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Research report

Functional symmetry of the primary visual pathway evidenced by steady-state visual evoked potentials

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ABSTRACT

The primary visual pathway exhibits a symmetrical anatomical structure, initially arising from the left and right retinas, passing through the lateral geniculate nucleus, and finally projecting to the left and right primary visual cortices. However, to our knowledge, studies based on scalp EEG have not provided adequate evidence of the functional symmetry of the primary visual pathway, as the usual visual ERP is often related to other higher-level brain areas. Steady-state visual evoked potentials (SSVEPs) can be considered as the direct response of the primary visual pathway to a repetitive stimulus, with a very limited correlation with responses of higher-level brain areas. Therefore, SSVEPs can be used to evaluate the functional symmetry of the primary visual pathway. In this study, we draw a comparison among the powers and distributions of SSVEPs of different frequencies when the left or right eye alone is stimulated, and when both the eyes are stimulated together. Our results indicate that the primary visual pathway is almost symmetrical in generating SSVEPs from either eye and that there is some functional interaction between the left and right primary visual pathways.

1. Introduction

Vision is the most important source of knowledge of the outside world for most people. Two main parameters that define vision are lightness and brightness. In the field of optics, reflectance is defined as the ratio of light reflected from a surface to the light incident on the surface, while luminance is defined as the amount of light an object emits or the amount of light that reflects back form the object. In vision study, lightness is the perceived reflectance, while brightness is the perceived luminance (Kingdom, 2011). The mechanism of perception of reflectance and luminance is still unclear, and has been the focus of many researchers. Sometimes, there is difference in the perception of some aspects of the physical stimulus either because of visual deficits in the individual or the stimulus style; this phenomenon is known as vision illusion. Extensive research on visual illusions has been conducted. While some studies have found new sets of visual illusions (Zavagno, 1999; Gori and Stubbs, 2006), some have tried to explain the mechanisms of various existing visual illusions (Agostini and Galmonte, 2002; Anstis et al., 2007; Gori et al., 2010), and some have made use of vision illusions to study vision deficits (Pammer and Wheatley, 2001; Gori et al., 2014, 2016). Although the neural mechanism of vision is not clear, the anatomical structure of the primary vision pathway is well-elucidated (Hankins and Lucas, 2002). When a visual stimulus presents in a visual field, stimulus-related information, such as reflectance and luminance, is first preprocessed by the temporal retina and the nasal retina, each of which projects to different optic nerves. Next, the optic nerves from the temporal retina project to the lateral geniculate nucleus directly, while the optic nerves from the nasal retina first project to the optic chiasm. In the optic chiasm, about half of the optic nerves project to the ipsilateral geniculate nucleus, while the other half project to the contralateral geniculate nucleus. The signals from these optic nerves are processed at the lateral geniculate nucleus and the processed signals project to the primary visual cortex through the optic radiations. In case there is a need for further processing, the signals are projected to the striate cortex or the extrastriate cortex. Fig. 1 shows the anatomical model of the primary visual pathway, which is evidently almost symmetrical. In this pathway, the lateral geniculate nucleus is not just a node for vision nerve distribution or transfer, but also processes the visual information to some extent. Some

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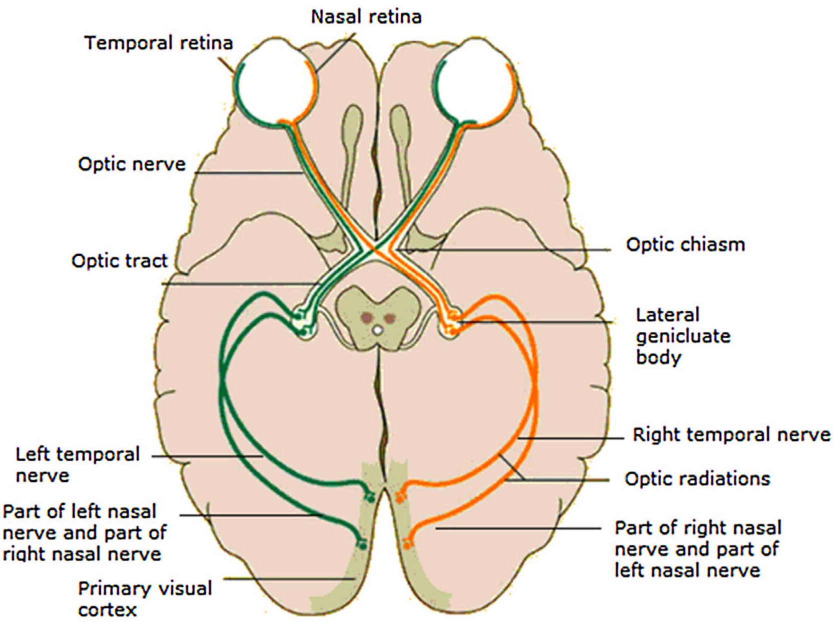

Fig. 1. An anatomical model of the primary visual pathway.

signals at the lateral geniculate nucleus have some special sense. In the Craik–Cornsweet–O'Brien (CCOB) illusion, the perceived lightness of a region of uniform luminance can be profoundly altered by the presence of a luminance gradient along the complete border or a part of the border enclosing the region. Functional magnetic resonance imaging (FMRI) shows that the CCOB illusion is strongly correlated with signals recorded by the human lateral geniculate nucleus (Elaine et al., 2009).

Much of the work related to the primary visual cortex has been performed using an intracranial electrode implanted in the mammalian brain, while recording its response to different stimulus styles. It has been observed that the stimulus style can significantly influence the neural responses. For example, periodic stimuli travel over longer distances than aperiodic stimuli at the neuron level (Chun et al., 2011), while a flicker can produce a strong simultaneous response to both brightness and color contrast, in the visual cortex (Sae and Ikuya, 2012). It was reported that the macaque primary visual cortex is slower to respond to surface interiors than to optimal bar stimuli (Xin and Michael, 2007). Another study reported a negative correlation between the response and the response 'history' of the cells, in that a larger response on one fixation was associated with a lower response on the subsequent fixation (Sean et al., 2007). Some findings suggest that brightness information is explicitly represented in the response of neurons of the striate cortex as part of a neural representation of object surfaces (Andrew and Michael, 1999). One study reveals that the stimulus parameters—color and motion—can be discriminated and matched between the normal and blind hemifields, whereas brightness cannot (Antony et al., 1999). The studies described above used intracranial electrode recordings, which can provide information related to only one or a few neurons' responses to the stimulus precisely. However, given the various kinds of neurons in the cortex, it is impossible to study these neurons one by one. Therefore, intracranial electrode recordings cannot be used to investigate the gross effect of stimuli, and thus cannot demonstrate the functional symmetry of the primary visual pathway. EEG recordings using scalp electrodes can be thought to reflect the total response of many neurons, and can be used to study brain function. A cognitive task based on visual stimuli is often used to study brain function related to vision. However, a usual visual ERP study cannot provide convincing evidence of functional symmetry of the primary visual pathway, since higher brain areas (in addition to the primary visual cortex) are also represented in the EEG recordings.

When a visual stimulus with a stable intensity and frequency, such as a flicker, presents a clear electronic signal in the visual field that can be recorded from the scalp, which has the same frequency as the stimulus or its harmonics. This signal is called the steady-state visual evoked potential (SSVEP). However, the mechanism through which SSVEPs are generated remains unclear. One theory suggests that an SSVEP is a cortical response to the stimulus presented at the peripheral retina projecting via the cortico-cortical loops. There exist three SSVEP neural networks corresponding to different frequency bands, i.e. low (5–12 Hz), medium (12–30 Hz) and high (30–50 Hz) (Silberstein, 1995; Herrmann, 2001). Some studies have illustrated the travelling phenomena in SSVEPs (Burkitt et al., 2000). Since the discovery of SSVEPs, they have been used in many ways. An important application is for studying the processing of cognitive tasks of long durations (Silberstein et al., 1990; Gray et al., 2003; Birca et al., 2006; Ellis et al., 2006; Camfield et al., 2012), while another is in developing an SSVEP-based Brain-Computer Interface (BCI) (Cheng et al., 2002; Lee et al., 2010; Luo and Sullivan, 2010; Ortner et al., 2010; Lopez et al., 2010). All these studies are based on dual eye stimulation, and the validity of single eye stimulation has not been discussed. Consequently, these studies do not provide insights into the symmetry of the primary visual pathway.

In this study, we used flicker stimuli of different frequencies to stimulate the subjects' left eye, right eye, and both eyes. The SSVEP in each condition was collected from the scalp, and the SSVEP power and distribution were used to evaluate the functional symmetry of the primary visual pathway. Based on the SSVEP power under the three different stimulus styles, a simple function model of SSVEP generation was proposed.

2. Methodology

2.1. Ethics statement

This study was approved by the Human Research and Ethics Committee of the University of Electronic Science and Technology