PNAS COMMENTARY

Blink and you see it

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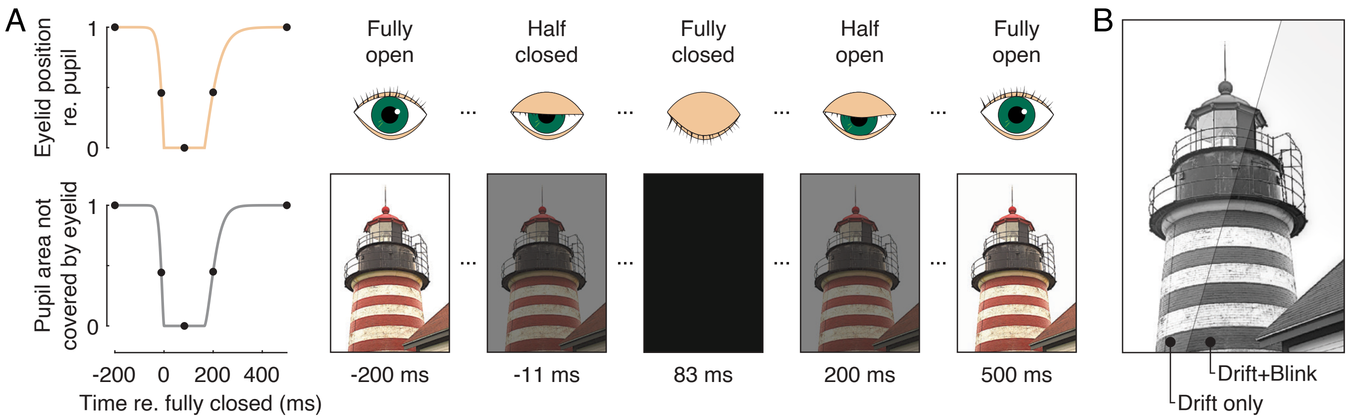

Fig. 1. Visual consequences of a blink. (*A*) Following measurements of the dynamics of eyelid closure, Yang et al. (1) modeled the pupil area not covered by the eyelid. An example image highlights the amount of light reaching the retina in different blink phases (time points correspond to black dots in the leftmost panels). (*B*) Schematic depiction of the visual benefit resulting from a blink—an enhancement of luminance contrast emphasizing lower spatial frequencies while leaving high spatial frequencies unaffected.

Every few seconds, our visual world disappears behind a thin fold of skin that maintains the tear film on the corneal surface and, for more than a tenth of a second, blocks light from falling onto the retina. "Blink and you miss it" is a common idiom that captures how we have conceived of those moments in time. A new study (1) now turns this idea on its head, showing that the transients caused by blinks effectively enhance visual contrast sensitivity. The authors argue that these movements are a computational component, not an inconvenience, of visual processing.

The human retina is ceaselessly exposed to strong and rapid luminance modulations caused by eye movements, from the microscopic scale of ocular drift while we fixate on a certain object, to the macroscopic scale of rapid saccadic gaze shifts from one location to the next. Consider this printed text—the small font size has a high variation of luminance over space (high spatial frequencies), such that even miniature eye movements cause strong modulations in the luminance reaching the retinal receptors. Neural activity is driven by these transient modulations conveying a stronger response to the visual stimulus in the presence than in the absence of eye movements (2, 3). In this rhythm of light, eye blinks can be considered the beat of a kettledrum: when the human eyelid closes and opens again, the intensity of light reaching the retina changes suddenly and drastically. In contrast to eye movements, however, luminance modulations that come with blinks depend on the motion of the eyelid rather than the gaze, and they are largely independent of the particular scene we observe.

Yang et al. (1) modeled the modulation of the luminance signal that reaches the retina as the eyes blink, including a closing, closed, and opening phase (Fig. 1*A*). They then estimated the spatial and temporal frequency spectrum that a static image would have before and after a blink, against a background of small fixational eye movements (ocular drift). To estimate the perceptual quality of this signal, the distribution of emerging temporal frequencies (rate of luminance changes in a certain space) was then filtered by the range of temporal frequencies that humans are sensitive to (4). Eye blinks would, in principle, increase the power across a wide range of spatial and temporal frequencies. But because fixational eye movements cause incessant transients in the range of high-spatial frequencies, the luminance variations resulting from eye blinks would most strongly affect visibility of stimuli with wider-spaced luminance variations (spatial frequencies lower than 5 cycles per degree; Fig. 1*B*).

In a highly controlled psychophysical setup, the authors took this prediction to the test while eye movements—including blinks—were meticulously recorded with a high-precision eye tracker for later analysis. Participants fixated their gaze on a screen while waiting for a faint luminance grating (alternating dark and light bars) to fade in. The grating had a particular orientation (+45 or −45 degrees), and its contrast was adjusted to each participant's visibility

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threshold. By design, the grating's spatial frequency was in a range predicted to benefit from a blink. While holding their gaze in place, participants were ready to blink once an auditory cue was played to them. Critically, the tone appeared at one of two possible times during a trial, such that the blink would be initiated either before the grating appeared or while it was on the screen. Moreover, to isolate the impact of blinks from any other transients that could affect stimulus visibility, the authors slowly ramped up stimulus contrast over time, long before blink onset, and took great care to discard trials in which microsaccades or saccades were observed. And, indeed, participants' reports revealed higher sensitivity to the grating's orientation when they executed the blink while (rather than before) the grating was displayed. This result is quite intriguing: The grating's orientation was perceived with higher accuracy when a blink significantly reduced the time for which the grating could be observed.

Yang et al.'s results add to the growing recognition that the retinal consequences of eye movements—from the fixational scale to large-scale eye-head gaze shifts—form an integral part of visual processing.

In additional experiments, the authors replicated this effect and tested additional conditions. They showed that the blink-contingent benefit was not observed for very fine spatial details, in agreement with their predicted specificity of the effect to lower spatial frequencies. The model simulations further predicted that any blink, largely independent of the movement's dynamics, should lead to measurable benefits in perception. As voluntarily executed blinks upon instruction are typically long in duration and reaction time, the authors next probed reflexive blinks. Participants performed the same task as before, but instead of a tone instructing a blink, their eyes were exposed to air puffs, triggering reflexive blinks that were faster in execution and shorter in duration than the voluntary ones. Again, participants showed increased visual sensitivity when the reflexive blink occurred in the presence of the grating rather than before the grating was displayed.

It is remarkable that the authors' model simulations focused entirely on visual processes, suggesting that the increase in sensitivity to low spatial frequencies is a consequence of the transient modulation of light that results from a blink. This predicts that the visual consequences of blinks alone would cause the observed perceptual benefits. Like any movement, however, blinks are initiated by neural motor signals, which—through corollary discharge (efference copy) signals (5–7)—may have an impact on visual processing (8, 9). In a final experiment, therefore, the authors tested whether or not a motor signal for the eyelid movement is required for a perceptual benefit to occur. To this end, they mimicked the visual consequences of a blink. During these simulated blinks, the luminance of the experimental display dropped transiently and then increased again, akin to the visualization in Fig. 1*A* (*Bottom* row). The durations and initiation times of the fake blinks mirrored those of actual blinks that participants had previously executed, and they occurred exclusively during the presentation of the grating. The results were rather clear: all tested participants showed a performance improvement after a simulated blink, compared to no simulated blink, and the improvement was of similar magnitude as that of the actual blinks.

Together, these results draw a consistent picture: the major transients that blinks impose on the visual input effectively enhance sensitivity to luminance contrast for a wide range of medium to low spatial frequencies. While the authors have shown this impressively in a comprehensive set of experiments, immediate next questions arise. First, what is the time course of a blink's perceptual benefit? When does it kick in and how long does it last? Establishing the dynamics of perceptual enhancement with respect to the blink will require limiting the time for which the stimulus is available before and after the blink. Second, the study investigated visual sensitivity at participants' individual perceptual threshold, using luminance contrasts at the edge of visibility. An intriguing question is how blinks affect visual sensitivity and appearance at higher levels of contrast, which are characteristic of natural scenes (an assumption we make in Fig. 1*B* is that the same mechanisms apply independent of the overall contrast level). Finally, an untested prediction of the author's model (at least in our reading) is that blinks would increase sensitivity to fine spatial detail as well, if the impact of fixational eye movements on retinal stimulation were eliminated. Such retinal stabilization can be achieved by inducing foveal afterimages (10). While eye blinks are known to prolong afterimage durations (11), it remains to be seen whether this prolongation applies across spatial scales.

New insights can shed new light on long-standing questions and, even more thrillingly, inspire new ones. One long-standing question regarding blinks, much like for saccadic eye movements (12), is the phenomenal perceptual continuity that we experience despite the marked temporal disruption in the visual input (13–15): How do we bridge the temporal gap that a blink creates? How do we integrate information from before and after? How do we keep track of moving objects during a blink? In the case of saccades, visual signals imposed by the rapid motion of the eyes contribute to these processes (16–18). Similarly, the visual consequences of blinks as described by Yang et al. (1) may contribute to perceptual continuity by emphasizing critical aspects of the visual input stream around the time of a blink.

An exciting new question that results from the paper is whether the visual system exploits the benefits of blinks systematically (see also ref. 19). It is known that humans strategically select periods of time for blinking during which a momentary loss of vision is least critical—in expectation of behaviorally relevant information (20) or in between scenes in the narrative of movies (21, 22). In a similar vein, blink rates transiently break down in response to the appearance of salient stimuli (23). Yang et al.'s (1) findings uncover the perceptual benefits of blinks, raising the question if we use blinks when their positive visual impact is likely to play out. Conditions in which blinks would make a difference involve coarse visual information (i.e., low spatial frequency content) that is behaviorally relevant. For instance, do we blink more often during night vision (when we lack the high resolution of foveal vision) or when we do not wear our prescription glasses? Indeed, the optimal rate of blinking may vary across different environments, when both the benefits and the costs of blinks are considered. Establishing such behavioral adaptations will benefit from investigating spontaneous blinks, a behavior that has not been explicitly tested by the authors. The blunt nature of the visual consequences of blinks-, however, appears to imply that the origin (reflexive, voluntary, or spontaneous) and exact kinematics of the movement are of little importance (1). In this aspect, blinks may be markedly different from saccadic eye movements, whose kinematics follow a specific relation of movement amplitude, velocity, and duration that relate to visual sensitivity in equally lawful ways (24, 25).

At large, Yang et al.'s (1) results add to the growing recognition that the retinal consequences of eye movements—from the fixational scale to large-scale eye-head gaze shifts—form an integral part of visual processing (16, 17, 24). Both blinks and saccades shared the same fate in that their visual consequences were long considered a nuisance to the visual system that required suppression. It becomes clearer that the sudden and rapid changes in retinal input that result from these movements are a feature, not a bug, that affects visual processing in efficient ways (26). Yang et al. (1) started their project with a mystery, asking why we blink more than necessary to keep the eyes from drying. Their results uncover visual functions of blinks that urge us to conceive of these movements not just as eye-closing, but also—and perhaps more importantly—as eye-opening.

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