Blink-related momentary activation of the default mode network while viewing videos

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It remains unknown why we generate spontaneous eyeblinks every few seconds, more often than necessary for ocular lubrication. Because eyeblinks tend to occur at implicit breakpoints while viewing videos, we hypothesized that eyeblinks are actively involved in the release of attention. We show that while viewing videos, cortical activity momentarily decreases in the dorsal attention network after blink onset but increases in the default-mode network implicated in internal processing. In contrast, physical blackouts of the video do not elicit such reciprocal changes in brain networks. The results suggest that eyeblinks are actively involved in the process of attentional disengagement during a cognitive behavior by momentarily activating the default-mode network while deactivating the dorsal attention network.

functional MRI | natural vision

We spontaneously generate an eyeblink every few seconds—15–20 per minute, on average. These spontaneous eyeblinks are believed to occur to lubricate the cornea, but the rate is several times more than required for ocular lubrication (1, 2). Therefore, it remains an open question why eyeblinks are generated so frequently at the cost of blocking visual input for a period amounting to 10% of our waking hours (3).

Spontaneous eyeblinks tend to occur at breakpoints of attention, such as the end of a sentence while reading (4), a pause by the speaker while listening to a speech (5), and implicit breakpoints while viewing videos (3). That eyeblinks occur not only at explicit but also at implicit breakpoints raises the possibility that spontaneous eyeblinks play an active role in the release of attention from external stimuli while attentively engaging in a cognitive task. Clinical neurological studies support this possibility. People who had a difficulty of voluntary eye movements often generate eyeblinks to terminate the spasms of visual fixations (6–8).

Assuming the role of the eyeblink in disengaging attention, each spontaneous eyeblink should be associated with inhibition of the dorsal attentional network that mediates the allocation of attention (9), and with an activation of the default-mode network (DMN), which is known to counteract the dorsal attention network (10) and is implicated in introspection (11, 12). We hypothesized that spontaneous eyeblinks control the disengagement of attention by momentarily deactivating the dorsal attention network while activating the DMN.

To test this hypothesis, we used fMRI to examine the cortical activity of 10 healthy participants (mean age: 21.7 y) in relation to the onset of each spontaneous eyeblink while the participants attentively viewed video clips from "Mr. Bean," a British television comedy. The story was chosen because our previous behavioral study demonstrated that the timing of spontaneous eyeblinks was synchronized across participants at the implicit breakpoints of the same video (3).

Results

The participants spontaneously generated an average of 17.4 eyeblinks per minute (ranging from 3.1–51.0) while viewing the videos. Event-related analyses revealed activation in the distributed cortical regions, including the medial visual area, the anterior cingulate cortex (ACC), the posterior cingulate cortex (PCC), the angular gyrus (AG), and the insular/secondary somatosensory (SII) cortex (Fig. 1*A* and Table S1). The activations in the ACC, PCC, and AG generally overlapped with regions previously implicated for the DMN (13). Event-related deactivation was found in the frontal eye fields (FEF) and the superior parietal lobe (SPL), which are implicated in the dorsal attention network (Fig. 1*B* and Table S1).

To further examine whether blink-related activation involved the DMN or resting state activation in this task, we examined the brain regions that showed greater activation at rest than while viewing the videos in the same participants. We found that the ACC, the AG, and the insular/SII exhibited resting state activation (Fig. 1*C*), and most of these areas showed blink-related activation (Fig. 1*D* and Table S2).

The time courses of the blood oxygen level-dependent (BOLD) signal demonstrated reciprocal increases in the DMN (Fig. 2 *A*–*C*) and decreases in the dorsal attention network (Fig. 2 *D* and *E*). The increase of the BOLD signal in the DMN generally reached a peak 4–5 s after blink onset and returned to the baseline at 7–8 s (Fig. 2 *A*–*C*). The decrease in the dorsal attention network reached a trough at 4–10 s and returned to the baseline at 15 s or later (Fig. 2 *D* and *E*). When the size of the peaks was measured for each participant, the peak height of the increase in the dorsal attention network generally correlated with the peak depth of the decrease in the DMN (Fig. 2*F*). That is, the larger the activation in the DMN, the larger the deactivation in the dorsal attention network. These results clearly demonstrate a momentary competitive interaction between the DMN and the dorsal attention network in close relation to the timing of each spontaneous eyeblink.

It may be argued, however, that the transient activation in the DMN was simply induced by a physical interruption of visual input and had nothing to do with the eyeblinks per se. To test this trivial possibility, we compared the cortical activations evoked by a spontaneous eyeblink and those evoked by comparable physical blackouts (165 ms in duration) (14) that were inserted in the same video clips pseudorandomly with a mean interval of 6.4 s. The DMN exhibited greater activation after an eyeblink than after a blackout (Fig. 3*A* and Table S3), clearly showing that the transient activation in the DMN was due to the eyeblink per se and not to the physical interruption of the visual input. In contrast, activation in the medial visual area was consistently observed for both eyeblinks and blackouts (Fig. 3*B*), suggesting that

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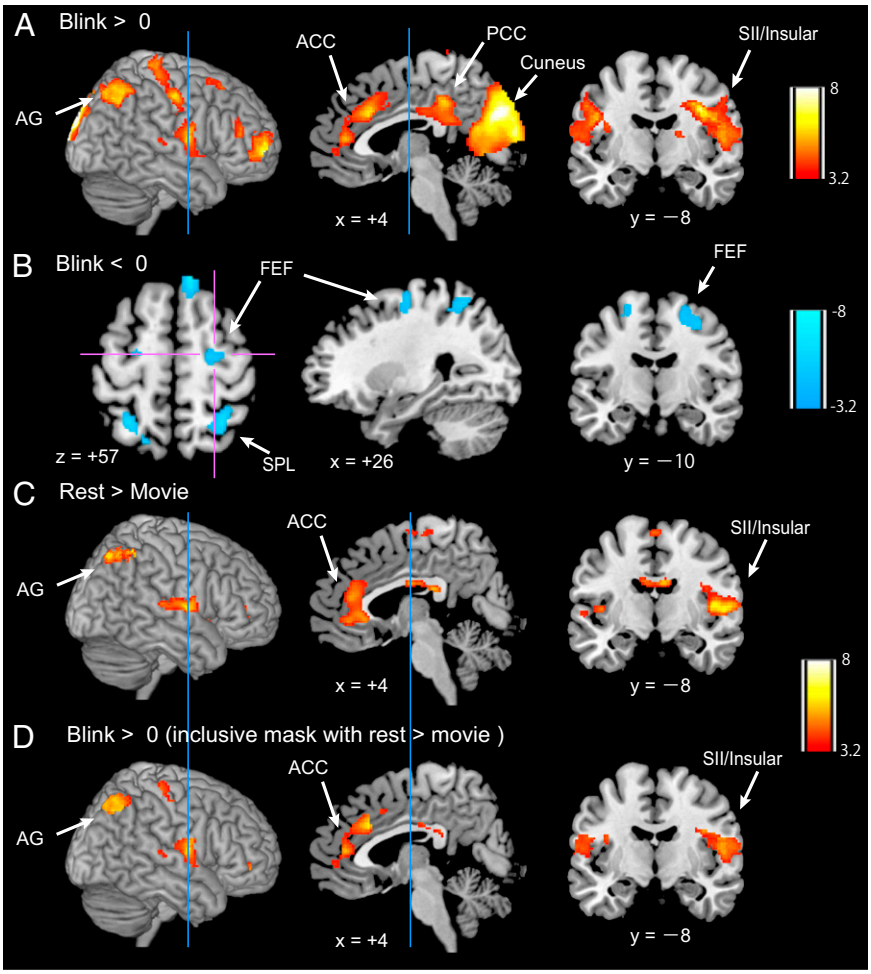

Fig. 1. Blink-related cortical activation and deactivation. (*A* and *B*) Areas with significant blink-related activation (*A*) and deactivation (*B*). (*C*) Distribution of the resting state network that exhibited significantly greater activation during the rest blocks relative to the movie blocks. (*D*) Areas of blink-related activation masked by resting state activation ($P < 0.05$, uncorrected). Note that the blink-related activation in the AG, ACC, and SII/Insular cortex survived, but the activation in the cuneus disappeared. The threshold of significance was set to $P < 0.005$ (voxel level, uncorrected), and the extent of the cluster size (k) was > 10. Numbers in the color bars show t statistics. Similar areas showed significant blink-related activation and deactivation with a more strict threshold ($P < 0.001$, uncorrected for voxel level, and $P < 0.05$, corrected for the cluster level), when we combined data from experiments 1 and 3 (20 participants in total; Fig. S1).

this activation was mainly caused by the change of luminance due to the closure of the eyelids.

It may be worth noting that activations in the superior colliculus, the middle temporal gyrus, the superior temporal sulcus, the precentral gyrus, and the inferior frontal gyrus were suppressed after an eyeblink compared with activations after a blackout (Fig. 3*C* and Table S3). We always notice blackouts, but the visual interruption of spontaneous eyeblinks is seldom noticed. The suppression of these cortical areas, constituting the so-to-speak ventral attention network (9), makes us unaware of blackouts caused by eyeblinks.

Discussion

This study reports momentary cortical activation in the DMN with reciprocal deactivation in the dorsal attention network in close relation to the onset of spontaneous eyeblinks. The reciprocal changes in the two networks have not been reported in previous studies of the neural correlates of eyeblinks (15–20). We suggest two critical differences that may explain the activation of the DMN in response to each eyeblink in the present study. First, eyeblinks were generated unconsciously in the present study, whereas eyeblinks were generated intentionally in previous studies. Therefore, activations in previous studies were predominantly observed in regions that are related to intentional motor generation (15, 16, 18). However, these areas were not activated in the present study. We infer that the DMN would be activated by natural unconscious blinks but not intentional eyeblinks. Second, the participants attentively viewed videos in the present study, but participants in previous studies viewed static crosses or simple visual stimuli, such as a checkerboard pattern (17, 19, 20). The attentional level of the participants should have been higher in the present study because the videos contained rich visual and social information that changed dynamically over time and left room for attentional disengagement. In contrast, the level of attention in previous studies would have been low and left little room for attentional disengagement or additional activation of the DMN.

Previous fMRI studies on event segmentation, which is the cognitive operation of constructing temporal boundaries between epochs in an ongoing narrative (see ref. 21 for review), have observed responses in the ventral and/or dorsal attention networks (22, 23). This observation raises the concern of why eyeblinks, which are associated with "implicit breakpoints" (3), do not activate these attention networks because the notions of implicit breakpoints and event segmentation appear similar in concept.

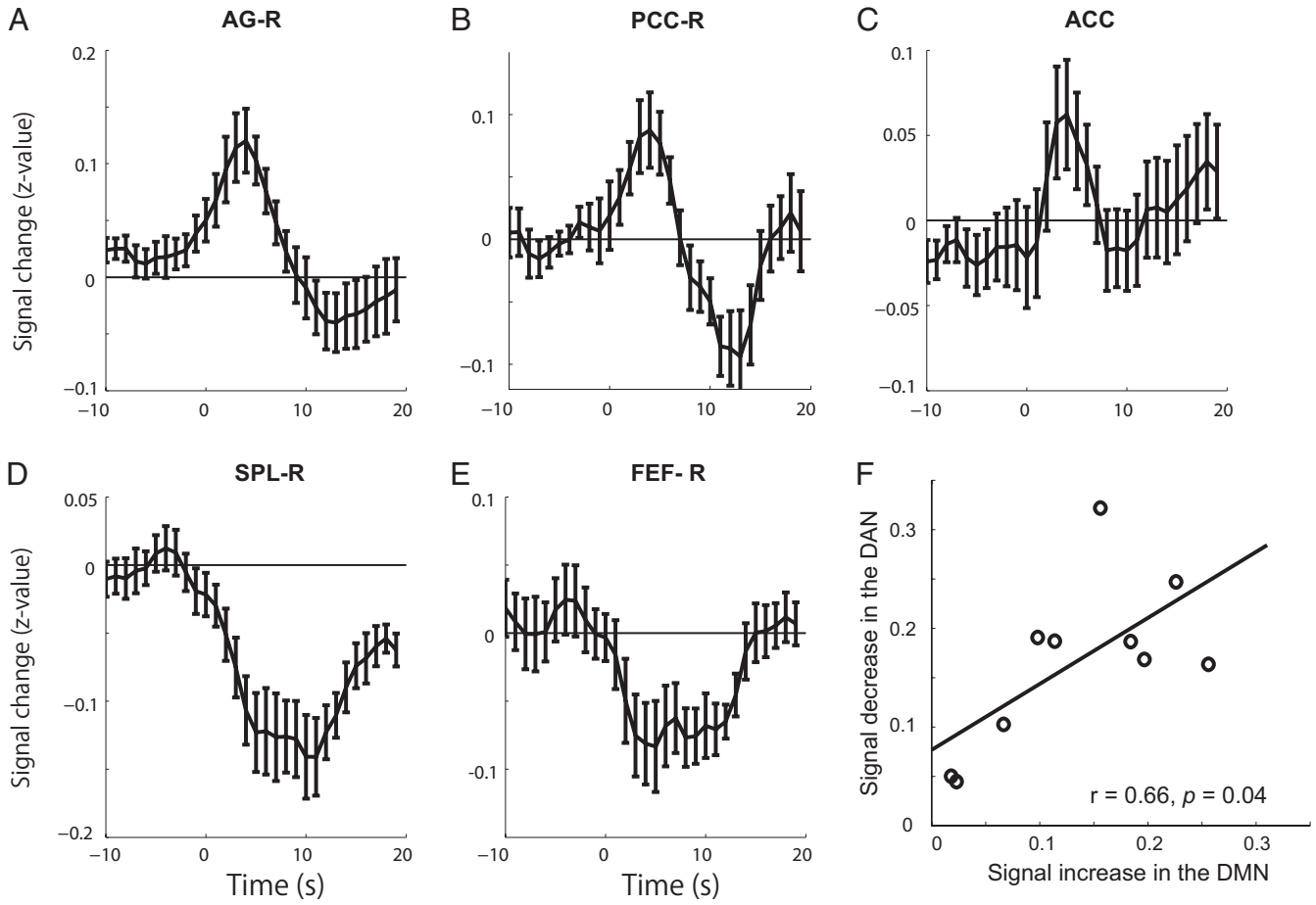

Fig. 2. Time courses of blink-related activations and deactivations. (*A*–*C*) The mean time courses of activations (across 10 participants) at three peak voxels in three typical areas in the DMN: the right AG [*A*; AG-R (50, −62, 44), the Montreal Neurological Institute (MNI)], the right PCC [*B*; PCC-R (8, −31, 30)], and the ACC [*C*; (−4, 43, 5)]. Error bars show the SEM. (*D* and *E*) The mean time courses of deactivation at two peak voxels in the dorsal attention networks (DAN): the right superior parietal lobule [*D*; SPL-R, (32, −44, 54)] and the right frontal eye field [*E*; FEF-R, (22, −9, 56)]. (*F*) The mean of the decrease in the DAN plotted against the mean of the increase in the DMN for each participant ($n = 10$). The mean decrease was calculated from the two peak values in the right SPL and FEF, and the mean increase was calculated from the three peak values in the right AG, PCC, and ACC.

Event segmentation in the previous literature has been based on "perceptually salient event boundaries," which are defined by participants by the pushing of a button (22). However, the MRI signals in the present study were aligned to the onset of each spontaneous eyeblink that went unnoticed by the participants. Eyeblinks occurred synchronously across participants at a moment when the salient events were most unlikely to occur, such as the disappearance of the main character (3). Therefore, we infer that the timings for event segmentation differed from the implicit breakpoints that are represented by spontaneous eyeblinks.

Posner et al. (24) proposed that the control of attention involves several distinct operations: attentional disengagement, shift, and allocation. Many previous studies have demonstrated that activation in the dorsal visual attention network serves the shift and allocation of endogenous visual attention (9). In contrast, the neural mechanism underlying the disengagement of visual attention has not been elucidated. Our results suggest that not only the inhibition of the dorsal attention network but also the momentary activation of the DMN serves the process of disengagement, and that this process is triggered by spontaneous eyeblinks.

It is generally believed that activity in the DMN is suppressed while attending to the external world (13). Accordingly, activation of the DMN during any cognitive task has been associated with degradation in task performance (25). However, given its key role in the disengagement of attention, repeated momentary activations in the DMN might be an essential process for any cognitive behavior. The causal relationship between spontaneous eyeblinks, momentary activations in the DMN, deactivation in the dorsal attention network, disengagement of attention, and performance in cognitive tasks merits further investigation.

Methods

Participants. Twenty healthy participants (15 male, 5 female, age range 20–24 y) took part in the study. All had normal or corrected-to-normal vision with no history of neurological disorders. Ten participants took part in experiment 1, the other 10 participated in experiment 3, and all 20 participated in experiment 2. Four other participants took part in the study but were excluded from further analysis because of one of the following reasons: (*i*) the rate of eyeblinks was too high (more than 60 per min) in two potential participants, (*ii*) one fell asleep during experiment 1, and (*iii*) one blinked in response to every blackout in experiment 3. The study was approved by the review boards of Osaka University and the National Institute of Information and Communications Technology, and all participants gave written informed consent before participation.

Task. All videos used in this study were taken from the British television comedy "The Best Bits" in "Rowan Atkinson in Mr. Bean 1" (26). To maintain the level of attention, the participants were informed in advance that they had to answer several questions regarding the content of the videos after each experiment. The mean correct score to the questions was very high (96%, ranging from 81% to 100%). In addition, the participants were

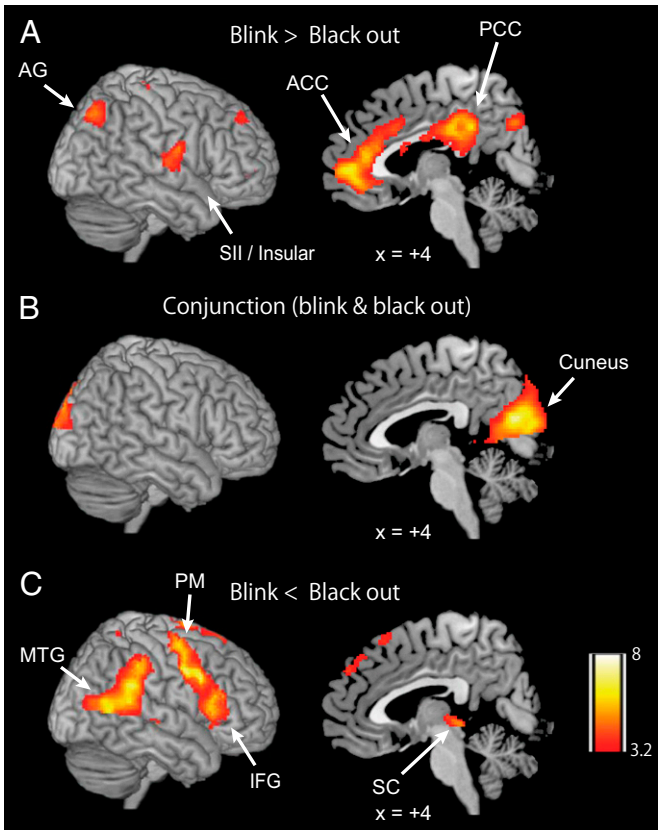

Fig. 3. Comparison of activations evoked by spontaneous eyeblinks and physical blackouts. (*A*) Regions activated more strongly by eyeblinks than by blackouts. (*B*) Regions activated by both eyeblinks and blackouts. Conjunction null (blink > 0 and blackout > 0) was tested. (*C*) Regions activated by blackouts more strongly than by eyeblinks. The threshold of significance was set to $P < 0.005$ (voxel level, uncorrected), and the extent of cluster size (k) > 10. IFG, inferior frontal gyrus; MTG, middle temporal gyrus; PM, premotor cortex; SC, superior colliculus (Fig. S2).

informed that their eye movements would be measured while watching a video stimulus. They were not told that their blinking was being measured.

In experiment 1, one of four video clips was continuously presented to each participant for 480 s during each run of scanning to examine blink-related cortical activations and deactivations while viewing the videos. Each participant was scanned four times with four different video clips.

In experiment 2, a block design was used to identify the brain regions showing greater activation at rest (rest block) than while viewing videos (movie block). During each movie block, participants viewed the video for 30 s. During each rest block, the participants were simply instructed to maintain fixation on a cross for 30 s. Each session began with a rest block, and seven movie blocks and seven rest blocks alternated thereafter (total 450 s). The mean blink rate during the movie block (27.0 ± 7.1 per min, mean ± SEM) was not significantly different from the rest block (22.4 ± 5.9). Each participant was scanned twice with two different video clips.

In experiment 3, videos with intermittent blank screens were continuously presented for 480 s to compare blank-related responses with blink-related responses. The visual stimuli were the same as those in experiment 1, except that blank screens, each lasting for five frames (165 ms), were inserted in the stimuli at pseudorandom intervals with a mean frequency of 9.4 per min. The interval distribution was derived from data collected from a particular participant in experiment 2. Each participant was scanned four times with four different videos.

Data Acquisition. Stimulus presentation was controlled by using Presentation software (Neurobehavioral Systems) on a Dell computer running Microsoft Windows XP. Visual stimuli were projected onto a screen at the back of the magnet's bore that participants viewed through a mirror. The screen display subtended ~9.5° × 7.1° of the visual angle. Structural images for each participant were collected by using a T1-weighted 3D MP-RAGE sequence on a Siemens 3-Tesla whole-body scanner [repetition time (TR) = 2 s, echo time (TE) = 4.38 ms, flip angle = 8°, field of view 256 mm, resolution 1 × 1 × 1 mm]. Functional images were collected by using a gradient echo, echo-planar sequence (TR = 1.5 s, TE = 30 ms, flip angle = 70°, isotropic nominal resolution: 3 mm, 25 adjacent contiguous slices with 0.5 mm gap, thickness 3.5 mm). The slice positions were located to cover the entire prefrontal and parietal cortices. Each participant completed four runs in experiment 1 (346 scans per run; 13 before, 320 during, and 13 scans after the task period), two runs in experiment 2 (300 scans per run), and four runs in experiment 3 (346 scans per run). The first 10 images of each run were discarded.

During scanning, pupil diameter and eyelid position were monitored continuously by using an infrared video eye-monitoring system with a sampling rate of 220 Hz (NAC Image Technology). Each eyeblink was initially detected automatically according to criteria in the time course of pupil size changes that were characterized by a combination of a rapid decrease of pupil size followed by an increase within 500 ms. Each onset time was subsequently confirmed individually by the experimenter.

Data Analysis. We used SPM8 (Wellcome Trust Centre for Neuroimaging) 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 based on voxelwise signal changes by using the general linear model with the standard hemodynamic function of SPM and random effects analysis. The threshold of significance was set to $P < 0.005$ (voxel level, uncorrected) and the extent of cluster size (k) > 10 (27).

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

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