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A better oscillation detection method robustly extracts EEG rhythms across brain state changes: The human alpha rhythm as a test case.

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Abstract

Oscillatory activity is a principal mode of operation in the brain. Despite an intense resurgence of interest in the mechanisms and functions of brain rhythms, methods for the detection and analysis of oscillatory activity in neurophysiological recordings are still highly variable across studies. We recently proposed a method for detecting oscillatory activity from time series data, which we call the BOSC (Better OSCillation detection) method. This method produces systematic, objective, and consistent results across frequencies, brain regions and task. It does so by modeling the functional form of the background spectrum by fitting the empirically observed spectrum at the recording site. This minimizes bias in oscillation detection across frequency, region and task. Here we show that the method is also robust to dramatic changes in state that are known to influence the shape of the power spectrum, namely, the presence versus absence of the alpha rhythm, and can be applied to independent components, which are thought to reflect underlying sources, in addition to individual raw signals. This suggests that the BOSC method is an effective tool for measuring changes in rhythmic activity in the more common research scenario wherein state is unknown.

Keywords: electroencephalography, alpha, brain rhythm, human, oscillation

Introduction

In 1929, Hans Berger was the first person to describe rhythmic oscillations of electrical potential recorded from the human scalp. This included a 10-Hz signal present over the occipital cortex which became known as the alpha rhythm (Berger, 1929). The alpha rhythm occurs at frequencies of 8-12 Hz, is most prominent during behavioural states of relaxed wakefulness with eyes closed, and is replaced by low-voltage, faster activity with eye opening. While alpha was long thought to represent a brain idling state, its role in neural processing now appears much more complex. Alpha power increases are elicited in tasks requiring top-down inhibition or highly selective processing, such as ignoring specific stimuli while attending to others (Freunberger et al., 2009; Klimesch et al., 2007; Worden et al., 2000). In addition, alpha power has been shown to increase with memory load during the retention interval in a modified Sternberg task (Jensen et al., 2002).

In the years since the discovery of alpha, many other electroencephalographic (EEG) oscillations have been described at various frequencies and locations, and have been associated with distinct brain processes and behavioural states. EEG oscillations represent the collective activity of rhythmically synchronized neuronal networks (reviewed in Niedermeyer and Lopes da Silva, 2005) and are thought to be essential for both ongoing modulation of behaviour and offline processing, for example, occurring during sleep or rest (Buzsaki and Draguhn, 2004).

Despite the fact that EEG oscillations have been studied for over 80 years, identifying oscillatory activity in EEG traces is still highly variable across studies (van Vugt et al., 2007). The primary method in the field is to calculate frequency spectra using either *Fourier* or wavelet transforms of the signal, and to visually inspect the resulting spectra for peaks in specific frequency bands. Each method has its own particular strengths and weaknesses. The Fourier transform efficiently decomposes any stationary signal as a series of sine waves of different frequencies and amplitudes (Brigham, 1974). Unfortunately, brain signals are rarely (if ever) stationary, and are often dynamic on time scales that are too fast to allow for an adequate representation of all frequency components using traditional Fourier-based computational methods. Wavelet transforms, on the other hand, fit more temporally discrete pieces of the signal using a family of mathematical functions (known as "wavelets") that vary both in frequency and time window (Kemerait and Childers, 1972; Schiff et al., 1994). Wavelet methods avoid the problem of nonstationarity by allowing spectral characteristics to change over time. Unfortunately, the presence of a spectral peak at a given frequency using either method does not necessarily imply underlying oscillatory activity at that frequency because non-oscillatory, large-amplitude artefacts and transient signals can produce power changes at specific frequencies. In addition, some functionally relevant oscillations are highly transient, and depending on the size of the analysis time window they can be obscured by other, larger amplitude, oscillatory activity or they can be overshadowed by the overall power in the background spectrum.

Autocorrelations of EEG signals are often performed to establish the presence of oscillatory activity, but this analysis method also has limitations: the fundamental frequency will dominate the autocorrelation function, and it is difficult to rigorously compute a significance value for rhythmicities that may be apparent in the autocorrelation plot. Further, the baseline for deciding when bandpass power reflects an oscillation varies from study to study. In some cases, the observation of a peak in the spectrum and/or autocorrelation is sufficient, whereas in other cases, a direct comparison to some baseline condition is used. In either approach, the determination of rhythmicity depends upon the variable characteristics of the signals themselves. Finally, pre-whitening (normalizing power across frequency) can help to overcome the frequency bias due to the colored-noise form of the EEG spectrum, but it can be overly conservative, overcorrecting when peaks (potentially reflecting oscillations – the signal of interest) are present. What is needed is a method of detecting oscillations that derives detection thresholds in a way that is consistent across frequency, electrode (brain region), task, electrophysiological state and species.

The BOSC method. With these issues in mind Caplan et al. (2001) , introduced a new method to detect oscillatory activity in EEG signals which we term the Better OSCillation detection method, or BOSC. This method is designed to take into account the functional form of "background," non-rhythmic portion of the signal and to reveal segments of the recording that deviate significantly from the spectral characteristics of the background. In BOSC, one calculates a power threshold (P_T) and a duration threshold (D_T) for oscillatory episode detection by modeling the known functional form of the background power spectrum. That is, at a given frequency, BOSC detects increases in power, above P_T, of a specific minimum duration, D_T, thereby rejecting increases in spectral amplitude that are non-repeating (Fig. 1). Briefly, an average wavelet power spectrum is calculated, and this spectrum is modeled as colored noise (power scaling as 1/frequency) with the possible addition of peaks at some frequencies that potentially reflect the presence of oscillations (Fig. 1D). The colored noise spectrum is a basic property of EEG as well as other natural autocorrelated signals (Schlesinger and West, 1988). This spectrum is then fit by linear regression in log-log space. In previous applications of BOSC, the power threshold (P_T) has been set to the 95th percentile of the theoretical probability distribution (with $\chi^2(2)$ form; e.g., Fig. 1E) of power values at a given frequency and the duration threshold (D_T) has been set at each frequency f to 3 complete cycles ($3/f$). Oscillations are only detected when both P_T and D_T are exceeded. The qualitative outcome of application of the method is robust to the exact choice of threshold values; Caplan et al. (2001) characterized how variations in P_T and D_T affect the frequency specificity and conservatism of oscillation detection. The BOSC method also lends itself to a useful quantitative measure: the proportion of time (within a trial or other time segment) that detected oscillations are present, which we have termed $P_{episode}$ (Caplan and Glaholt, 2007; Caplan et al., 2001; Caplan et al., 2003; van Vugt et al., 2007).

This BOSC method has been used successfully to identify and quantify theta oscillations in the human neocortex that are correlated with memory encoding and retrieval and sensorimotor integration (Caplan and Glaholt, 2007; Caplan et al., 2001; Caplan et al., 2003). It has also been applied to oscillatory activity from intracranial recordings in the human hippocampus (Ekstrom et al., 2005). Previous work has demonstrated that the BOSC method provides standardized detection criteria across frequency, electrode and task. Ideally, this method can be generalized to extend to all types of EEG recordings, providing standardized oscillation detection criteria across electrophysiological state and species (Hughes et al., 2009). Thus, we sought to more systematically evaluate the BOSC method on a well known and easy-to-induce oscillation that occurs during wakefulness: Alpha. An ancillary goal was to determine whether the BOSC method is compatible with independent component analysis (ICA) which has been increasingly adopted as means of inferring activity of presumed underlying sources (Makeig et al., 1997). This would only work if the power spectrum of an independent component also exhibited a colored-noise functional form. Our final goal was to determine whether state changes that occur during wakefulness present a challenge to the method. Because the method relies on estimating the background spectrum, if the background spectrum were to change sufficiently across state, this would very likely result in false positives or false negatives or a bias across frequency. We show in the present study that the BOSC method is robust to state changes and reveals features that are entirely consistent with previous research on the alpha rhythm.

Methods

Data collection

Twelve human participants recruited from the University of Alberta community were fitted with a 256-channel HydroCell geodesic sensor net (Electrical Geodesics Inc., Eugene, OR) with electrode impedances kept below 50 kΩ (Ferree et al., 2001). Data were amplified by the EGI NetAmps 300 amplifier with a 400 Hz anti-aliasing hardware filter; digitized at a rate of 250 Hz and acquired via Net Station software using a 24-bit A/D converter.

Experimental protocol

The task was presented in E-prime (Psychology Software Tools Inc., Pittsburgh, PA); subjects received verbal and written instructions to begin with their eyes open (or closed) and to close (or open) their eyes gently upon hearing a beep. The beep was presented every 5 seconds, with 10 beep presentations in total constituting 45 seconds.

Data analysis

Data were analyzed in MATLAB (v. 7.4; The Mathworks, Natick, MA) using EEGLAB (Delorme and Makeig, 2004) and filtered from 0.5 to 45 Hz. Independent component analysis (Makeig et al., 2004) was performed following an initial dimensionality reduction using a principal component analysis, keeping the first 20 components. Because independent components (ICs) have been suggested to reflect underlying sources, ICs representing alpha oscillations were selected for further analysis with the BOSC method based on a peak in the conventional power spectrum in the 8-12 Hz bandwidth accompanied by a clear dipole-like topography with a maximum electrode weight at occipital loci. This allowed us to test whether the BOSC method could be successfully applied to ICs. Individual electrodes were selected for analysis based on their weighting in the IC alpha components.

The Better OSCillation detection method

The BOSC method identifies episodes in the signal where the power at a given frequency exceeds a power threshold, P_T that is derived from the theoretical background distribution of power values at each frequency, for a minimum duration, D_T that scales with frequency (D_T=3/f). First, spectral analysis of the selected component or electrode was performed using a Morlet wavelet transform (Grossmann and Morlet, 1985) with a window of 6 cycles and frequency sampled in 18 logarithmic steps covering the bandwidth from 2 to 38 Hz. A background window was selected (see below) and this window was used to calculate the average background spectrum. The background EEG spectra were assumed to be colored noise of the form $Af^{-\alpha}$ (e.g., Fig. 2b), typical of natural autocorrelated signals (Schlesinger and West, 1988). This assumption allows us to estimate the spectrum by fitting it with a linear regression in log-log coordinates (Fig. 1D). P_T was set to the 95th percentile of the expected $\chi^2(2)$ distribution of power values at each frequency with the distribution mean set to the estimated mean from the linear regression in the previous step (Fig. 1E). The $\chi^2(2)$ distribution is a characteristic that results from Fourier-transforming a Gaussian-distributed signal (recorded EEG in the time domain), which yields a complex number. Squaring this complex number to compute power amounts to constructing a value from the sum of two squared Gaussian values, one for the real part and one for the imaginary part of the complex number, hence χ^2 with 2 degrees of freedom (Percival and Walden, 1993). D_T was calculated based on the duration of three complete oscillation cycles at each frequency, 3/f. Epochs when both P_T and D_T were exceeded were tagged as oscillations. The measure, $P_{episode}$, the proportion of time during which oscillations at a given frequency were present, was used to assess performance of the method.

Background window

To test the robustness of the method to electrophysiological state changes, we asked whether the core assumption of the method, that one can model and estimate the background spectrum, might pose a problem for the BOSC method when analyzing data that includes more than one state. To this end, we compared four different types of background window to derive the BOSC threshold P_T: First, the entire epoch of the task (45 s) was used as the background, which is similar to what has been used in previous applications of the method. For comparison, background spectra were also calculated from exclusively eyes-open or eyes-closed epochs, which should represent the optimal match between background and signal of interest, or from data segments that overlapped both conditions, which should represent the worst-case scenario, in which two different states are treated as though they were one. For these calculations, the spectra from eight 2.5-s epochs (totalling 20 s) that represented eyes-open, eyes-closed or overlapping segments were averaged and used as the background spectrum.

Results

Detecting alpha

In 11/12 subjects we found ICs with clear spectral peaks in the alpha (8-12 Hz) band. Figure 2 illustrates the detection of alpha oscillations in a single independent component by BOSC. The component was chosen for further study based on an 8-12 Hz peak in the conventional spectrum (Fig. 2B) and a clear dipole-like topography with a maximum weight in electrodes overlying occipital cortex (Fig. 2A). Consistent with the peak in the conventional power spectrum, the BOSC method detected oscillations in the alpha band (Fig. 2C), and these oscillations were present more of the time during the eyes-closed epochs. When the proportion of time during which oscillations were present ($P_{episode}$) was compared between conditions, there was a clear difference between the eyes open and eyes closed conditions in the alpha bandwidth (Fig. 2D). The relative flatness of non-peak frequencies in this figure highlights the fact that the $P_{episode}$ method removes the frequency bias present in the original spectrum, putting all frequencies on an even footing. This is one advantage of the method as described previously (Caplan et al., 2001; Caplan et al., 2003). A plot of the raw EEG trace with periods of identified 9.5-Hz oscillations highlighted in red confirms that these oscillations occur preferentially during the eyes-closed condition (Fig. 2E), and that the identified oscillations indeed look rhythmic when inspected visually (Fig. 2F). Furthermore, Fig. 2F shows that these alpha oscillations have a spindle-like appearance, waxing and waning in amplitude within the eyes-closed condition, as has been observed previously (Niedermeyer and Lopes da Silva, 2005).

To evaluate the oscillations detected by BOSC, across all subjects who had a clear alpha independent component, $P_{episode}$ (see Methods) for the peak alpha frequency in the representative alpha component was calculated for both eyes-open and eyes-closed conditions (Fig. 3A). Average $P_{episode}$ for eyes-closed was 0.62 ± 0.05 (mean ± SEM) compared to 0.13 ± 0.02 for the eyes-open, and these were significantly different (paired two-tailed t-test: $t(10) = -11.61$, $p < 0.05$). It should be noted that these are actually conservative estimates of the difference in alpha-frequency $P_{episode}$ for the two conditions, since conditions were divided by the time-points of the audible beep. Due to the delay between the beep onset and the subjects' actual reaction times to the beep, this is likely offset from the actual time-points of eye-closure and opening.

ICA vs *individual electrodes*

The application of BOSC to ICs is novel; for comparison, we applied BOSC to the raw signals derived from individual electrodes, as conventionally done in the past. Electrodes of interest were selected as sites with the maximum (Fig. 4) and minimum (Fig. 5) weighting from the representative alpha independent component. While the amplitude of alpha oscillations recorded over the occipital cortex (Fig. 4) was clearly larger, alpha specific to the eyes-closed condition was still detected by the method from the electrode with the smallest weighting in the representative alpha component (Fig. 5). In theory, all electrodes should detect activity from all sources within the brain. The similarity of $P_{episode}$ values for both electrodes shown (Figs. 4D and 5D) highlights the sensitivity of the method. In accounting for the background spectrum in each case, it produces similar $P_{episode}$ values despite differences in the power of the oscillation. This suggests that the BOSC method is relatively resilient to other signals that might accompany the signal of interest. Note that this does not mean the BOSC method is blind to differences between recording sites; rather, one could straight-forwardly follow up oscillation detection with analyses that quantify amplitude (not to mention phase) of oscillations once detected –

this type of measure would reveal the difference in relative weighting of the alpha rhythm for different electrodes.

The similarity of the spectra for the ICs and the individual electrodes was confirmation that the colored-noise background spectrum assumption of the method was valid for both ICs and individual electrodes. A second assumption of the method is that the background signal power values at each frequency have a $\chi^2(2)$ probability distribution function. In Figure 6, the distribution of wavelet power values for an alpha component is plotted (histogram) with a $\chi^2(2)$ probability distribution function (line plot), for the peak alpha frequency (Fig. 6A), as well as two other nearby frequencies (Figs. 6B-C). The same plots are shown for a single electrode in Figs. 6D-F. First, note that when oscillations are not thought to be present (non-peak frequencies in Figs. 6B-C, E-F), the distribution of power values is quite close to the expected $\chi^2(2)$ form. For the peak frequency, the probability distribution deviates substantially from $\chi^2(2)$, due to the presence of more oscillatory activity, which produces a power distribution weighted more to higher values (a thicker tail). The vertical lines mark the 90^{th}, 95^{th} and 99^{th} percentile levels of the $\chi^2(2)$ distribution, to demonstrate how the selection of the percentile threshold would affect the detection of oscillations. A more conservative threshold could result in more false negatives, while a less conservative threshold would let more oscillations through, resulting in potential false positives (Caplan et al., 2001).

Background window

A principal aim of this study was to find out whether state changes during wakefulness could present a problem to the BOSC method. Thus, we systematically varied the epochs included in the background window that were used to derive the averaged background spectrum. In the analyses reported to this point the background window spanned the entire experiment. This window therefore averaged across the state changes elicited by the eyes-open and eyes-closed protocol. In this case, changes in the background spectrum could affect the model fit (i.e. the threshold) and thus be inappropriate for one or both states. To examine the effects of brain state on the background fit (and thus, power thresholds as a function of frequency and, ultimately, detected oscillations) three separate background spectra were calculated: one using the average spectrum from exclusively eyes-open epochs, one using the average spectrum from exclusively eyes-closed epochs, and one using the average spectrum from epochs that overlapped both states (see Methods section).

The theoretical form of the background spectrum is a straight line in log-log coordinates. Thus, we can characterize the shape of the background spectrum (disregarding any peaks) by inspecting the values of slope and intercept of the regression line. The average slope of the regression line fitting the background spectrum for the bilateral alpha component using the full experiment as the background window was -1.00 ± 0.07dB/Hz, which was not significantly different (paired two-tailed t-test) from the slope for the eyes open condition (slope = -0.98 ± 0.08dB/Hz, $t(10) = -0.64$, $p>0.05$), nor from the slope for the eyes closed condition (slope = -0.99 ± 0.09, $t(10) = -0.40$, $p>0.05$). The average y-intercept of the regression line using the full experiment to calculate the background window was 1.66 ± 0.15, which was again not significantly different from the y-intercept for the eyes open condition (y-intercept = 1.56 ± 0.13, $t(10) = 2.10$, $p>0.05$) nor from the y-intercept for the eyes closed condition (y-intercept = 1.76 ± 0.16, $t(10) = -1.91$, $p>0.05$), although both of these were nearly significant ($p<0.1$).

Despite the lack of significant differences in the parameters used to fit the background spectrum (slope and y-intercept), there was a difference in the detected oscillations using the different background windows. More oscillations were detected when the eyes-open condition was used to calculate the background spectrum, and fewer oscillations were detected when the eyes-closed condition was used as the background. This can be seen for a single experiment in Figure 7 and is displayed as averages across all experiments in Figure 8.

Two alpha components

In 10/11 subjects, more than one alpha IC was detected. In most of these cases, the strongest alpha component was distributed symmetrically over the occipital cortex, (Fig. 2), whereas the weaker alpha component was lateralized (Fig. 9). In all cases, the peak alpha frequency was identical in both components (mean peak alpha frequency 11.4 ± 0.4 Hz; Fig. 3C). Despite the fact that the peak frequencies were identical, the fact that the two components were extracted separately by ICA indicates that they were temporally independent. This is illustrated in figure 10, where the alpha oscillation in the lateralized component (Fig. 10B) appears maximal when alpha in the bilateral component (Fig. 10A) is weak, and the bilateral component starts to show rhythmic activity just before the lateralized component. The $P_{episode}$ values for the lateralized alpha components were qualitatively similar to the bilateral alpha components (Fig. 3B), and were significantly different across states (eyes closed $P_{episode} = 0.58 \pm 0.05$; eyes open $P_{episode} = 0.18 \pm 0.02$; significantly different via paired two-tailed t-test: $t(9) = -8.45$, $p < 0.05$). This finding of multiple alpha components is consistent with other ICA-based alpha studies (Jeong et al., 2004; Makeig et al., 2002), and is consistent with the idea that alpha arises from the synchronization of multiple alpha generators (Nunez et al., 2001). This confirms that the BOSC method is succeeding in identifying the features of alpha that have already been described, but unlike previous methods it provides a more quantifiable and reproducible means of characterizing those features.

Alpha harmonic

In 4/11 subjects, an alpha harmonic at twice the alpha frequency was detected by the BOSC method (Fig. 11). For these experiments, the average $P_{episode}$ at the harmonic frequency for the eyes closed condition was 0.18 ± 0.03 compared to 0.024 ± 0.009 for the eyes open condition, and these were significantly different in a paired two-tailed t-test ($t(3) = -6.05$, $p<0.05$).

Discussion

Our findings support the BOSC method as a powerful tool for identifying oscillations in neural data. It does so by setting parameters in a manner that minimizes bias across frequency, electrode and task (as shown previously), electrophysiological state (shown here) and species (Hughes et al., 2009). The alpha rhythm was an ideal candidate for testing the validity of this method: It is large in amplitude, it dominates the recording when present, and it is easily evoked. In addition to evaluating detection of alpha, two corollary predictions were made as tests of the method: alpha oscillations should be larger in amplitude in electrodes near vs. distant from the occipital cortex, and alpha oscillations should be more prominent during eyes-closed vs. eyes-open conditions. The method succeeded in both of these tests, for both raw signals at individual electrodes and for ICs, although it was also shown that the method could detect small-amplitude alpha oscillations from electrodes distant from the presumed source.

The characteristics of the alpha components extracted by ICA and the presence of both bilateral and lateralized components were consistent with previous studies on alpha (Jeong et al., 2004; Makeig et al., 2002). Moreover, the BOSC method also extracted a harmonic at about 20 Hz in a subset of our subjects, a feature of subject variability which has been reported previously (Niedermeyer and Lopes da Silva, 2005).

One of our objectives was to determine whether the BOSC method would succeed at identifying oscillations in IC timecourses. We found that the critical assumptions about the background spectrum that underlie the method, that is, a colored-noise background spectrum and a $\chi^2(2)$ distribution of wavelet power values at each frequency, were shown to be valid for ICs and not only recordings from individual electrodes. This is important because ICA is becoming increasingly adopted as a means of artefact removal as well as data analysis. Because the functional form of the background spectrum is the same for

ICs as for the original electrodes, the BOSC method could be applied to ICs, which are thought to reflect discrete underlying sources, without modification.

The eyes-open and eyes-closed conditions can be thought of as inducing different brain "states." A key question was whether the modeled background spectrum would vary substantially enough across waking states to present a problem to the method. By looking at background windows exclusively from one state or spanning both states, we were able to assess the effects of state on the parameters that affect the detection of oscillations. Although the selection of background window affected the absolute $P_{episode}$ for each frequency, the detected oscillations were still qualitatively similar (Figs. 10 and 11). When the optimal background (same-state) was used, the method became more conservative, detecting fewer oscillations, particularly at non-alpha frequencies. Considering that the BOSC method is typically used for exploratory research, in which the timing and task dependence of oscillations are by definition unknown and any potential state changes are unknown as well, our findings suggest that changes in the background spectrum and their estimates over unrecognized state changes may not be a major concern. However, as we elaborate below, it is still important to cross-check the form of the spectra to determine whether or not the colored-noise background assumption is violated; if so, then the assumptions underlying the method are invalid and the method may produce unpredictable results. The above results also suggest that an initial run of the analysis could be performed to identify gross state changes, and a subsequent analysis using a within-state background window once state changes are known would produce more stringent identification of oscillatory activity.

The colored-noise form of EEG signals has been used elsewhere to estimate the background spectrum. For example, with a different application in mind – online spectral analysis for use with brain-computer interfaces – Blankertz et al. (2010) model the spectrum in the same way as we have, namely, as colored noise plus peaks. The BOSC method differs in how the spectrum estimate is used. Blankertz et al. use it to identify peaks in the spectrum. The BOSC method does not require peaks to be identifiable and is, instead, used to estimate the background signal compared with which runs of rhythmic activity may be inferred. Thus, the BOSC method includes the additional assumption of the chi-square probability distribution function of wavelet power values at a given frequency as well as the duration threshold, which makes the method conservative about identifying oscillations in a signal.

The BOSC method shares some features with other existing time-frequency analysis methods such as EEGLAB's event-related spectral power (ERSP) method (Makeig et al., 2004). However, as has been elaborated elsewhere (van Vugt et al., 2007), the BOSC method goes further in several ways, which means that the BOSC method enables the researcher to ask questions about oscillations in different ways. First, most other methods, including ERSP, use a baseline condition as a control with which to compare the signal of interest, with the consequence that significance will depend on the precise choice of comparison condition. The BOSC method fits the signal's own background spectrum, both the colored-noise form of the mean spectrum, and the chi-square form of the expected probability distribution of wavelet power values. The power threshold can be seen as a stand-in for the background-signal modeling aspect of the BOSC method. We have shown elsewhere (Caplan et al., 2001, Figure 6, parameter varying across rows) that when the power threshold is made more liberal (inclusive), bringing the method closer to conventional spectral analysis methods, the signal-to-noise ratio (ratio of rate of detected oscillations relative to an approximate false-positive rate) goes down. In addition, other methods lack a duration threshold, which helps to restrict findings to segments of signal that would be interpreted as rhythmic even by more conservative standards. We have shown elsewhere (Caplan et al., 2001, Figure 6, parameter varying across columns) that when the duration threshold is shortened, the frequency specificity becomes worse, suggesting that non-oscillatory signal is detected yielding false-positive findings if we are only interested in truly rhythmic activity.

Recommendations:

First, it is possible to apply the method to independent components. For both independent components and raw EEG signals, it is important to check the form of the background spectrum to ensure that the coloured-noise assumption is met. Further to this, some care must be taken in selecting the appropriate frequency range over which to estimate the background spectrum, particularly because the 1/f spectrum form must be adhered to for the linear-regression to be a meaningful fit of the background spectrum. As rigorously laid out by Miller et al. (2009, see also their supplementary materials), roll-off frequencies due to bandpass filtering can be problematic and should be avoided. Miller and colleagues also point out that a "noise floor" due to non-physiologic (e.g., instrumental) noise is typically present, with approximately white spectrum. This could potentially affect the background fit, in particular at higher frequencies. Ideally, this white noise could be estimated and included in the fit of the backround spectrum. Alternatively, the frequency range could be adjusted to avoid the potentially problematic higher frequencies. In addition, examining the fit of power values at each frequency to the theoretical $\chi^2(2)$ distribution, as shown in figure 6, could help determine if the white noise floor introduces substantial bias at a particular frequency.

When applying the method in situations where state changes are known in advance, a within-state background window is optimal for the detection of oscillations. If these state changes are not known in advance, they can be identified by initial analysis using the method with a non-state-specific background. Finally, once oscillatory episodes are detected, they can be used as a starting point for further analyses to examine amplitude, frequency and phase characteristics.

Conclusion

This study presented a test case for the BOSC method in detecting an oscillation that is strong, easy to elicit and well described in the literature. The results show that the method can detect alpha oscillations that are temporally restricted to periods when they are expected (eyes-closed condition) in both ICs and single electrodes. Furthermore, the detection of alpha oscillations is robust to the selection of the background window. These findings, along with recent validation of the method applied to hippocampal recordings from rats (Hughes et al., 2009), suggest that the BOSC method will play an important role in comparing oscillatory activity across frequency, brain region, task, electrophysiological state and species.

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Figures

Figure 1: *The oscillatory episode detection method.* A schematic representation of the application of a power threshold (P_T) and a duration threshold (D_T) to an EEG signal. In A, both thresholds are exceeded and the method identifies this epoch as oscillatory. In B and C, P_T or D_T are not exceeded and therefore these epochs are not identified as oscillatory. D. An example power spectrum with a peak potentially reflecting alpha oscillations (blue), and the modelling of the background spectrum with a linear regression (green). E. The probability distribution function of power values at frequency f* can be fit by a $\chi^2(2)$ distribution (see text), which is used to determine the power threshold (P_T) for oscillation detection, in this case based on the 95th percentile of the $\chi^2(2)$ distribution.

Figure 2: *Oscillation detection in an ICA alpha component.* A. The spline-interpolated scalp distribution of an alpha component extracted by ICA. Color scale denotes electrode weight (unitless). B. Background wavelet power spectrum mean and standard deviation (blue) and the linear regression fit to the background (green). C. Oscillations detected across all frequencies by the oscillatory episode detection method. Red vertical lines indicate when participants were instructed to close their eyes and black vertical lines indicate when participants were instructed to open their eyes. D. The proportion of time ($P_{episode}$) during the eyes-closed condition (red) and eyes-open condition (black) that oscillations were detected at each frequency. E. The time-domain representation of the chosen component, with detected oscillations at the peak alpha frequency (9.5 Hz) highlighted in red. Vertical lines are the same as above. F. An expansion of the highlighted section in E, to show the spindle-like appearance of the alpha oscillation. F.

An expansion of the highlighted section in E, to show the spindle-like appearance of the alpha oscillation.

Figure 3: $P_{episode}$ *for bilateral and lateralized alpha components.* A. $P_{episode}$ values for the eyes open and eyes closed conditions for all subjects, as well as averages ± SEM across subjects for the bilaterally distributed alpha component from ICA. B. $P_{episode}$ values for the eyes open and eyes closed conditions for all subjects, as well as averages ± SEM across subjects for the lateralized alpha component from ICA. C. Peak alpha frequency for the bilateral and lateralized alpha components within each experiment.

Figure 4: *Oscillation detection in a single electrode with strong alpha.* The electrode was selected from the same subject as in Figure 2. A. The 256-electrode array with the selected electrode highlighted in yellow. B. Background wavelet power spectrum mean and standard deviation (blue), and the linear regression fit to the background (green). C. Oscillations detected across all frequencies by the oscillatory episode detection method. Red vertical lines indicate when participants were instructed to close their eyes and black vertical lines indicate when participants were instructed to open their eyes. D. The proportion of time ($P_{episode}$) during the eyes-closed condition (red) and eyes-open condition (black) that oscillations were detected at each frequency. E. The raw signal from the chosen electrode, with detected oscillations at the peak alpha frequency (9.5 Hz) highlighted in red. Vertical lines are the same as above. F. An expansion of the highlighted section in E, to show the spindle-like appearance of the alpha oscillation.

Figure 5: *Oscillation detection in a single electrode with weak alpha.* The electrode was selected from the same subject as in Figs. 2&4. A. The 256-electrode array with the selected electrode highlighted in yellow. B. Background wavelet power spectrum mean and standard deviation (blue), and the linear regression fit to the background (green). C. Oscillations detected across all frequencies by the oscillatory episode detection method. Red vertical lines indicate when participants were instructed to close their eyes and black vertical lines indicate when participants were instructed to open their eyes. D. The proportion of time ($P_{episode}$) during the eyes -closed condition (red) and eyes-open condition (black) that oscillations were detected at each frequency. E. The raw signal from the chosen electrode, with detected oscillations at the peak alpha frequency (9.5 Hz) highlighted in red. Vertical lines are the same as above. F. An expansion of the highlighted section in E, to show the spindle-like appearance of the alpha oscillation.

Figure 6: *Distribution of power values.* For all panels, the blue bars represent the empirical probability distribution function of power values from the signal used to estimate the background spectrum (signal from the entire recording) in 25 equally spaced bins for a given frequency. The red line represents the theoretical $\chi^2(2)$ probability distribution function based on the estimated mean power at the same frequency derived from the linear-regression fit. Vertical lines represent the 90^{th}, 95^{th} and 99^{th} percentile thresholds (left to right). Note that for alpha frequencies, a great proportion of the power values are far beyond the range plotted here; those are summed in the right-most bin. A-C are for the bilateral alpha component from ICA; D-F are for the individual electrode

analysed in Fig. 4. A&D are from the peak alpha frequency of 11.3 Hz. B&E are from a lower frequency (6.7 Hz) and C&F are from a higher frequency (19.0 Hz).

Figure 7: *The effect of background window on oscillation detection.* For A. (eyes open background window); B. (eyes closed background window) and C. (across state background window): ***i***. The average wavelet power spectrum with standard deviation. Overlaid are the regression lines calculated using the whole experiment (black), the eyes open epochs (blue), the eyes closed epochs (green), and the state-overlap epochs (red). ***ii***. Detected oscillations across all frequencies using the background estimates illustrated in *i*. Red vertical lines indicate when participants were instructed to close their eyes and black vertical lines indicate when participants were instructed to open their eyes. ***iii***. $P_{episode}$ plots for eyes-closed (red) and eyes-open (black) conditions, using the background estimates illustrated in *i*. ***iv***. Component time courses with detected oscillations at the alpha frequency (9.5 Hz) highlighted in red, using the background estimates illustrated in *i*. ***v***. An expansion of the highlighted section in *iv*.

Figure 8: *The effect of background window (summary).* A. Slope of the regression line for all experiments using the four background windows calculated as in Figure 10A&B. B. Y-intercept of the regression line for all experiments using the four background windows calculated as in Figure 10A&B. C. $P_{episode}$ during the eyes-open condition for all experiments using the background windows calculated as in Figure 10A&B. D. D. $P_{episode}$ during the eyes-closed condition for all experiments using the background windows calculated as in Figure 7A&B.

Figure 9: *Lateralized alpha component.* From the same subject as Figs 2 & 4-5. A. The spline-interpolated scalp distribution of an alpha component extracted by ICA. Color scale denotes electrode weight (unitless). B. Background wavelet power spectrum mean and standard deviation (blue), and the linear regression fit to the background (green). C. Oscillations detected across all frequencies by the oscillatory episode detection method. Red vertical lines indicate when participants were instructed to close their eyes and black vertical lines indicate when participants were instructed to open their eyes. D. The proportion of time ($P_{episode}$) during the eyes-closed condition (red) and eyes-open condition (black) that oscillations were detected at each frequency. E. The time-domain representation of the chosen component, with detected oscillations at the peak alpha frequency (9.5 Hz) highlighted in red. Vertical lines are the same as above. F. An expansion of the highlighted section in E.

Figure 10: *Temporal independence of two alpha components.* A. An 8-second epoch from the alpha component shown in Figure 2, with detected alpha-frequency oscillations highlighted in red. B. The same time segment as in A, from the alpha component in Figure 6. Note the alpha oscillation is maximal in B when the oscillation is at a minimum in A, demonstrating why these were extracted as temporally independent components.

Figure 11: *Alpha harmonic in an independent component.* This is from a different subject from Figs. 2, 4-5 & 9-10. A. The spline-interpolated scalp distribution of an alpha component extracted by ICA. Color scale denotes electrode weight (unitless). B.

Background wavelet power spectrum mean and standard deviation (blue), and the linear regression fit to the background (green). C. Oscillations detected across all frequencies by the oscillatory episode detection method. Red vertical lines indicate when participants were instructed to close their eyes and black vertical lines indicate when participants were instructed to open their eyes. D. The proportion of time ($P_{episode}$) during the eyes-closed condition (red) and eyes-open condition (black) that oscillations were detected at each frequency. E. The time-domain representation of the chosen component, with detected oscillations at the alpha harmonic frequency (19.0 Hz) highlighted in red. Vertical lines are the same as above. F. An expansion of the highlighted section in E.