NeuroImage 152 (2017) 50–59

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage

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

ARTICLE INFO

Keywords:
Attention
Bistable perception
EEG
Necker cube
Perceptual switching
Point process

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 instanta-

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

http://dx.doi.org/10.1016/j.neuroimage.2017.02.068
Received 20 December 2016; Received in revised form 30 January 2017; Accepted 23 February 2017
Available online 24 February 2017
1053-8119/

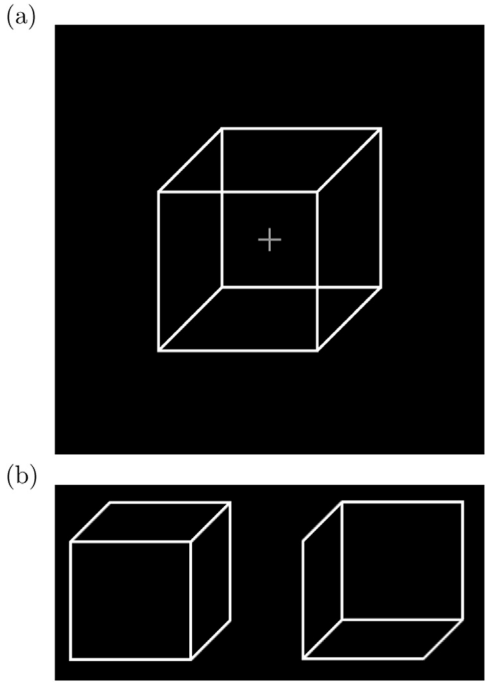

Fig. 1. (a) Necker cube presented to participants. (b) Left: top view, right: bottom view.

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