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Eye blinks as a visual processing stage

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Humans blink their eyes frequently during normal viewing, more often than it seems necessary for keeping the cornea well lubricated. Since the closure of the eyelid disrupts the image on the retina, eye blinks are commonly assumed to be detrimental to visual processing. However, blinks also provide luminance transients rich in spatial information to neural pathways highly sensitive to temporal changes. Here, we report that the luminance modulations from blinks enhance visual sensitivity. By coupling high-resolution eye tracking in human observers with modeling of blink transients and spectral analysis of visual input signals, we show that blinking increases the power of retinal stimulation and that this effect significantly enhances visibility despite the time lost in exposure to the external scene. We further show that, as predicted from the spectral content of input signals, this enhancement is selective for stimuli at low spatial frequencies and occurs irrespective of whether the luminance transients are actively generated or passively experienced. These findings indicate that, like eye movements, blinking acts as a computational component of a visual processing strategy that uses motor behavior to reformat spatial information into the temporal domain.

spatial vision | visual encoding | retina | fixational eye movements | saccade

Significance

Humans spend a remarkable fraction of their awake time while blinking. Here, we show that eye blinks are not simply a mechanism for refreshing the tear film but act as an information processing stage. By modulating the visual input to the retina, blinks effectively reformat spatial information in the temporal domain, yielding luminance signals that emphasize low-resolution information about the global structure of the visual scene. We show that human observers benefit from these transients and that this perceptual enhancement occurs independently from motor signals associated with blinks. Thus, contrary to common assumption, blinks facilitate—rather than disrupt—visual processing, amply compensating for the loss in stimulus exposure.

Humans blink their eyes every few seconds. While the frequency of blinks varies greatly across individuals and tasks (1–3), blinking is critically important: It lubricates the eye (4, 5), regulating the precorneal tear film (6) and improving the optical quality of the image on the retina (7). In exerting these beneficial actions, however, blinks appear to challenge visual processing, as they temporarily occlude the external scene. Since each blink can last as long as 300 ms (8–10), blinking significantly disrupts the acquisition of visual information and may substantially delay motor responses to important visual events.

This problem is further exacerbated by the attenuation in visual sensitivity that occurs around the time of an eye blink (8, 9, 11). Humans are normally not aware of the interruptions imposed by blinks in the visual stream entering the eye. This is a remarkable accomplishment considering that comparable input changes would be startlingly obvious if resulting from the external scene rather than eye blinks. This process seems to be partly mediated by an internal suppression mechanism that attenuates visual sensitivity, akin to the one occurring during saccadic eye movements (12–18). Since this suppression precedes and outlasts each blink (13), it leads to reduced visibility lasting even longer than the blink duration.

These considerations, together with the observation that humans blink more often than necessary for keeping the eye well lubricated (6, 7, 19), suggest that eye blinks also serve other functions. In principle, there are two complementary ways in which blinks could contribute to visual perception: by intervening in visual processing via their associated extraretinal signals and by directly affecting neural responses via the luminance changes they cause on the retina. Whereas the former possibility has been the subject of recent investigations (20, 21), the perceptual consequences of the luminance modulations exerted by blinks have been only marginally investigated.

Several considerations suggest that these signals could be beneficial. Given that neurons in the early visual system tend to be strongly sensitive to input changes (22–24), one would expect blinks to sharply modulate neural activity. Indeed, transient responses have been observed in the visual cortex at the time of eye blinks, with activity first decreasing as the eyelids close and then rapidly recovering at the reappearance of the stimulus (25, 26). Notably, immediately following a blink, activity rebounds to a higher level than that present before closure of the eyelid (26), an effect driven by the reafferent stimulation that may facilitate visual encoding.

Although they possess different characteristics, the luminance modulations caused by other types of motor actions, eye movements, play critical roles in visual perception (27–31). Both saccades (32–35) and ocular drifts (36, 37)—the incessant fixational motion of the eye in between saccades (38–40)—yield luminance transients that are

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perceptually beneficial. These signals enhance vision in complementary ways, as expected from their specific characteristics, i.e., the distinct ways saccades and drifts transform an external spatial scene into a spatiotemporal flow onto the retina (31, 41). The abrupt luminance changes delivered by blinks differ considerably from the modulations induced by eye movements. But, as is the case for saccades (42), one may expect that, in a sufficiently low spatial frequency range, blinks will yield a more effective input than what would be available in their absence.

Here, we focus on the perceptual consequences of the luminance changes resulting from blinks. We show that blinks enhance contrast sensitivity as predicted by the characteristics of their transients, specifically the spatial information conveyed within the temporal range of retinal sensitivity. We further show that this enhancement occurs for both instructed and reflexive blinks and also during passive exposure to similar transients, even if they are not actively generated by blinks.

Results

To predict the visual consequences of eye blinks, we first examined how their occurrence alters the luminance flow normally impinging onto the retina (Fig. 1*A*). In the fixation periods in between saccades, ocular drifts continually modulate visual input signals. These modulations depend on the stimulus, increasing both in amplitude and speed as the spatial frequency of the stimulus increases (37, 43) (Fig. 1*B*). In contrast, the modulations resulting from blinks do not depend on spatial frequency, as blinks deliver signals with identical dynamics irrespective of the stimulus. Thus, if blink transients are used by the visual system, one may expect them to exert a stronger influence in the low spatial frequency range, where the modulations resulting from fixational eye movements are smaller.

We quantitatively explored this idea in simulations of the visual input signals present during fixation (Fig. 1 *C*–*E*). We modeled the fixational eye movements normally performed by healthy observers as Brownian motion (44, 45), while blinks acted by transiently interrupting the spatiotemporal luminance flow. Fig. 1*C* shows the power spectrum of the simulated visual input signal during observation of a stationary white noise stimulus, i.e., a stimulus that contains all spatial frequencies with equal amplitude. As shown by these data, the occurrence of an eye blink greatly increases power at low spatial frequencies, an effect visible over a broad range of temporal frequencies (arrows in Fig. 1*C*). In contrast, at high spatial frequencies, the luminance modulations from blinks are comparable in amplitude to those continually delivered during fixation by ocular drift.

To understand the efficacy of these input signals in driving perceptual responses, we estimated the total power delivered by blinks within the range of temporal sensitivity of the visual system. To do this, the distribution in Fig. 1*C* was weighted by the temporal function of human contrast sensitivity (46)

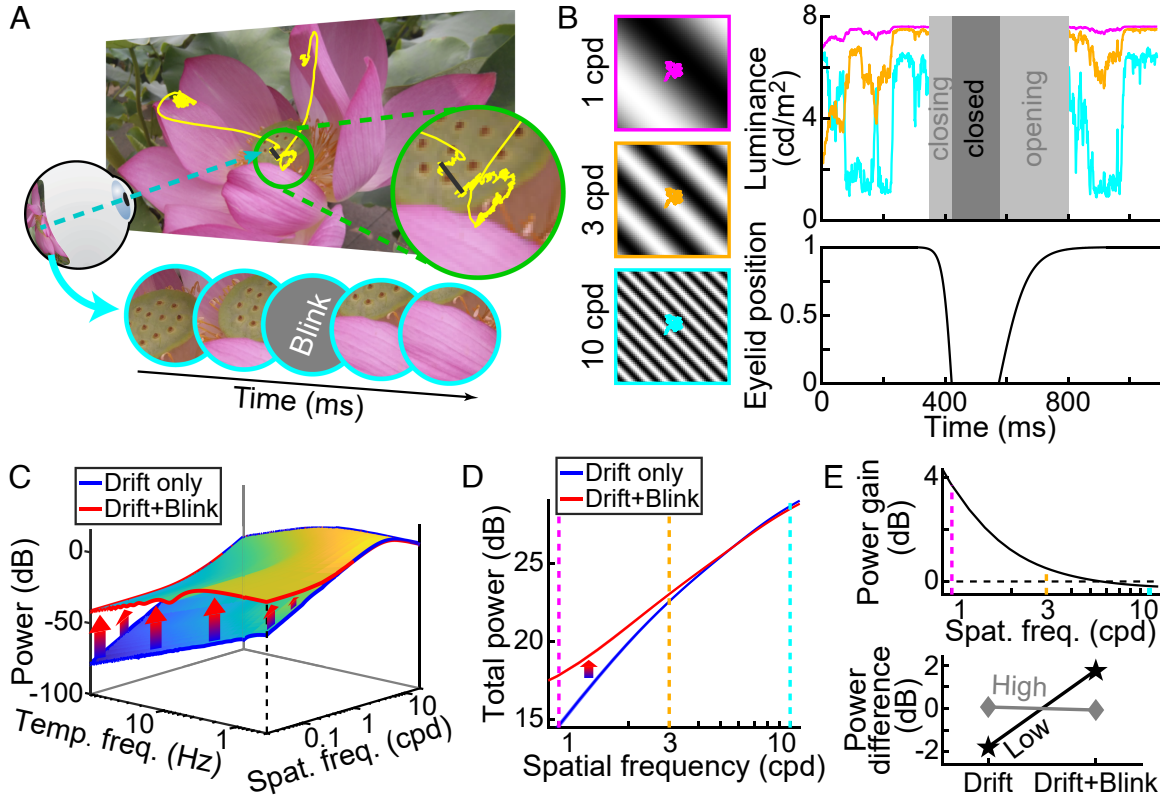

Fig. 1. Predicted consequences of blink transients. (*A*) A sequence of eye movements (yellow trace) is interrupted by a blink (dark segment), which transiently occludes the visual input to the retina (*Bottom*). The insert zooms in on the eye movements always present during fixation (ocular drift). (*B*) Luminance modulations experienced by a small retinal area (3′ diameter) during exposure to the same eye drift trajectory over gratings at three different spatial frequencies (cyan: 10 cpd; orange: 3 cpd; magenta: 1 cpd). Input changes become larger and faster with increasing spatial frequency. The *Bottom* graph shows the motion of the eyelid over the pupil. Gray bars mark the periods when the eyelid closes, fully covers the pupil, and reopens. (*C*) Power spectra of simulated visual input in the presence (Drift+Blink; surface with red edges) and absence of eye blinks (Drift only; surface with blue edges). Ocular drift was modeled as Brownian motion and blinks as transient attenuation in luminance. The arrows mark the power enhancement exerted by eye blinks. (*D*) Power of the resulting input signals within the temporal range of human sensitivity. (*E*) Blinks are expected to increase the power up to ~5 cpd (*Top* panel), yielding stronger visual input signals at low (*Bottom*; black line, 1 cpd) but not high spatial frequencies (gray, 10 cpd).

and integrated across temporal frequencies. Blinks increase the strength of input signals up to approximately 5 cycles/deg (Fig. 1*D*). These considerations suggest that, like eye movements (31), blinks may improve visibility by delivering luminance modulations that effectively increase the contrast of the stimulus on the retina. This effect is expected to occur selectively at low spatial frequencies (Fig. 1*E*) and to not depend on motor signals associated with the active production of eye blinks.

We tested these predictions in a discrimination task (Fig. 2*A*). Subjects reported whether a 3-cpd grating was rotated by 45° clockwise or counterclockwise. The spatial frequency of the grating was chosen near the peak of human sensitivity, within the range where blink transients are predicted to be beneficial. In two separate conditions, subjects were cued to blink either during the presentation of the stimulus (Stimulus-Blink condition) or before its appearance (No-Stimulus-Blink condition; namely, no blink during stimulus presentation). Great care was paid to limit sources of temporal modulations other than eye blinks, both by slowly ramping up the contrast of the stimulus and by discarding all trials in which subjects performed saccades of any amplitude, including microsaccades, during stimulus presentation.

As expected, all subjects were able to blink reliably when prompted, resulting in reaction times and blink characteristics comparable to those previously reported in the literature (9, 10, 47). The average reaction time ± SD across participants was 398 ± 93 ms (Fig. 2*B*), and the average blink duration was 165 ± 61 ms (Fig. 2*C*), which effectively shortened by ∼15% the exposure to the stimulus at maximum contrast. Reaction times and durations were not correlated ($r = -0.16$, $P = 0.674$), and their characteristics were virtually identical in the two conditions of No-Stimulus-Blink and Stimulus-Blink.

As shown in Fig. 2 *D* and *E*, eye blinks occurring during the examination of the stimulus were beneficial to the task. Despite the reduction in stimulus exposure resulting from the blinks themselves, proportions of correct responses were significantly higher when blinks occurred during the presentation of the stimulus than before its appearance, ($t(8) = 3.36$, $P = 0.010$, paired t-test; Cohen's $d = 1.12$). This perceptual enhancement was consistent across participants and reached statistical significance in the individual data from four subjects ($P < 0.034$, one-tailed Z-test corrected for continuity). Similar results were also obtained by quantifying performance in terms of the discrimination sensitivity index d', with an average improvement of 0.52 ($t(8) = 3.63$, $P = 0.007$, paired t-test; Cohen's $d = 1.21$), which reached statistical significance in the individual data from five subjects ($P < 0.048$, bootstrap one-tailed Z-test).

These results provide support to the proposal that blink transients are beneficial for vision. To confirm that blinks indeed increased the strength of visual input signals, we estimated the power spectrum of the spatiotemporal luminance flow experienced by the subjects in our experiment. For every participant, we reconstructed the visual input resulting in each trial from observing the stimulus in the presence of the recorded eye movements and—when performed—blinks, and estimated its spectral density. Without blinks, the power of the luminance modulations resulting from ocular drifts decreased approximately proportionally to temporal frequency, as previously reported in

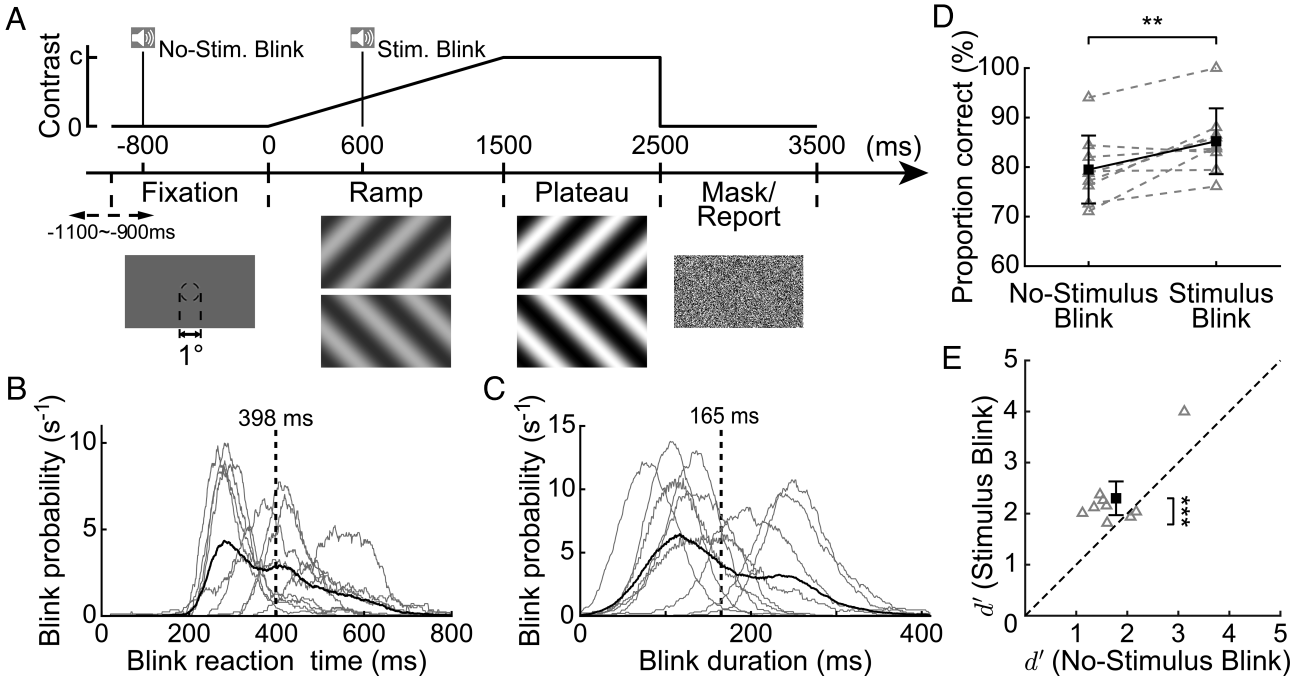

Fig. 2. Experimental paradigm and behavioral results. (*A*) Subjects were asked to report the orientation (±45°) of a full-field (21.2° × 11.9°) grating displayed in the presence or absence of blinks. A trial started with the subject fixating at the center of the monitor for a random interval (900 to 1,100 ms). The stimulus then appeared, ramping up in contrast up to an individually selected value. A white-noise mask ended the trial. A 50-ms beep instructed subjects to blink either during stimulus presentation (Stimulus-Blink condition; cue 600 ms after stimulus onset) or during the initial period of fixation before the stimulus presentation (No-Stimulus-Blink condition; cue 800 ms before stimulus onset). (*B* and *C*) Blink characteristics. (*B*) Probability distributions of blink reaction times. Both the distributions from individual subjects (gray lines) and the average distribution across observers (black line) are shown. The dashed vertical line marks the mean reaction time. (*C*) Probability distributions of blink duration, the period in which the pupil was fully covered by the eyelid. Graphic conventions are as in *B*. (*D* and *E*) Comparison of performance in the presence and absence of blinks during stimulus presentation. The two panels show proportions of correct responses (*D*) and d' (*E*). Both averages across subjects (black) and individual subjects' data (gray) are shown. Error bars represent ± one STD in *D* and 95% CIs in *E* (**$P = 0.010$, ***$P = 0.007$; paired t-tests; $N = 9$ participants).

the literature (45). In keeping with the predictions of Fig. 1*C*, eye blinks during stimulus presentation significantly increased input power over a broad band of temporal frequencies (Fig. 3*A*). As a consequence, blinks yielded a more effective signal in driving visual responses within the temporal range of human sensitivity (Fig. 3*B*). On average, power increased by approximately 22% across subjects ($t(8) = 6.732$, $P = 1.5\text{E}-4$, 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. 3 *A* 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. S1*A*). However, our power spectra do include the effects of possible offsets in gaze position measured before and after a blink (*SI Appendix*, Fig. S2*A*). As reported in *SI Appendix*, Fig. S2*B*, these gaze shifts contributed for approximately 18% of the power gain resulting from blinking ($t(8) = 8.659$, $P = 2.5\text{E}-5$, 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. 3*C*). 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. 3*D*). 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. 3 *C* and *D* suggest that blink modulations should be beneficial also for blinks that differ greatly in their

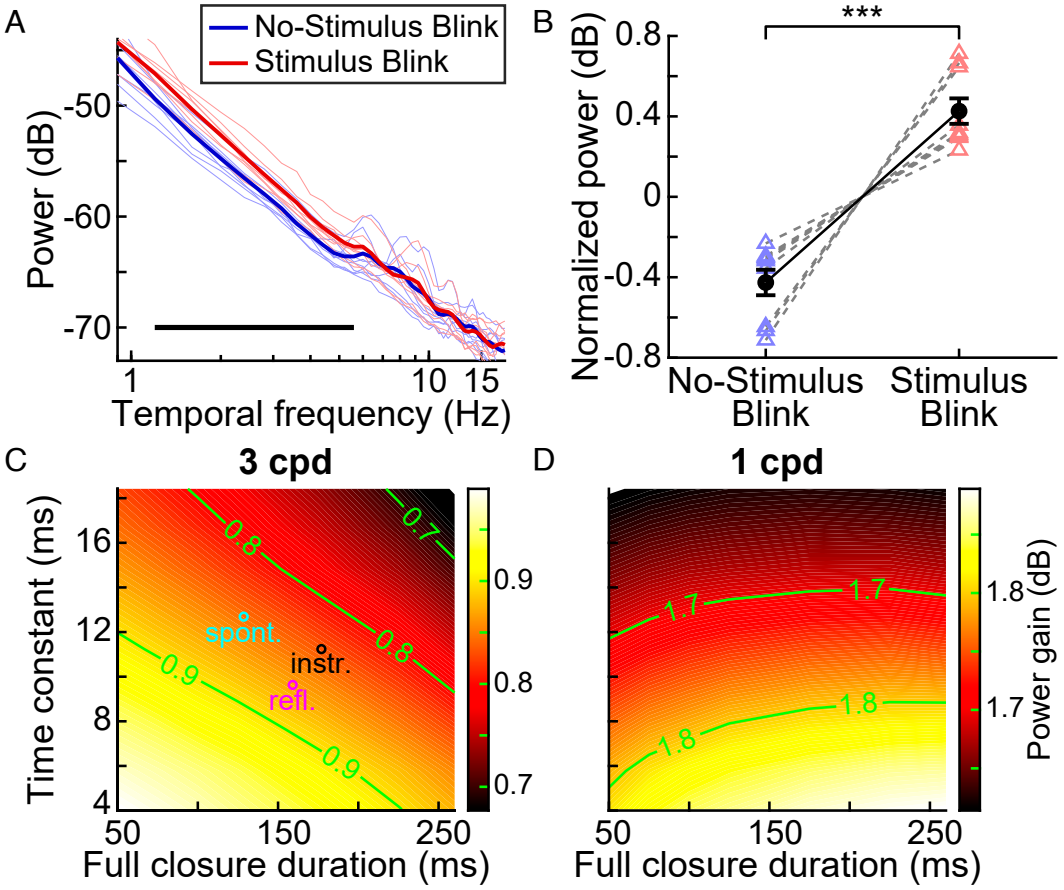

Fig. 3. Consequences of eye blinks on visual input signals. (*A*) Power spectra of the spatiotemporal luminance signals experienced by subjects in the two experimental conditions of Fig. 2. Both averages across subjects (thick lines) and the individual data (thin lines) are shown. The horizontal bar 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 ± one SEM (***$P = 1.5\text{E}-4$, 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 $P = 1.000$

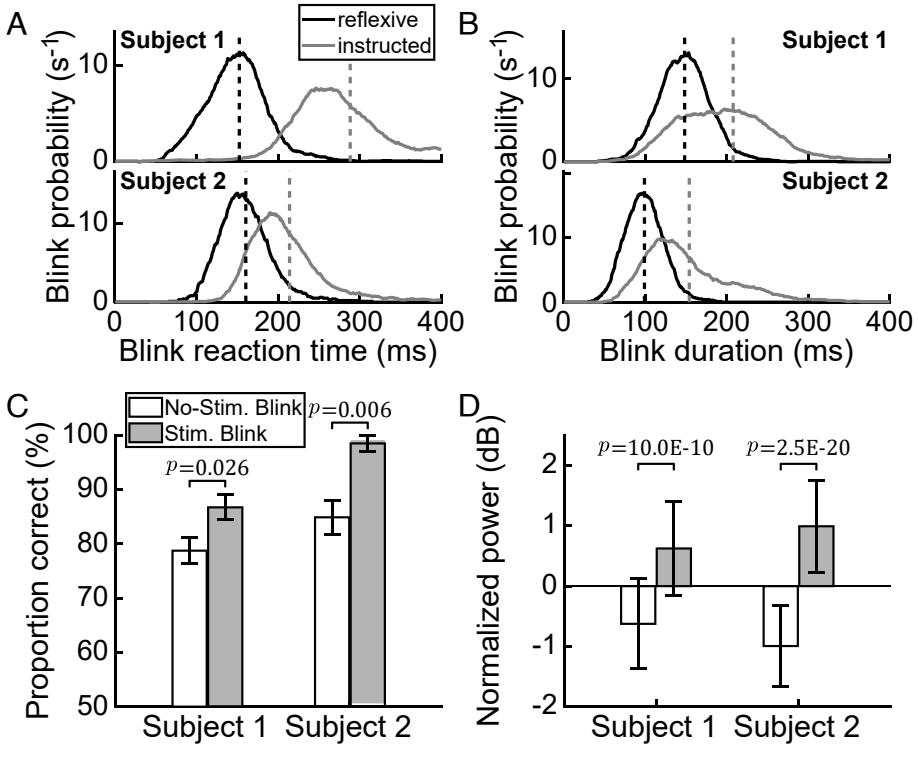

Fig. 4. Perceptual enhancement from reflexive blinks. (*A* and *B*) Comparison between the characteristics of reflexive blinks elicited by air puffs (black lines) and the instructed blinks of Fig. 2*A* (gray lines). Data represent the probability distributions for blink reaction times (*A*) and durations (*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 ± 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 ± one SEM. Probability values are the results of Z-tests corrected for continuity in *C* and two-sample t-tests in *D*.

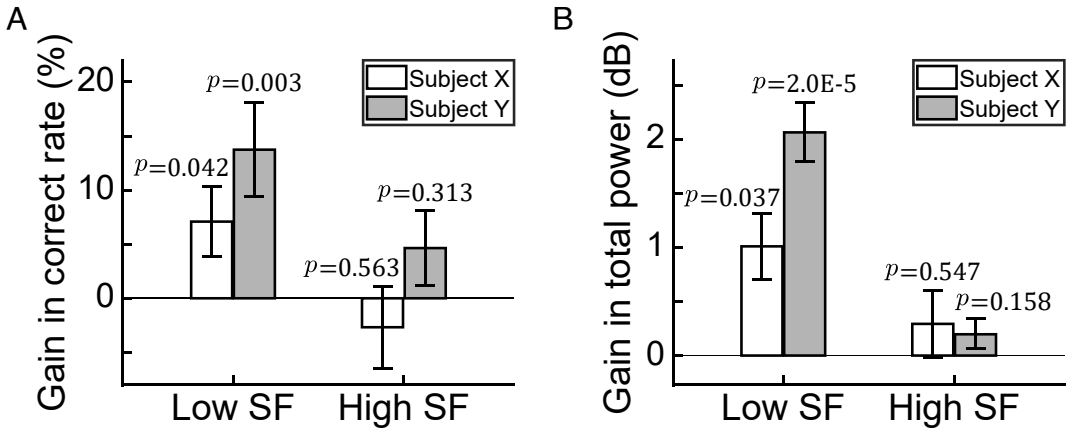

Fig. 5. Eye blinks selectively benefit low spatial frequencies. (*A*) Changes in performance between Stimulus-Blink and No-Stimulus-Blink conditions during the presentation of a 1-cpd (low spatial frequency) or 10-cpd grating (high spatial frequency). Data from two subjects are shown on separate bars. Error bars represent ± one STD. (*B*) Gain in the power of retinal stimulation resulting from blinking. Data represent the ratios of power delivered within the temporal range of human sensitivity by the eye movements and blinks recorded in the two experimental conditions. Error bars indicate ± one SEM. Probability values are the results of *Z*-tests corrected for continuity in *A* and two-sample *t*-tests in *B*.

for correct rate and d', respectively; Wilcoxon rank-sum test). This enhancement was highly consistent across subjects: All participants exhibited higher performance in the simulated-blink condition, as directly visible in their individual data (Fig. 6 *B* and *C*). Thus, passive exposure to brief luminance transients similar to those resulting from eye blinks enhances visual sensitivity.

Discussion

Humans blink their eyes frequently during normal viewing, more often than it seems necessary for refreshing the tear film (6, 7, 19). Since each blink lasts 100 to 300 ms, it is estimated that an individual can spend as much as 10% of their awake time while blinking (55). It has long been questioned how the visual system deals with the associated interruptions in the input to the retina (8, 9, 56) and whether eye blinks serve other functions besides lubricating the eye (4, 5). The results of this study provide a possible answer to these questions; rather than impairing visual processing as commonly assumed, blinks serve a computational function: They enhance sensitivity to low spatial frequencies via their luminance transients.

Specifically, our data show that a) discrimination of spatial patterns is facilitated when blinks occur during stimulus presentation (Fig. 2); and that b) blink transients deliver powerful luminance modulations within the temporal range of visual sensitivity, increasing the strength of input signals relative to sustained fixation (Fig. 3). These effects only occur for stimuli at sufficiently low spatial frequencies (Fig. 5), as predicted by a model of the spatiotemporal luminance flow to the retina (Fig. 1). Furthermore, they occur for both instructed and reflexive blinks (Fig. 4), and irrespective of whether abrupt luminance transients are actively generated by blinks or passively experienced (Fig. 6), an observation that controls for possible extraretinal contributions as well as changes in retinal image quality with blinks. The resulting perceptual improvements are considerable, sufficient in our experiments to overcome the temporal loss in stimulus exposure, so that eye blinks effectively contribute to the processing of visual information.

At first sight, our findings appear to conflict with the considerable evidence of a perceptual suppression accompanying blinks (8, 9, 11). Ingenious experiments that projected light directly onto the retina through the mouth (8) or used specula to keep the eyelids open (11, 57) have revealed an attenuation in sensitivity that precedes and outlasts the blink itself (13). These studies, however, focused on a different question than the one investigated here: how blinks affect the visibility of transient events, such as a briefly displayed probe. These events are rare under natural viewing conditions, and their luminance modulations interact with those normally resulting from blinks. In contrast, here we focused on how blinks influence the representation of a stationary scene continuously present throughout the blink, as it normally occurs outside the laboratory. To this end, in our experiments, we were careful to minimize all transients other than those caused by eye movements and the blinks themselves.

In fact, our results provide a possible explanation for the reports of previous studies that did not temporally manipulate stimuli, including the observations that blinks counteract and prevent image fading during prolonged fixation (58, 59). This effect is what one would expect from a visual system that exploits blink transients to enhance sensitivity to low spatial frequencies. Our results are also consistent with the neural modulations measured at the time of eye blinks. Intracranial electrocorticographic recordings in humans (26) indicate that the changes in visual stimulation elicited by blinks sharply modulate neural responses, with an initial drop in activity followed by a strong overshoot at stimulus reappearance. This signal is consistent with the spatiotemporal redistribution of power in Fig. 3, which predicts strong responses when the eyes reopen.

It is worth pointing out that the perceptual improvement measured in our study differs from the attentional influences previously reported in the literature (21). Blinks have been found to be beneficial in rapid serial visual presentations (RSVP), in which subjects identify target stimuli in random streams of distractors. This effect has been attributed to an attentional facilitation following blinks (20) and, unlike the enhancement we observed, only occurs with real blinks, not simulated ones. In fact, this facilitation is unlikely to be caused by the luminance modulations delivered by blinks, which, in an RSVP procedure, are swamped by the transients resulting from the rapid succession of images. In contrast, the perceptual enhancement measured in our experiments follows the structure of blink-induced luminance modulations: It occurs with both real and simulated blinks; and is present at low but not high spatial frequencies.

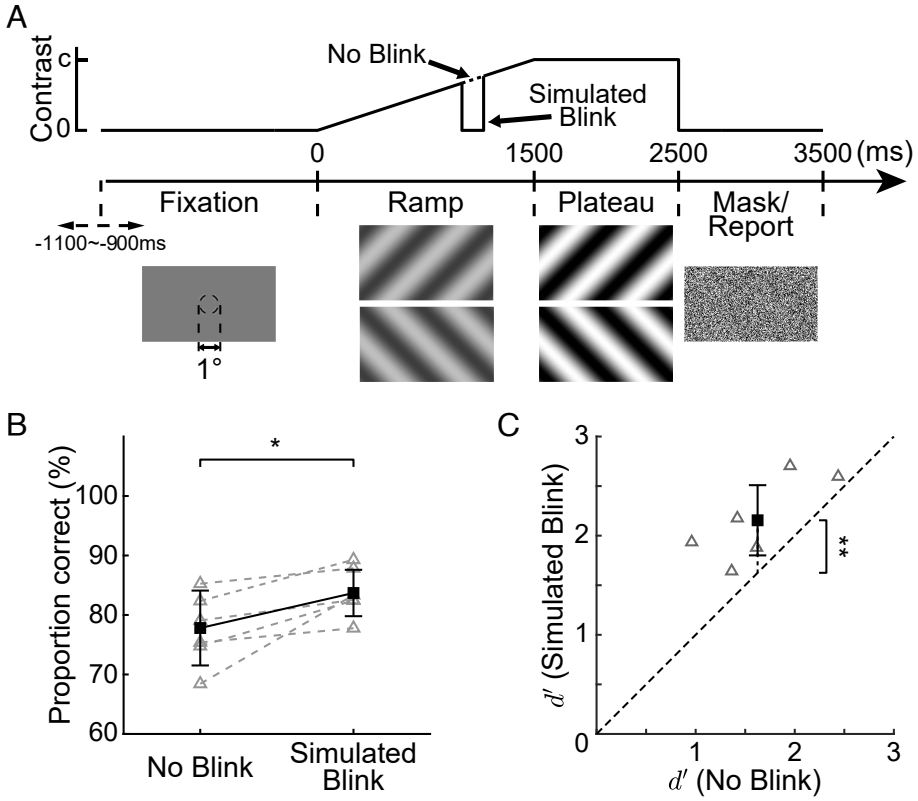

Fig. 6. Perceptual consequences of simulated blinks. (*A*) In an experiment similar to that of Fig. 2*A*, subjects were exposed to changes in the stimulus that resembled the luminance transients elicited by eye blinks. Each simulated blink consisted of a brief period of stimulus blanking with onset and 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 ± 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. S1*A*). 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. 1*D*, 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

in sensitivity that accompanies saccades (13, 15, 18), blink suppression is believed to serve the purpose of reducing visibility to abrupt changes in retinal stimulation, thus facilitating the establishment of stable visual representations. However, the possibility emerges that, rather than mechanisms for suppressing sensitivity to sensory changes, these effects may be consequences of using brief probes to test neural pathways tuned to extract information from luminance transients. That is, reduced visibility may reflect the interference between the neural responses to the probes used to measure sensitivity and the process of extracting spatial information from oculomotor-induced input transients. This hypothesis is consistent with the observations that both saccade and blink suppression are stronger for low spatial frequency (11) and achromatic stimuli (57), which is the type of information expected to be conveyed by saccade and blink transients.

In sum, we have shown that the luminance transients resulting from eye blinks enhance contrast sensitivity to low spatial frequencies, an effect that occurs despite the loss of exposure imposed by the blink itself. Thus, in addition to lubricating the eye, blinks also appear to serve an information-processing function by shaping the spatial content of the signals that fall within the temporal range of visual sensitivity. It is known that humans plan blinks to avoid missing salient events (68). Further work is needed to investigate whether blinks are also strategically executed according to the role played by their transients in the acquisition of visual information.

Materials and Methods

Subjects. Data were collected from 12 subjects (four females and eight males; average age 22 y). Nine and six subjects participated, respectively, in the main experiments of Figs. 2 and 6. Two subjects took part in each of the control experiments of Figs. 4 and 5. All subjects were paid to participate and possessed normal emmetropic vision, as assessed via a standard eye-chart test. With the exception of one of the authors, all subjects were naïve about the purposes of the experiments. The full study protocol was approved by the Research Subjects Review Board at the University of Rochester, and informed consent was obtained from every subject.

Stimuli and Apparatus. Stimuli consisted of gray-scale gratings that were either displayed over the entire monitor (visual angle of $21.2^\circ \times 11.9^\circ$; experiments of Figs. 2, 5, and 6) or within a Gabor window (SD 1.7°; experiment of Fig. 4). Stimuli were displayed for a period of 2.5 s. The frequency of the gratings was either 3 cycles/degree (cpd; Figs. 2, 4, and 6) or alternated randomly between 1 or 10 cpd in the experiment of Fig. 5. In all experiments, the gratings varied randomly across trials in both orientation ($\pm 45^\circ$ relative to the vertical meridian) and phase (0°, 90°, 180°, or 270°).

Stimuli were displayed on a calibrated LCD monitor (Acer Predator XB272) at a 200-Hz refresh rate and a resolution of 1366×768 pixels. To increase the contrast resolution beyond the 256 gray levels provided by the monitor, stimuli were rendered using simultaneously the bit-stealing (69) and the random dithering (70) techniques. This approach ensured that increments in the stimulus contrast appeared perceptually smooth even at low values. Stimuli were observed binocularly from a distance of about 160 cm, with each pixel subtending $\sim 1'$. The head of the observer was immobilized by means of a head-rest and a custom dental-imprint bite bar.

The movement of the right eye was continuously monitored by a Dual Purkinje Image eye tracker, either the analog commercial device (a generation 6 DPI; Fourward Technology) or an in-house developed digital apparatus the dDPI (71). Both systems operate by measuring the relative displacement between the first and fourth Purkinje reflections of an infrared beam and provide subarcminute resolution with artificial eyes. In the DPI, the analog oculomotor signal was first low-pass filtered at 500 Hz and then sampled at 1 kHz. The dDPI directly delivers digital measurements at either 331 Hz or 1 kHz. We measured only one eye because of the conjugacy of eye blinks (47).

Experimental Procedures. Data were collected in blocks of 50 trials. A typical experimental session consisted of five blocks, lasting approximately 1 h. Before each block of trials, the subject was carefully positioned within the apparatus and the eye tracker tuned to ensure robust tracking of the Purkinje images. Oculomotor measurements were subsequently converted into visual angles following procedures described in previous publications (66). Breaks in between blocks allowed the subject to rest.

Subjects were asked to report whether a grating was tilted 45° clockwise or counterclockwise. Each trial started with the subject maintaining fixation at the center of the monitor, indicated by four arches (radius 0.5°) on a uniformly dark gray field (luminance 3.8 cd/m^2; Fig. 2*A*). After a random interval of 900-1100 ms, the contrast of the grating gradually increased reaching an individually predetermined level over a period of 1.5 s. It then remained constant for an additional 1 s. A high-contrast white-noise mask was then displayed for 1 s over the entire monitor to end the trial, and the observer entered their perceptual response by pressing one of two buttons on a joypad.

In each trial, an auditory cue (a 50-ms beep) instructed the subject to execute a blink. In half of the trials the cue occurred during the presentation of the stimulus, 600 ms after the onset of the contrast ramp (the Stimulus-Blink condition). In the other half of the trials, the cue was given 800 ms before the ramp onset, so that the blink occurred when the stimulus was not present (No-Stimulus-Blink condition). Trials from the two conditions were randomly interleaved within each block.

The specific contrast value reached by the stimulus was adjusted for each individual subject to obtain $\sim$80% correct responses. This was achieved in a preliminary calibration procedure via the PEST method (72). In some cases, due to variability in the subject's performance, the contrast was slightly adjusted across experimental sessions to remain close to threshold. These small adjustments always occurred in both Stimulus- and No-Stimulus-Blink conditions, so that the contrast was identical in the two sets of trials. Across subjects, the mean contrast was 0.0039 in the experiment of Fig. 2, 0.0053 in Fig. 4 and 0.0033 in Fig. 6. For the experiment in Fig. 5, the mean contrasts were 0.0067 and 0.0450 for the low and high spatial frequency stimuli, respectively.

In the experiment of Fig. 4, the auditory cue instructing subjects to blink was replaced by a puff of air, so that blinks were elicited reflexively. An air spray nozzle at a distance of $\sim$2 cm from the eye directed air toward the outer canthus from the side of the body. The nozzle was connected via a flexible plastic tube and a solenoid valve to an oil-free compressor (California Air Tools 2010A). The pressure of the air puff was set to the minimum necessary to reliably elicit an eye blink by means of a flow-regulating valve attached to the compressor with a maximum pressure setting of 10 psi. An Arduino board (MEGA-2560) controlled the solenoid valve to deliver the air puff either 800 ms before (No-Stimulus-Blink condition) or 600 ms after (Stimulus-Blink condition) the stimulus onset, like the auditory cues in Fig. 2.

To examine whether abrupt luminance transients qualitatively similar to those caused by blinks are perceptually beneficial, in the experiment of Fig. 6, rather than executing a blink, subjects were exposed to sudden changes in the stimulus. Specifically, the luminance of the monitor was transiently minimized (0.02 cd/m^2) for an interval similar to that of an eye blink. Modulating the monitor intensity was sufficient for this purpose, as most of the light in the experimental room came from the monitor itself. In this experiment, we only simulated the period of full eye closure, without attempting to replicate the phases of eyelid opening and closing. Both the time of occurrence of a simulated blink and its duration were randomly sampled with replacement from each individual's pool of blink data previously collected. Each subject underwent a similar number of trials with instructed and simulated blinks. Subjects informally reported being aware of the blank period. However, since the experiment made no attempt to faithfully replicate the subjective visual experience of a blink, we did not ask subjects to report on their perception of the interruption in stimulation.

Data Analysis. Recorded eye traces were segmented into nonoverlapping periods of blinks, saccades, and drifts. Blinks were marked by the eye tracker as

the periods of disappearance of the first Purkinje reflection (P_1), which in a DPI device only happens when the cornea is covered by the eyelid. Given that in our apparatus P_1 is located in the lower portion of the pupil, the interval between P_1 disappearance and reappearance (blink duration) approximately matched the period that the pupil was fully covered by the palpebrae (*SI Appendix*, Fig. S1*A*).

Periods in which the eye moved faster than $3°/s$ were labeled as saccades or microsaccades based on the displacement amplitude, whether greater or smaller than 30′, respectively. Only trials with continuous, uninterrupted eye tracking, except in correspondence of the prompted blink, were selected for data analysis. Furthermore, to avoid other sources of luminance modulations, in the experiments of Figs. 2, 4, and 6, we discarded all trials that contained saccades of any amplitude, including microsaccades. Thus, in the trials selected for data analysis, the eye only moved via ocular drift and contained only one blink or no blinks at all. Across all experiments, the number of valid trials for an individual subject in a single condition ranged from 141 to 563.

To investigate the visual consequences of blinks, we compared performance between the Stimulus-Blink trials and the No-Stimulus-Blink trials. Performance was quantified by means of both proportions of correct responses and discriminability index, d'. The d' was estimated relative to the $+45°$ orientation, i.e., false alarms were the instances in which subjects reported this orientation when the grating was actually at $-45°$. To avoid infinite d' with hit or false alarm rates of 0 or 1, we replaced rates of 0 and 1 with $0.5/n$ and $1 - 0.5/n$, respectively, where n is the number of trials (73). Subjects were run extensively to quantify individual effects. Differences in performance between conditions were evaluated for each subject using Z-tests and on average across subjects using paired t-tests (8 dof in Fig. 2 and 5 in Fig. 6). For both the main experiments of Figs. 2 and 6, the probability that effects do not generalize to the majority of the population is smaller than 0.05 (74). The probability density distributions of blink reaction times (the delay between the onset of the auditory cue and the onset of blink; Fig. 2*B*) and blink durations (Fig. 2*C*) were estimated by averaging data over 50-ms sliding windows.

Visual Input Modeling. To examine the spatiotemporal signals resulting from eye blinks, we reconstructed the luminance flow impinging onto the retina and estimated its power within the range of human temporal sensitivity. Given an image $I(\boldsymbol{x})$, where $\boldsymbol{x}$ represents space, the visual flow $L_{I,\boldsymbol{\xi}}(\boldsymbol{x}, t)$ resulting from observing $I(\boldsymbol{x})$ during a sequence of eye movements $\boldsymbol{\xi}(t)$ and blinks can be expressed as

$$L_{I,\boldsymbol{\xi}}(\boldsymbol{x}, t) = B(t)A(t)I\big(\boldsymbol{x} - \boldsymbol{\xi}(t)\big), \qquad [1]$$

where t indicates time. $A(t)$ represents the temporal modulations resulting from the time-varying contrast profile of the stimulus in our experiments (the 1.5-s ramp followed by the 1-s plateau), and $B(t)$ models the input modulations resulting from an eye blink.

To estimate $B(t)$, we first modeled the motion of the eyelid relative to the pupil using high-speed video recordings of blinks (*SI Appendix*, Fig. S1*B*). The function

$$E(t) = \begin{cases} \dfrac{2}{1 + e^{-(t-t_c)/\tau_c}} - 1, & t <= t_c \quad \text{closing phase} \\ 0, & t_c < t < t_o \quad \text{eyelid fully closed} \\ \dfrac{2}{1 + e^{-(t-t_o)/\tau_o}} - 1, & t >= t_o \quad \text{reopening phase} \end{cases} \qquad [2]$$

assumes the value 1 when the eyelid is in its resting position for a normally clear pupil and the value 0 when the pupil is fully closed. The instants t_c and t_o represent the end of the closing phase of the blink and the start of the opening phase, respectively. The eyelid speed in these two phases is determined by the two time constants, τ_c and τ_o.

Since our experimental measurements indicate that τ_c and τ_o are strongly correlated ($r = -0.81$, $P = 1.3\text{E} - 9$; *SI Appendix*, Fig. S1*C*), we randomly sampled τ_c from a Gaussian distribution based on our video database of blinks (mean: −11.2 ms; SD: 2.8 ms) and correspondingly determined τ_o as

$$\tau_o = -2.79\ \tau_c + 3.93 + \varepsilon, \qquad [3]$$

where ε is a zero-mean Gaussian random variable (5.6 ms SD) estimated from the residual of the correlation in the experimental data of *SI Appendix*, Fig. S1*C*. Thus, the entire eyelid trajectory was modeled with just two parameters, τ_c and the duration of the period of full eyelid closure (see examples in *SI Appendix*, Fig. S1*D*).

The term $B(t)$ in Eq. **1** varied proportionally to the amount of energy reaching the retina during the course of an eye blink. Because of the proximity of the eyelid to the pupil, the irradiance on the retina was assumed to be proportional to the pupil area not occluded by the eyelid (*SI Appendix*, Fig. S1*B*):

$$B(t) = 1 - \frac{1}{\pi}\left[\arccos\big(2E(t) - 1\big) - \big(4E(t) - 2\big)\sqrt{E(t) - E(t)^2}\right], \qquad [4]$$

which varies between 1 and 0 for a clear and fully covered pupil. Eq. **4** models the eyelid as a sharp line, neglecting possible smoothing from the eyelashes. We also assumed no eyelid transparency, as only a minimal fraction (less than 2% according to (9)) of light makes its way through. However, the data in Fig. 3 *C* and *D*, which examines the power of the blink modulation as a function of eyelid speed and duration of pupil coverage, indicate that our results are very robust with respect to the dynamics of visual stimulation during blinks. Results also changed little assuming a greater eyelid transparency.

For every trial in the experiments of Figs. 2, 4, and 5, we reconstructed the visual input experienced by the subject given the stimulus (I in Eq. **1**) with its dynamics and the subject's individual contrast ($A(t)$), the recorded sequence of eye movements ($\xi(t)$), and–in the Stimulus-Blink condition–the blink modulation ($B(t)$). Given the optical arrangement of our apparatus, t_c and t_o in Eq. **2** were assumed to correspond to the blink start and end time provided by the eye tracker. To avoid possible oculomotor artifacts as the eyelid covers the pupil, eye movements in the 90 ms preceding t_c and in the 200 ms following t_o were not included in the spectral analyses. Thus, our reconstructions of visual input signals at the time of eye blinks do not include the eye movements that accompany blinks (48, 49), which could not be reliably measured by our apparatus (*SI Appendix*, Fig. S1*A*), but which presumably further increase the strength of blink transients by introducing additional luminance modulations. Our input reconstructions, however, do include the consequences of possible shifts in gaze position before and after a blink (*SI Appendix*, Fig. S2*A*), and $\xi(t)$ was assumed to move from the pre- to the postblink position when the pupil was fully covered. *SI Appendix*, Fig. S2*B* quantifies the contribution of these gaze shifts to the blink modulation by examining how power changes if the eye remained immobile over the course of the blink.

In Fig. 1, to examine how blinks alter the luminance flow impinging onto the retina during normal fixational instability, we compared the power of visual input signals delivered by gratings at various spatial frequencies in the presence and absence of blinks. Ocular drift (the term $\boldsymbol{\xi}(t)$ in Eq. **1**) was modeled as Brownian motion (44, 45) with a diffusion constant of 10 arcmin^2/s (36, 37). The term $A(t)$ was here assumed to remain constant to model the consequences of blinks on a stationary scene. $B(t)$ was modeled as in Eq. **4** with τ_c = -7 ms and a duration of 100 ms.

Spectral Estimation. In all cases, the power spectrum of the visual input was estimated by means of the periodogram:

$$L(\boldsymbol{k}, f) = \left\langle \left| \mathcal{F}(L_{I,\boldsymbol{\xi}}(\boldsymbol{x}, t)) \right|^2 \right\rangle_{I,\boldsymbol{\xi}}, \qquad [5]$$

where $\mathcal{F}$ represents the Fourier Transform operator, $\langle\rangle_{I,\boldsymbol{\xi}}$ indicates averaging across stimuli and recorded eye trajectories, and $\boldsymbol{k}$ and f are the spatial and temporal frequencies. We used the spatiotemporal factorization approach proposed in previous studies (42, 45). This method enhances spectral resolution by assuming that the image on the retina and its motion are independent–a plausible assumption on average across the visual field:

$$L(\boldsymbol{k}, f) = I(\boldsymbol{k}) \left\langle \left| \int A(t)B(t)e^{-2\pi i \boldsymbol{k}\cdot\boldsymbol{\xi}(t)} e^{-2\pi i f t} dt \right|^2 \right\rangle_{\boldsymbol{\xi}}, \qquad [6]$$

where $I(\boldsymbol{k})$ is the power spectrum of the stimulus and the second term represents the temporal redistribution of power caused by eye movements, blinks, and the dynamics of stimulus presentation. In our experiments, we used a grating at spatial frequency k_0: $I(\boldsymbol{x}) = \sin(2\pi k_0 \boldsymbol{x})$. Power spectra were estimated separately for each participant using the individual traces of blinks and recorded

eye movements (directly sampled or interpolated at 1 kHz), and then averaged across subjects.

To understand how this input signal may affect perception, we computed its power within the temporal range of human sensitivity. To this end, $L(\boldsymbol{k}, f)$ was filtered by the known temporal sensitivity function of the human visual system (46):

$$H(f) = \gamma[(i2\pi f\tau + 1)^{-n_1} - \zeta(i2\pi f\tau\kappa + 1)^{-n_2}], \quad [7]$$

where $\kappa = 1.33$, $n_1 = 9$, $n_2 = 10$, $\tau = 4.94$, $\zeta = 1$, and $\gamma = 200$ as in ref. 46. That is, we first weighted $L(\boldsymbol{k}, f)$ by $H(f)$ and then integrated across temporal frequencies. In Figs. 3*B* and 4*D*, to emphasize the similar consequences of blinks irrespective of the individual stimulus contrast, the total power for each subject was normalized by their mean in the two compared conditions, i.e., with and without blinks during stimulus presentation.

Data, Materials, and Software Availability. Anonymized experimental data and analysis code. Data have been deposited in GitHub (https://github.com/Brainsanity/YangEtAlPNAS2024) (75).

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