Spontaneous eyeblinks during breaking continuous flash suppression are associated with increased detection times

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An eyeblink has a clear effect on low-level information processing because it temporarily occludes all visual information. Recent evidence suggests that eyeblinks can also modulate higher level processes (e.g., attentional resources), and vice versa. Despite these putative effects on different levels of information processing, eyeblinks are typically neglected in vision and in consciousness research. The main aim of this study was to investigate the timing and the effect of eyeblinks in an increasingly popular paradigm in consciousness research, namely breaking continuous flash suppression (b-CFS). Results show that participants generally refrain from blinking during a trial, that is, when they need to detect a suppressed stimulus. However, when they do blink during a trial, we observed a sharp increase in suppression time. This suggests that one needs to control for blinking when comparing detection times between conditions that could elicit phasic changes in blinking.

Introduction

It has been estimated that eyeblinks block visual input up to about 10% of our waking time (Nakano, Yamamoto, Kitajo, Takahashi, & Kitazawa, 2009). Yet, this is seldom noticed in everyday life. This lack of awareness of the temporary suppression of visual information could partly stem from the fact that spontaneous eyeblinks are not uniformly distributed in time. Eyeblinks tend to happen at implicit breakpoints in information processing, e.g., when listening to a speaker who pauses during a speech (Nakano & Kitazawa, 2010), at the end of a sentence, or when turning over a page while reading (Hall, 1945; Orchard & Stern, 1991). The observation of such temporal relationships between blinking and information processing has led to the suggestion that spontaneous eyeblinks reflect cognitive processing (Lee, Ojha, Kang, & Lee, 2015; Nakano, Kato, Morito, Itoi, & Kitazawa, 2013; Pivik & Dykman, 2004; Siegle, Ichikawa, & Steinhauer, 2008; Sirevaag et al., 1999; Van Bochove, Van Der Haegen, Notebaert, & Verguts, 2013).

In vision research, both the temporal occlusion of visual information caused by blinking and its relation to attention need to be carefully considered in any experimental design. Earlier work on the perception of visually ambiguous figures, for example, revealed that continuous presentation of the pattern is required to initiate perceptual switching. Intermittent presentations, in which the pattern was briefly removed, stabilized perception, that is, decreased the switch rate between the ambiguous figures (Leopold, Wilke, Maier, & Logothetis, 2002). It could thus be expected that blinking during the continuous presentation of ambiguous figures—which can be taken to be functionally

Citation: Van Opstal, F., De Loof, E., Verguts, T., & Cleeremans, A. (2016). Spontaneous eyeblinks during breaking continuous flash suppression are associated with increased detection times. *Journal of Vision*, *16*(14):21, 1–10, doi:10.1167/16.14.21.

doi: 10.1167/16.14.21 Received May 27, 2016; published November 30, 2016 ISSN 1534-7362

similar to intermittent presentation—also decreases the perceptual switch rate. Indeed, when looking at ambiguous figures, a perceptual switch is often preceded by a reduction in the frequency of eyeblinks (Ito et al., 2003; Nakatani & Van Leeuwen, 2005), and a negative correlation between an individual's eyeblink rate (EBR) and switch rate has been observed (Nakatani & Van Leeuwen, 2005). Further, in studies that use binocular rivalry instead of ambiguous figures, a relation between blinking and perceptual switches has also been found. In contrast to studies using ambiguous figures, however, the occurrence of eyeblinks before a switch increased rather than decreased in binocular rivalry (Kalisvaart & Goossens, 2013). One possible interpretation of this result is that in the case of binocular rivalry, eyeblinks could elicit perceptual switches between the eyes rather than coincide with or result from them (Kalisvaart & Goossens, 2013).

The hypothesis that eyeblinks could modulate a perceptual switch between the eyes is of critical importance for studies in which the occurrence and/or time of this switch constitutes the dependent variable. Whereas this is clearly the case in binocular rivalry and for ambiguous figures, it is also true in an increasingly popular paradigm to study visual consciousness, namely breaking continuous flash suppression (b-CFS; Jiang, Costello, & He, 2007). This b-CFS is a variant of binocular rivalry in which a dynamic noise pattern is presented to one eye, while the other eye is presented with a static target stimulus. The dynamic presentation to one eye suppresses the conscious visibility of the static target stimulus. The b-CFS enables the presentation of a visual stimulus below the threshold for conscious perception for a long duration without suppressing the unconscious processing of the identity of the target stimulus (Tsuchiya & Koch, 2005). In b-CFS, participants need to respond as fast as possible when the suppressed stimulus breaks through suppression. Their response time is then typically used to make inferences about unconscious processing (e.g., De Loof, Poppe, Cleeremans, Gevers, & Van Opstal, 2015; Mudrik & Koch, 2013; but also see Stein, Kaiser, & Peelen, 2015). While the limits of b-CFS have been abundantly discussed recently (e.g., Gayet, Van der Stigchel, & Paffen, 2014; Stein, Hebart, & Sterzer, 2011), the potential effect of eyeblinks on b-CFS has not yet been considered. This is all the more surprising given that if eyeblinks can elicit a perceptual switch from one eye to the other, they could also modulate the timing of the break through suppression and hence constitute a potential confound in any b-CFS paradigm. It is well known, for instance, that EBR changes depending on cognitive load (Fukuda, 1994, 2001; Ohira, 1996) or on the availability of information processing resources (Ichikawa & Ohira, 2004). Therefore, studies comparing b-CFS between conditions with unequal load (e.g., when studying the relation between working memory and visual consciousness; De Loof et al., 2015; experiments 1 and 5 of Gayet, Paffen, & Van der Stigchel, 2013), or with differences in processing resources (e.g., when comparing cued versus noncued conditions; Lupyan & Ward, 2013; Stein, Thoma, & Sterzer, 2015), could be potentially confounded by differences in blinking behavior between conditions. It is not always clear, however, whether participants are explicitly instructed to refrain from blinking during a b-CFS trial.

In light of these considerations, the main goal of the present study was to explore the time course of blinking during a b-CFS trial and to clarify the potential effect of eyeblinks on b-CFS. To do so, we registered the timing of spontaneous blinks during a b-CFS experiment and probed how blinking influences detection performance. If blinks indeed elicit perceptual switches between the eyes, a close temporal relationship between a blink and the conscious experience of the stimulus is expected, with a blink occurring briefly before the break through suppression. If, on the other hand, blinking during the presentation of the stimulus decreases the switch rate (e.g., Ito et al., 2003; Leopold et al., 2002; Nakatani & Van Leeuwen, 2005) and temporally occludes all visual information, the time it takes for a stimulus to break through suppression would increase when a blink occurs during a b-CFS trial. Finally, we also investigated if a blink before the start of a trial, i.e., during the intertrial interval, influences breakthrough time. Such preblinks, indeed, could initiate attentional preparation to enhance performance on the upcoming trial (Lee et al., 2015; Nakano et al., 2013; Siegle et al., 2008; Sirevaag et al., 1999).

A secondary aim of this study was to investigate the relationship between individual differences in EBR and b-CFS. Recent PET research suggests a close link between dopamine receptor density in the striatum and visual consciousness. In one study, a correlation was found between the size of the attentional blink and receptor density, suggesting that striatal activity is related to the detection of a visual stimulus (Slagter et al., 2012). Another PET study demonstrated that striatal dopamine receptor density correlates with detection performance in a visual masking task (Van Opstal et al., 2014). Here, both objective classification and subjective visual experience of a masked stimulus were related to striatal receptor density, indicating that the availability of visual information for conscious processing (e.g., in working memory) depends on striatal activity. In the current study, we further investigated the relation between striatal activity and visual detection performance by using b-CFS as a measure for visual detection and by using EBR as a proxy for striatal dopamine receptor density (e.g., Groman et al., 2014; Karson, 1983). If dopamine receptor density is related to making visual information available for conscious processing, one would expect that an individual's EBR correlates with the average time it takes for the person to become aware of the suppressed stimulus.

Methods

Participants

Twenty-seven undergraduate students (eight males, 19 females; mean age: 23.7 years) participated in this study. Exclusion criteria for participating were (a) prior history of neurological or psychiatric disorders, (b) wearing spectacles, and (c) illegal substance use. All participants gave informed consent prior to the experiment and were naive about the purpose of the experiment. Participants were paid 10 Euros for their participation. Because of missing triggers in the recordings caused by technical issues with the EOG-system, the data of seven participants could not be analyzed. The final sample therefore consisted of 20 participants.

Apparatus and stimuli

The stimulus set consisted of ten pictures of Caucasian faces from the Face Database of the Park Aging Mind Laboratory (five males, aged 19–79; Minear & Park, 2004). All pictures ($3.6° \times 3.6°$ visual angle) were luminance scaled to avoid additional luminance-based variation in response times (RTs). Twenty Mondrian masks were created ($8.8° \times 8.8°$ visual angle), consisting of squares with a width and height ranging from 0.7° to 3.2° visual angle in all possible RGB palette colors. Stimuli were generated using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) in MATLAB (MathWorks) and were shown on a 19 inch monitor (Samsung Syncmaster B1940; screen resolution: 1280×1024; refresh rate: 60 Hz). The screen was divided into a left and a right half. At the center of each half of the screen, an image display extended over an $8.8° \times 8.8°$ visual angle square that was surrounded by a checkerboard frame to facilitate binocular fusion (checkers measuring $0.95° \times 0.95°$ visual angle). The target stimulus was presented at 2.2° above or below the center of the image display.

Procedure

Prior to the experiment, ocular dominance was determined with the standard Porta test, i.e., by aligning a finger with a distant point under binocular view and seeing how it matches with monocular view. For the main experiment, participants were seated about 60 cm from the screen and were asked to wear a pair of stereoscopic mirror goggles (http://www.nvp3d.com). These mirror goggles ensure that the image presented on the left side of the screen is visible for the left eye only, and the image on the right side of the screen for the right eye only, and that they are merged into one visual percept through binocular fusion (see Figure 1). To further prevent the possibility that information from the left/right hemifield could be spotted by the right/left eye, a black screen was placed between both eyes, perpendicular to the screen.

A trial started with the presentation of the Mondrian masks at a rate of 10 Hz on the image display of the dominant eye. With the onset of the Mondrians, the stimulus was presented on the image display of the nondominant eye. However, while the Mondrian masks are immediately presented at full contrast, stimulus presentation was progressively faded from zero contrast (i.e., no stimulus) to full contrast over a period of 6 s, so as to prevent an immediate breakthrough (Jiang et al., 2007). The stimulus is presented until the participants respond, and could appear at the top or bottom of the image display. Participants were instructed to detect the stimulus, and to press the up- or down-arrow of the keyboard corresponding to the location of the face in the image display (i.e., at the top or bottom of the display respectively). The response of the participants thus reflects the moment at which the stimulus breaks through suppression. As soon as a key was pressed, the trial was stopped, and the stimulus and Mondrian masks were removed from the screen. The intertrial interval (ITI) was set to 800 ms. Before the main experiment, participants performed a short training session until they indicated sufficient familiarity with the procedure. A total of 180 trials were then presented during the main experiment, which lasted about 15 min.

Eyeblink measurements

A BioSemi ActiveTwo system (BioSemi Inc., Amsterdam, The Netherlands) was used to record the eyeblinks during the experiment. Eyeblinks were recorded with two electrodes, one placed below and one above the right eye of the participant. Electrodes over the left and right mastoids were used as reference. The ground electrodes were placed on the right arm. Because the EBR is known to be stable during daytime but increases in the evening (from 8:30 p.m. onwards; Barbato et al., 2000), data were always collected before 6:00 PM. Participants were told that the electrodes served to register eyeblinks during the experiment. They were asked to blink freely during the experiment,

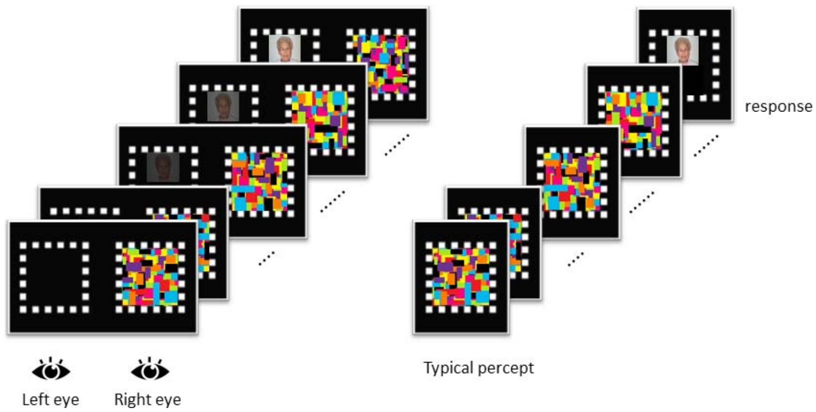

Figure 1. The left side of the figure presents the outline of a typical b-CFS trial. The trial starts with the presentation of a Mondrian mask to the dominant eye (here, the right eye). Together with the onset of the Mondrians, the stimulus is presented to the nondominant eye at zero contrast. While a different Mondrian mask is presented every 100 ms (i.e., at a rate of 10 Hz), the stimulus slowly fades in to full contrast. The typical percept experienced by the participants is presented on the right. The trial ends when the stimulus breaks through the suppression of the Mondrian masks and the participant has pressed the up or down key.

but were instructed that it was not allowed to cheat by continuously closing the one eye to which the Mondrian masks were presented.

Data analysis

The vEOG data were down-sampled to 100 Hz and filtered (band-pass filter ranging from 1 to 20 Hz). Eyeblinks were detected by calculating the average and standard deviation of the signal for the complete duration of the experiment. Whenever the signal exceeded one standard deviation above the average, it was marked as the onset of a potential eyeblink. A further constraint for an event to be labeled as an eyeblink was that the voltage should increase at least 100 μV within 200 ms (e.g., Colzato, Slagter, Spapé, & Hommel, 2008). The time of the eyeblink was set at the peak amplitude following the marked onset. After performing this protocol on all data, visual inspection of the data and the marked eyeblinks was then carried out to detect false positives (e.g., related to, for example, eye movements or spikes) or misses, by looking at the typical bell-shaped waveform of eyeblinks.

To formally investigate the temporal relationship between an eyeblink and a response, we looked at the cross-correlation between the binary time series of eyeblinks and responses. We therefore converted the vEOG data into a binary times series in which ones and zeroes marked the occurrence or absence of a blink respectively. For the response time series, ones (zeroes) marked the presence (absence) of a response. Similar to cross-correlation analyses in binary neuronal spike time analyses (e.g., Luccioli, Ben-Jacob, Barzilai, Bonifazi, & Torcini, 2014), the cross-correlations for the time series were calculated as follows:

$$C_{ab}(\tau) = \frac{\sum_{t=\tau}^{T} a_{(t+\tau)} b_t}{\min\left(\sum_{i=1}^{T} a_i, \sum_{k=1}^{T} b_k\right)} \quad (1)$$

in which a and b represented the time series for eyeblinks and responses respectively, T the total duration of the time series (in ms), and τ the latency between the time series with a negative (positive) value of τ indicating that the eyeblink time series is shifted backwards (forwards) in time relative to the response time series. The value of $C_{ab}(\tau)$ represents the strength between the two time series. A maximum value of $C_{ab}(\tau)$ at a negative (positive) value of τ indicates that a blink occurred approximately τ ms before (after) the response. Based on prior research that suggested that blinking in a Stroop task often occurs about 210 ms prior to the response (Oh, Han, Peterson, & Jeong, 2012), and on the ITI that was set to 800 ms in the current experiment, latencies within a period of 800 ms before and 800 ms after a response were investigated (i.e., $-800 \leq \tau \geq 800$).

Results

Trials with incorrect responses (1.1 % of the data), and trials with RTs larger than 10 s (1.1 %) were removed from further analysis. The mean RT to detect the stimulus was 2153 ms ($SD = 755$ ms).

Temporal relation between an eyeblink and response time

The vEOG were epoched in segments of 1600 ms centered on a response and averaged per participant.

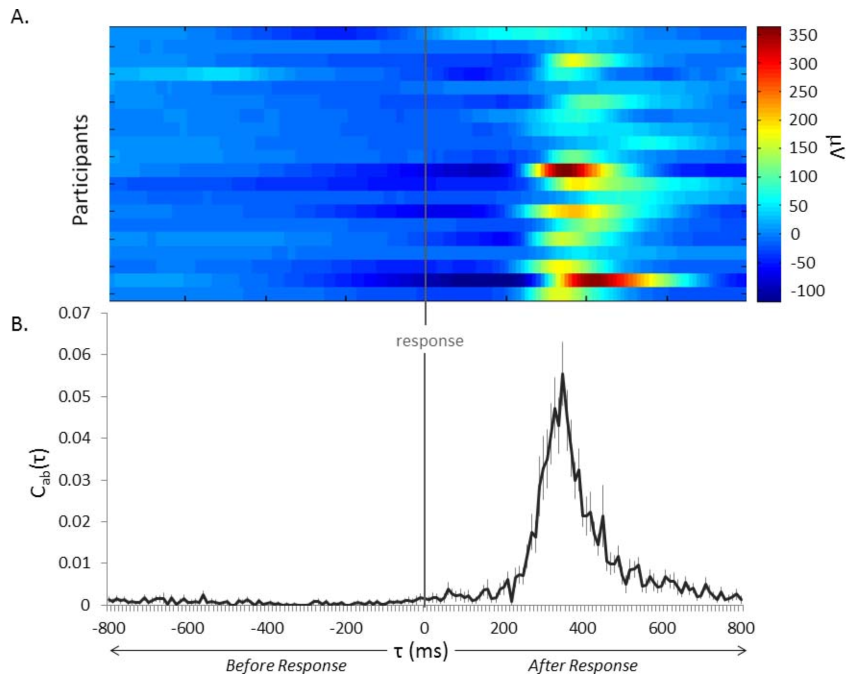

Figure 2. (A) Shows the average vEOG waveform for a period of 800 ms before and after the response. Every line in the heat map represents the average of a single participant. The highest voltages are consistently observed in the post-response period. (B) Illustrates the average cross-correlogram for the temporal correlation between the response and eyeblink time series. The cross-correlation peaks at a positive value of $\tau = 350$ ms, indicating that a blink tended to follow a response. Error bars denote the squared error of the mean.

As can be seen in Figure 2A, this revealed that the highest amplitudes in the vEOG signal were reached after a response was recorded, i.e., after the detection of the suppressed stimulus, during the intertrial interval. Results from the cross-correlational analysis furthermore showed that the highest value of $C_{ab}(\tau)$ was at a positive value of τ for all participants, indicating that eyeblinks tended to occur about 350 ms after the response (Figure 2B).

Trial-by-trial effects of eyeblinks on reaction times

Whereas the previous analysis showed that participants mostly blinked after they gave a response, there were occasional trials in which a blink occurred during the CFS trials. The average number of trials with no blink (mean = 51), a blink during the trial (mean = 30), and a blink during the ITI (mean = 113) are presented in Figure 3A. To further investigate if a blink affected RTs because of a change in switch rates or the temporal occlusion from visual information, we looked at those trials where an eyeblink did occur before the response, and investigated the extent to which the occurrence of an eyeblink affected the RT on that trial. Likewise, we also investigated if an eyeblink that occurs during the ITI would initiate attentional preparation and hence influence the RT in the upcoming trial. We therefore performed a multiple regression analysis according to Lorch and Myers's (1990) individual equation method. Here, regression weights are obtained for each factor in the analysis on the subject level; these regression weights are subsequently tested at the group level (i.e., a simple paired t test against zero). The two factors were the absence (0) or presence (1) of a blink during the ITI, and the absence (0) or presence (1) of a blink during the trial. Because one participant never blinked during a trial, the analyses for the effect of blinks

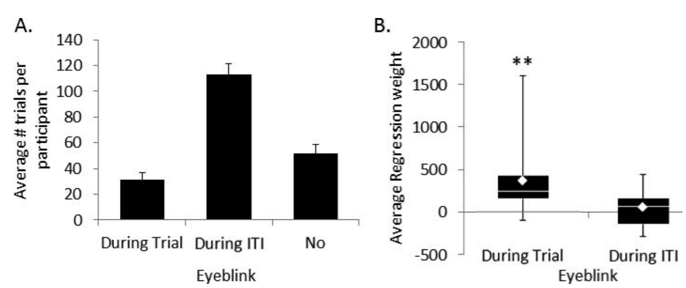

Figure 3. (A) Shows the average number of trials in which participants blinked during the trial, during the intertrial interval (ITI), or did not blink. (B) Boxplots of the results from the regression showing that a blink during the ITI was not related to the RT on the trial following the ITI. In contrast, eyeblinks occurring during a trial are related to higher RTs.

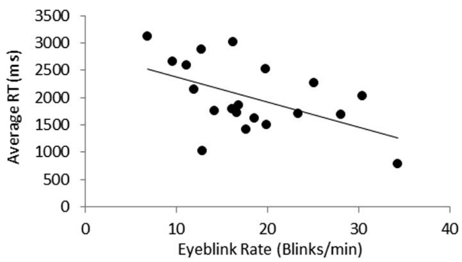

Figure 4. A significant negative correlation is found between the overall EBR and average RT. An individual with a higher EBR is on average faster to detect the suppressed stimulus.

during a trial and during the ITI were performed on only 19 participants.[1]

Results of the regression analyses showed that a blink during the ITI had no effect on RT of the next trial, average $\beta = 35$, $t(18) = 0.74$, $p = 0.47$. In contrast, there was a very strong relation between the occurrence of a blink during a trial and RT, average $\beta = 388$, $t(18) = 3.95$, $p = 0.0009$ (Figure 3B), indicating that the stimulus was detected on average 388 ms later when a blink occurred during the trial compared to when no blink occurred during the trial. Wilcoxon rank sum tests revealed very similar results. No significant effect is observed when contrasting the betas for the intertrial interval blinks to zero, $Z = 1.47$, $p = 0.14$, but a very strong effect is observed when contrasting the beta values from the trial blinks, $Z = 4.43$, $p < 0.001$. A direct comparison between the two types of trials with a Wilcoxon rank sum test also showed a significant difference, $Z = 3.21$, $p = 0.0013$.

To investigate the possibility that the relation between blinking during a trial and longer RTs was caused because of fatigue to the eye, we looked at the time of blinking during a trial. When a blink during a trial would occur at the end of the trial, this could indicate that long RTs caused participants to blink rather than that a blink caused an increase in RTs. Results showed that the average blink occurred 106 ms ($SD = 46$ ms) after the onset of the trial, indicating that the blink during a trial was not caused by the long duration of the trial.

Relation between EBR and visual detection

The relationship between EBR and detection performance was investigated with a between subjects correlation analysis on the individual's EBR and average RTs. Because the previous analysis showed that RTs were affected when blinks occurred during the trial, only trials without a blink were used for this analysis. The EBR was calculated as the average number of blinks per minute, measured for the complete duration of the experiment.

The EBR ranged between 6.8 and 34.3 blinks per minute ($M = 18.1$; $SD = 7.1$), similar to what is typically found with the spontaneous EBR (e.g., Colzato et al., 2008; Oh et al., 2012). Results showed a significant negative correlation between EBR and RT, $r = -0.52$, $p = 0.020$, indicating that participants with a higher EBR exhibited faster RTs (Figure 4).[2] Whereas at first sight this might seem to contradict the earlier result showing that a blink during a trial increased RTs, this is not necessarily the case because blinking occurred mainly during the ITI, which did not affect RTs.

Although the participants received no instructions with respect to blinking behavior, it could be argued that blinking during the experimental task is different from spontaneous blinking which is generally measured while participants are not performing any task. To investigate how a spontaneous EBR relates to the EBR during task performance, we investigated blinking behavior from two other experiments in which eyeblinks were measured both during and outside task performance. Because these experiments were designed for completely different purposes, only the results about the relation between spontaneous EBR and the EBR during task performance are discussed. In a first experiment, the spontaneous EBR, measured while participants ($n = 17$) looked at a fixation cross for 3 min, strongly correlated with the EBR measured during the experiment, $r = 0.78$, $p < 0.001$. When these participants returned one week later for a similar follow-up experiment, again a significant correlation was observed, $r = 0.67$, $p < 0.005$. This correlation was also observed in another similar experiment in which the spontaneous EBR was measured for 5 min prior the experiment, $r = 0.89$, $p < 0.001$. This close relation between the spontaneous EBR measured outside and during task performance suggests that the EBR as measured in the current experiment reflects the spontaneous EBR.

Discussion

In this study we investigated the effect of eyeblinks on breaking continuous flash suppression (b-CFS). Results showed a temporal correlation between the moment an eyeblink occurred and the timing of the break through suppression. However, in general, blinks were more likely to follow a response rather than to precede it. Participants appeared to spontaneously refrain from blinking during a b-CFS trial. Further analysis revealed that blinking before the onset of the next trial (during the ITI) was unrelated to RTs on the upcoming trial. In contrast, when an eyeblink did occur during a trial, this had a direct relation with RTs: The time it takes to detect the suppressed stimulus increased when participants blinked during the trial.

These results indicate that a spontaneous eyeblink does not directly elicit a perceptual switch from one eye to the other during b-CFS. Indeed, such a process would have decreased RTs after a blink. Whereas this appears to contradict earlier results in which an increase in blinking was observed prior to a switch in a binocular rivalry experiment (Kalisvaart & Goossens, 2013), it is important to note that in that study, the increase was only observed for switches from the nondominant to the dominant eye and not from the dominant to the nondominant eye. In our study, similar to most experiments that use b-CFS, the target stimuli were consistently presented to the nondominant eye only. Our results are therefore consistent with results from binocular rivalry and allow concluding that it is highly unlikely that spontaneous eyeblinks cause breaks through suppression if the target stimuli are presented to the nondominant eye in a b-CFS experiment.

Although an eyeblink may not directly elicit a break through suppression, the strong relation between the presence of a blink during a b-CFS trial and breakthrough time is a strong indication that it is necessary to carefully control eyeblinks in b-CFS experiments. Interestingly, the observed increase in RT caused by an eyeblink (i.e., 388 ms) closely matches the duration of a spontaneous eyeblink (about 340 ms as measured with electromyographic recordings of the orbicularis oculi muscles; VanderWerf, Brassinga, Reits, Aramideh, & Ongerboer de Visser, 2003).

The observed increase in the RT when a blink occurs during a trial is perhaps not so surprising. First, it resonates with findings with ambiguous figures in which intermittent presentations stabilize perception (Leopold et al., 2002). Because a blink during a trial is similar to an intermittent presentation, it can be expected that a perceptual switch between the eyes is delayed. In contrast to binocular rivalry, however, the dynamical presentation of the masks in CFS could also be regarded as involving intermittent presentation (although there is no real absence of a stimulus), and it could be questioned if a blink would have any additional effect. Furthermore, a blink might not be subjectively experienced as an intermittent perception and could therefore be different from an intermittent presentation. A more plausible explanation for this observation might be that a blink causes temporary occlusion of visual information, and thereby momentarily halts the accumulation of such information. The increase in detection time would then merely be a consequence of the absence of information accumulation during the blink. The observation that a blink during a trial increases the RT with a duration that is similar to the duration of a blink further supports this explanation. Irrespective of the mechanism that causes the increase in b-CFS time, however, it should be clear that carefully controlling for eyeblinks is essential in b-CFS experiments.

The need to control for eyeblinks is particularly acute in cases where there is a reason to assume that blinking behavior could be different between conditions. It is, for example, known that eyeblink bursts follow high cognitive load (Fukuda, 1994, 2001; Ohira, 1996) or information processing (Ichikawa & Ohira, 2004). Differences in b-CFS between conditions in which these factors are not matched (e.g., cued versus noncued, or load versus no-load) could therefore be contaminated by blinking. Similarly, phasic changes in EBR caused by reward, effort anticipation (Peckham & Johnson, 2015), or mood changes induced through emotional stimuli (Akbari Chermahini & Hommel, 2012) could affect detection times in b-CFS experiments. The delayed break through suppression for emotional compared to nonemotional words may be caused by phasic increases in blinking when emotional words are presented (Prioli & Kahan, 2015; Yang & Yeh, 2011). Whereas we do not want to claim that the results of the studies referred to above are all caused by confounding effects of eyeblinks, it is noteworthy that the size of the effect of an eyeblink on reaction times in our experiment is in the same order of magnitude as the effects found in many of these studies (i.e., about 250–500 ms).

Our results also show a significant negative correlation between EBR and break through suppression, indicating that the higher the EBR of a participant, the smaller the overall RT for that participant. This result does not necessarily contradict the finding that a blink during a trial increased RTs because the blinking occurred mainly during the ITI. The observed within-participants increase in suppression duration when a blink occurs during the trial is relatively independent from the between-participants negative correlation between EBR and suppression duration. The observed relation between the EBR and average RT is reminiscent of a study in which the relation between the EBR and the size of the attentional blink was investigated (Colzato et al., 2008). Colzato and colleagues (2008) showed that individuals with a higher spontaneous EBR generally showed a smaller attentional blink, indicating better visual detection. Similarly, the results of the present study also show that detection performance of the suppressed stimulus is better for individuals with a higher EBR. One way to understand the relation between EBR and detection performance is through the relation between spontaneous EBR and dopamine D2 receptor density in the striatum. According to earlier work with patients (e.g., Karson, 1983) and to a recent study with monkeys (Groman et al., 2014), the spontaneous EBR correlates with dopamine D2 receptor density in the striatum. The correlation between EBR and b-CFS time therefore echoes earlier findings with PET in which a relation between D2 receptors in the striatum and visual consciousness was found (Slagter et al., 2012; Van Opstal et al., 2014). It could, however, be argued that the EBR in the present study is not identical to a spontaneous EBR because it was measured during task performance and participants overall refrained from blinking during a trial. Although our results indeed indicate that the timing of blinking is different during task performance compared to spontaneous blinking, it could still be assumed that participants with a high spontaneous EBR also blink more while performing a task, for example during the ITI.

In conclusion, this study showed that eyeblinks during a b-CFS trial increase the time it takes for the stimulus to overcome suppression, and is thus suggestive that eyeblinks need to be carefully controlled when comparing conditions that may elicit differences in blinking behavior. Furthermore, the present study adds to a growing body of evidence that emphasizes the role that dopaminergic pathways into the striatum play in visual awareness.

Keywords: continuous flash suppression, eyeblink, consciousness, visual awareness

Acknowledgments

The authors would like to thank—in alphabetical order—Albert Debeir, Lauriane Hill, Jeromy Hrabovecky, and Antoinette Vandekerckhove for their help in acquiring the data. Filip Van Opstal is a scientific collaborator of the F.R.S.-FNRS (Belgium). EDL is a doctoral researcher at the Fund Scientific Research, Flanders. Axel Cleeremans is a Research Director of the F.R.S.-FNRS (Belgium). This work was partially funded by ERC Advanced Grant RADICAL to Axel Cleeremans.

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Footnotes

[1] Three participants had less than 10 trials during which they blinked. When the analyses were performed without these participants, the same results were obtained: no effect of a blink during the ITI, $\beta = 51$, $t(15) = 0.98$, $p = 0.34$, but a strong effect of a blink during the trial, $\beta = 367$, $t(15) = 3.36$, $p = 0.0043$. Similar results were found with a Wilcoxon rank sum test: no significant effect for the intertrial blinks, $Z = 1.27$, $p = 0.20$, but a strong effect for the blink trials, $Z = 3.85$, $p < 0.001$.

[2] To ensure that the significant correlation was not caused by outlier values, a robust regression method was performed that uses iteratively reweighted least squares with a bisquare weighting function. This also showed a significant correlation, $p = 0.0231$.

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