) system so that the power is represented by a square wave in which the low values stand for no power and the high values for full power. The frequency of this modulation is higher than the integration time of the led, this implies that an higher frequency corresponds to an higher power. The duty cycle, defined as the time of high values of the square wave is a useful measure of this frequency (and of the power of the led). We used a PWM system because an intensity modulation system based on resistors fluctuates over time. This was not a problem using a fixed decrement intensity as in the described design, but the board was build to allow a good control of power too. As with standard displays, the relation between power and emitted light was not linear, and a calibration procedure of the light at different duty cycle values was needed.

### Psychophysical stimuli and procedure

In each trial, the light was set at an intensity level determined by preliminary psychophysical measures. Because the psychophysical paradigm was based on a 2-Intervals Forced Choice task, two identical sounds (2,000 Hz) defined each interval and lasted one second, with 0.5 s in between. The signal, consisting on a decrement of luminance of 100% of the duty cycle ( $\Delta L$ ) of varying duration (that in the given range of intervals, 1–12 ms, translates linearly to its detectability), was presented randomly in the 1st or the 2nd interval after an interval of at least 296 ms from the beginning of the sound with an additional 1–255 ms random delay. An entire trial lasted 2,500 ms.

We used the psychophysical method of constant stimuli, using eight randomly selected durations linearly spaced within the range 1–12 ms. This range was established on the basis of pilot observations and resulted well suited to generate a complete psychometric function. The experiment was controlled by a MATLAB script. The experimental variable was time instead of light intensity, as in the original work by Volkman et al. (1982), because it is more stable across subjects than luminance differences since it is not affected by differences in the filtering of light by the palate. Subjects were asked to detect which interval contained a brief light decrement. A pre-recorded verbal signal instructed the subjects to open or close their eyes and when they were ready they had to press a button to begin the trial.

Eyeball movements were controlled instructing the subject to rotate their eyes up as much as they could and to stare at a virtual fixation point placed in the topmost vertical position they could reach by rotating their eyes but without slanting their heads. A similar request seems to be well accomplished by subjects, with an average error of 5° (Merton 1961).

We measured 60 trials for each stimulus duration and eye condition ( $60 \times 8 \times 2$ ), for a total of 960 trials. Data were fitted with a Gaussian cumulative using a maximum likelihood estimation method, parameters errors were estimated by the Bootstrap resampling method (Efron and Tibshirani 1994).

#### EEG experimental procedure

In the EEG experiment, subjects wore completely dark glasses and stood in a dark environment with the retinae stimulated only through the palatine bone, resulting in conditions identical to the psychophysical experiment. However, in this case, there was no behavioral task to perform. The only request to the subjects was to invert the close and open their eyelids when signaled by a brief sound (40 ms, 2,000 Hz) and according to a pattern of durations of openings and closure that was fully consistent with the psychophysical experiment. More specifically, the sound was played every 3 s plus a jitter of  $\pm 0.5$  s. The sound was written in MATLAB, and it was played and triggered to the EEG data by E-PRIME software. The signal was divided in epochs by using this sound as trigger. Every experiment lasted about 10 min, with 100 epochs for each eyes conditions. The scalp currents were sampled at 1,000 Hz.

#### EEG recordings and data analysis

The electrophysiological recording was made in AC mode, by using a Neuroscan NuAMP amplifier and a Quickcap with Ag/AgCl electrodes, from three locations: O1, Oz and O2 against linked mastoids (left and right). For all electrodes, impedance was reduced to less than 5 k $\Omega$ . Electrical activity was amplified with a bandpass of 0.01–100 Hz and digitized at 1000 Hz.

Vertical and horizontal electro-oculographic activity was recorded by an electrode below and on the side of the left eye, respectively.

In offline analysis, the data were epoched (no Epochs were divided) by taking the last 2.5 s before the next trigger for every eyes conditions, then these were averaged and their spectrum was analyzed by a Fast Fourier Transform implemented in Neuroscan software. We have used the last 2.5 ms in order to minimize the impact of eye opening/closure, even though they should already be minimal in occipital electrodes. Trials with eye blinks, eye movements and muscular or other artifacts (defined as a voltage deviation greater  $\pm 60$   $\mu$ V) were excluded. Every difference in the signal spectrum should not be attributed to a luminance difference, because the retinae received the same stimulation in both conditions. The eyeball movements were controlled as in the former experiment to avoid a major retinae' stimulation in the steady closed eye condition, due to the retinal proximity to the light source.

However, a bad control of the Bell's phenomenon (Bell 1823), consisting in an upward and outward rotation of the eyeballs during the eye closure, could not explain an alpha spectral contribution increment in the steady closed condition, because a major visual stimulation should entail an occipital desynchronization, with a reduction in alpha power. The spectrum was analyzed in the alpha range (8–12 Hz) with a frequency resolution of .5 Hz. Spectral energy ( $\eta V^2$ ) was plotted against the frequency, leading to an alpha power measure. Analyzing only occipital activity in the alpha frequency allowed the signal confusion by closing and opening movements of the eyes that could affect the recordings in the first tens of milliseconds after the trigger to be avoided.

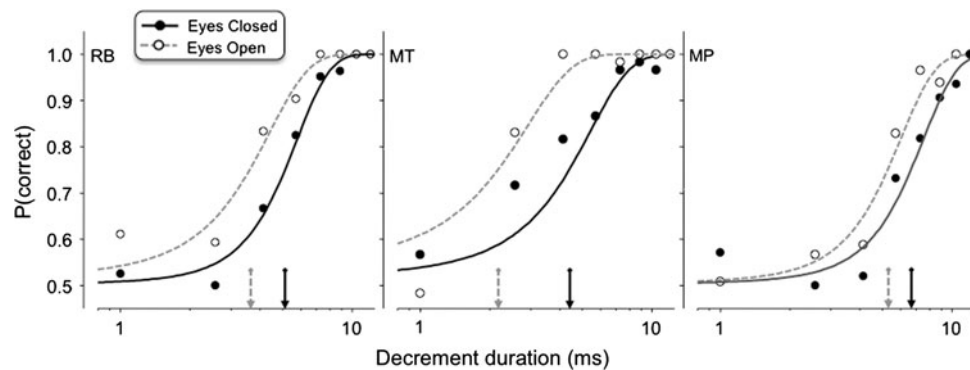
## Results

#### Psychophysical experiment

The psychophysical performance for the closed eyes condition is worse than the opened eyes condition throughout the stimulus range (Fig. 1). For all the subjects, the psychometric functions for the opened eyes condition are shifted to the left relative to the psychometric function for the closed eyes condition. This means that when the eyes are closed the detection of very brief luminance decrements is worse even when the effects of eyelids and of eye movements are taken under control, thus confirming the visual suppression effects reported by Volkman et al. (1982). Since eyes movements were controlled behaviorally, when subjects moved their eyeballs in the Eyes Closed condition one would expect an upper rotation of eye globe (Bell's phenomenon), by which retinae would be more stimulated by light from the palate relative to the Eyes Open condition. Data show the opposite pattern, with no relevant effect of eye movements.

#### EEG experiment

This experiment is designed to investigate the pattern of alpha oscillations during the same experimental conditions of the psychophysical experiment. Figure 2 plots the amplitude of the EEG signal in the alpha range, between 8 and 12 Hz and at a resolution of 0.5 Hz, showing that the spectral power for the closed eyes condition is higher than the opened eye conditions for almost all the data points. There are subtle differences across observers in the distribution of the spectral powers across bins, but this is clearly an effect of the variability of the measure that does not affect the meaning of our results. As a further support to the fact that we are probing effectively the alpha spectrum, the data of the subject showing the weakest spectral power, RB, are plotted in a wider spectrum (8–20 Hz), showing that for all the electrodes both conditions elicit well alpha activity that



**Fig. 1** Psychometric functions for the three participants (RB, MT and MP, from *left to right*) and the two conditions, Eyes Closed (*filled symbols*) and Eyes Open (*empty symbols*). The sigmoidal functions represent the best fit of cumulative Gaussians through the eight accuracies measured at each decrement duration for the two conditions (*straight and dashed lines*, respectively). For all subjects, the psychometric

function for the Eyes Open condition is shifted to the left relative to the Eyes Closed condition. Visual thresholds, taken at 75% accuracy and indicated by the *arrows* along the abscissae, are hence higher in the former condition, implying a decrease in sensitivity when the eyes are closed even though the visual stimulus was administered through the palate

is stronger when the eyes are closed. This fits with the hypothesized correlation between alpha power and visual suppression. The bar plot plotted in the leftmost column of Fig. 2 shows the average spectral power in the alpha band (8–12 Hz) across electrodes and subjects. As expected, the Eyes Closed condition has a much greater alpha power than the Eyes Open condition for the three occipital electrodes examined and for all experimental subjects.

We tested an ANOVA (on individual subjects) to the log-transformed data with eye conditions (2 levels) and electrodes (3 levels) as factors showing no interaction between the two factors (all  $p$ -values  $> .96$ ) and no electrode effect ( $P > .67$  for AM,  $P > .97$  for RB and  $P > .16$  for MT), but only a strong main effect of the eye condition for all the subjects ( $P < .001$  for AM and  $P < .01$  for RB and MT). The lack of an electrode effect on occipital lobe is coherent with previous studies, in which a spatiotopic effect of attentional alpha waves modulation was found (Worden et al. 2000; Rihs et al. 2007), because in the present study retinae were stimulated diffusely. This effect should not be considered an effect of a difference in visual stimulation because light was constantly stimulating the retinae through the palate. Therefore, this alpha modulation was probably related to some form of central modulation bound to the eye condition. This modulation took place in correlation with a difference of visual threshold also related to the eye condition. This result is coherent with the predictions of the ‘gating function’ theory applied to the visual suppression phenomenon found in the behavioral experiment.

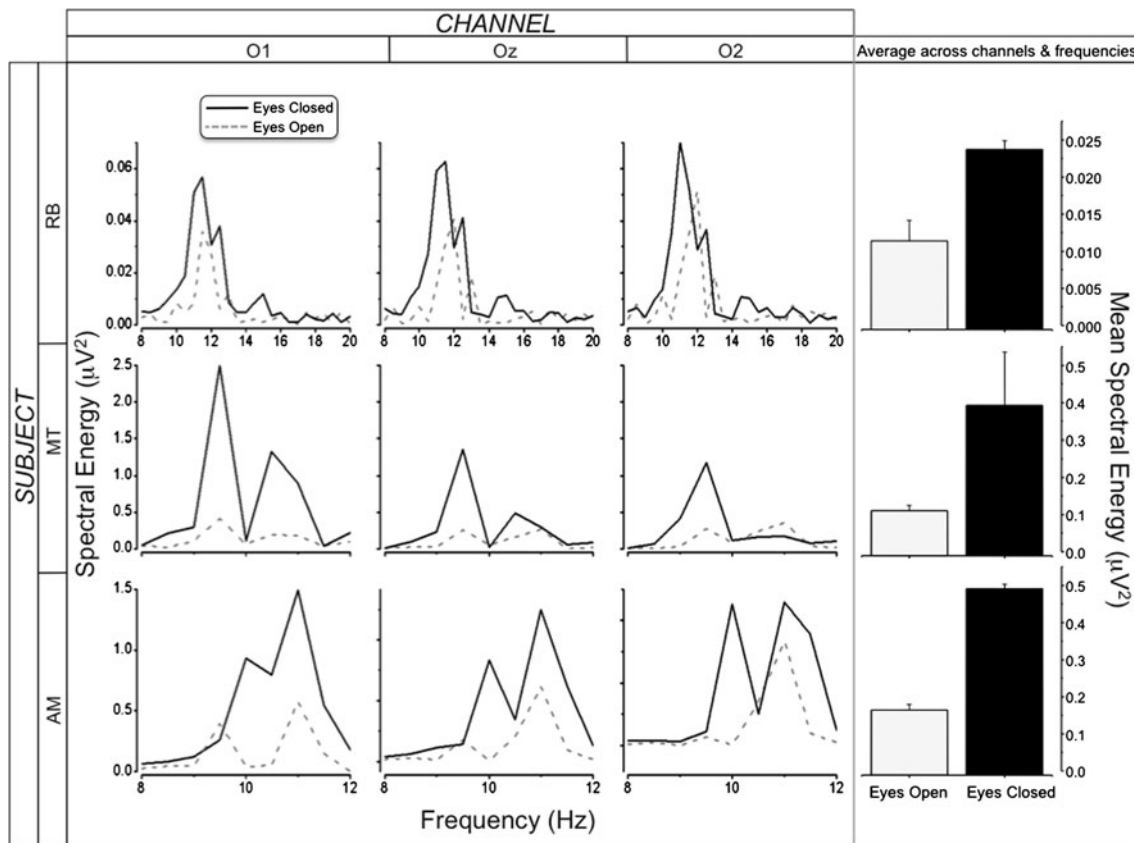
## Discussion

In this study, we elicited visual suppression in young adult subjects by simply requiring them to shut their eyes tran-

siently. Relying on the well-known phenomenon that closing the eyes increases alpha activity recorded through EEG (see Cantero et al. 2002 for a review), we found a time-locked increase in alpha oscillations during a short closure of the eyelids relative to when eyes were open in conditions where light was projected to the retinae through the palate. This simple paradigm, derived from a previous study by Volkmann et al. (1982) turned out to be very easy to control and because it lasts just enough to allow an EEG oscillatory response in the alpha band, an effect that we hypothesize to be linked to the sensory inhibition of early levels of the visual system. Visual thresholds for detecting a light decrement of variable length were higher with closed eyes relative to the open eye condition, and the energy of alpha oscillations was significantly higher in the former condition. This effect could not be explained with a change in the retinal stimulation because the retinae were stimulated from the oral cavity through the palate. The only physical change that could affect the illumination of the retinae was the rotation of the eye when the eyelids were closed. The Bell’s phenomenon (Bell 1823) consists in an upward and outward rotation of the eyeballs during a blink that exposes the retinae toward the palate, hence allowing, in principle, to get more light through. Our observers were instructed to fixate a virtual point at the highest position allowed by the upward rotation in the vertical axis, but, if this control failed somehow, the Bell’s phenomenon would expose the retinae even more to light from the palate, implying higher rather than lower sensitivity, as we actually found.

We probed visual suppression by varying the interval of a light decrement, while Volkmann et al. (1982) varied the intensity of a decrement while keeping its interval constant to measure the psychometric functions. Then, the visual suppression found is consistent across different measures. The main goal of our study was to correlate visual suppres-





**Fig. 2** Spectral Energy in the alpha band. In the first three columns, recordings from electrodes O1, Oz and O2 are represented from the left to the right, while the three subjects, RB, MT and AM from *top to bottom*, respectively. The leftmost column report bar plots of the average across electrodes and frequencies. The six plots represent the spectral power measured in squared microvolts sampled every 0.5 Hz. The data for subjects MT and AM (*middle and bottom line*, respectively) are plotted in the alpha frequency range (8–12 Hz). Data for subject RB (*top line* of plots) show a spectrum extending beyond the alpha range as it was the subject with the weakest spectral power and we wanted to show that (A) we have significantly measured alpha activity and the results are not simply noise and (B) that different fre-

quencies are not modulated by our experimental conditions. The straight lines represent the spectral power measures for the Eyes Closed condition, while the dashed lines represent the spectral power recorded in the Eyes Open condition. Spectral power in the alpha band appears higher in the closed eyes condition than in the other condition for all the electrodes for the three subjects. The bar graphs of the leftmost column represent the mean energy across frequencies and channels for the two conditions (*black bars* for the Eyes Closed, *gray bars* for the Eyes Open condition), with the *error bars* showing the S.E.M. across channels. Coherently with our main hypothesis, the Eyes Closed condition shows at least twice the spectral energy than the Eyes Open condition

sion to one of its possible neural correlates, within the hypothesis that an alpha wave increment may increase in relation to early sensory inhibition. Our results show an alpha wave modulation according to the eyes condition that entails a visual suppression phenomenon. This is coherent with the hypothesis that alpha waves underlie the neural mechanism of inhibition of incoming sensory information. The light was presented from the oral cavity though the palatine bone. Alpha waves are known to decrease with visual stimulation, but in our experiment the eyelid could not cause any change in the light that reaches the retinae, so the difference in the alpha waves could not be explained as a difference in the visual stimulation. Subject wore dark glasses and stood in a dark environment, so there was no change in the light from the external environment. Eye movements have been controlled in the same way as the

former experiment, but even here the failure of this control could only cause a reduction of the measured effect, because in case of eyeball rotation with the eye closure, participants' retinae were more exposed to the light causing an alpha waves reduction according to the typical alpha waves behavior. Our results instead showed an increment in alpha waves, as expected from the 'gating function theory'. This issue does not imply that there is causal relationship between alpha waves and this kind of visual suppression, but affords the possibility, as evidenced by the occurrence of visual suppression in that visual areas where alpha waves are generated, the attentional modulation of alpha waves, and the analogy with the sleep spindles. A recent study suggests that our correlation may involve a causal relationship between alpha oscillations and the gating of visual information. Romei and colleagues (2010) have indeed observed a

reduction of visual performance in the emifield contralateral to TMS pulses at alpha frequency that was significantly larger than with stimulation at theta (< alpha) or beta (> alpha) frequencies.

While we cannot be certain that the suppression observed is the same early suppression that occurs in blinks and saccadic eye movements, it is plausible and parsimonious that the visual system uses the same resource for the same function in different situations. The suppression of visual sensitivity when observers have their eyes closed is an interesting kind of visual suppression because it is easy to generalize to novel experimental setups. For example, it could be easily studied in animal paradigms without timing problems, in a similar way to the paradigms used to probe the sleep spindles, i.e. by electrophysiological recordings of thalamo-cortical activity in vivo and in vitro (Lopes da Silva 1991). All the alpha waves modulation studies described earlier, including the present, are of a correlational nature and are open to interpretations alternative to the ‘gating function’ theory. For example, in the classical (Adrian and Matthews 1934) alpha rhythm’s view, a reduction of sensory stimulation entails alpha wave synchronization. Therefore, if a visual suppression or an attentive mechanism would act at a level earlier than the alpha waves generation site, the results described in the present study and in other studies on attentional modulation could be explained as a passive consequence of a lack of activity. In this view, the present study can play an important role in locating the visual suppression site occurring before the alpha wave generation areas.

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