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Blink-related dynamic switching between internal and external orienting networks while viewing videos

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ABSTRACT

Humans spontaneously generate eyeblinks every few seconds. However, because this blink rate is several times more common than is required for ocular lubrication, the function of most spontaneous eyeblinks remains unknown. Because spontaneous eyeblinks tend to occur at implicit breakpoints in video stories, I hypothesized that spontaneous eyeblinks play an active role in attentional disengagement from external stimuli. Consistent with this, we previously found that spontaneous eyeblinks involve the concurrent deactivation of the dorsal attention network and activation of the default mode network when individuals are viewing videos. However, this previous study examined only the upper brain regions to increase the temporal resolution of the data. Therefore, the present study examined whether the temporal and subcortical regions exhibited blink-related activations or deactivations using the same visual stimuli as in the previous study. Data revealed that the bilateral hippocampus and cerebellum showed a prominent but momentary activation after the blink onset. In contrast, a blink-related deactivation was observed in both the right ventral and dorsal attention networks. These results suggest that spontaneous eyeblinks are involved in the attentional disengagement from external visual information via the massive and dynamic alteration of brain activity between the external and internal orienting networks.

1. Introduction

Humans generate a spontaneous eyeblink every few seconds, and ultimately spend 10% of their waking hours in darkness (Nakano et al., 2009; Stern et al., 1984). It is generally accepted that eyeblinks are necessary for ocular lubrication, but spontaneous eyeblinks occur several times more frequently than is necessary for ocular lubrication (Doane, 1980; Karson, 1983). Therefore, the functional role of most spontaneous eyeblinks remains unknown.

The timing of blink generation is synchronized between individuals at the attentional breakpoints of video stories or speech (Nakano and Kitazawa, 2010; Nakano et al., 2009). In addition, people who have difficulty in voluntary eye movements unconsciously generate eyeblinks to terminate visual fixation spasms (Holmes, 1936; Wadia and Swami, 1971). These observations raise the possibility that spontaneous eyeblinks are actively involved in the attentional disengagement from external stimuli. To investigate this possibility, we previously used functional magnetic resonance imaging (fMRI) to examine the brain activity related to the onset of spontaneous eyeblinks while viewing videos (Nakano et al., 2013). Data revealed that the dorsal attention network (DAN), including the frontal eye field (FEF) and the superior parietal lobe (SPL), exhibited blink-related deactivation, whereas the default mode network (DMN), including the anterior cingulate cortex (ACC), the posterior cingulate cortex (PCC), and the angular gyrus (AG), showed blink-related momentary activation (Fig. 1). In contrast, physical blackouts of the video for durations that were comparable with eyeblinks did not activate the DMN or deactivate the DAN. Therefore, spontaneous eyeblinks are specifically involved in the attentional disengagement from external stimuli by switching brain activity between DMN and DAN.

The DMN, which exhibits reduced activity during externally oriented tasks, is implicated in internally driven cognition and memory (Buckner et al., 2008; Raichle et al., 2001; Shulman et al., 1997). The DMN regions play pivotal roles in connecting to other regions, and serve as network hubs with a significantly higher functional connectivity density (Tomasi and Volkow, 2011). In particular, the PCC has a strong anatomical and functional connection with the medial temporal lobe, including the hippocampus, which

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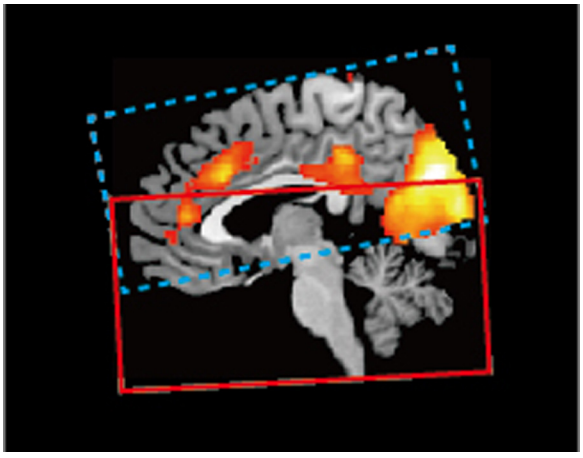

Fig. 1. The brain areas scanned by the MRI scanner. The red rectangle represents the brain area scanned in the present study. The blue dotted rectangle represents the brain area scanned in the previous study (Nakano et al., 2013). The yellow and red colored brain regions represent the blink-related activation reported in the previous study (Nakano et al., 2013). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

is a central region for episodic memory processing (Greicius et al., 2004, 2009). For example, many neuroimaging studies reported that the hippocampus often shows concurrent activation with the DMN, particularly during tasks that require self-referenced memory retrieval (Greicius et al., 2004; Vincent et al., 2006). In addition to the hippocampus, the recent fMRI studies revealed that the cerebellum cortex has a strong functional connectivity with the DMN (Buckner et al., 2011; Halko et al., 2014). Thus, I speculate that these brain regions which have dense functional connectivity with the DMN also showed blink-related activation. However, since our previous study examined blink-related neural activity only in the upper region of the brain to increase the temporal resolution of the data (Fig. 1, blue dotted area). Therefore, the present study examined the blink-related neural activity in the lower region of the brain, including the medial temporal lobe and the cerebellum, when individuals were viewing the same videos used in the previous study (Fig. 1, red circled area).

2. Materials and methods

2.1. Participants

Fourteen healthy participants (eight male and six female aged 21–24 years), who were not enrolled in the previous study, participated in the study. All had normal vision and no history of neurological disorders. Two other participants who took part in the study were excluded from further analysis because of an extremely high blink rate (>60 per min) and large head motions (>10 mm). The study was approved by the review boards of Osaka University and the National Institute of Information and Communications Technology, and all participants provided written informed consent before participation.

2.2. Task

All videos used in this study were taken from the British TV comedy "The Best Bits" of "Rowan Atkinson in Mr. Bean 1" (2004, Universal Studios). One of four video clips was continuously presented to each participant for 480 s during each scan to examine the blink-related cortical activations and deactivations that occurred while they were viewing the video. Each participant was scanned four times using different video clips. To ensure that participants maintained their attention, they were informed in advance that they had to answer several questions regarding the content of the video after each experiment. The mean percent of correct answers to the questions was very high (96%, range 92–100%). In addition, the participants were informed that their eye movements would be measured while watching the video. They were not told that their blinking was being measured.

2.3. Data acquisition

Stimulus presentation was controlled using presentation software (Neurobehavioral Systems, CA) on a Dell computer running Microsoft Windows 7. Visual stimuli were projected onto a screen at the back of the magnet's bore that participants viewed through a mirror. Structural images were collected for each participant using a T1-weighted 3D MP-RAGE sequence on a Siemens 3-Tesla whole-body scanner (TR = 2 s, TE = 4.38 ms, flip angle = 8°, field of view = 256 mm, resolution = 1 mm × 1 mm × 1 mm). Functional images were collected using a gradient echo with an echo-planar sequence (TR = 1.75 s, TE = 28 ms, flip angle = 70°, isotropic nominal resolution = 3 mm, 27 slices with no gap). The slice positions were oriented to cover the entire cerebellum, striatum, brain stem, and limbic systems. Each participant completed four runs (275 scans per run); the first 10 images from each run were discarded.

During scanning, the pupil diameter and eyelid position were continuously monitored using an infrared video eye-monitoring system with a sampling rate of 240 Hz (NAC Image Technology, Tokyo, Japan). Each eyeblink was initially detected automatically according to the rate at which the pupil size changed, which was characterized by the combination of a rapid decrease in pupil size followed by an increase within 400 ms.

2.4. Data analysis

SPM8 (Wellcome Trust Center for Neuroimaging, London, UK) was used for data preprocessing [slice timing, realignment for head motion correction, normalization to the standard brain template (Montréal Neurological Institute template), and smoothing with an 8-mm full-width half-maximum Gaussian filter] and statistical analyses. The statistical significance of brain activation was evaluated on the basis of voxel-wise signal changes using a general linear model with the standard hemodynamic function of SPM and random effects analyses. The threshold of significance was set at $p < 0.001$ (voxel level, uncorrected) and the extent of cluster size (k) was >10 to balance the type I and type II errors (Lieberman and Cunningham, 2009; Woo et al., 2014).

Next, the blink-related temporal dynamics of the blood oxygen level-dependent (BOLD) signal changes, which occurred while the videos were being viewed, were analyzed. The time course of the signal intensity in each voxel was extracted. The time series was high-pass-filtered (cut-off cycle, 128 s), converted to a z-score, and interpolated linearly at 100-ms resolution. The time course was averaged over all blink events for each participant, and then averaged across participants. The peak height and trough depth of the time series were measured within a time window between 0 and 15 s after the blink onset.

3. Results

The participants spontaneously generated a mean of 16.8 eyeblinks per minute (range, 3.4–35.6) while viewing the videos. Consistent with the previous study, blink-related brain activation was found in the ACC, the precuneus, and the medial visual areas. In addition, the present study revealed blink-related activation in the distributed brain regions, including the hippocampus, the orbital frontal cortex (OFC), the caudate nucleus, the ventral striatum, and