

the literature (45). In keeping with the predictions of Fig. 1C, eye blinks during stimulus presentation significantly increased input power over a broad band of temporal frequencies (Fig. 3A). As a consequence, blinks yielded a more effective signal in driving visual responses within the temporal range of human sensitivity (Fig. 3B). On average, power increased by approximately 22% across subjects ($t(8) = 6.732$, $P = 1.5E - 4$, paired t -test; Cohen's $d = 2.244$), an effect that also reached statistical significance in the individual data from seven observers ($P < 0.041$, one-tailed Wilcoxon rank-sum test). The gain in power was positively correlated with the change in performance, so that the subjects who experienced stronger transients were also the ones who improved the most in the blink trials ($r = 0.6$, $P = 0.09$).

It is worth noting that the spectral estimations of Fig. 3A and B likely underestimate the real strength of blink transients, as they do not include the additional modulations introduced by the eye movements that accompany blinks (48, 49), which could not be reliably measured by our apparatus (SI Appendix, Fig. S1A). However, our power spectra do include the effects of possible offsets in gaze position measured before and after a blink (SI Appendix, Fig. S2A). As reported in SI Appendix, Fig. S2B, these gaze shifts contributed for approximately 18% of the power gain

resulting from blinking ($t(8) = 8.659$, $P = 2.5E - 5$, paired t -test; Cohen's $d = 2.886$).

Considering that the dynamics of blinking may affect luminance modulations, we examined how the strength of the visual input signal varies with blink characteristics. High-speed video recordings of eye blinks showed that two parameters are sufficient to reliably capture the overall time course of light intensity on the retina during the course of a blink: a) the speed of the eyelid, which in our model is determined by the time constant of the eyelid trajectory; and b) the duration of the period of full eyelid closure (SI Appendix, Fig. S1). The Bottom row of Fig. 3 shows how the power of the input modulation varies as these two parameters change systematically. During exposure to a 3-cpd grating, power decreased with decreasing eyelid speed (increasing time constant) and/or increasing blink duration (Fig. 3C). However, changes in power were limited to about 8% over a five-fold variation in parameter values. A lower frequency stimulus yielded even smaller changes (see data for 1 cpd in Fig. 3D). Thus blinks appear to deliver a more effective visual input than an equivalent period of fixation irrespective of their exact dynamics.

The data in Fig. 3C and D suggest that blink modulations should be beneficial also for blinks that differ greatly in their

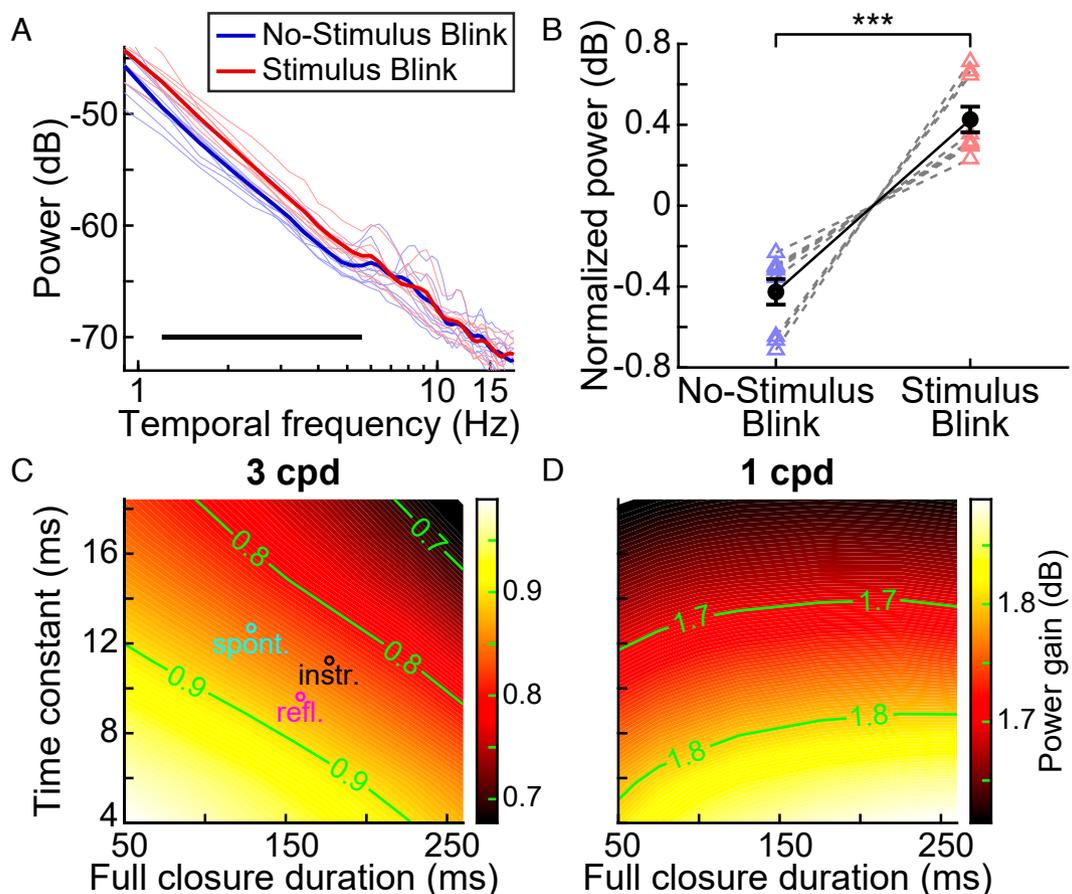


Fig. 3. Consequences of eye blinks on visual input signals. (A) Power spectra of the spatiotemporal luminance signals experienced by subjects in the two experimental conditions of Fig. 2. Both averages across subjects (thick lines) and the individual data (thin lines) are shown. The horizontal bar marks statistical significance ($P < 0.05$, paired t -test, FDR corrected). (B) Blink-induced changes in the effective strength of input signals. The power in A is here weighted by the temporal sensitivity of the human visual system and integrated across frequency. For each subject, data are normalized by the individual average in the two experimental conditions. Circles and triangles show means across subjects and individual subjects' data, respectively. Error bars represent \pm one SEM ($***P = 1.5E - 4$, paired t -test, $N = 9$). (C) Gain in power as a function of blink characteristics. Each data point represents the average power ratio in the presence/absence of blinks for a specific combination of eyelid speed (ordinate) and interval of full eyelid closure (abscissa). The stimulus is a 3 cpd grating. Circles mark the mean parameters measured for instructed (black), reflexive (magenta), and spontaneous blinks (cyan). (D) Same analysis as in C for a 1 cpd grating.

temporal characteristics. To test this prediction, in a control experiment, we examined the consequences of reflexive blinks, which are known to have faster dynamics than the instructed blinks of Fig. 2 (10, 50–52) and are also known to be associated with different brain states (53, 54). To this end, we substituted the auditory cues with air puffs. As expected, the reflexive blinks elicited by an air puff possessed significantly shorter reaction times (Fig. 4*A*) and durations (Fig. 4*B*) than the instructed blinks of the previous experiment. In this experiment, we also used smaller stimuli to further test the robustness of the effects. Despite these differences, subjects continued to benefit from the presence of blinks. For both participants, performance was higher when reflexive blinks were triggered during stimulus presentation than before its appearance (Fig. 4*C*). Again, this perceptual improvement was accompanied by an increment in the power of retinal stimulation during blinks (Fig. 4*D*). Thus, both instructed and reflexive blinks enhance visual sensitivity, and the effect seems not to depend on stimulus size.

The model in Fig. 1 makes a more specific prediction: If the transients delivered by eye blinks are indeed responsible for the perceptual enhancement shown in Figs. 2 and 4, one may expect this improvement to be confined to low spatial frequencies, the range in which the modulations from fixational eye movements are small. To test this hypothesis, we repeated the experiment using gratings at either low (1 cpd) or high (10 cpd) spatial frequency. Apart from the stimulus change, the task and procedures were otherwise identical to those described in Fig. 2. As before, with a low spatial frequency stimulus, the occurrence of an eye blink enhanced performance (Fig. 5*A*). In contrast, blinks had no effect during viewing of the high-frequency grating, and

discrimination performance was virtually identical when blinks occurred before and during stimulus presentation. In keeping with these findings and the predictions of Fig. 1, blinks also increased the efficacy of the visual signals impinging onto the retina during exposure to a 1-cpd grating, but not with a 10-cpd grating (Fig. 5*B*). Thus, these results corroborate the idea that the perceptual consequences of blinks measured in our experiments originated from their luminance transients.

Our predictions are purely based on the characteristics of the visual signals delivered by blinks: These abrupt transients redistribute the spatial power of the stimulus across temporal frequencies, effectively yielding a stronger driving input at low spatial frequencies. These considerations imply that the visual system should benefit from these transients irrespective of their origin, i.e., whether caused by blinks or generated from the external stimulus.

To investigate this hypothesis, in a fourth experiment, rather than instructing subjects to actively blink, we passively exposed them to reconstructions of blink transients obtained by directly modulating the luminance of the stimulus on the display (Fig. 6*A*). The results in Fig. 6 show that exposure to simulated blinks is beneficial. Performance was significantly higher in the simulated-blink trials than in the absence of the abrupt luminance changes, an effect evident both in the percentages of correct responses ($t(5) = 3.254$, $P = 0.023$, paired t -test; Cohen's $d = 1.329$; Fig. 6*B*) and in the discriminability index ($t(5) = 3.847$, $P = 0.012$, paired t -test; Cohen's $d = 1.571$; Fig. 6*C*). The extent of the improvement obtained with simulated blinks was comparable in magnitude to that measured with real eye blinks in the experiment of Fig. 2 ($P = 0.864$ and $P = 1.000$

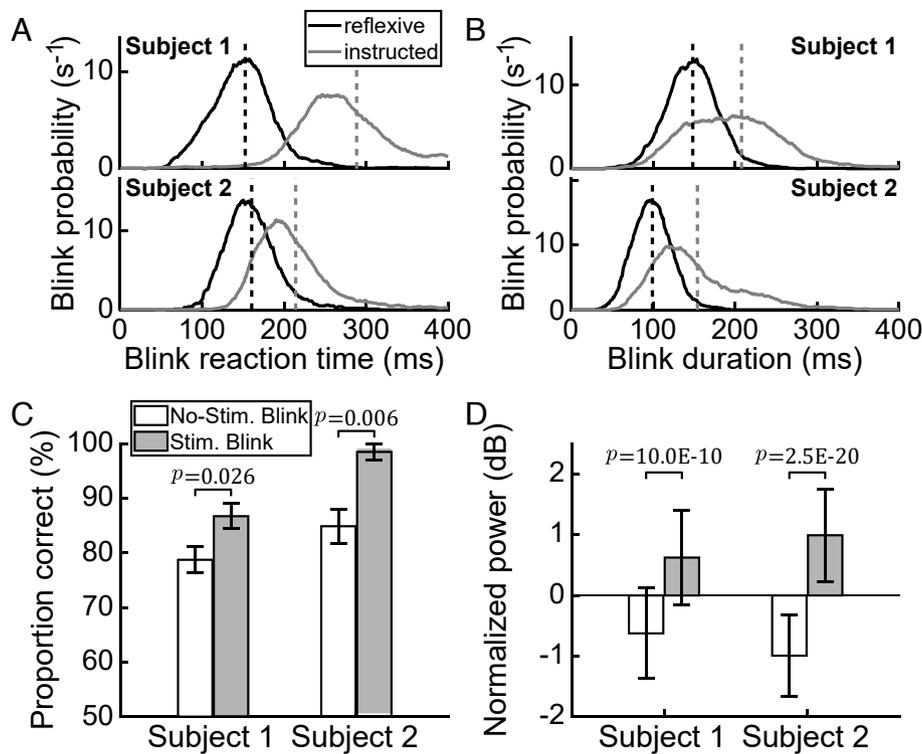


Fig. 4. Perceptual enhancement from reflexive blinks. (A and B) Comparison between the characteristics of reflexive blinks elicited by air puffs (black lines) and the instructed blinks of Fig. 2*A* (gray lines). Data represent the probability distributions for blink reaction times (A) and durations (B). Separate panels show data from different subjects. Dashed lines mark the distribution means. (C) Proportion of correct responses when reflexive blinks occurred before (white bars) and during stimulus presentation (gray bars). Error bars are \pm one STD. (D) Comparison of the strength of retinal stimulation in the two conditions, as in Fig. 3*B*. Graphic conventions are as in panel C. Error bars represent \pm one SEM. Probability values are the results of Z-tests corrected for continuity in C and two-sample t -tests in D.

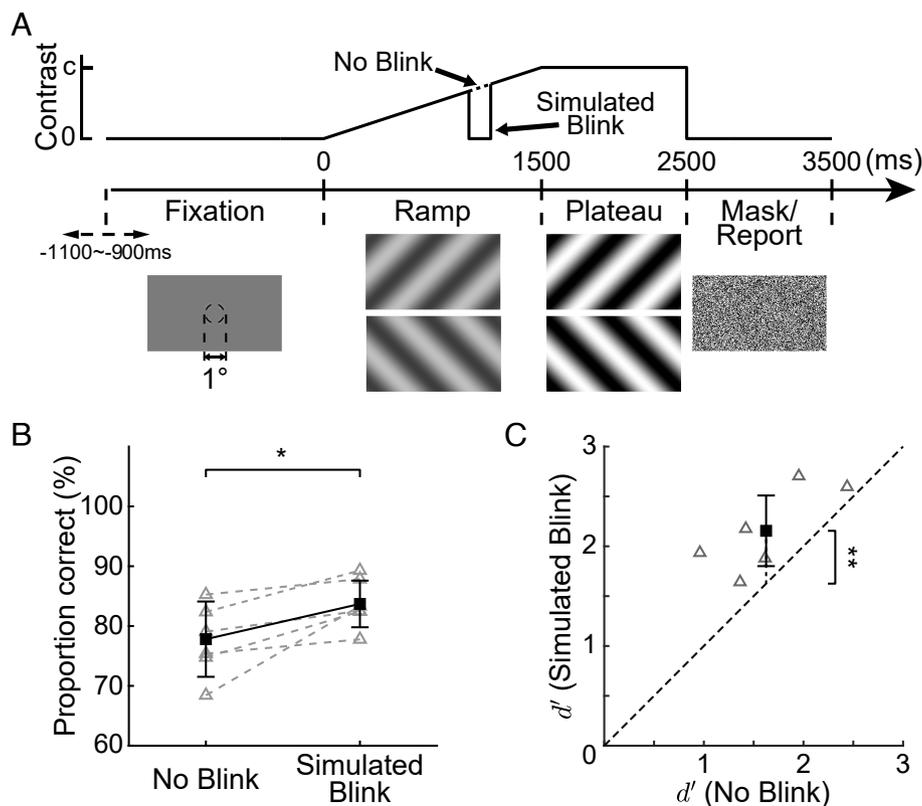


Fig. 6. Perceptual consequences of simulated blinks. (A) In an experiment similar to that of Fig. 2A, subjects were exposed to changes in the stimulus that resembled the luminance transients elicited by eye blinks. Each simulated blink consisted of a brief period of stimulus blanking with onset and duration randomly sampled from the previously collected individual blink data. (B and C) Comparison of performance in the presence and absence of a simulated blink. The two panels show proportions of correct responses (B) and d' (C). Both averages across subjects ($N = 6$; black) and individual subjects' data (gray) are shown. Error bars represent \pm STD in B and 95% CIs in C (** $P = 0.012$, * $P = 0.023$; paired t -test).

While in this study we have focused on instructed (Fig. 2) and reflexive blinks (Fig. 4), the robustness of luminance transients to blink kinematics (Fig. 3 C and D) suggest that our findings extend to the spontaneous blinks that occur during natural viewing. In fact, several considerations suggest that our data may underestimate the role of blink transients. Our spectral analyses did not take into account the eye movements that occur during blinks (48, 49), which could not be reliably measured by our apparatus (SI Appendix, Fig. S1A). These movements likely add temporal power by introducing modulations similar to those resulting from saccades (42). For example, in the experiment of Fig. 2, including some of the eye movements present during the blink opening and closing phases (up to a conservative speed threshold of 5 degrees/s) increased power by 11%. Furthermore, as shown in Fig. 1D, eye blinks deliver progressively stronger luminance modulations than ocular drifts as the spatial frequency of the stimulus decreases. Since natural scenes contain prominent power at low spatial frequencies, blinks are expected to provide very effective transients outside the laboratory, enhancing sensitivity to the coarse structure of the visual scene. Little is presently known about the dependence of blinks on the spatial frequency content of the stimulus, but a number of studies indicate that blinks tend to be less frequent when examining high, rather than low, spatial frequencies (60, 61), which is consistent with our results.

The finding that the visual system takes advantage of blink modulations acquires further importance in the context of visual perception theories arguing for a temporal encoding of spatial information (27, 62–64). During natural viewing, the retina is continually exposed to changes in luminance, as saccades alternate

with fixational eye movements (38–40). This behavior appears to confound the processing of spatial information (14, 15, 18, 65). However, evidence is increasingly accumulating for an alternative viewpoint that casts a more positive light on these input changes (31). According to this view, spatial information is not just conveyed by the location of neurons within maps, but also by the way motor behavior shapes the temporal structure of neural responses (27–29). This idea builds on the observation that the resulting visual input signals stimulate the retina with temporal changes rich in spatial information, which critically depend on how the eye moves.

A number of findings from our laboratory support this proposal of active space-time encoding. We showed not only that fixational eye movements critically enhance—rather than degrade—vision of fine spatial detail (40, 66), but also that their luminance modulations are matched to the statistics of natural scenes (45), forming a continuum with the modulations from larger eye movements (42). The current study adds to this previous body of work by showing that the strong luminance transients exerted by eye blinks are also useful. Like saccades, the luminance signals from blinks enhance low spatial frequencies relative to ocular drift and possess temporal frequencies that are expected to strongly activate retinal neurons (67). However, unlike eye movements, blinks modulate luminance equally at all spatial frequencies, thus not counterbalancing the power spectrum of natural scenes. This implies that blinks deliver much stronger signals than saccades at low spatial frequencies.

In the context of theories advocating for a temporal encoding of spatial information, the notion of blink suppression acquires an alternative conceptual interpretation. Like the attenuation

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2 **Supporting Information for**
3 **Eye Blinks as a Visual Processing Stage**

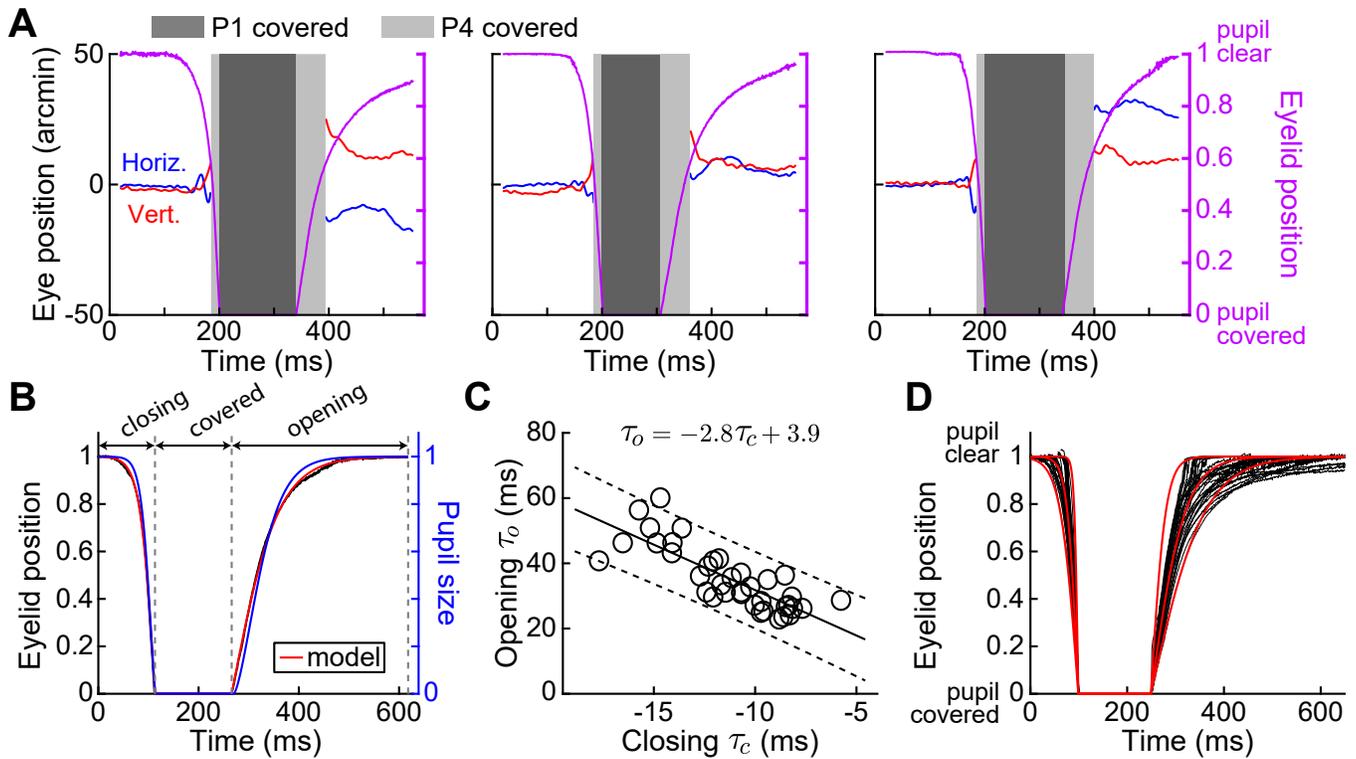
4 **Bin Yang, Janis Intoy and Michele Rucci**

5 **Michele Rucci.**

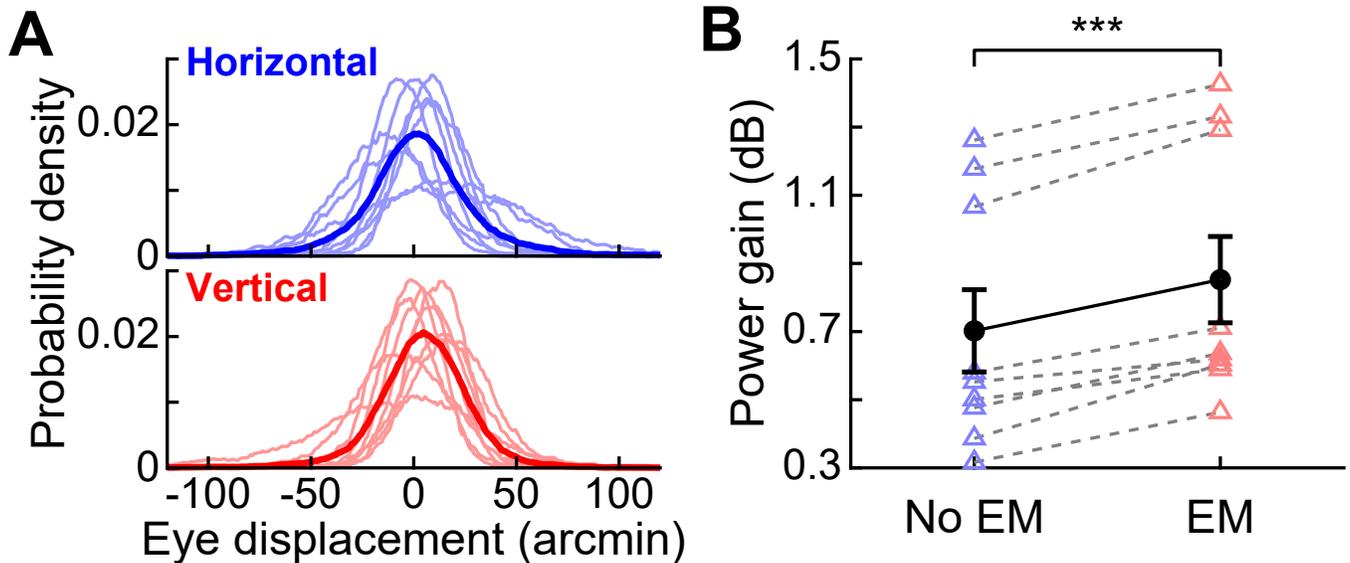
6 **E-mail: mrucci@ur.rochester.edu**

7 **This PDF file includes:**

8 Figs. S1 to S2



9 **Fig. S1.** Blink detection and dynamics. (A) Three examples of blink detection in a Dual Purkinje
 10 Image (DPI) eye-tracker. Oculomotor data from the DPI (blue line: horizontal position; red line: vertical
 11 position; left ordinate) are synchronized with the eyelid trajectory (purple line; right ordinate), estimated
 12 from videos of the eye acquired at a 1-kHz frame rate. Values of 0 and 1 indicate full eyelid closure
 13 and normal opening, respectively. The blink duration reported in our study refers to the period of
 14 occlusion of the first Purkinje image (P_1) of the eye-tracker beam (dark gray rectangle). Given the
 15 position of P_1 in our setup, this interval approximately matches the period in which the pupil is fully
 16 covered by the eyelid. On average, over 39 videos of spontaneous, instructed, and reflexive blinks
 17 from two subjects, P_1 occlusion preceded full pupil closure by 4 ± 3 ms and followed reopening by
 18 8 ± 9 ms. Note that eye movements are no longer available from the moment in which the fourth
 19 Purkinje image (P_4) is covered by the eyelid (light gray rectangles). (B-D) Modeling blink kinematics.
 20 (B) An example of measured (black line; left ordinate) and modeled (red line) eyelid trajectory. In all
 21 recorded videos, eyelid opening and closing phases were well captured by half-sigmoid functions. The
 22 blue line represents the estimated area of the pupil unobstructed by the eyelid (right ordinate). (C)
 23 The time constants of the opening and closing phases of a blink, τ_o and τ_c , are strongly correlated
 24 ($r = -0.81$, $p = 1.3E - 9$; black line). Dashed lines mark the 95% confidence interval. Thus, the full
 25 eyelid trajectory can be modeled with just two parameters: τ_c (or τ_o) and the length of the period of
 26 full eyelid closure. (D) This model captures the variability in eyelid trajectories measured for various
 27 types of blinks (black traces; here aligned by normalizing the period of eyelid closure). Red lines are
 28 the trajectories given by the model for three values of τ_c .



29 **Fig. S2.** Eye movements associated with blinks and their consequences on luminance transients. (**A**)
 30 Distributions of blink-induced gaze displacements in the experiment of Fig. 2. Data represent the
 31 offsets in horizontal (top) and vertical eye position (bottom) between the times at which the eyelid starts
 32 moving and its return to normal opening. Based on the video recordings of eyelid trajectories, these
 33 instants were respectively estimated as occurring 90 ms before P_1 disappearance and 200 ms after its
 34 reappearance. Thin lines are the distributions from individual subjects. The bold line represents the
 35 average across subjects. The mean horizontal and vertical displacements across participants were
 36 $19.3' \pm 9.6'$ and $16.4' \pm 7.3'$, respectively. (**B**) Contributions of eye movements to the strength of the
 37 luminance modulations caused by blinks. The data reported in the article include consideration of gaze
 38 displacements. Assuming the eye to remain stationary throughout a blink (No EM) attenuates the gain
 39 in power delivered by the modulation within the range of human temporal sensitivity by approximately
 40 21% (***) $p = 2.5E - 5$, paired t -test). Error bars represent \pm SEM.