Fluctuations in Neuronal Synchronization in Brain Activity Correlate with the Subjective Experience of Visual Recognition

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Abstract The scientific study of subjective experience is a current major research area in the neurosciences. Coordination patterns of brain activity are being studied to address the question of how brain function relates to behaviour, and particularly methods to estimate neuronal synchronization can unravel the spatio-temporal dynamics of the transient formation of neuronal assemblies. We report here a biophysical correlate of subjective experience. Subjects visualised figures with different levels of noise, while their brain activity was recorded using magnetoencephalography (MEG), and reported the moment in time (corresponding to a noise level) of figure recognition, which varied between individuals, as well as the moment when they saw the figure more clearly, which was mostly common among the participants (thus less subjective). This latter moment is considered to represent psychophysical stochastic resonance (PSR). Fluctuations in neuronal synchronization, quantified using a diffusion coefficient, were lower in occipital cortex when subjects recognised the figure, for a certain noise level, but did not correlate with the moment of PSR. A different pattern was observed in frontal cortex, where lower values of the diffusion coefficient in neuronal synchronization was maintained from the moment of recognition to the moment of PSR. No specific pattern was found analysing signals from temporal or parietal cortical areas. These observations provide support for distinct synchronization patterns in different cortical areas, and represent another demonstration that the subjective, first-person perspective is accessible to scientific methods.

Keywords Visual perception · Diffusion · Fluctuations · Synchrony · Noise · Brain · Magnetoencephalography

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1 Introduction

The brain has for long been considered a ‘noisy processor’ [1]. While a classical view regards noise as a degrader of information processing in nervous tissue, early wisdom already considered that biological noise could “produce important physiological effects” [2]. More recent studies have established the constructive nature of noise, or of the interaction between what is called “noise” and signal processing in nervous systems. For instance, more efficient processing occurs for certain noise levels, which in signal processing is associated with the phenomenon of stochastic resonance (SR), a general phenomenon in which noise improves the response of a nonlinear system [3, 4]. This concept can be extended to what can be termed psychophysical stochastic resonance (PSR), when there is improved sensory discrimination for certain noise levels [5]. For example, noise-enhanced sensorimotor discrimination in human subjects has been shown in several modalities [3, 6–11]; indications of stochastic resonance in the mammalian nervous system have been obtained using other preparations [12, 13]. It should be noted that it is one thing to determine stochastic resonance occurring in the brain and another to study how the brain (perception) responds to stimuli constructed according to the principles of SR. Thus, some of these studies address the latter rather than the former [7] while others provide a more accurate investigation of the phenomenon of SR within the brain circuitries [6].

While the most common trend in this area of brain research is to assess the magnitude and extension of synchronized neuronal activity, in this study we look at the *fluctuations in synchrony*. The spatio-temporal dynamics of transient formation of neuronal assemblies, that, according to some proposals, is the essence of brain function [14–16], can be revealed by the study of fluctuations in neuronal synchronization [17]. Some have called this phenomenon the “turnover” of neuronal assemblies [18]. A diffusion coefficient (D_{eff}) that represents the fluctuations in phase synchronization, previously described [19, 20], can be used as a measure to determine the spatio-temporal dynamics of the transient formation and dissolution of neuronal assemblies in brain activity and during perceptual tasks in particular. Based on studies where behavioural stochastic resonance was related to brain electrophysiological activity in the human visual system [21], and considering that peak amplitudes in evoked responses coincided with a maximum in the signal to noise ratio of visual stimuli “degraded” by noise [22], we sought to investigate whether a decrease in fluctuations in phase synchronization in the occipital cortex (visual cortex) would correlate with psychophysical stochastic resonance (PSR) in subjects visualising figures embedded in different noise levels. On the contrary, we found that this was not the case; rather, lower D_{eff} in the visual cortex (occipital area) correlated with the subjective moment of recognition of the image by the participants, and not with the instant of PSR. In addition, we also studied the fluctuations in representative areas of the other major cortical lobes: frontal, parietal and temporal.

2 Methods

Ten healthy participants (four males), ages 23–44, who gave informed consent to participate in the study, visualised images of objects and faces embedded in increasing levels of noise (Fig. 1 shows one example), while their magnetoencephalographic (MEG) recordings were acquired. The images, figures of objects and persons, were converted from colour to grayscale, that is, each pixel was assigned a value between 0 (black) and 1 (white). As a result, each figure is transformed into a matrix M of numbers running from 0 to 1, with

Fig. 1 Upper panel displays an example of the images shown to the participants in this study (but note that the noise is dynamic, not static). Lower panel shows the schematic head with all MEG sensors, and those selected for the study in four cortical lobes: frontal, parietal, temporal and occipital (*encircled*), to assess the diffusion coefficient (D_{eff}) in phase synchronization as detailed in the text

dimensions that depend on the size and pixel density of the original figure. To add noise, the original image in greyscale is quantified using three values (0, 0.5 and 1, for black, grey and white respectively). To achieve this, upper and lower thresholds were created, in such a way that whenever the matrix values were above 1 or below 0 (because of the added noise) the values remained 1 and 0, respectively (this procedure is similar to the one described in reference [7], although in that study only one threshold was used). For values between 0 and 1, the pixels are shown in grey (with assigned value of 0.5). Hence, since there are three states (0, 0.5 and 1) the information content in each pixel is $\log_2 3 = 1.58$ bits. If noise is added to this matrix that represents the figure (M'), more points will appear black or white, thus resulting in more contrast; this is done by adding to the grey-scaled matrix M' a random number “ r ” normally distributed with mean 0 and standard deviation of 1. The resulting matrix is $M' + r$, and multiplying “ r ” by a random number running from 1 to 20, 20 levels of noise were created for each figure and the corresponding films consisting of the series of one image with superimposed noise were presented to the subjects.

The resulting noisy figures were presented to the participants via a video projector in our MEG recording set-up. In total, 23 images were shown to participants, and with 20 levels of noise per image we had about 460 noise levels in total. The total number was used to estimate statistics on the effective diffusion coefficient detailed below. By increasing the noise level, the recognition of the figures monotonically increases until a maximum value, because contrast is created; we call this instant, when images are most clearly perceived, the moment of PSR. Beyond this moment, for increasing noise levels, the recognition progressively decreases and the perception of the image finally becomes lost. Contrast and luminance of the images were the same throughout the experiment. Participants pressed a button to signal the time when they recognized the image, a time that of course corresponded to a certain noise level. As a control for the motor action of the button press, participants were asked to press the button at a different time, towards the end of the image series.

Magnetoencephalographic (MEG) recordings were acquired at 625 Hz sampling rate, using a CTF Omega 151 channel whole head system (CTF Systems, Port Coquitlam, Canada), as previously described [23]. The head position relative to the MEG sensors in the helmet was recorded at the start and end of each recording. Recordings were analysed in MATLAB as described below. Visual inspection of the recordings was performed during acquisition and before analysis, to remove (or repeat the acquisition of) segments with artefacts. For our study, we chose MEG sensors that record activity in prefrontal, parietal, occipital and temporal areas, depicted in Fig. 1. We then calculated the effective diffusion coefficient (D_{eff}) of the phase differences between MEG signals in each of these cortical areas, as described in references 19 and 20. This coefficient represents the spread of a distribution of phase differences, measuring the number of phase slips (2π -jumps) of the phase difference per unit time [20]. The instantaneous phase and corresponding D_{eff} were evaluated at frequencies from 5 to 42 Hz, with D_{eff} given by,

$$D_{\text{eff}} = \frac{1}{2} \frac{d}{dt} \left[\langle \phi^2(t) \rangle - \langle \phi(t) \rangle^2 \right],$$

ϕ is the phase difference between two MEG signals.

To calculate phase differences between two MEG signals, we extracted the instantaneous phase using the Hilbert transform, as described in detail in [23]. Thus, phase differences were assessed on band-passed signals, using a constrained least square finite impulse response filter (FIRCLS), with a specified central frequency “f” and cut-offs $f \pm 2$ Hz; we studied D_{eff} in the range 5–42 Hz. We did not evaluate instantaneous phases past 42 Hz due to the limitations imposed by the sampling acquisition of our equipment and the requirements for a reliable interpretation of the operation done by the Hilbert transform [24]. This frequency range encompasses the most important physiological frequency bands, theta (4–8), alpha (8–14), beta (15–29) and gamma (>30 Hz). To summarize, the D_{eff} calculation runs as follows: for a specific set of MEG signals, in the frontal lobe for example, (depicted in Fig. 1), the instantaneous phases are evaluated at the relevant frequencies for all the signals and the phase differences between two signals are computed for all possible combinations, and then the computation according to the above equation gives us the D_{eff} . We then averaged the series of D_{eff} for specific time windows of choice, which in general were those corresponding to one noise level (between 2 and 3 s).

As a standard procedure in this type of analysis, we performed the same calculations with surrogates obtained from the original series, by applying a time shift between each pair of signals; in this way we ensure that the series are not phase-locked on average while at the same time maintaining the same temporal structure. The time shift was randomly selected from 1/sampling frequency, to the highest possible allowed by our data. A population of 20 D_{eff} values were obtained from 20 pairs of surrogate signals. Using more than 20 surrogates did not alter the estimated D_{eff} and standard deviation of this population. We then looked for values of D_{eff} in the original signals, which were above or below the standard deviation of the mean D_{eff} for the surrogates.

3 Results

Initially, as a preliminary study, we determined whether the D_{eff} estimated in the occipital (visual) cortex was dependent on the noise the subjects observed in an image. An alternate sequence of noise and static black-and-white images were presented to subjects, and the D_{eff} of the phase synchronization was estimated for central frequencies (as defined in

methods) 5, 15, 20, 30, 36 and 42 Hz. D_{eff} was found to be significantly higher when participants were shown a purely noisy image, as opposed to the static black and white images. This observation, while not surprising, indicates that input dynamic noise is associated with more fluctuations in the phase differences in visual cortex, and therefore we may expect a higher D_{eff} as the noise increases, in the next set of experiments. In these, subjects visualised images, such as shown in Fig. 1, with increasing dynamic noise levels (20 noise levels in total; in the graphs shown in Figs. 2 and 4 the noise intensity increases from left to right), and were instructed to press a button at the moment when they first recognised the image. This moment of image recognition was variable between individuals:

Fig. 2 Values of D_{eff} calculated for the occipital MEG sensors (**a** and **b**), or randomly selected sensors in (**c**), while one subject visualised images with ~20 noise levels (16 are shown in the graph). Each noise level is presented between two vertical lines (which is the duration of the presentation of one noise level, between 2 and 3 s). Noise intensity increases from left to right. The three graphs correspond to same subject, and D_{eff} was evaluated at 40 ± 2 Hz. Each vertical line represents the presentation of the image with a new noise level. The first dotted line signals recognition of the image by the participant (marked *Rec*), which was the moment when the participant pressed the button to signal recognition; the second dotted line represents the moment when the subject was asked to press the button, as a control for a possible motor effect of button press. Asterisks represent the D_{eff} values, calculated for each noise level, according to the equation presented in “Methods.” The line across the graph with the standard deviations (vertical bars) is the average D_{eff} calculated for 20 surrogates, as explained in the text. Notice that, around the recognition episode in (**a**) and (**b**), there are values of D_{eff} below the standard deviation for the surrogates. This is not observed in (**c**). *PSR*, in (**a**), is the instant (noise level) when the participant best viewed the image, but is not associated with D_{eff} values below the surrogate standard deviations

an example comparing the instant of recognition of a series of ten images, in four participants, is shown in Table 1. However, when they were asked to identify the moment when they best perceived the image, which we call here psychophysical stochastic resonance (PSR), the responses of all participants were very uniform: it occurred between noise levels 9 and 11. The evaluation of the noise level at which PSR occurred was done after the MEG session, each subject was shown the series of images three to four times and the PSR instant for each image, that occurred for a specific noise level, was taken. In this way, the instant of PSR was reliably determined for each participant.

We then calculated the D_{eff} from the MEG sensors that record the activity in the occipital cortex (encircled in Fig. 1). Figure 2 shows several examples. In Fig. 2a and b we show typical graphs obtained from these experiments, and in Fig. 2c) the results obtained when other MEG channels were selected randomly from the whole head, done as a control. Figure 2a and b correspond to a participant visualising two different images with the corresponding superimposed noise levels. As detailed in the figure legend, values of D_{eff} below the standard deviation for the surrogates were observed frequently (in nine of ten subjects) corresponding to the time window when subjects signalled the recognition of the image. However, this phenomenon was not observed when the same calculations were performed on a set of randomly selected MEG channels from the total of 146 (this set had same number of signals as that used in the previous calculations), or when recordings from the prefrontal, parietal or temporal cortices (those marked in Fig. 1) were analysed. To quantify this observation, we counted the number of times a D_{eff} value was below the standard deviation of the surrogate values, and, from this count, a frequency (probability) was obtained, which is represented in Fig. 3 by the bar graphs. This figure shows the grand average for all subjects, and the average for one in particular, in order to illustrate that the grand average follows the same trend as that of the individual. The probability is significantly higher (after an initial ANOVA test, a Student's t -test was performed to compare one group versus another) during the moment of subjective recognition, but did not correlate with the moment of PSR, as we originally hypothesised. This phenomenon was observed more clearly for frequencies in the range 38–42 Hz, while for other frequencies studied (mentioned in Methods) there was no clear trend. As explained in the legend of Fig. 3, several “control” probabilities were also determined, in particular that associated with the motor action that the subjects were required to perform to signal image recognition: a button press; in this way, we account for a possible motor effect on the measured phase synchronization (however unlikely, since we are looking at activity in visual occipital cortex and not in motor cortex).

While this phenomenon was not observed when prefrontal MEG signals (those encircled in Fig. 1) were analysed, a different pattern was noticed in this case. Specifically, the D_{eff} was of lower value during a sustained period of time, between the moment of recognition and the moment of PSR (Fig. 4). Note the difference with those patterns shown in Fig. 2a

Table 1 Noise levels at which four participants first recognised a series of 10 images

Subject	Noise levels at which recognition occurred									
#1	5	5	11	5	4	5	4	5	5	9
#2	7	9	11	7	5	8	8	11	7	9
#3	11	12	5	—	3	2	7	5	5	4
#4	8	6	4	4	3	4	4	4	4	5

Note the variability. Subject #3 did not recognize the fourth image. In general, for all the ten participants, these ranged from level 3 to 13, of a total of 20 noise levels.

Fig. 3 Average, for all subjects (a) and for one participant (b), of the probability that the D_{eff} (evaluated at central frequency of 40 Hz) calculated for the activity in the occipital cortex was below the standard deviation of the surrogates during the episode of image recognition (bars marked *Recogn*). In (a), *Global* is the probability to find a D_{eff} below the standard deviation of the surrogates in the whole experiment (which consisted of more than 300 presentations of noise levels), *Press* is the probability associated with control button presses, *PSR* is that during the PSR window, and *Rand. Chan* is that probability associated with recognition but using randomly selected channels, as in Fig. 2c. The probability of finding D_{eff} values below the standard deviation of the surrogates is much higher in the occipital cortex during the window of recognition of the image; p values are shown when compared with the other conditions. None of the other four groups were statistically different from each other (ANOVA followed by t -test). The same trend is shown for one subject (La), in (b). This pattern was seen in nine of ten participants

and b. This prefrontal pattern was seen in 80% of the subjects. The bar graph in Fig. 4 shows the averages of D_{eff} in prefrontal areas for four subjects, during the period between recognition and PSR as well as before the recognition and during the window of button press. In the case of the analysis done on the signals recorded in the parietal or temporal cortex, no specific pattern was observed.

4 Discussion

In general, these observations provide support for distinct synchronization patterns in different cortical areas associated with perception, and complement related observations using functional neuroimaging that demonstrated a role of the visual cortex in the phenomenon of PSR [25]. Our measurements, using an effective diffusion coefficient, are related to those using the more common measure of SR, the signal-to-noise ratio [8, 21]. Considering that, in noisy systems like the brain, synchronization can be defined only in a statistical sense, as widely discussed in many articles and books [14, 16, 24, 26], it is important to think in terms of fluctuations in synchrony, in addition to the more usual determination of the strength of the synchronization between brain regions. Other methods have been recently used to assess the dynamic formation (and dissolution) of neuronal

Fig. 4 Values of D_{eff} for phase differences among prefrontal channels, for one subject visualising an image with ~20 noise levels (16 are shown), graphed as those shown in Fig. 2. Unlike the case of the occipital cortex channels, in this case we see lower absolute values of the D_{eff} between the moment of recognition (*Rec*, first dotted line) and PSR. The *second dotted bar* is the moment of a control button press. The *bar graph below* shows the averages of the values of D_{eff} in four subjects, in the time windows (indicated in the upper plot) between recognition and PSR (black bars), before recognition (white bars), and around control button press (grey bar). Note that the mean values are lower between recognition and PSR. Asterisks denote statistical significance comparing the three averages in each participant

assemblies. One of these is specifically based on phase differences [17], thus similar to our computations; one advantage of this method is that it is possible to document the dynamics of synchronization and desynchronization, since the method is based on the time derivative of the phase differences. In our study, using D_{eff} , we look at the ensemble of fluctuations, rather than fine details.

Using a related visual paradigm, indications for SR in the alpha frequency range (~10 Hz) measured in visual cortex associated with varying noise levels were reported [21]. In contrast, the phenomenon we describe here occurred for gamma frequencies (38–42 Hz) however, but differences in the paradigms have to be considered. A main difference is the recording method, EEG versus MEG, as the possible effects of the reference electrode in EEG recordings are well known [27]. A second difference is the visual signal used: in reference [21], different inputs were shown to each eye; we chose not to show a different signal to each eye as we were interested in the subjective experience of figure recognition as well as in the PSR, and these are not feasible using separate inputs to each eye, because of the well-known phenomenon of binocular rivalry that appears under these conditions [28]. Thus, in our experiments we are also observing possible processing at the level of the retina, as mentioned in reference [21], but we consider this processing as part of the

cognitive process as well. Our results complement those of Sorrentino et al. [22], who showed that evoked magnetic responses peaked at the maximum signal to noise ratio of the stimuli and the visual cortex showed sharper peaks than longer latency sources located elsewhere in the brain. However, all these other studies normally dealt with stochastic resonance and its equivalent in psychophysics, while our study is the first, to our knowledge, that reveals a decrease in fluctuations in phase synchrony (which is indicative of stochastic resonance phenomena) associated with the conscious perception of an image, and not with the period of PSR. One relevant issue to consider is that we cannot assert whether SR is really happening in the brain neuronal networks in these experiments. Rather, what can be clearly said about our experiments and those of others [7] is that we constructed the stimuli (noisy images) according to the concept of SR: signal with superimposed noise. But whether this phenomenon is occurring in the brain is difficult to ascertain (see reference 5 for a detailed discussion of the psychophysics of SR).

The possible physiological interpretation of our findings can be conceived by the consideration of the numerous observations that reported synchronization of brain rhythms during visuomotor events and conscious perception [14, 29–31], and, particularly related to our results, transient phase locking in the gamma frequency range was observed associated with conscious (somatic) perception [32]. Using D_{eff} , we in fact measure the fluctuations in phase locking, and a lower value in occipital visual cortex during the subjective moment of recognition indicates that there could be an enhanced coordinated activity that supports conscious perception, as proposed by some investigators [30, 33]. As expressed by Tononi et al. [34]: “meaningful, association-rich stimuli should lead to an increase in the mutual information between many subsets of neuronal groups”. Further indications of brain synchronization associated with behavioural SR have been obtained using a different paradigm where a signal is fed to one eye and noise to the other [35]. We interpret these observations as a physiological correlate of the statement by Tononi et al.

On the other hand, the presence of a sustained period of less synchronized fluctuations in frontal cortex supports the proposed patterns of re-entry excitation in this brain area [36, 37] and, as a consequence, longer-lasting coordinated activity can be expected. In general, our results represent one more indication that the subjective, first-person perspective is accessible to scientific methods, as also observed in binocular rivalry experiments in humans [30, 38], and suggest that relationships between conscious experience and biophysical parameters can be defined in sensory processing. Thus, these investigations raise new questions related to psychological experience and brain coordination dynamics [16], and suggest that the study of the fluctuating patterns of activity in nervous system function may reveal clues as to the relation between brain and behaviour.

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