1 Title:

2 **Boosted visual performance after eye blinks**

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Abstract

We blink more often than required for maintaining the corneal tear film. Whether there are perceptual or cognitive consequences of blinks that may justify their high frequency, is unclear. Previous finding showed that blinks may indicate switches between large scale cortical networks, such as dorsal attention and default-mode networks. Thus, blinks may trigger a refresh of visual attention. Yet, this was not confirmed behaviourally. We tested the effect of blinks on visual performance in a series of rapid serial visual presentation (RSVP) tasks. In Experiment 1, participants had to identify a target digit embedded in a random stream of letter distractors, presented foveally for 60 ms each. Participants blinked once during the presentation stream. In a separate condition, blinks were simulated by shutter glasses. Detection performance was enhanced (up to 15% point increase in accuracy) for targets appearing up to 300 ms after eyeblinks. Performance boosts were stronger for voluntary blinks than artificial blinks. This was replicated for object recognition with naturalistic stimuli (Experiment 2), but not in a numerosity task (Experiment 3), and spatially distributed stimuli (Experiment 4). We conclude that eye blinks lead to attentional benefits for object recognition in the period after reopening of the eyelids and may be used strategically for temporarily boosting visual performance.

Keywords: Eye blinks, Attention, Default Mode Network, Attention Network

Introduction

We blink more often than required for maintaining the corneal tear film. Blink frequencies fluctuate greatly depending on task. For instance, people tend to blink more frequently when they are engaged in a conversation and less during reading (Bentivoglio et al., 1997). These fluctuations of blink frequencies are unlikely due to different requirements for cornea lubrication during different cognitive states. The precorneal tear film starts drying up on average 25 s after a blink (Norn, 1969). This would suggest that 2-3 blinks per minute would be enough to maintain the tear film.

More plausibly, different blink rates reflect different mental processing states. For example, reduced blink frequencies during reading (Bentivoglio et al., 1997) might be attributed to the increased visual bandwidth required for efficient absorption of information. However, the benefits of increased blink frequencies during conversations are less apparent. What could be the benefit of increased blink rates in certain cognitive or perceptual scenarios? Do blinks trigger other physiological responses with consequences for perception or cognition?

Blink frequencies could reflect neural activity in major cognitive neural networks. For example, the Dorsal Attentional Network (DAN) and the Default Mode Network (DMN) — respectively associated with externally motivated attention-demanding tasks (Vanhaudenhuyse et al., 2011) and internal mental processes such as mind wandering (Mason et al., 2007) — are anti-correlated in their activities (Fox et al., 2005). A recent study found eye blinks to be associated with activation of the DMN and simultaneous deactivation of the DAN, when blinks were measured while participants viewed a movie clip (Nakano et al., 2013). Interestingly, blinks tended to occur at specific and consistent time points during the movie across participants

(Nakano et al., 2009). Blinks may reflect transitions in cognition, during which previously attended visual information is consolidated and processed by the internal cognition-oriented DMN. Each blink might thus indicate the onset of a new episode of 're-freshed' attention.

Blinks are costly to perception. The eyelids cover the pupil for a period of up to 300 ms (Stern et al., 1984), impairing spatial information at the retina and introducing strong global transient signals. At typical blink rates about 10% of overall time is spent with the eyes closed (Lawson, 1948). Yet, the disruptions caused by spontaneous eye blinks are typically not perceived. Behavioural experiments suggest that the transients induced by eye blinks are suppressed. Light flashes presented through the roof of the mouth to bypass the pupil and eyelids are less detectable when they coincide with eye blinks (Manning et al., 1983; Riggs et al., 1981; Volkmann et al., 1980).

Blinks trigger neural activity in the posterior parietal cortex (Hari et al., 1994). This activity did not occur, however, for blinks made in complete darkness, and was therefore hypothesized to be related to maintaining perceptual continuity throughout the blink. Conversely, a functional magnetic resonance imaging (fMRI) study found suppression of activity in visual areas: Stimulation of the retina with a flashing light through the roof of the mouth exhibited reduced activity in parietal as well as frontal regions, when participants blinked as compared to no blinking (Bristow et al., 2005). Electrooculography measures during visual stimulus presentations showed a drop of neural activity in higher ventral visual regions, when participants observed brief screen blanking, followed by an immediate rebound activity that overshoot baseline activity (Golan et al., 2016). This response drop was attenuated for blinks. These studies show that extraretinal signals, e.g., motor signals signifying the execution of

a blink, seem to reduce transients resulting from the blink, which may result in the lack of awareness of the abrupt visual disruption and thus allow for perceptual continuity across a blink.

To look for potential cognitive benefits of eye blinks, we investigated the effect of eye blinks on perception and attention. We used a modified rapid serial visual presentation (RSVP) task. Participants were asked to identify a single target that was embedded at a random time point in a rapid stream of successive distractor stimuli. In three conditions, viewing was interrupted by a voluntary eye blink, by an artificial blink caused by shutter glasses, or remained continuous throughout the presentation. In seven experiments with different stimuli, we evaluated target identification performance as a function of presentation time after voluntary and artificial blinks and compared this to performance in control conditions without blinks. Participants were either asked to identify digit target embedded in letter distractors (Experiment 1A, 1B), identify animal target embedded in scene distractors (Experiment 2A, 2B, 2C), count number of white dots amount other shape distractors (Experiment 3) and identify target digit placed in a random spatial location amount letter distractors (Experiment 4). The B experiment variants were modified to have blinks occurring in the middle of a trial and the C variant, to have participants manually initiating the artificial blink.

Blink-induced suppression (Bristow et al., 2005; Golan et al., 2016; Volkmann et al., 1980) may predict that visual performance is affected right after a blink. In contrast, a 'refresh' of attention induced by eye blinks (Nakano et al., 2013) may predict better performance just after a blink. Here, we looked at the behavioural implication of eyeblinks.

General Methods

Participants

118 participants (40 males, age range: 18-40 years, mean: 23.6 years, *SD*: 3.8 years) were recruited from Nanyang Technological University and received course credits or S\$10 per hour for their participation. 10 participants participated in Experiment 1A, 2A, 3 and 4. Experiment 2C has 14 participants. Experiment 1B and 2B, had 32 participants. All participants had normal or corrected-to-normal visual acuity (only contact lenses were used for correction to allow for use of the occlusion goggles). Informed consent was obtained from all participants. The study was approved by the Institutional Review Board of Nanyang Technological University.

Apparatus

Stimuli were presented on a 21-inch CRT monitor (FD Premium SUN Microsystems) with a screen resolution of 1152 x 864 at a refresh rate of 100 Hz. Participants sat 58 cm from the monitor with their heads rested on a chin rest. Stimuli were generated using the PsychoPy software package (Peirce, 2007). Eye blinks were detected in real-time using an Eyelink 1000+ (SR Research, Ottawa, Canada). A 5-point monocular calibration procedure was used to calibrate the eye tracker to each participant's right eye. To simulate eye blinks artificially, participants wore Plato Occlusion Goggles (Translucent Technologies, Toronto, Canada), controlled by the stimulation software via an Arduino microcontroller board.

Procedure

We presented participants with a single target stimulus embedded in a stream of distractor stimuli. The precise nature of the stimuli was different in each experiment and are described below in Figure 1. Each trial started with 1000 ms of

fixation before the RSVP stream commenced. Each frame in the stream was presented for 60 ms (6 refresh frames of the monitor).

Figure 1. Experimental Paradigm. Stimuli and procedure of the RSVP task. **a.** In Experiment 1A, a single target digit was embedded in a rapid stream of distractor letters, each frame presented for 60 ms. In the VB condition, the target was presented at a random delay (here, in the first frame) after the end of a voluntary blink. In AB, occlusion goggles simulated a blink and the target was shown afterwards, accordingly. In the control condition (and in Experiment 1B), the target appeared randomly at any time during the trial (except the first and last five frames). **b.** Experiment 2 used natural scene distractors and animals as target. Participants had to respond whether an animal was present and which category the animal belonged to. **c.** Experiment 3 used random numbers of shapes as distractors and white filled circles as targets. The task was to report the number of circles. **d.** Experiment 4 used four distractor letters dispersed over the central region of the screen in each frame. The target frame contained one number target among 3 letter distractors.

In the Control condition without blinks or disruptions by shutter glasses, the target appeared at a random frame of the trial, excluding the first and last five frames. At the end of each trial, participants were asked to indicate their response via a key press.

In the Voluntary Blink condition (VB), for Experiments 1A, 2A, 3 and 4, we asked participants to blink once anytime they wished during the trial, but preferably not too late. Blinks were detected in real time, when the eye tracker's pupil area estimate was zero; the first frame with pupil size > 0 thereafter was marked as the end of a blink. The target was initially set to be presented at a random frame (except the first and last 5 frames). When a blink was detected before the pre-set target frame, the target was re-programmed to appear after a delay chosen as follows: On half of the trials, the target appeared with equal probability in frames 1, 2, or 3 after the end of the blink; in the other half of the trials, the target appeared with equal probability in any of the remaining frames (excluding the last 5 frames of the trial). This unequal distribution between early and late frames was chosen to collect more data for short delays up to 180 ms after a blink.

To ensure that any post-blink boost in performance is not solely due to an implicit expectation that targets are more likely to appear after a blink, Experiments 1B, 2B and 2C used a uniform distribution of target times (excluding only the first and last 5 frames of the sequence) independent of the timing of the blink. Here, blinks were cued to be initiated roughly half-way through the trial, upon hearing an auditory 50 ms beep (432 Hz pure tone) through stereo speakers after 1260 ms (total trial duration 3600 ms) from trial onset. Experiment 2C allowed participants to initiate the artificial blink by pressing the space bar.

Trials in which blinks occurred after the target were also classified as Control. Trials with more than one blink before target appearance or with excessive noise in the tracking data were discarded.

In the Artificial Blink condition (AB), blinks were simulated by closing the occlusion goggles. For Experiments 1A, 2A, 3 and 4, the occlusion was triggered randomly before two-thirds of the duration of a trial. For Experiments 1A, 2A, 3 and 4, the occlusion was triggered to occur 1500-1740 ms into the trial (shortly after the beep cue at 1260 ms). The occluding duration was set to each participant's mean individual blink duration (± 1 SD) measured from a resting baseline blink rate (see below).

Baseline Resting Blink Duration

Before the main experiment, we measured baseline blink durations for each participant to adjust the duration of artificial blinks for each participant. Participants were asked to relax, do nothing, and fixate a white cross on a black background on the monitor screen for 3 minutes, while the eye tracker was used to record blinks. Subsequently, participants could roam their eyes around (but not off) the screen for another 3 minutes.

Analysis

We plotted average target identification performance (percent correct) as a function of target presentation time after the end of a blink (for VB and AB). Data was plotted in bins of 60 ms, smoothed by a rolling-average window of 120 ms (± 60 ms). As targets were scattered over many times bins with limited trials, data from all participants were collapsed together to reach sufficient number of trials for all time bins. Similar results were found, when we repeated the analysis with different bin spacings or averaging window sizes (see Figure S1).

Each bin's performance was then compared to the no-blink control condition (control data collapsed across two sessions) and the other conditions using

bootstrap tests. We resampled data from the collapsed dataset with replacement over 10,000 iterations, before performing the binning and smoothing procedure and calculated the bootstrap standard error (standard deviation of the bootstrap distribution). Significant differences between conditions were detected, if bootstrapped samples lead to better performance in one condition over another condition on more than 97.5% or less than 2.5% of iterations.

The bootstrapped data were then corrected for multiple comparisons using the False Discovery Rate (FDR), Benjamini-Hochberg procedure, with the threshold value set at 0.05. Performance data before the blink onset were not included into the comparisons as they were not the primary focus of the current study.

Experiment 1A and 1B: Number Identification Task

Methods

We tested the effect of voluntary and artificial blinks on target identification performance in an RSVP task with a number digit target in a sequence of letter distractors (Figure 1A). Distractor stimuli consisted of single capital letters from the Roman alphabet (Arial font) presented in the centre of the screen, subtending 0.69 degree of visual angle (vertical extent). Targets consisted of single Arabic numeral digits (Arial font), omitting digits 0, 1, and 2 due to their similarity to O, I, and Z, respectively, which were also omitted from the distractor list. All stimuli were white (132 cd/m²) presented on a grey (66.4 cd/m²) background. Each stimulus frame in the sequence was shown for 60 ms.

For Experiment 1A, participants performed both 4 blocks of 50 trials for Voluntary Blink (VB) and Artificial Blink (AB) conditions and 1 block of the No-blink Control condition in two separate sessions (order counterbalanced) of about 1 hour each. Half of the participants completed the control condition first, while the other half completed the experimental conditions first. Each trial consisted of 70 frames and lasted 4.2 s. Target times were biased, so that on 50% of trials, the target appeared in the 180 ms after the end of a blink or the reopening of the shutter glasses. This was to increase the number of trials during the time immediately after the blink.

However, the biased target times in Experiment 1A might have introduced an implicit expectation and therefore heightened attention at the time following the blink. Therefore, in Experiment 1B the timing of the target was fully randomized to occur at any point in the trial. Blinks were cued by a beep. Trials lasted for 60 frames (3600 ms). The beep occurred at 1260 ms, so that the end of the subsequent blink would be approximately half way through the trial. In the AB condition, the glasses shut at a random delay 240-480 ms after the beep. Targets could occur at any frame during the trial apart from the first and last 5 frames (300 ms). Experiment 1B consisted of 6 blocks of 50 trials for VB and AB with one additional block of control condition in each session, for a total of 14 blocks per participant over two days. In addition, a larger sample size of 32 participants was collected.

Results

Performance for the control condition without blinks was reliably above chance (chance = 14.3% correct), Mean = 69.8%, $SD = 1.0$. Note that all standard deviations reported in this paper are bootstrap standard deviations (See General Methods).

254 Figure 2A shows performance in the control condition (horizontal green lines), and
255 for the VB and AB conditions as a function of target time after a blink. Performance
256 for after both voluntary and artificial blinks exceeded the control performance when
257 the target was presented shortly after a blink. VB reached peak performance at ~180
258 ms with 84% ($SD = 4.1\%$) correct responses, with the boost lasting the duration of
259 ~60-300 ms after the blink. AB reached peak performance of 91.7% ($SD = 4.0\%$)
260 correct at ~300 ms, with the boost lasting ~10-360 ms after the blink.

Figure 2. Visual Performance. Task performance as a function of target presentation time after voluntary and artificial blinks for all experiments. Responses were binned in 120 ms bins, plotted every 60 ms, time-locked to the end of the blink. Shaded areas are bootstrap standard errors. Horizontal lines at the top show periods with significant differences ($p < 0.05$) after correcting for multiple comparisons from the respective control condition (blue and red) or between VB and AB (black). **a.** Experiment 1A ($N = 10$). **b.** In Experiment 1B ($N = 32$), trials with targets appearing up to 1.5 seconds before and after the blink are shown. Blinks generally appear during mid trial, after an audio cue prompt was play 1260 ms into the trial. **c.** Experiment 2A ($N = 10$). **d.** Experiment 2B ($N = 32$). **e.** Experiment 2C ($N = 14$). **f.** Average error is shown for the numerosity task of Experiment 3 ($N = 10$). Larger errors are plotted down, i.e., better performance is up. Percentage correct is shown in Figure S1D. **g.** Experiment 4 ($N = 10$).

A bootstrap analysis revealed significant differences ($p < 0.05$, see Analysis) between the VB and Control conditions immediately from the end of the blink until ~300 ms after the blink. AB was also different from Control immediately after the blink for ~360 ms.

Both voluntary and artificial blinks caused a boost in performance immediately after blinks for about 360 ms. As this boost was not specific to real blinks, it is likely that this effect is based on the sudden stimulus onset after both voluntary and artificial blinks, or alternatively, reduced forward masking from stimuli that were invisible during the blink (Breitmeyer et al., 1984).

In Experiment 1B, performance for the no-blink control condition was somewhat higher than Experiment 1A (75.0%, $SD = 0.8\%$), possibly due to shorter trial durations (3.6 vs 4.2 s). As in Experiment 1A, we found a significant boost in the VB condition after the blink up to ~300 ms (Figure 2B), peaking at ~180 ms (86.7%, $SD = 1.8\%$). AB peaked early at ~120ms (82.4%, $SD = 1.9\%$), but this boost is less pronounced and sustained as compared to VB. Later significant boosts for VB were also observed at ~600–900 ms (peak: 83.2%, $SD = 3.2\%$), at ~1080ms and ~1260ms.

The performance boost is unlikely to be attributed to the beep cue: When performance is plotted as a function of time, locked to the beep onset, performance did not consistently spike after the beep (Figure S2B).

In summary, Experiment 1 found a boost in target recognition performance immediately after eyeblinks, both when targets were more likely to occur right after a blink (Experiment 1A) and when their timing was completely random (Experiment 1B). Artificial blinks with shutter glasses also led to better performance right after the opening of the glasses. However, this boost is mild in Experiment 1B, suggesting

that in the absence of presentation bias, voluntary eye blinks elicited a stronger boost in attention performance.

Some of the boost may in part, be an effect of the visual transient of reopening of the eyelids (or shutter glasses). But voluntary blinks (Experiment 1B and subsequent experiments) seemed to produce an even stronger effect compared to artificial blinks. At least, it should be noted that eye blinks could be used strategically to generate such a boost at time points, at which temporal attention is required (Hoppe et al., 2018). The performance boost might also be a consequence of activity switches between large scale neural networks (Nakano et al., 2013).

Experiment 2A, 2B, 2C: Naturalistic stimuli, animal identification task

Methods

To assess whether the results from Experiment 1 are robust to the kind of stimulus and task used, we employed a naturalistic stimulus set in Experiment 2. Stimuli consisted of photographs of natural scenes, with target photos containing an animal. The task was to detect whether an animal was present and to identify the category that the animal belongs to (Figure 1B).

Stimuli were taken from a published image data set (Li et al., 2002), including a collection of 1088 natural scenes as distractors and 24 target images, consisting of 6 animals from each of 4 categories (birds, insects, mammals, and reptiles). Random distractor images were presented consecutively for 60 ms each at a size of 600 x 400 pixels ($19.76^\circ \times 13.47^\circ$) centred on the screen on a grey background.

In Experiment 2A, targets were embedded within the stream of distractors as described in Experiment 1A, with higher probability for targets immediately after a blink. Each trial had 60 frames and lasted for 3.6 s. Participants responded at the end of the presentation stream whether they saw an animal and if they did, what category the animal belonged to. We also included 50% target-absent trials. Therefore, we increased the number of blocks in each session. There were 2 control and 4 experimental blocks of 48 trials each during the VB and AB sessions, respectively. Target-absent trials were used to additionally calculate false alarm rates.

As with Experiment 1B, Experiment 2B aimed to independently replicate these findings in a larger sample ($N = 32$) and with completely randomized target timing. No-target trials were removed in Experiment 2B and replaced with more targets (ie., 12 animals instead of 6 in each of the 4 categories).

Experiment 2C was identical Experiment 2B, the only difference being that the shutter glasses were manually triggered by the participants. Participants were told to press the space bar immediately after hearing the beep tone, which in turn, initiated the artificial blink. This was to rule out the possibility that a lack of physiological initiation of blinks in the artificial blink conditions confounded the result.

Results

For Experiment 2A, hit rates were 71.3% and 68.6% of trials with targets present for VB and AB, respectively; false alarm rates were 0.9% and 1.7% of target absent trials. Due to negligible false alarm rates, no further signal detection analysis was performed.

Performance on the categorization task in the control condition was above chance level (25%), mean = 65.5%, $SD = 1.2\%$. Figure 2C shows performance as a function of time after the blink. We again found a boost in the VB condition 60-180 ms after a blink, performance peaking at 75.9% ($SD = 1.9\%$) correct ~120 ms after the blink. AB reached peak performance of 74.2% ($SD = 2.7\%$) immediately after blinks but did not survive correction for multiple comparisons.

The bootstrap analysis revealed significant differences between the VB and Control conditions from immediately until ~240 ms after the blink (Figure 2C). There is another later boost from 900–1020 ms, peaking to 80.0% ($SD = 5.7\%$) correct, but it did not survive correction for multiple comparisons. AB performance did not significantly differ from control performances.

For Experiment 2B, performance on the categorization task in the control condition was above chance level (25%), mean = 57.9%, $SD = 0.9$ (Figure 2D). VB led to increase performance from ~60-240 ms after the blink, reaching peak performance of 67.1% ($SD = 2.6\%$) correct at ~180 ms, showing significant differences to both control and AB performance. VB performance also peaked again at ~1380 ms (mean = 64.3%, $SD = 2.5\%$). AB performance did not differ from baseline performance at any timepoints (other than during the closure of the shutter glasses, where performance obviously dropped).

For Experiment 2C, control performance was above chance (63.4%, $SD = 1.3\%$) (Figure 2E). VB performance of 2B was replicated in 2C, where there was a significant boost after the eyeblink to ~120 ms, peaking at ~60 ms (mean = 76.8%, $SD = 3.6\%$). There was also a second boost observed at ~540 ms (mean = 76.6%, $SD = 3.5\%$). No boost was observed in the AB condition.

In summary, the general pattern of results from Experiment 1 was replicated in Experiment 2 for a completely different set of stimuli. Like in Experiment 1, there was a significant performance boost immediately after the end of a blink. This boost was more pronounced for voluntary than for artificial blinks in Experiment 2A, and altogether absent for artificial blinks in Experiment 2B and 2C, indicating that eye blinks have effects on visual performance over and above their optical effects. In both experiments we also found more sustained performance improvements in later periods after voluntary blinks. This boost effect is unlikely to be confounded by the lack of physiological response in earlier (and subsequent) artificial blink conditions as performances remain constant in Experiment 2C. One possible explanation as to why boosts from voluntary blinks were stronger in Experiment 2 could be due to the increased visual complexity of the images used. This could have attenuated any kind of superficial performance boost resulting from transient pop-up of targets at blink offset, leaving the remaining boost effect driven by eye blinks instead.

Experiment 3: Numerosity Task

Methods

The tasks used to measure perceptual performance in Experiments 1 and 2 are object recognition tasks, thought to be based on the ventral temporal stream of visual processing (Goodale & Milner, 1992). Some of the neuroimaging literature on eye blinks, however, stressed the importance of parietal regions for the maintenance of perceptual continuity across eye blinks (Bristow et al., 2005; Hari et al., 1994). We therefore aimed to test behavioural consequences by repeating the RSVP paradigm of Experiments 1 and 2 with a numerosity task, which is thought to involve processing in parietal stream areas (Piazza & Izard, 2009).

In Experiment 3, distractors consisted of several identical shapes or symbols chosen at random for each frame (sinusoidal grating in a rectangle or square, square outline, cross, bar, + sign, + sign in a square). Each symbol measured $0.41^\circ \times 0.41^\circ$ and was randomly placed within the central area of the screen of $4.11^\circ \times 4.11^\circ$. The target frame consisted of white, filled circles, numbering between 1 and 7 (see Figure 1C). Participants had to indicate at the end of each trial, how many white circles they saw during the RSVP stream.

Each trial consisted of 70 frames and lasted 4.2 s. Each session consisted of 5 experimental blocks of 50 trials with voluntary or artificial blinks and one control block. The procedure was otherwise identical to Experiment 1A.

Results

Performance for no-blink trials was poorer than in Experiments 1 and 2, but still above chance level (14.3%) in both the VB (mean = 36.4%, $SD = 4.0\%$) and AB sessions (mean = 35.5%, $SD = 1.3\%$) (Figure S1F). Evidently, the task was harder than the object recognition tasks in Experiments 1 and 2. Analysing the response patterns in more detail, we found that a sizable amount of wrong responses had the tendency to be close to the correct number of circles, suggesting that participants were still able to roughly judge the quantity of circles. We therefore analysed the average error, i.e., the distance of the response from the correct number, instead of percentage correct (percentage correct is shown in Figure S1F). The average error in the control conditions was 1.30 ($SD = 0.03$).

Figure 2F shows the average errors in the VB and AB conditions as a function of target presentation time after the end of the blink. Note that larger errors are

plotted downwards, i.e., better performance is up, for easier comparisons to the other experiments.

There was no clear indication of an early performance boost as in Experiments 1 and 2. In fact, the bootstrap analysis revealed significantly poorer performance for VB as compared to Control from 450-510 ms (highest average error = 1.93, $SD = 0.21$). The only increase in performance compared to baseline was for VB from 1020-1140 ms, peaking to 0.81 ($SD = 0.11$) averaged error. This window corresponds closely to the later performance boosts found for VB in most earlier Experiments, notably in 1B, where the boost was significant.

AB average error early after the artificial blink were not significantly different from Control, but was significantly better than VB ~60 ms after blinks.

In summary, the early boost after voluntary and artificial blinks observed in Experiments 1 and 2 was not evident in a numerosity task presumably based on parietal stream processing (Piazza & Izard, 2009). Here, we found a general performance decrement for VB compared to AB. Potentially, this can be explained by parietal processing resources being recruited for continuity-preserving mechanisms (Hari et al., 1994), and thus limiting the ability to process numerosity. This is supported by the finding that AB performance was not negatively affected immediately after the artificial blink.

Experiment 4: Digit identification across different locations

Methods

In previous experiments, there is no spatial uncertainty about the location of the target. It was always foveated and thus likely in the focus of spatial attention during

the task. The parietal cortex, which has been discussed to be involved in eyeblinks and numerosity, is also widely known to be responsible for spatial processing (Corbetta et al., 1995; Mesulam, 1999). In Experiment 4, we tested to see if the deficit observed in Experiment 3 also applies to a different parietal-related task. Here, the target could occur at spatially dispersed locations to see whether the performance boosts are specific to the foveal region or spread over larger areas of the visual field.

We used the same stimuli as in Experiment 1. However, there were 4 distractors on each frame, placed randomly within a diameter of 6.7° around a low contrast fixation mark. Each item measured $0.56^\circ \times 0.56^\circ$. In the target frame, one of the letter distractors was replaced by a digit (Figure 1D). Participants had to identify the number target by a key press at the end of each trial. There were 54 trials in each of 5 experimental blocks and 1 control block for each blink condition. Each trial had 63 frames and lasted for 3.78 s. The task and procedure were otherwise identical to Experiment 1A.

Results

Performance for the no-blink trials was consistently above chance (14.3%), mean = 70.2%, $SD = 1.0\%$. Figure 2G shows performance in the VB, AB, and control conditions. The bootstrap analysis revealed no significant differences across all conditions and time points.

In summary, like in Experiment 3, results from Experiment 4 did not show the performance boosts observed in earlier experiments, suggesting that the visual performance enhancement as a result of an eye blink is only seen in object recognition tasks. While Experiment 4 is also an object recognition task, the spatial

uncertainty of the object requires the recruitment of the spatial processing parietal region. Tasks that are presumably utilising the parietal regions of the brain do not enjoy such benefit. This could once again, be due to resource competition between the execution of eyeblinks – also related to the parietal cortex - and the processing of the parietal related numerosity or spatial tasks

Discussion

RSVP paradigms, as employed here, are oftentimes used in the study of the ‘attentional blink’, where the ability to detect a second target, which appears shortly after the first target, is very poor (Pashler, 1994; Raymond et al., 1992). Here, there was only one target. And we studied the effect of *real* eye blinks—rather than ‘blinks’ of attention—on visual performance.

We hypothesized that changes in large scale network activity after eye blinks (Nakano et al., 2013) might lead to an ‘attentional refresh’ and thus improve perceptual performance immediately after blinks. However, suppression of blink-induced transients (Bristow et al., 2005; Golan et al., 2016; Volkmann et al., 1980) might also be expected to impair perceptual performance immediately after blinks. We found an early boost in performance immediately after eye blinks lasting for up to ~300 ms in object recognition tasks with simple letter and number (Experiment 1) and more complex natural stimuli (Experiment 2). Both experiments (Experiments 1B, 2B, 2C) also showed signs of a second later boost after the end of a blink, which was also evident in a numerosity task (Experiment 3). Early boosts after blinks were not evident, however, in a numerosity task in Experiment 3 or for spatially dispersed stimuli in Experiment 4.

The early boost for object recognition may in part be stimulus-driven, as artificial blinks produced by occlusion goggles led to a similar early boost (Experiment 1A), akin to attention-grabbing sudden stimulus onsets (Yantis & Jonides, 1984). This initially suggests that eye blinks can facilitate object recognition, but in the form of a physical aid rather than a cognitive boost. By removing the visual input for a fraction of a second, the blink reduces forward-masking effects (Breitmeyer et al., 1984) in the RSVP stream. However, the early boost after artificial blinks may be partly due to the predictable nature of the target in Experiment 1A. Targets were more likely to appear in the first 180 ms after the blink. Removing this bias in target timing in Experiment 1B still led to a performance boost after voluntary blinks, but much less so after artificial blinks.

In Experiment 2, only voluntary blinks enjoyed significant performance boosts after eye blinks. Stimuli complexity in Experiment 2 might have untangled the boost effects of transients evident in Experiment 1 from boost effects obtained from eye blinks per se. We observed no early boost in a numerosity task (Experiment 3) that presumably recruits parietal cortex regions. This is in line with neuroimaging studies suggesting that parietal cortex activity plays a role in maintaining perceptual continuity during eye blinks (Bristow et al., 2005; Hari et al., 1994), and thus might have reduced processing resources for the numerosity task immediately after the blink. Similarly, when the target was spatially less predictable (Experiment 4), no early boost was observed, which could also be based on unavailable parietal resources to attentively monitor multiple target locations.

These performance boosts may be consistent with changes in large scale cortical network activity triggered by eye blinks, as reported in an earlier fMRI study (Nakano et al., 2013). While the exact timing of these neural events is hard to

determine with fMRI methods only, we propose that the behavioural boost found in the present study could be the consequence of newly refreshed attention following the blink-induced release of attention. Electrophysiological measures may be better suited to look for neural signatures of this effect in the future.

The attentional “refresh” in this view may also re-focus attention to foveal regions, which may explain the lack of a performance boost in Experiment 4, where the target could be spatially distributed over a larger region of the visual field.

Alternatively, our results might be related to a phase reset of attentional rhythms. Previous studies using visual detection paradigms have identified attentional rhythms, oscillating at about 4 Hz (Landau & Fries, 2012). Stimulus transients or saccadic eye movements may be able to reset the phase of these rhythms, or saccades may be triggered to occur at fixed phases of attentional oscillations (Hogendoorn, 2016; Landau & Fries, 2012). Given the many similarities between saccades and eye blinks and the transients triggered by blinks, it is possible that eye blinks cause a phase reset for such rhythms or occur at a specific phase. In this view, the early and late windows with performance enhancements after eye blinks identified above might be the consequence of synchronized performance fluctuations. Unfortunately, the RSVP paradigm employed in our study does not lend itself to an analysis of behavioural performance rhythms time-locked to the blink. There are insufficient numbers of trials per participant to analyse performance robustly in the frequency domain.

The post-blink boost may be consistent with the view that both visual attention and eye blinks are related to cortical dopaminergic mechanisms. Several studies found that increasing dopamine levels lead to increased spontaneous blink rates (Karson, 1983; Kleven & Koek, 1996). Furthermore, infusing dopamine D1 receptors

in monkeys' Frontal Eye Fields (FEF) with D1-receptor agonist resulted in monkeys being more likely to choose stimuli targets that fell within the corresponding FEF response field (Noudoost & Moore, 2011), highlighting the role of dopamine in influencing attention. It is plausible that dopamine levels influence both eye blink generation and attentional modulation.

Some low-level, optical effects of eye blinks should be considered, as they might also bear on perceptual abilities as measured in the current experiments. Blinks are known to induce changes in pupil size as the eye adapts to different light levels during and after the lid closure (Winn et al., 1994). Pupil sizes fluctuate in a prototypical pattern after blinks and may thus affect perceptual properties of a viewed stimulus. Examining pupil size in our data revealed no obvious relationship between pupil sizes and performance (see Figure S1). VB and AB have distinct but consistent pupil size change patterns across all 5 experiments, yet, changes in behavioural performance did not follow similar time courses.

Another low-level effect of eye blinks—and some might argue their primary physiological function—is the renewal of the tear film layer over the cornea, which aids refraction and increases the acuity of vision (Montés-Micó, 2007; Montés-Micó et al., 2010). However, the refractive properties of the corneal surface as a function of time after a blink are optimal at about 6 s after a blink (Montés-Micó et al., 2005), which is outside of the time scale we examined here.

Blinks can be categorized as voluntary (consciously initiated), spontaneous (unconsciously initiated) or reflexive (initiated by foreign objects). Eye blinks in the current study were all voluntary, potentially limiting the generalizability of our results to other situations. However, some studies have argued that all types of blinks share similar mechanisms to a certain extent. E.g., suppression of detection performance

after blinks is similar for reflexive and voluntary blinks (Manning et al., 1983). Blink adaptation, in which position changes of a fixation target across a blink lead to adaptive gaze shifts, occurs similarly for spontaneous, voluntary, and reflexive blinks (Lau & Maus, 2019). Post-blink neural transient characteristics in Golan et al. (2016), too, are somewhat similar between voluntary and spontaneous blinks. Thus, the behavioural consequences of voluntary eye blinks could be similar to spontaneous eye blinks to some extent. At the very least, it is interesting to note that in the case of voluntary blinks, perceptual performance can be modulated by eye blinks. The resulting boost comes over and above effects of visual transients.

The timing of eye blinks can occur strategically during times of lower target probability (Hoppe et al., 2018), and in a more ecological situation of watching a video, blinks occur at highly consistent time points not overlapping with meaningful actions (Nakano et al., 2009). Both these findings highlight the importance of suppressing blinks during behaviourally relevant time periods, since obviously our eyes should remain open when relevant information is present. However, our results suggest that in situations where the timing of relevant events is predictable during intentional visual search, it might be beneficial to blink just before an event.

Conclusions

Our results show for the first time that eye blinks are accompanied by subsequent boosts in performance in object recognition tasks. These performance boosts are most prevalent for object recognition tasks and at foveal locations but absent in tasks that presumably recruit the parietal cortex. Our results shed light on

how eye blinks influence visual performance apart from the obvious occlusion of the visual field, and the consequences of blinks for spatial and temporal visual attention.

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Appendix

Figure S1. Performance plotted against pupil size. Performance, as in Figure 2, plotted with a rolling average window of 200 ms on each millisecond on the x-axis, with bootstrapped standard error of mean (shaded areas). Additionally, averaged time courses of size (normalized to the pre-blink pupil size) are shown (not recorded in AB condition of Experiment 1 due to technical issue). Each condition was plotted against their own respective control (that was held on the same day) rather than against control performance collapsed over two separate days (which was done for the official analysis in Figure 2). Control performance across sessions generally tended to be consistent. **a.** Experiment 1A. **b.** Experiment 1B. **c.** Experiment 2A. **d.** Experiment 2B. **e.** Experiment 2C. **f.** Experiment 3, plotted in raw percentage correct rather than averaged error. **g.** Experiment 4.

Figure S2. Performance for all experiments as in Figure 2, but time locked to the beginning of the trial. The histograms at the bottom of each panel show the number of trials with a blink ending in this bin. Bins with less than 15 trials (usually the first and last few bins) are not shown. **a.** Experiment 1A. **b.** Experiment 1B: The vertical dashed line shows the time of the auditory beep that cued participants to blink (at 1.26 s). **c.** Experiment 2A. **d.** Experiment 2B. **e.** Experiment 2C. **f.** Experiment 3. **g.** Experiment 4.

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