

A point process modeling approach for investigating the effect of online brain activity on perceptual switching



Takeru Matsuda^{a,*}, Keiichi Kitajo^{b,c}, Yoko Yamaguchi^c, Fumiyasu Komaki^{a,c}

^a Graduate School of Information Science and Technology, The University of Tokyo, Tokyo, Japan

^b RIKEN BSI-Toyota Collaboration Center, RIKEN Brain Science Institute, Wako, Saitama, Japan

^c RIKEN Brain Science Institute, Wako, Saitama, Japan

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ABSTRACT

When watching an ambiguous figure that allows for multiple interpretations, our interpretation spontaneously switches between the possible options. Such spontaneous switching is called perceptual switching and it is modulated by top-down selective attention. In this study, we propose a point process modeling approach for investigating the effects of online brain activity on perceptual switching, where we define online activity as continuous brain activity including spontaneous background and induced activities. Specifically, we modeled perceptual switching during Necker cube perception using electroencephalography (EEG) data. Our method is based on the framework of point process model, which is a statistical model of a series of events. We regard perceptual switching phenomenon as a stochastic process and construct its model in a data-driven manner. We develop a model called the online activity regression model, which enables to determine whether online brain activity has excitatory or inhibitory effects on perceptual switching. By fitting online activity regression models to experimental data and applying the likelihood ratio testing with correction for multiple comparisons, we explore the brain regions and frequency bands with significant effects on perceptual switching. The results demonstrate that the modulation of online occipital alpha activity mediates the suppression of perceptual switching to the non-attended interpretation. Thus, our method provides a dynamic description of the attentional process by naturally accounting for the entire time course of brain activity, which is difficult to resolve by focusing only on the brain activity around the time of perceptual switching.

1. Introduction

When watching an ambiguous figure that allows for multiple interpretations, our interpretation spontaneously switches among the various possible views. This phenomenon is called multistable perception and spontaneous switching is also known as *perceptual switching* (Blake and Logothetis, 2002; Leopold and Logothetis, 1999; Pastukhov et al., 2013). An example of an ambiguous figure is the Necker cube (Fig. 1), which allows for two interpretations as a three-dimensional object (Necker, 1832). Perceptual switching is thought to reflect the stochastic nature of information processing in the brain (Braun and Mattia, 2010) and many experimental studies have investigated its underlying mechanism (Sterzer et al., 2009). These previous studies are classified according to the use of one of the following two approaches: bottom-up approach or top-down approach. Although the bottom-up approach assumes that perceptual switchings passively result from early visual processing, the top-down approach focuses on the active decision-making process involved in multistable perception.

From the latter viewpoint, multistable perception is expected to be affected by attention. Indeed, similar to other visual phenomena (Reynolds and Chelazzi, 2004; Yamagishi et al., 2003), multistable perception is modulated by selective attention (Meng and Tong, 2004) such that the duration of the attended interpretation increases when an observer intentionally focuses on one interpretation of an ambiguous figure. Thus, switching to the attended interpretation is facilitated by selective attention, whereas switching to the non-attended interpretation is suppressed by it.

Previous experimental studies on multistable perception have mainly focused on the brain activity around the time of perceptual switching such as evoked and induced activity, e.g., alpha activity was found to decrease around the time of perceptual switching (Isoglu-Alkac et al., 2000; Isoglu-Alkac and Struber, 2006; Struber and Herrmann, 2002). In contrast, consideration of the entire time course of brain activity is important for understanding selective attention in multistable perception because attentional facilitation and suppression of perceptual switching are continuous processes rather than instant-

* Corresponding author.

E-mail address: Takeru_Matsuda@mist.i.u-tokyo.ac.jp (T. Matsuda).

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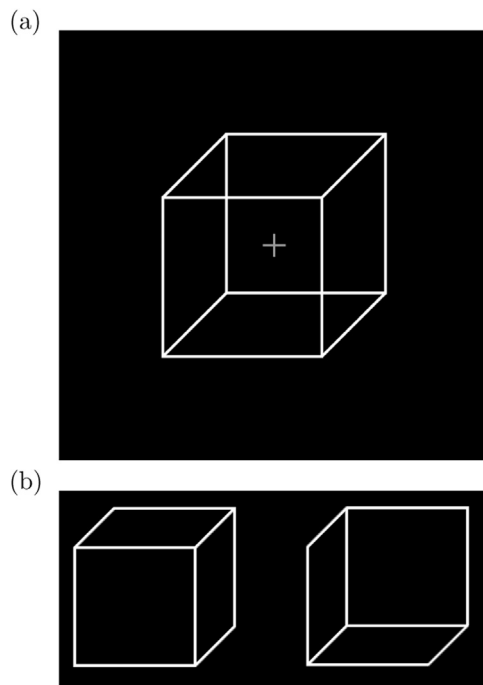


Fig. 1. (a) Necker cube presented to participants. (b) Left: top view, right: bottom view.

neous events. We define *online activity* as this continuous brain activity that includes spontaneous background and induced activities. Therefore, we are interested in the dynamic relationship between online brain activity and perceptual switching. In the present study, we develop a data analysis method that is suitable for this purpose.

Many neuroimaging studies suggest that oscillatory activity such as alpha and gamma are crucial for sensory processing (Engel et al., 2001). In previous studies on multistable perception, the alpha activity has been mainly associated with bottom-up processing (Ehm et al., 2011; Isoglu-Alkac et al., 2000; Isoglu-Alkac and Struber, 2006; Mathes et al., 2010; Struber and Herrmann, 2002) whereas the beta (Hipp et al., 2011) and gamma activities (Basar-Eroglu et al., 1996; Ehm et al., 2011; Mathes et al., 2006; Nakatani and van Leeuwen, 2006; Struber et al., 2000, 2001) have been associated with top-down processing. However, few studies have evaluated the interaction between top-down and bottom-up processes. We note that the modulation of online alpha activity has been found to be associated with visual attention. For example, the visual discrimination ability decreases as the prestimulus alpha power increases (Hanslmayr et al., 2007; van Dijk et al., 2008). In addition, when covert visual attention is directed to the left or right of the visual field, online occipital alpha activity is suppressed in the hemisphere contralateral to the attended side (Kajihara et al., 2015; Thut et al., 2006; Worden et al., 2000). We investigate whether attentional control over perceptual switching is also mediated by the modulation of online alpha activity.

To explore the relationship between perceptual switching and online brain activity, we employ a statistical modeling approach that regard the perceptual switching phenomenon as a stochastic process and we construct a model of perceptual switching in a data-driven manner. Perceptual switching can be represented as a series of events on the time axis (Fig. 4A). In statistics and probability theory, a series of events over time can be described as a point process (Daley and Vere-Jones, 2003), which is a type of stochastic process. Point process models are widely used for the analysis of phenomena such as neuronal firings (Truccolo et al., 2005) and earthquakes (Ogata, 1999). In point process models, the probability of an event occurring is described by a function called the *intensity*. In this study, we model perceptual switching using an *online activity regression model*, which describes a point process in which the intensity depends on online brain activity.

By fitting online activity regression models to experimental data, our method reveals whether online brain activity has excitatory or inhibitory effects on perceptual switching.

Using online activity regression models, we analyze experimental data collected from participants while they viewed the Necker cube. Based on the likelihood ratio testing with correction for multiple comparisons, we explore the cortical regions and frequency bands that are associated with attentional control during multistable perception. The results demonstrate that online occipital alpha activity suppresses perceptual switchings to the non-attended interpretation. Thus, our point process modeling approach provides a framework for investigating the relationship between cognitive events and online brain activity.

2. Material and methods

2.1. Experimental settings

We use the experimental data regarding selective attention in multistable perception from Shimaoka et al. (2010), who focused on the phase-synchrony across distant cortical areas and found that phase-locked clusters transiently merge together around the time of perceptual switching with a stronger connection in the switch to the attended interpretation. Thus, they did not consider online brain activity. In the present study, we reanalyze their data to investigate the relationship between online brain activity and perceptual switching with a particular emphasis on selective attention.

2.1.1. Participants and visual stimuli

Sixteen right-handed adult volunteers with normal or corrected-to-normal vision (mean age, 24.7 years; SD, 4.7 years; seven females) participated in the study after providing informed consent. The study was approved by the ethics committee at RIKEN (Saitama, Japan). Participants were seated in a dark room at 95 cm from a 19-in. CRT monitor (100 Hz refresh rate), and presented with a gray Necker cube (width and height=4.2° in visual angle) on a black background in the center of the monitor (see Fig. 1) in time blocks of 180 s. The participants were instructed to focus on a gray fixation cross (width and height=0.4° in visual angle) displayed in the center of the cube and to avoid making eye movements or blinks. Throughout the experiment, the head position of each participant was maintained by a chin rest. Participants were instructed to depress a specific keyboard key with their right index finger while they perceived the “top view” (i.e., as if seen from above), and to depress another key with their right middle finger while they perceived the “bottom view” (i.e., as if seen from below). When the Necker cube was perceived as intermediate or flat, the participants made no response. Four experimental conditions and instructions were given to each participant, as follows:

- Neutral view condition; “Just look at the cube passively.”
- Top view biasing condition; “Attempt to perceive the cube from the top view for as long as possible.”
- Bottom view biasing condition; “Attempt to perceive the cube from the bottom view for as long as possible.”
- Self-paced key pressing condition without the Necker cube; “Press the keys at your own pace.”

Two biasing conditions were included to investigate selective attention in multistable perception. Meng and Tong (2004) reported that voluntary control with “maintain” instructions actually induced top-down selective attention and that the duration of the attended interpretation was significantly longer. The self-paced key pressing condition was a control for motor activity.

After a 1-min practice block under each condition and a 3-min resting block, the participants received the four conditions in a mixed randomized order (five blocks/condition, Fig. 2). During the resting block, the Necker cube was not presented and participants were asked

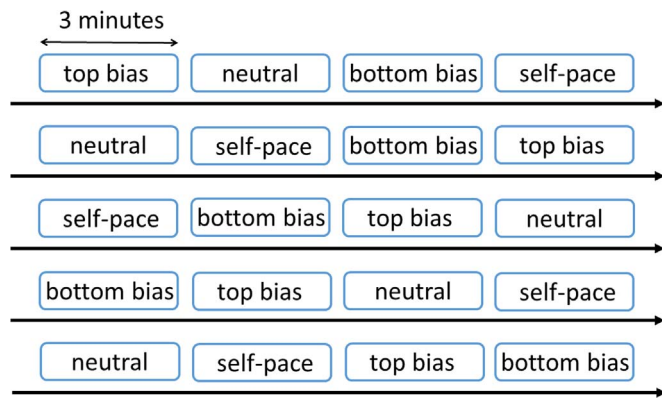


Fig. 2. Blocking scheme used in the experiment. Participants received the four conditions (neutral, top biasing, bottom biasing, and self-paced) in a mixed randomized order. Each experimental block lasted 3 min and five blocks were assigned to each condition.

to fixate on the cross. Participants were given a short break between blocks.

2.1.2. Electroencephalography (EEG) recordings

The EEG signals were recorded from 62 electrodes, which were placed according to the international 10-10 placement system (Fig. 3). Horizontal and vertical electrooculogram (EOG) signals were recorded bipolarly with the electrodes positioned 1 cm from the outer canthi of both eyes, and above and below the left eye. Electrode impedances were kept below 5 kΩ. After amplification, the EEG and EOG signals were band-pass filtered between 0.1 and 100 Hz, and digitized at 500 Hz (Synamps, Neuroscan Inc. El Paso, Texas, US). The EEG signals were referenced to a linked earlobe reference. Further details of this process were reported by Shimaoka et al. (2010).

2.2. Data preprocessing

Based on the raw 62-ch EEG data, we obtained the 62-ch EEG power time series in five frequency bands for each subject, each condition, and each direction of switching (top to bottom view or vice versa), as shown in Fig. 4. First, we rejected ocular artifacts in the EEG using ADJUST (Mognon et al., 2011), by referring to the horizontal and

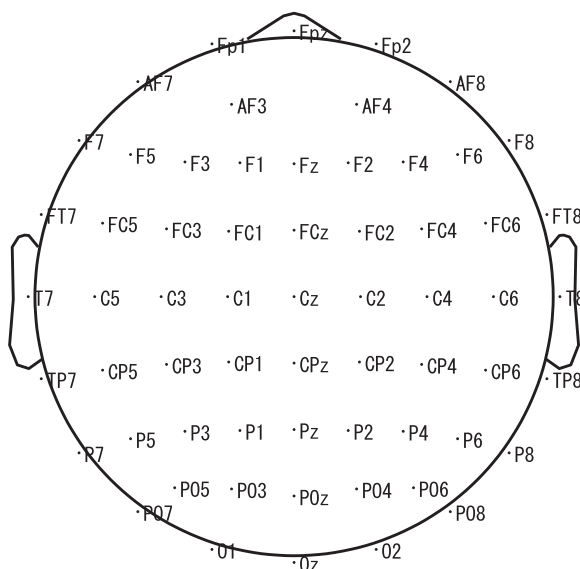


Fig. 3. Locations of the 62 electrodes, which were placed according to the international 10-10 placement system.

vertical EOG. Next, we extracted the timings of the participants’ key-pressing activities as the beginning of key-holdings. We regarded each key-pressing activity as perceptual switching. In Fig. 4A, red lines represent the switch from top to bottom view and magenta lines represent the switch from bottom to top view, respectively, and the EEG obtained from one electrode is plotted in blue. Then, we divided each experimental block into several sub-blocks based on the key-pressing timings and classified the sub-blocks into two types according to the direction of the switch at the end. Sub-blocks of the same type were concatenated over the five experimental blocks (Fig. 4B). Here, we divided the data according to the direction of switch because selective attention controls the two types of switching in different ways. Finally, we computed the EEG power in the delta band (0.5–4 Hz), theta band (4–8 Hz), alpha band (8–13 Hz), beta band (13–30 Hz) and gamma band (30–50 Hz) by applying the short-time Fourier transform (STFT; Cohen, 2014) to the EEG obtained from each electrode (Fig. 4D). Here, the window width and window shift were set to 1000 ms and 100 ms, respectively. Namely, the EEG obtained from each electrode was separated into frames of 1000 ms, which overlapped by 900 ms, and the Fast Fourier Transform (FFT) was then applied to each frame to obtain the band-specific power (Fig. 4C). We required the EEG power as a continuous time function for our analysis, so we interpolated the EEG power by spline smoothing.

2.3. Point process modeling of perceptual switching

We explore the relationship between perceptual switching and online brain activity, where we are particularly interested in whether online oscillatory activity (e.g., alpha) have excitatory or inhibitory effects on perceptual switching. We address this problem by a statistical modeling approach. Namely, we consider the data as an output from a stochastic data generation process and construct statistical models of this process in a data-driven manner. Perceptual switching is represented as key-pressing time series in our data, which is regarded as a series of events on the time axis (Fig. 4A). In statistics and probability theory, such a series of events over time is described as a point process (Daley and Vere-Jones, 2003), which is a type of stochastic process. Intuitively, the probability of event occurrence is specified by a point process. Point process modeling is usually applied to neuronal firings (Truccolo et al., 2005), earthquakes (Ogata, 1999), and other series of events. For example, sensory information (Pillow et al., 2008) or functional connectivity (Stevenson et al., 2012) can be inferred from multi-neuron spiking data using point process models. In addition, point process models enable to assess the influence of a concurrent time series on the occurrence of events (Ogata et al., 1982). In this study, we evaluate the excitatory or inhibitory effects of online brain activity on perceptual switching by fitting point process models to our data.

First, we describe the general framework used for point process modeling (Daley and Vere-Jones, 2003). Suppose that events have occurred at time points $t_1, \dots, t_n (0 \leq t_1 < \dots < t_n \leq T)$ during time interval $[0, T]$. A point process model is specified by a function on $[0, T]$ called the *intensity function*: $\lambda(t)$. Intuitively, the value $\lambda(t)$ of the intensity function at time t represents the rate of event occurrence around time t (Fig. 5 (a)). Mathematically, the probability of an event occurring in time interval $[t, t + dt)$ is given by $1 - \exp(-\lambda(t)dt) \approx \lambda(t)dt$, where dt is an infinitesimal time length. We investigate the data generation process underlying the series of events by constructing a parametric model of the intensity function $\lambda(t|\theta)$ and estimating the unknown parameter θ from the data.

In this study, we describe perceptual switching by a point process model. Our data comprise the key-pressing timings and the concurrent EEG power time series (Fig. 4). We divided the data according to the direction of switch, so we use different intensity functions for each direction of switch: one is for switch from the top to bottom view $\lambda^{(t \rightarrow b)}(t)$ and the other is for switch from the bottom to top view $\lambda^{(b \rightarrow t)}(t)$

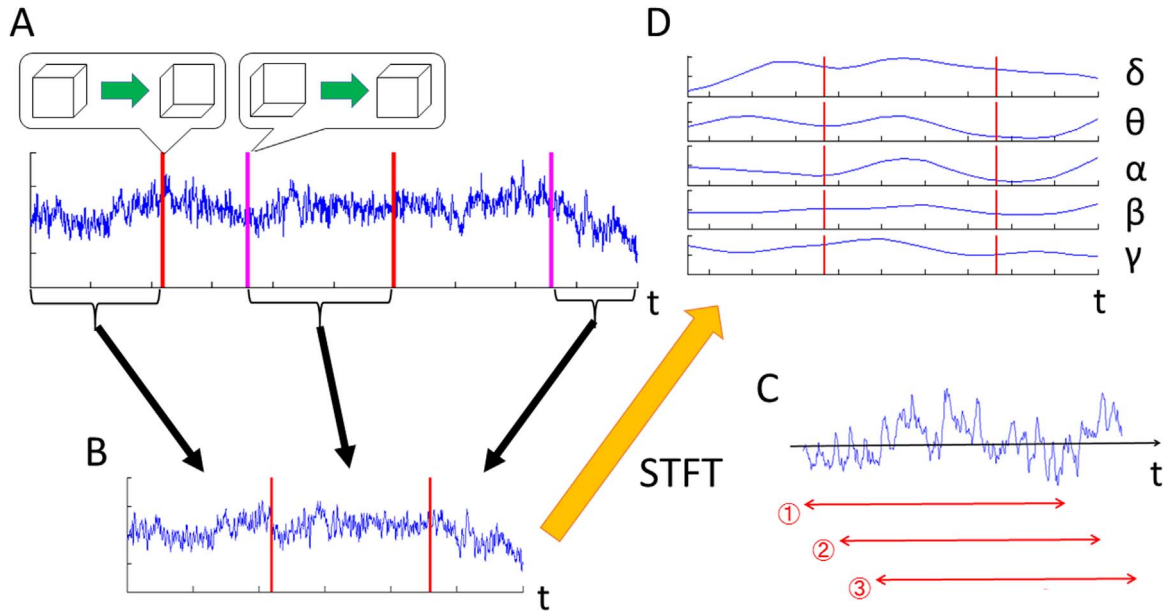


Fig. 4. Procedure employed for data preprocessing. Here, we show how to extract the EEG power time series on one electrode for switch from top to bottom view. A: Original data. The EEG obtained from one electrode is plotted in blue and key-pressing timings are shown in red (switch from top to bottom view) and magenta (switch from bottom to top view). The EEG is divided into sub-blocks based on key-pressing timings. B: Extracted EEG time series for switch from top to bottom view. Sub-blocks are concatenated. C: Schematic of the short-time Fourier transform. Red arrows indicate the sliding windows. D: EEG power in five frequency bands.

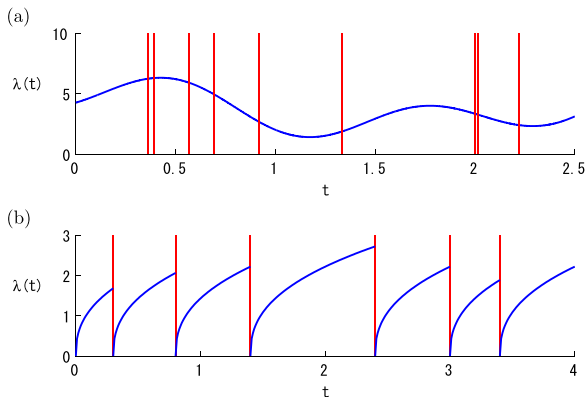


Fig. 5. (a) Relationship between the intensity function $\lambda(t)$ (blue) and the series of events t_1, \dots, t_n (red). A larger value $\lambda(t)$ of the intensity function at time t leads to a higher probability of event occurrence around time t . (b) The Weibull-type intensity function (4) with $\theta_0 = 1$, $\theta_1 = 0.4$ (blue) and the series of events (red). Here, the first event occurred at $t_1 = 0$. By definition (4), the intensity drops to zero immediately after each event, thereby preventing very short intervals between events (cf. (a)).

(Fig. 6). The parametric model developed for these intensity functions includes two effects: the effect of online brain activity and the refractory effect, each of which is explained in the following. For simplicity, we do not distinguish between $\lambda^{(t \rightarrow b)}(t)$ and $\lambda^{(b \rightarrow t)}(t)$ in the remainder of this subsection.

In general, suppose that we observe a concurrent time series $x(t)$ and a series of events. To evaluate the influence of $x(t)$ on event occurrence, the following model of the intensity function is useful:

$$\lambda(t|\theta) = \exp(\theta_0 + \theta_1 x(t)). \quad (1)$$

The term $\theta_1 x(t)$ in (1) represents the contribution of $x(t)$ to event occurrence. When $\theta_1 > 0$ ($\theta_1 < 0$), the probability of event occurrence becomes higher when $x(t)$ is larger (smaller). In other words, $x(t)$ has an excitatory effect if $\theta_1 > 0$ and an inhibitory effect if $\theta_1 < 0$, respectively. When $\theta_1 = 0$, $x(t)$ makes no contribution to event occurrence. Therefore, by taking $x(t)$ as the EEG power in (1), we can include the effect of online brain activity on perceptual switching.

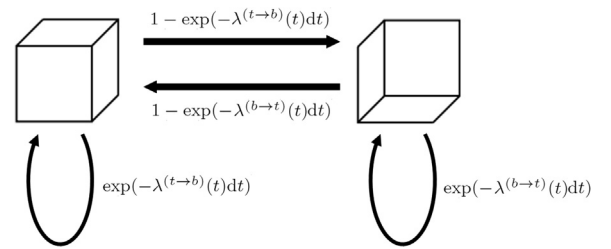


Fig. 6. Schematic of the point process modeling of perceptual switching. Here, we focus on the interval $[t, t + dt)$, where dt is an infinitesimal time length. Four transition patterns of the Necker cube interpretation are shown by arrows. Curved arrows represent the case where no perceptual switching occurs, whereas straight arrows represent the case where one perceptual switching occurs. The possibility of more than one perceptual switching within the infinitesimal interval $[t, t + dt)$ is negligible. The expressions on each arrow represent the transition probabilities. Therefore, if the top view is perceived at time t , then the probability that the top view is still perceived at time $t + dt$ is $\exp(-\lambda^{(t \rightarrow b)}(t)dt) \approx 1 - \lambda^{(t \rightarrow b)}(t)dt$ and the probability that the interpretation is changed to the bottom view at time $t + dt$ is $\lambda^{(t \rightarrow b)}(t)dt$. If the bottom view is perceived at time t , then $\lambda^{(b \rightarrow t)}(t)$ appears instead of $\lambda^{(t \rightarrow b)}(t)$.

In practice, the probability of event occurrence often depends on the duration from the last event. For example, aftershocks tend to repeat after a major earthquake (Ogata, 1999). In contrast, neurons cannot fire immediately after the last firing and this property is called refractoriness (Citi et al., 2014). Borsellino et al. (1972) reported that perceptual switching also has the refractory property and the distribution of the intervals between perceptual switching can be approximated well by the gamma distribution. In point process modeling, such an interaction between events is expressed by making the intensity function conditional on the history H_t of the series of events, where H_t represents the set of event timings in the interval $[0, t)$. For example, consider a conditional intensity function of the following form:

$$\lambda(t|H_t) = \frac{f(t - t_*)}{1 - F(t - t_*)}, \quad (2)$$

where t_* is the time of the last event before time t (if there are no events before t , then $t_* = 0$), $F(s)$ is a probability distribution function, and

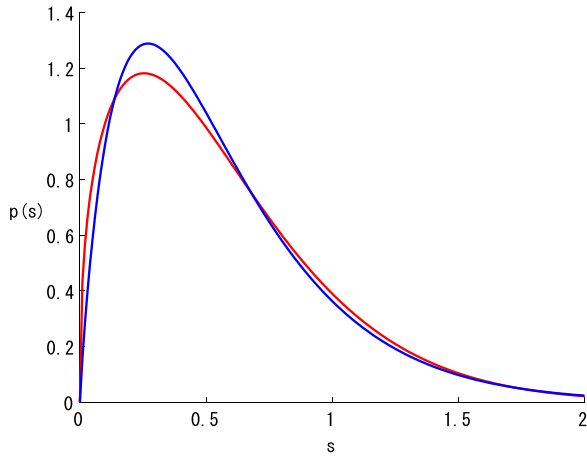


Fig. 7. Comparison of the probability density functions of the Weibull distribution (red) and the gamma distribution (blue). The unit of s is seconds. In the Weibull distribution, the parameters are set to $\theta_0 = 1$, $\theta_1 = 0.4$. In the gamma distribution, the parameters are set to make the mean and variance equal to those in the Weibull distribution.

$f(s) = F'(s)$ is the corresponding probability density function. The point process with intensity function (2) is called renewal process. In a renewal process (2), the intervals between events $s_i = t_{i+1} - t_i (> 0)$ are independent and identically distributed with a probability distribution function $F(s)$. Thus, the results reported by Borsellino et al. (1972) imply that the renewal process with the gamma distribution as the interval distribution describes perceptual switching well. However, the corresponding intensity function (2) is computationally inconvenient. Therefore, we instead consider the Weibull distribution

$$p(s|\theta) = \exp\left(\theta_0 + \theta_1 \log s - \frac{1}{\theta_1 + 1} \exp(\theta_0 + (\theta_1 + 1) \log s)\right), \quad (3)$$

which is commonly used in survival analysis (Kalbfleisch and Prentice, 2002). As shown in Fig. 7, the Weibull distribution has a similar shape to the gamma distribution but yields a more tractable form of the conditional intensity function (2):

$$\lambda(t|H_t, \theta) = \exp(\theta_0 + \theta_1 \log(t - t_*)), \quad (4)$$

which leads to a concave log-likelihood as explained in the next subsection. If $\theta_1 > 0$, the intensity $\lambda(t|H_t, \theta)$ increases with the time from the last event, thereby resulting in refractoriness (Fig. 5 (b)). We confirmed that the fit of the Weibull distribution to the intervals between perceptual switchings was not worse than the gamma distribution. In the following, we refer to the point process model with the conditional intensity function (4) as *Weibull-type model*.

In summary, by merging models (1) and (4), we obtain the conditional intensity function:

$$\lambda(t|H_t, \theta) = \exp(\theta_0 + \theta_1 \log(t - t_*) + \theta_2 x(t)). \quad (5)$$

This model enables to evaluate the effect of online brain activity while accounting for the refractory effect. By testing the hypothesis that $\theta_2 = 0$, we can assess the significance of the effect of $x(t)$. Note that the model (5) reduces to the Weibull-type model (4) when $\theta_2 = 0$. In the following, we refer to the point process model with the conditional intensity function (5) as the *online activity regression model*, because it indicates the contribution of online brain activity to the occurrence of perceptual switching.

After data-preprocessing (Section 2.2), we obtained the 62-ch EEG power time series in five frequency bands. Let the EEG power obtained from the i -th electrode in the j -th frequency band be $x_{i,j}(t)$, where $j = 1, 2, 3, 4, 5$ represent the delta, theta, alpha, beta, and gamma bands, respectively. Then, we have $(62 \times 5 =)$ 310 online activity regression models

$$\lambda_{i,j}(t|H_t, \theta) = \exp(\theta_0^{(i,j)} + \theta_1^{(i,j)} \log(t - t_*) + \theta_2^{(i,j)} x_{i,j}(t)) \quad (i = 1, \dots, 62; j = 1, \dots, 5). \quad (6)$$

By fitting these models to the data, we identify the scalp location and frequency band that contribute significantly to perceptual switching. This process employ likelihood ratio testing with correction for multiple comparisons, as explained in the next subsection.

Due to the inevitable time lag between perceptual switching and key pressing, it may be inappropriate to incorporate the EEG power $x_{i,j}(t)$ at time t into the value of the intensity function $\lambda_{i,j}(t|H_t, \theta)$ at time t in (6). Therefore, we checked whether the results were altered by replacing $x_{i,j}(t)$ in (6) with $x_{i,j}(t - \Delta t)$, where Δt is 0.5 s. The same Δt was used by Struber and Herrmann (2002). The results changed little, so we hereafter use (6) without time lag.

2.4. Likelihood ratio testing of point process models

To identify the part of the brain and frequency band with significant effects on perceptual switching, we test the hypothesis that $\theta_2^{(i,j)} = 0$ in (6) by likelihood ratio testing with correction for multiple comparisons.

First, we fit the Weibull-type model (4) and online activity regression models (6) to the experimental data. In general, the log-likelihood of the point process model with conditional intensity function $\lambda(t|H_t, \theta)$ is given by

$$\log L(\theta) = - \int_0^T \lambda(t|H_t, \theta) dt + \sum_{k=1}^n \log \lambda(t_k|H_t, \theta), \quad (7)$$

where $t_1 < \dots < t_n$ are event times and $[0, T]$ is the observation interval (Daley and Vere-Jones, 2003). We estimate the parameter θ by maximizing the log-likelihood (7) using numerical optimization. Note that the log-likelihood (7) becomes concave for the Weibull-type model (4) and online activity regression models (6). We obtain the maximum likelihood estimates using the Newton method.

Next, we test the hypothesis that $\theta_2^{(i,j)} = 0$. The online activity regression models (6) reduce to the Weibull-type model (4) when $\theta_2^{(i,j)} = 0$, so the hypothesis that $\theta_2^{(i,j)} = 0$ can be tested by likelihood ratio testing for nested models. Let $L(\hat{\theta})$ and $L_{i,j}(\hat{\theta}^{(i,j)})$ be the likelihood functions evaluated at the maximum likelihood estimates $\hat{\theta}$ and $\hat{\theta}^{(i,j)}$ of the Weibull-type model (4) and online activity regression models (6), respectively. Then, the likelihood ratio (LR) statistic is defined as

$$\text{LR}_{i,j} = 2 \log \frac{L_{i,j}(\hat{\theta}^{(i,j)})}{L(\hat{\theta})}. \quad (8)$$

If $\theta_2^{(i,j)} = 0$, $\text{LR}_{i,j}$ asymptotically follows the chi-squared distribution with one degree of freedom. Now, it should be noted that we consider each subject, each condition, and each direction of switch separately. For the s -th subject under the c -th condition, let $\text{LR}_{i,j}^{(t \rightarrow b)}(s, c)$ and $\text{LR}_{i,j}^{(b \rightarrow t)}(s, c)$ be the likelihood ratio statistics (8) for switch from top to bottom view and switch from bottom to top view, respectively. Here, $c = 1, 2, 3$ represent neutral, top biasing, and bottom biasing conditions, respectively. Thus, the p-values (without correction for multiple comparisons) of the null hypothesis that $\theta_2^{(i,j)} = 0$ in (6) for each condition and each direction of switch are calculated as

$$p_{i,j}^{(t \rightarrow b)}(c) = \Pr \left[\chi^2(16) > \sum_{s=1}^{16} \text{LR}_{i,j}^{(t \rightarrow b)}(s, c) \right], \quad (9)$$

and

$$p_{i,j}^{(b \rightarrow t)}(c) = \Pr \left[\chi^2(16) > \sum_{s=1}^{16} \text{LR}_{i,j}^{(b \rightarrow t)}(s, c) \right]. \quad (10)$$

Finally, because we are simultaneously testing 310 hypotheses $\theta_2^{(i,j)} = 0$ with $i = 1, \dots, 62$ and $j = 1, \dots, 5$, we correct for multiple comparisons using the Bonferroni correction. Namely, the original p-value is multiplied by the total number of null hypotheses 310.

Therefore, the p-values (with correction for multiple comparisons) of the null hypothesis $\theta_2^{(i,j)} = 0$ are calculated as

$$\tilde{p}_{i,j}^{(t \rightarrow b)}(c) = 310 p_{i,j}^{(t \rightarrow b)}(c), \quad (11)$$

and

$$\tilde{p}_{i,j}^{(b \rightarrow t)}(c) = 310 p_{i,j}^{(b \rightarrow t)}(c). \quad (12)$$

Based on these p-values, the electrodes and frequency bands with significant effects on perceptual switching are identified for each condition and each direction of switch.

All of the EEG preprocessing steps and statistical analyses were performed using custom-written MATLAB (2013a) code. To visualize the results, we used the function *topoplot* in EEGLAB (Delorme and Makeig, 2007).

3. Results

As discussed by Shimaoka et al. (2010), under both biasing conditions, the duration length of the attended interpretation was significantly longer than that of the non-attended interpretation, which agrees with the results obtained by Meng and Tong (2004). Therefore, the participants actually viewed the Necker cube with top-down selective attention.

3.1. Fitting of the Weibull-type models

Before investigating the effects of online brain activity on perceptual switching, we fitted the Weibull-type model (4) to the key-pressing data. Fig. 8 presents a histogram of the perceived bottom view durations and the probability density function of the fitted Weibull distribution (3) for one subject under the neutral condition. Here, the estimated parameter $(\hat{\theta}_0, \hat{\theta}_1)$ was $(-1.11, 0.45)$ and the mean of the fitted Weibull distribution was 2.53 s. In addition, the p-value of the null hypothesis that $\theta_1 = 0$ was 1.53×10^{-7} according to the likelihood ratio testing. Similar results were obtained for other participants, conditions, and direction of switch. As $\hat{\theta}_1 > 0$, perceptual switching does not follow the previous switching immediately (Fig. 5(b)). Thus, perceptual switching exhibits refractory behavior, in a similar manner to the neuronal firings (Truccolo et al., 2005).

We tested for differences in the Weibull distributions across conditions and directions of switch. Namely, we compared six types of perceptual switching corresponding to the three conditions and two directions of switch. For all 15 paired comparisons, the null hypotheses that (θ_0, θ_1) is common were rejected with $p < 1.7 \times 10^{-15}$. Therefore, the Weibull distributions of the duration lengths vary among condi-

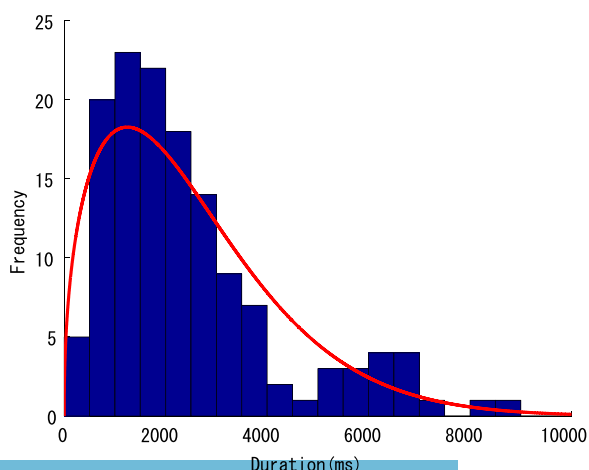


Fig. 8. Histogram of the perceived bottom view durations (blue) and the fitted Weibull distribution (3) (red) for one subject under the neutral condition.

tions and directions of switch, thereby confirming the findings obtained by Meng and Tong (2004) in another way.

3.2. Fitting of online activity regression models

Next, we fitted online activity regression models (6) to the experimental data. By testing the hypothesis that $\theta_2^{(i,j)} = 0$ in (6) by likelihood ratio testing with correction for multiple comparisons, we identified the part of the brain and frequency band with significant effects on perceptual switching. Among the five frequency bands considered (delta, theta, alpha, beta, and gamma), significant results were obtained for the alpha band. We present the results for the alpha band ($j=3$) in the following.

Fig. 9 maps the likelihood ratio statistic (8) summed over 16 participants for each condition and each direction of switch. The upper row shows the mapping for switch from top to bottom view $\sum_s \text{LR}_{i3}^{(t \rightarrow b)}(s, c)$ and the lower row shows the mapping for switch from bottom to top view $\sum_s \text{LR}_{i3}^{(b \rightarrow t)}(s, c)$, respectively. From the relation (9) and (11) between the likelihood ratio statistics and the Bonferroni-corrected p-values, we find that $\text{LR} > (\chi_{16}^2)^{-1}(1 - 0.05/310) = 44.6$ and $\text{LR} > 100$ correspond to $p < 0.05$ and $p < 310(1 - \chi_{16}^2(100)) = 1.1 \times 10^{-11}$, respectively, where χ_{16}^2 denotes the distribution function of the chi-squared distribution with 16 degrees of freedom. Therefore, online alpha activity in the green, yellow or red regions have highly significant effects on perceptual switchings.

According to Fig. 9, six pairs of the condition and the direction of switch are classified into two types. The significance of online alpha activity is low for the first type, which includes the switch from top to bottom view under the neutral and top-view biasing conditions as well as the switch from bottom to top view under the bottom-view biasing condition. However, online occipital alpha activity has highly significant effects for the second type, which includes the switch from top to bottom view under the neutral and top-view biasing conditions as well as the switch from bottom to top view under the bottom-view biasing condition. This clear contrast is interesting. Then, we investigate whether the effect of online occipital alpha activity is excitatory ($\hat{\theta}_2^{(i,3)} > 0$) or inhibitory ($\hat{\theta}_2^{(i,3)} < 0$). Fig. 10 maps the number of participants with negative $\hat{\theta}_2^{(i,3)}$ for each condition and each direction of switch. The online alpha activity in the red regions has an inhibitory effect on perceptual switchings for most of the participants (more than 12 out of 16). Therefore, for the second type of switchings discussed above, it can be seen that online occipital alpha activity has an inhibitory effect on perceptual switchings. In summary, online occipital alpha activity has a highly significant inhibitory effect on the switch from top to bottom view under the neutral and top-view biasing conditions as well as the switch from bottom to top view under the bottom-view biasing condition.

The results given above are naturally interpreted as follows. Under the top- and bottom-view biasing conditions, the participants attempt to maintain a fixed perception of the Necker cube. For example, under the top view biasing condition, perceptual switching from the bottom to top view is “desired,” whereas the opposite switch is “undesired.” Thus, we conclude that the switch to the “undesired” view is suppressed by online occipital alpha activity.

Although the participants did not watch the Necker cube with selective attention under the neutral condition, we found a strong difference between the two directions of switch. Combined with the above conclusion, one possible explanation is as follows: once the perceptual switching to the top view occurs, the participants prefer to maintain this interpretation because the top view is perceived more naturally than the bottom view. In other words, the top view is implicitly “desired” under the neutral condition. Our point process modeling approach can capture such implicit bias in addition to explicit selective attention.

As a control for motor activity, we conducted a similar analysis on

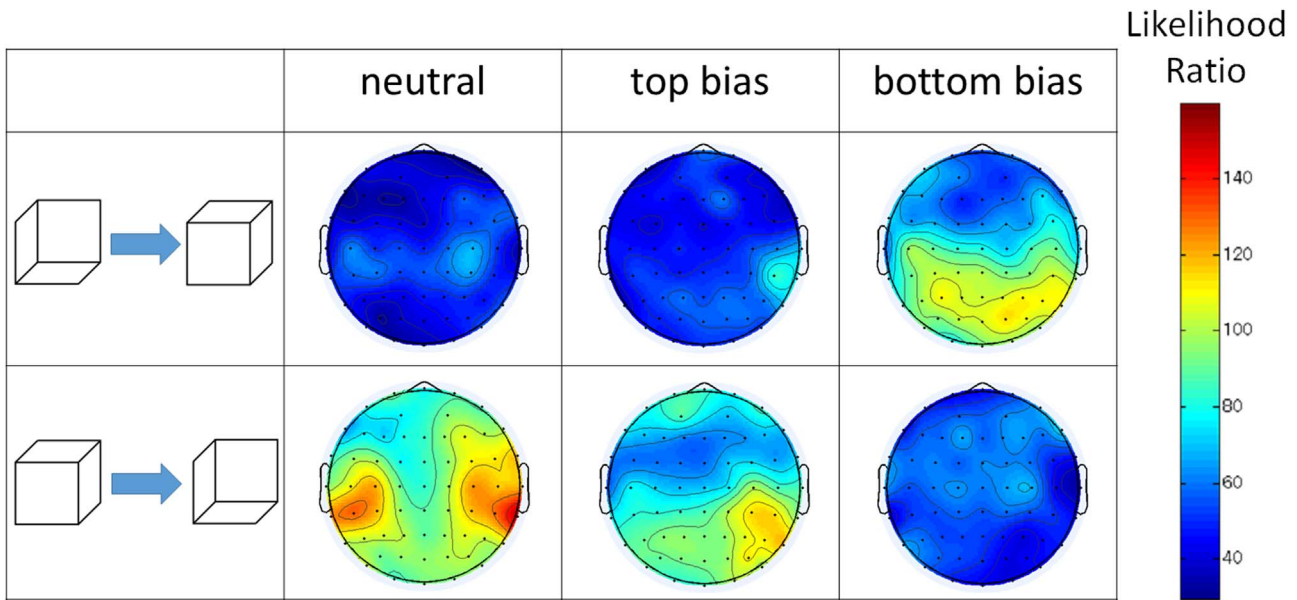


Fig. 9. Mapping of the likelihood ratio statistics for the alpha band (upper row: $\sum_{s=1}^{16} LR_{i,3}^{(t \rightarrow b)}(s, c)$, lower row: $\sum_{s=1}^{16} LR_{i,3}^{(b \rightarrow t)}(s, c)$), where each $LR_{i,j}(s, c)$ is defined as (8). The likelihood ratio statistics exceeding 100 corresponds to $p < 1.1 \times 10^{-11}$, so the online alpha activity in the green, yellow or red regions have highly significant effects on perceptual switchings.

the self-paced key pressing condition. Under this condition, the participants pressed the keys at their own pace without watching the Necker cube. Therefore, we did not divide the data into sub-blocks as in Fig. 4B. We concatenated five experimental blocks into one for each subject and applied the same analysis described above. Fig. 11 maps the likelihood ratio statistics for each frequency band and Fig. 12 maps the number of participants with negative $\hat{\theta}_2^{(i,j)}$ for each frequency band. Online alpha activity does not have significant effects on key-pressing events. In contrast, the parietal beta activity seems to have a significant effect. Among 16 participants, nine showed high significance of the parietal beta activity. The fitted parameter $\hat{\theta}_2^{(i,j)}$ was negative for all these participants. Therefore, the parietal beta activity appears to have inhibitory effects on key-pressing events. This result is plausible, because key-pressing events cause event-related desynchronization,

which results in decreased beta activity in the motor cortex (Pfurtscheller and Lopes da Silva, 1999).

4. Discussion

In this study, we proposed a point process modeling approach for studying the effects of online brain activity on perceptual switching and analyzed experimental data regarding selective attention in multistable perception. We developed online activity regression models (6), which enable to determine whether online brain activity has excitatory or inhibitory effects on perceptual switching. By fitting online activity regression models to the data and applying the likelihood ratio testing with correction for multiple comparisons, we determined the part of the brain and frequency band with significant effects on perceptual

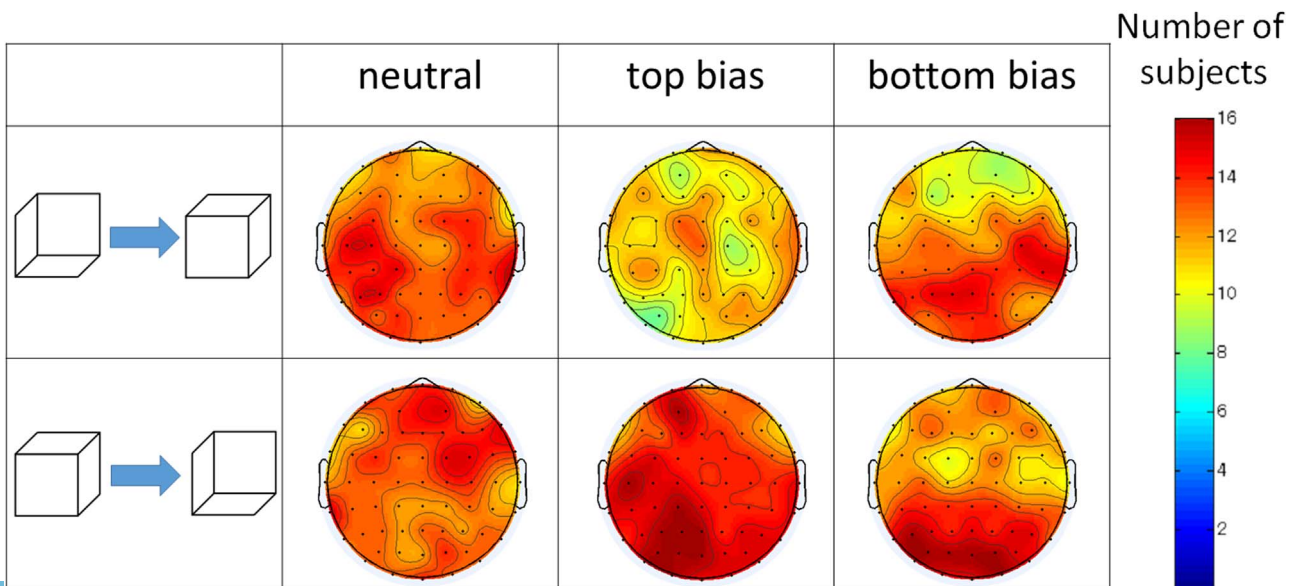


Fig. 10. Mapping of the number of participants with $\hat{\theta}_2^{(i,3)} < 0$ at each electrode for each condition and each direction of switch. Note that we analyzed 16 participants in total. The online alpha activity in the red regions has an inhibitory effect on perceptual switchings, the significance of which can be evaluated by Fig. 9.

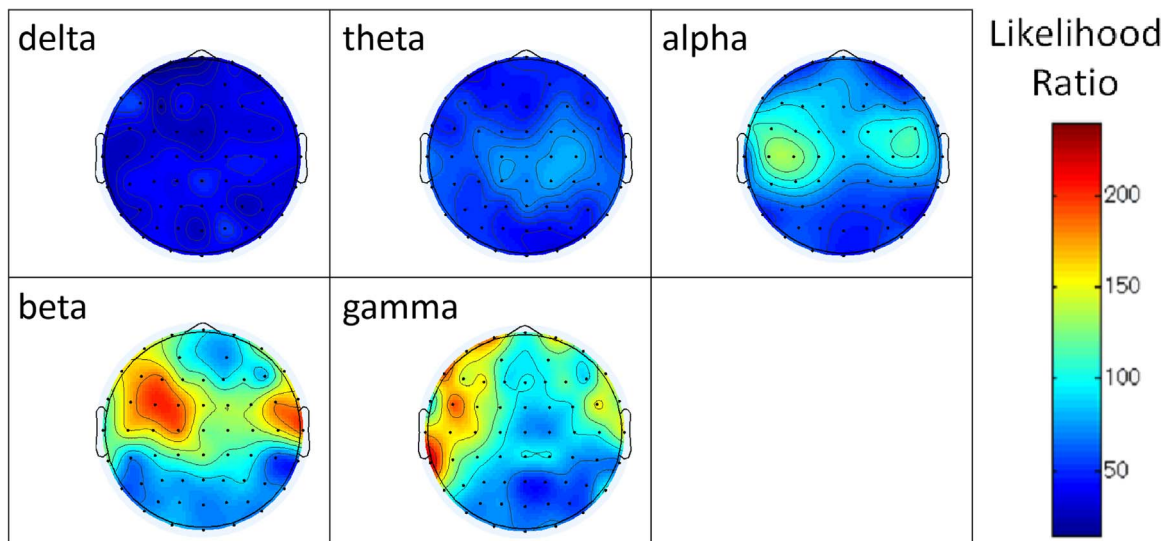


Fig. 11. Mapping of the likelihood ratio statistics $\sum_{s=1}^{16} LR_{i,j}(s)$ for each frequency band under the self-paced key pressing condition.

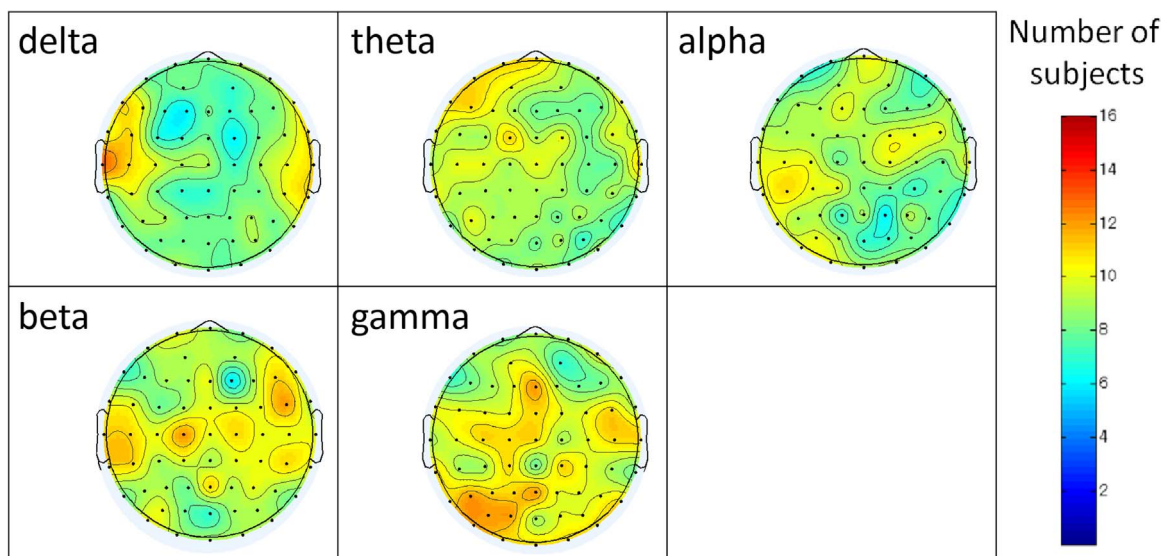


Fig. 12. Mapping of the number of participants with $\hat{\theta}_2^{(i,j)} < 0$ at each electrode for each frequency band under the self-paced key pressing condition. Note that we analyzed 16 participants in total.

switching. As a result, we found that online occipital alpha activity suppresses perceptual switching to the non-attended interpretation.

4.1. Attentional control over perceptual switching

Our results demonstrate that online occipital alpha activity maintains the attended interpretation. This finding is consistent with previous findings that alpha activity decreases around the time of perceptual switching (Isoglu-Alkac et al., 2000; Isoglu-Alkac and Struber, 2006; Struber and Herrmann, 2002). Such a relationship between occipital alpha activity and visual attention has been already reported. For example, when covert visual attention is directed to the left or right of the visual field, occipital alpha activity is suppressed in the hemisphere contralateral to the attended side (Thut et al., 2006; Worden et al., 2000). Our results suggest that occipital alpha activity also stabilizes the attended interpretation in multistable perception;

these results also support the hypothesis of Jensen and Mazaheri (2002) that alpha activity mediates the inhibition of information processing, because the participants in the present study tried to maintain the attended interpretation by inhibiting an alternative interpretation. Jensen et al. (2010) also reported that parietal alpha activity increases with memory load during retention.

Online occipital alpha activity holds the attended interpretation much more strongly than the non-attended interpretation. The online activity regression models (6) evaluate the effect of online brain activity (expressed by the parameter θ_2) while accounting for the change in the baseline switching rates (expressed by the parameter θ_0) across conditions separately. Therefore, suppression of perceptual switching to the non-attended interpretation is mediated not only by the decrease in the baseline switching rate θ_0 , as found by Meng and Tong (2004), but also by the significant change of θ_2 to negative. In other words, top-down processes related to the selective attention during the Necker

cube perception, which are controlled by the prefrontal cortex, are considered to interact with bottom-up information processing via the modulation of online alpha activity. Unlike previous studies (de Graaf et al., 2011; Windmann et al., 2006), we found no significant effects of frontal activity on perceptual switching, possibly because online activity regression models (6) are insensitive to instantaneous activity changes, i.e., the frontal cortex may become active only around the time of perceptual switching.

4.2. Advantages of the point process modeling approach

In the present study, we described perceptual switching using online activity regression models (6). Several theoretical models of perceptual switching have already been proposed. For example, Haken (1983) described multistable perception as a dynamical system with several attractors, whereas Braun and Mattia (2010) described perceptual switching using a noise-driven attractor dynamics model where each competing interpretation corresponds to one attractor of the dynamical system and noise fluctuations in the dynamics drive the stochastic transitions from one attractor to another. These models provide an intuitive understanding of multistable perception, but they are phenomenological in nature, thereby precluding any quantitative analysis of experimental behavioral and neurophysiological data. In contrast, our point process modeling approach allows quantitative evaluations of the effects of online brain activity.

The part of the brain that actually governs perceptual switching remains unknown. It is considered that manipulative experiments such as transcranial magnetic stimulation (TMS) are useful for investigating causality. In terms of multistable perception, experimental results obtained using TMS (de Graaf et al., 2011) and lesions (Windmann et al., 2006) suggest a causal role of the prefrontal cortex. Namely, the prefrontal cortex is essential for selecting and intentionally switching between competing interpretations. Windmann et al. (2006) also noted that the prefrontal cortex may not be necessary for maintaining conscious representations of continuously perceived visual objects. We suggest that online activity regression models (6) may be useful for elucidating causal relationships between online brain activity and perceptual switching. Specifically, by replacing $x(t)$ with $x(t - \Delta t)$ in (6), we can evaluate the effect of online brain activity on perceptual switching with a time lag Δt . We confirmed that this modification slightly altered the results given above when Δt was 0.5 s. This result may suggest a causal role of online occipital alpha activity in multistable perception. In addition, an analysis that incorporates a time lag may allow the prediction of perceptual switching from online brain activity. The probability of perceptual switching around time $t + \Delta t$ is obtained at time t .

Spontaneous brain activity has recently been shown to be important for various types of information processing (Arieli et al., 1996; Fiser et al., 2004; Laird et al., 2011; Luczak et al., 2009). Many neuroimaging studies suggest that spontaneous oscillatory activity such as alpha and gamma are crucial for sensory processing including visual perception (Busch et al., 2009; Dougherty et al., 2015; Freyer et al., 2009; Ruhnu et al., 2014). However, conventional analyses of cognitive events such as perceptual switching have mainly focused on the brain activity only around the time of events such as evoked and induced activity. In contrast, our point process modeling approach can investigate the dynamic relationship between cognitive events and online brain activity, in conjunction with brain signals such as EEG and fMRI. Therefore, our method has many potential applications in future studies.

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