

Optimizing the temporal dynamics of light to human perception

Hector Rieiro^{a,b,c}, Susana Martinez-Conde^a, Andrew P. Danielson^{a,b}, Jose L. Pardo-Vazquez^d, Nishit Srivastava^{a,b}, and Stephen L. Macknik^{a,b,1}

Departments of ^aNeurobiology and ^bNeurosurgery, Barrow Neurological Institute, Phoenix, AZ, 85013; ^cDepartment of Signal Theory and Communications, University of Vigo, 36310 Vigo, Spain; and ^dDepartment of Physiology, University of Santiago de Compostela, 15705 Santiago de Compostela, Spain

Edited by Dale Purves, Duke-NUS Graduate Medical School, Singapore, Republic of Singapore, and approved October 12, 2012 (received for review July 30, 2012)

No previous research has tuned the temporal characteristics of light-emitting devices to enhance brightness perception in human vision, despite the potential for significant power savings. The role of stimulus duration on perceived contrast is unclear, due to contradiction between the models proposed by Bloch and by Broca and Sulzer over 100 years ago. We propose that the discrepancy is accounted for by the observer's "inherent expertise bias," a type of experimental bias in which the observer's life-long experience with interpreting the sensory world overcomes perceptual ambiguities and biases experimental outcomes. By controlling for this and all other known biases, we show that perceived contrast peaks at durations of 50–100 ms, and we conclude that the Broca–Sulzer effect best describes human temporal vision. We also show that the plateau in perceived brightness with stimulus duration, described by Bloch's law, is a previously uncharacterized type of temporal brightness constancy that, like classical constancy effects, serves to enhance object recognition across varied lighting conditions in natural vision—although this is a constancy effect that normalizes perception across temporal modulation conditions. A practical outcome of this study is that tuning light-emitting devices to match the temporal dynamics of the human visual system's temporal response function will result in significant power savings.

psychophysics | experimental design

Artificial lighting ranks among the most significant of human technological advances. Few inventions have had an equivalent impact on the billions of people who use it on a daily basis (1). Despite artificial lighting accounting for ~22% of the electrical power consumption in the United States (2), light-emitting devices are not tuned to the temporal dynamics of vision. The temporal characteristics of a visual stimulus are critical to its perception (3–6), although the role of stimulus duration in perceived contrast has been debated since the publication of Bloch's (7) and Broca and Sulzer's (8) contradictory studies at the turn of the 20th century (Fig. 1A). Bloch's results indicated a monotonic increase in perceived brightness up to stimulus durations of 50 ms. Shortly thereafter, dozens of experiments were built on Bloch's research to show that this effect plateaued as duration increased over 100–150 ms (9). Broca and Sulzer, instead, found a peak in perceived contrast with increased duration. Bloch's result prevailed as the accepted model of basic temporal vision (10, 11), so much so that it was elevated to the status of a perceptual law. Yet the discrepancy between Bloch's law and the Broca–Sulzer effect remains unexplained.

All scientific measurements are susceptible to bias (12). In vision research, even first-time experimental subjects who are naive to a study's hypothesis have spent their lives analyzing ambiguous percepts and developing expertise through trial-and-error, at times unconscious of any perceptual learning (13). None of the standard methods to address experimental/subject bias (e.g., use of naive subjects, stimulus randomization, double-blind analyses) eliminate the bias caused by the subject's inherent expertise: naive subjects lack knowledge about the hypothesis, but remain knowledgeable

about stimulus conditions that they have previously addressed in life, a problem that randomization cannot solve. We call this confound "intrinsic expertise bias." Because no studies have previously controlled intentionally for this form of bias, many experimental observations fundamental to current perceptual models may be inaccurate, including the experimental bases for prevalent models of brightness and contrast perception. Here we developed an experimental design to explicitly control for intrinsic expertise bias and thus address the outstanding contradiction in perhaps the most fundamental issue in temporal vision: the effect of stimulus duration on perceived contrast. By solving this discrepancy, we further determine how to best tune light-emitting devices to the temporal characteristics of the human visual system to reap significant power-saving advantages.

Results

Single-Flash Experiment. We asked naive subjects to perform a counterbalanced two-alternative forced choice contrast discrimination task (Fig. 1B) to establish the unbiased relationship between stimulus duration and contrast perception (14) and to determine if intrinsic expertise bias explains the discrepancy between Bloch's law and the Broca–Sulzer effect. The study's participants discriminated between a "comparator"—a stimulus that did not change in physical contrast (i.e., 40%) but varied in duration—and a "standard"—a stimulus that did not change in duration (i.e., 500 ms) but varied in contrast (Fig. 1C). We assessed the effect of duration on the comparator's contrast by comparing the reported contrast to that of the standard. The pilot studies revealed an important caveat: the experimental design, albeit counterbalanced in the traditional sense, allowed subjects to distinguish between the comparator and the standard. This distinction was possible because—despite both stimuli being spatially identical—the standard always had a single duration and the comparator always had a single contrast. Over the course of the experiment, the subjects learned, either consciously or unconsciously (13), to discern between the two sets of stimuli, allowing them to apply intrinsic expertise bias, i.e., their intrinsic perceptual hypotheses about how stimulus duration affects perceived contrast.

To counteract the subjects' inherent expertise bias, we developed a principle of experimental design: the principle of stimulus equivalence. Following this principle, the comparator and the standard must be indistinguishable from each other, thereby making it impossible for the subjects to apply intrinsic expertise bias. We enacted this principle by running four different randomly interleaved versions of the experiment described above,

Author contributions: H.R., S.M.-C., J.L.P.-V., and S.L.M. designed research; H.R., A.P.D., J.L.P.-V., and N.S. performed research; H.R. analyzed data; and H.R., S.M.-C., and S.L.M. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence should be addressed. E-mail: macknik@neuralcorrelate.com.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1213170109/-DCSupplemental.

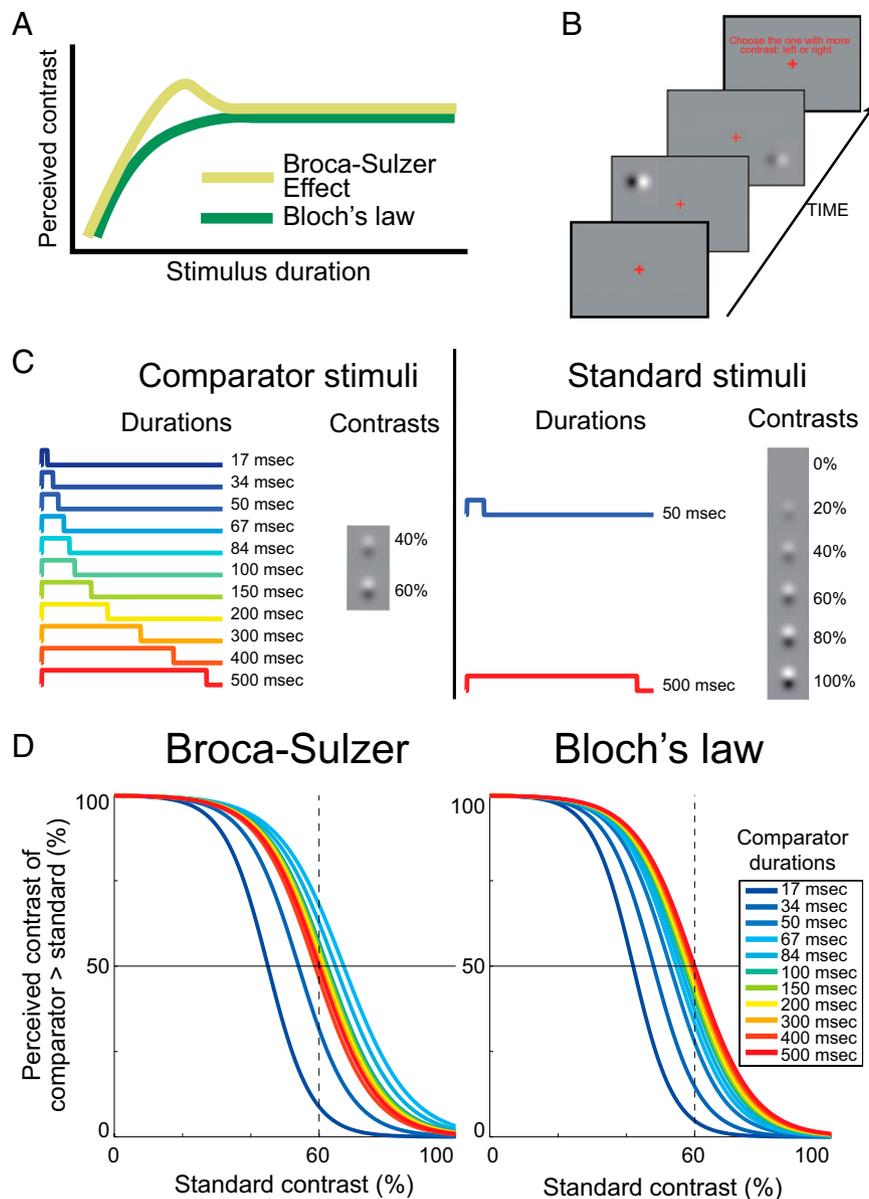


Fig. 1. Experimental design and potential outcomes. (A) Two competing models of temporal vision. Bloch's law postulates a monotonic increase in perceived contrast with increased duration, whereas the Broca-Sulzer effect postulates a peak in perceived contrast with increased duration. (B) Temporal structure of a trial. Subjects fixated on a central cross, and two Gabor patches flashed in succession on opposite sides of the screen. Following stimulus presentation, subjects reported which Gabor had higher contrast. (C) Physical contrasts and stimulus durations used for the comparator and standard stimuli. In the unblocked experiment, all possible combinations were randomized. In the blocked experiment, the different conditions were grouped into four sequential sets of trials or blocks, each with a constant comparator contrast and standard duration and an internally randomized trial sequence. (D) Psychometric curve models of the two possible experimental outcomes, color-coded for different comparator durations. If contrast perception has a peak, as in the Broca-Sulzer effect, the curves will first shift right and then left as stimulus duration increases. If contrast perception follows Bloch's law, the curves will shift monotonically to the right.

with two different comparator contrasts (with varied durations) and two different standard durations (with varied contrasts) (Fig. 1C). The structure of the experimental design was too complex for subjects to identify the comparator versus the standard, allowing us to determine the role of stimulus duration in contrast perception in an unbiased fashion (Fig. 1D). We called this experiment "unblocked" because all trials were completely randomized and not blocked in any way.

Next, subjects were tested in a blocked version of the same experiment, in which the four different permutations of comparator and standard were grouped into separate blocks (although otherwise the conditions were randomized across trials

within blocks). The unblocked experiment prevented the distinction between comparator and standard, but the blocked experiment did not. Therefore, in the blocked experiment, naive subjects could potentially apply intrinsic expertise bias to the perceived contrast of the stimuli.

The unblocked (i.e., bias-free) experiment resulted in a peak in contrast perception as a function of duration, consistent with the Broca-Sulzer effect (Fig. 2A and Fig. S1). The blocked experiment (conducted with the same naive subjects with the same randomized, but blocked, stimuli), produced a response pattern consistent with Bloch's law (Fig. 2A and Fig. S2). Because the two experiments were identical except for the presence/absence

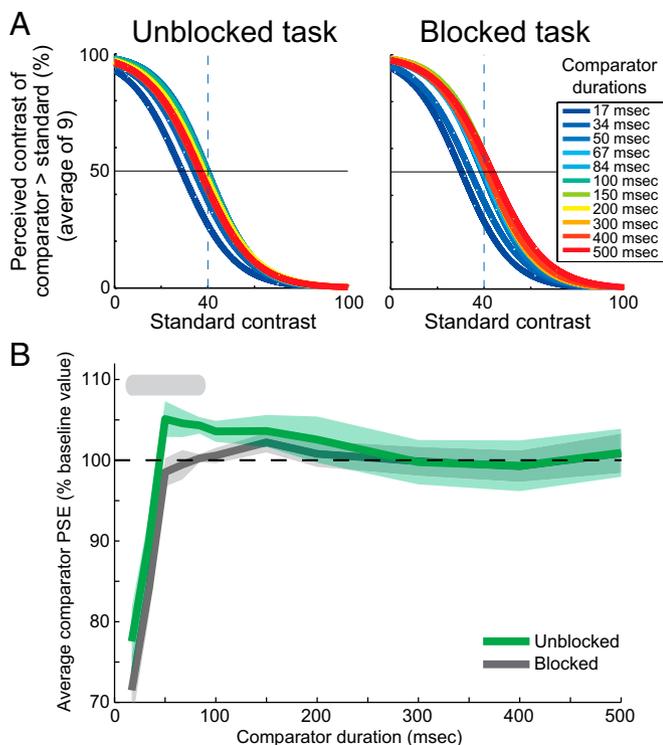


Fig. 2. Contrast perception peaks with stimulus duration. (A) Psychometric curves, averaged across subjects ($n = 9$) for the unblocked and blocked experiments, with a 50-ms duration standard and a 40% contrast comparator (see Figs. S1 and S2 for full results). The unblocked results follow Broca and Sulzer's predictions, whereas the blocked results are consistent with Bloch's law. (B) PSE for the comparator as a function of its duration (average \pm SE from the mean). The unblocked results (green) reveal a peak in perceived contrast as a function of duration. The blocked results (gray) indicate that Bloch's law is an artifact of uncontrolled intrinsic expertise bias. Horizontal bar at top indicates the range of durations showing a statistically significant difference between the unblocked and blocked experiments.

of blocking, the difference in results must be due to the naive subjects' ability to distinguish between the comparator and the standard and apply their own a priori conscious or unconscious interpretations of contrast based on stimulus duration. Thus, uncontrolled intrinsic expertise bias explains the discrepancy between Bloch's law and the Broca–Sulzer effect.

We quantified and statistically verified the findings by calculating the points of subjective equality (PSE) between stimulus durations (the 50% crossing points for each curve in the unblocked and blocked data from Fig. 2A; see *Materials and Methods* for details on the data analysis). PSEs differed significantly between the unblocked and blocked experiments for stimulus durations of 50–100 ms [two-tailed paired t test, controlled for false discovery rate (FDR) (15); $q = 0.05$] (Fig. 2B). The perceived contrast of unblocked stimuli with durations of 50–100 ms, moreover, was $\sim 5\%$ higher than the actual contrast (two-tailed t test, FDR corrected, $q = 0.05$). These findings indicate that contrast perception of single flashes is maximized for a small range of stimulus durations. This optimal range may be exploited to tune perception to maximize energy savings. Stimuli outside this peak require more energy; thus, they are less energy efficient for human perception.

If it is correct that criterion effects are responsible for the discrepancies in results across previous studies of Bloch's law versus the Broca–Sulzer effect, it follows that the variability between subjects in our blocked (and relatively uncontrolled) design should be higher than the same subjects' responses in the unblocked design (which was controlled for intrinsic expertise

bias). That is, if our hypothesis is correct, most subject responses should follow the Broca–Sulzer effect in the unblocked design, whereas subject responses should sometimes exhibit Bloch's law and sometimes exhibit the Broca–Sulzer effect in the blocked design. To test this prediction, we compared, for each individual subject, the maximum PSE (i.e., the perceptual peak response) for comparator durations ranging from 50 to 100 ms to the average PSE response for a 500-ms comparator. In the unblocked design, eight of nine subjects peaked higher than the 500-ms comparator, a significantly different response from what is expected if subjects were maximally variable and split between those following Bloch's law versus the Broca–Sulzer effect (binomial test, $P < 0.05$). By comparison, only three of nine subjects did so in the blocked design. This latter proportion was not significantly different (binomial test, $P > 0.05$) from what would be expected from an even split in the population. Thus, the blocked results are less cohesive and more variable than the unblocked results.

Flicker Experiment. The experiments above presented single flashes as stimuli: these stimuli are relevant to optimizing pulsed warning lamps and other single-pulse lighting systems. However, most modern artificial lighting relies on alternating current (AC)- or direct current (DC)-driven continuous or flicker-fused illumination systems. We set out to test whether continuously flickering stimuli also might benefit from tuning to the temporal dynamics of human vision. We recruited a different set of naive subjects to perform an unbiased contrast discrimination task, equivalent to the unblocked task in the single-flash experiments above, but using flicker-fused stimuli in which the on-period (duty cycle) of the flicker varied, whereas the duration of the off-period (interstimulus interval) remained constant at 17 ms to ensure that all flickering stimuli were perceptually fused and appeared continuous (16–18) (Fig. 3A). Previous research has shown that visibly flickering stimuli (as opposed to flicker-fused stimuli) appear enhanced in contrast with the same stimuli presented continuously, as in the classical Brucke–Bartley effect and other subsequent studies (17–22), but contrast enhancement of flicker-fused stimuli, like the stimuli used here, has not been reported previously. A previous study found contrast enhancement in sinusoidally modulated stimulus using a luminance-matching paradigm (23). Wu et al. (23) reported conducting pilot experiments with both blocked and unblocked designs and finding similar effects, although the results were not presented in the article. Wu et al. made no reference to attempting to control for intrinsic expertise bias, and in the final experiments they used a blocked structure and also the authors as subjects, so the study included several potential sources of experimental bias. Our results indicate an optimal perceived contrast of flicker-fused stimuli as a function of a peak in the duty cycle (Fig. 3B and C and Fig. S3).

Discussion

Bloch's law (i.e., the no-peak hypothesis) has remained the primary dogma in the field of temporal vision under both single-flash and flickering conditions, to the extent that quantitative models reject the existence of the Broca–Sulzer effect (i.e., the peak hypothesis) (11, 24). However, to the best of our knowledge, no previous study has fully controlled for subject criterion, including the intrinsic expertise bias. The presence of the Broca–Sulzer effect in some of the previous studies, but not in others, suggests that the lack of adequate criterion controls can lead to sporadic results. Here we show, by controlling for all known sources of experimental bias, that contrast perception can be enhanced by carefully choosing the temporal dynamics of the stimulus under single-flash and flickering conditions. We also show that failure to control for even a single criterion confound, such as intrinsic expertise bias, can account for Bloch's law. We propose that the literature is strewn with studies having dissimilar results, such as some previous studies that exhibit responses following Bloch's

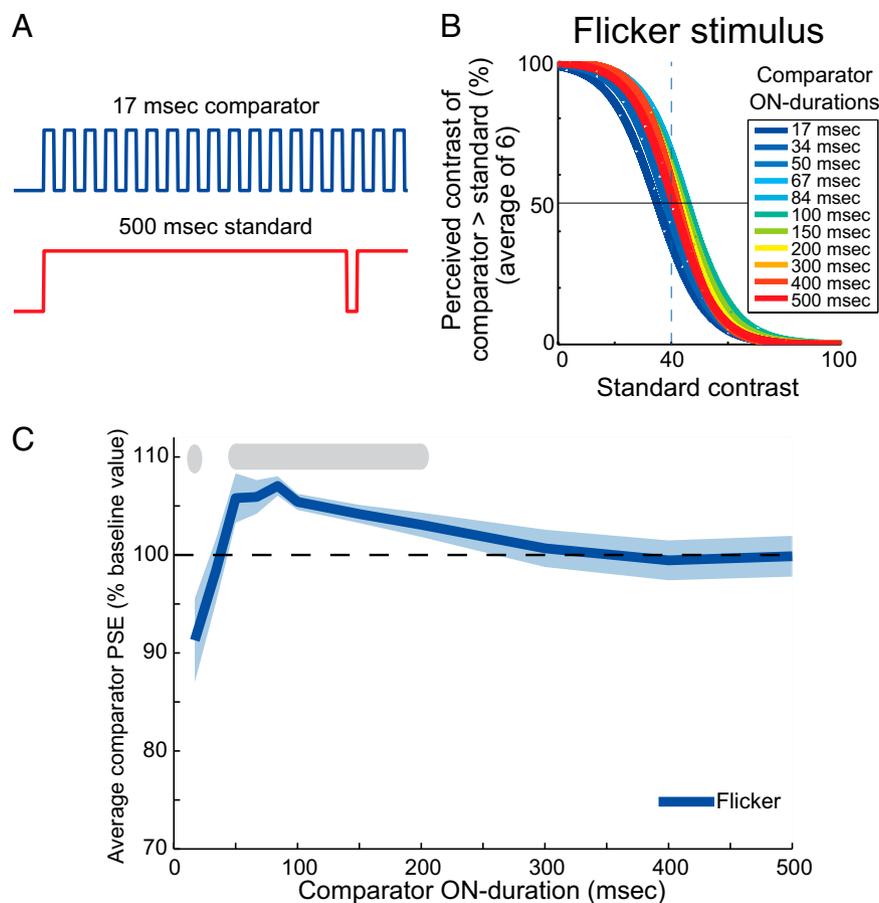


Fig. 3. Perceived contrast of a flickering stimulus peaks with flash duration. (A) Two sample time courses of the flickering stimuli, with the high level of the square-wave signal representing periods of time during which the stimulus was on and the low level periods of time during which the stimulus was off. Interstimulus interval was kept at 17 ms for all duty cycles, ensuring flicker fusion of all stimuli tested. (B) Average ($n = 6$) psychometric curves for the conditions having a 500-ms flash length for the standard and a 40% comparator (see Fig. S3 for full breakdown of results by subject). The curves indicate a peak in perceived contrast as a function of increasing flicker duty cycle (Fig. 1 A and D). (C) PSE as a function of the on-time internal to each cycle of flicker (average \pm SE from the mean). Perceived contrast peaks for flash durations between 50 and 200 ms. Shaded gray bar indicates the points that differ significantly from baseline.

law, some that follow the Broca–Sulzer effect, and others that exhibit a mix of both, in part due to the lack of control of the intrinsic subject bias (as we find in our own blocked and therefore uncontrolled results) or other criterion experimental biases. Therefore, our results not only explain an important phenomenon in brightness perception and natural vision, but also reveal a critical aspect of experimental design that must be taken into account for accurate perceptual measurement.

Previous studies have suggested that the Broca–Sulzer effect is restricted to low spatial-frequency gratings or uniform-brightness fields (11, 25, 26), yet our experiments produced the Broca–Sulzer effect and Bloch’s law with spatially identical stimuli, proving that differential spatial frequency cannot explain the effects found here. We note that these previous studies were not properly controlled for subject criterion; thus, the differential effects of spatial frequency, if any, may not have been measured accurately.

One previous study suggested that different classes of observers exist (27) and that some of them fail to report the Broca–Sulzer effect or report it under specific conditions. Bowen and Markell (27) proposed that this could explain why some experiments find a peak in perceived contrast whereas others do not and pointed to subject criterion as a likely explanation of the differences. We have now shown that subject criterion is a factor by asking subjects to perform two versions of the same experiment, differing only on one type of criterion control between conditions. Our data

indicate that Bloch’s law applies only when criterion controls are not complete and that even those subjects whose perception follows Bloch’s law in the uncontrolled design exhibit responses following the Broca–Sulzer effect when criterion controls are complete. Therefore, we conclude that it is the experimental design, and not the class of observer, that best explains the result.

It has always been clear that at very short stimulus durations (i.e., less than ~ 100 ms) the visual system cannot differentiate between duration and contrast, and so perceived contrast rises linearly with duration as light is integrated by the visual system, as seen in the early linear phase of both Bloch’s law and the Broca–Sulzer effect. However, why do our brains apply Bloch’s law to our perception, such as in experiments that are uncontrolled for intrinsic expertise bias, if contrast instead peaks as a function of duration? The answer may be that our brains function to ensure that objects seen under different lighting conditions will have the same appearance to minimize errors in object recognition, such as in brightness and color constancy effects (28, 29). Despite our finding that short-duration flashes are perceived as brighter, our brains appear to decrease the perceived contrast of objects illuminated by short-duration flashes so that, when the same object is illuminated under long-duration stable lighting conditions, such as direct sunlight, the object remains easily recognizable. Brightness constancy is desirable from an evolutionary point of view, as many objects are commonly viewed both under dim light (at dusk

or indoors) and under direct sunlight. It follows that brightness constancy across different temporal lighting conditions (for example, under the flickering conditions of a forest canopy versus on the savannah) would further promote high-quality object recognition. We propose that, although temporal responses fundamentally follow the Broca–Sulzer effect as a function of the underlying neurophysiology, the visual system has evolved a temporal contrast constancy mechanism: Bloch's law. This constancy effect normalizes perception so that a given object retains its appearance across different temporal lighting conditions. As with all constancy mechanisms, Bloch's law thus serves natural vision to enhance object recognition despite the visual system's differential response to stimuli of different durations. This brightness constancy effect adjusts perceived contrast on the basis of the temporal dynamics of light. Humans are therefore intrinsically expert at interpreting the temporal dynamics of their lighting conditions to apply Bloch's law as needed, such as within experiments that are not specifically controlled for such an eventuality.

However, the fact that apparent contrast does peak as a function of tuned temporal dynamics can be applied to light-emitting devices to save energy. It follows from our results that much of the prevailing AC and DC light sources are suboptimal for human perception. Modern AC lighting and visual presentation equipment typically flicker in relation to the 50- to 60-Hz AC power grid. A single flash from any of this equipment has a typical duration of 4–17 ms, a range lower than those tested here. As the perceived contrast of a 17-ms duration flash is ~30% lower than optimal, contrast perception from modern AC lighting devices is impoverished.

In contrast, DC lighting sources, such as non-pulse-width-modulated light-emitting diodes, do not modulate light temporally. This is also suboptimal, because contrast perception is not well tuned for stimulus durations over 200 ms (Figs. 2B and 3C). We propose that introducing optimal duration pulses of ~67 ms, combined with a powered-down period in each pulse cycle of ~10 ms or less, would result in ~13% power savings and ensure that the pulses of light fuse perceptually and are not seen as flickering (16–18). Powering down the device for a fraction of each pulse, and combining the savings with the increase in perceived contrast at the optimal pulse widths that are afforded by the visual system, would result in power savings of ~20% in modern DC lighting without the appearance of flicker. In summary, one could optimally tune lighting systems to the temporal dynamics of human vision by making them flicker at ~13 Hz with an 87% duty cycle without degrading perception and saving a significant amount of energy in the process.

The improvements described here would not be possible in a scenario in which Bloch's law holds. Under Bloch's law, brightness linearly increases for durations under 100 ms and then plateaus. So, for example, a 10-ms flash requires half the energy to be generated than a 20-ms one, but also has half the perceived brightness. The fact that perceived brightness is reduced for shorter durations would make it necessary to increase the luminous intensity, removing any potential energy savings. Therefore, in these conditions, the energetic cost of generating perceptually equal flashes would be constant when flash duration is under 100 ms, with the costs going up with longer flashes. The perceptual peak in the contrast–duration relationship of the human visual system that we report here allows for energy savings because the peak represents an optimal duration for contrast perception.

Why should we optimize stimulus duration to the temporal dynamics of human vision when our visual systems will decrease the perceived contrast to match Bloch's law? The answer is that constancy mechanisms make objects under different lighting conditions appear unchanged even though the image of the object projected in the retina is physically different (28, 29). Previous research has shown that perceived brightness of any light returned to the eye is more closely correlated to what is assumed to be its origin than with its actual physical magnitude (29), but

object recognition nevertheless functions better with bright light than with dim light due to the higher signal-to-noise ratio in the former scenario. Our results suggest that humans likewise will benefit from the increased contrast perception and visibility, and increased power savings, when performing tasks such as reading, independently of whether or not the visual system adjusts the appearance of the light according to Bloch's law. The effects described here are relevant to natural vision in our everyday lives and, by extension, will afford energy savings under any light-emitting device. Whereas highly controlled and artificial experimental conditions are needed to undermine temporal brightness constancy mechanisms (Bloch's law) and expose the Broca–Sulzer effect as the human visual system's genuine temporal vision response function in the laboratory, observers will benefit from improved perception under peak temporal durations in the natural world.

Materials and Methods

Single-Flash Experiment: Stimulus and Task. Nine naive subjects performed a two-alternative forced choice task in which they reported, via keyboard button press, which of two Gabor patches, presented in sequence, the standard and the comparator, had higher contrast compared with the 50% luminance gray background, on a Barco Reference Calibrator V video monitor (Barco) (Fig. 1B).

The Gabor patches were created by multiplying a sinusoidal grating, 0.5 cycles/degree, by a Gaussian function with a SD of 1.5°. The standard stimulus had two possible durations (50 and 500 ms) and six different contrasts (0, 20, 40, 60, and 80–100% peak-to-trough.) The comparator had 11 different durations (17, 34, 50, 67, 84, 100, 150, 200, 300, 400, and 500 ms) and two possible contrasts (40 and 60%) (Fig. 1C). Subjects fixated on a small red cross centered on the screen; eye position was monitored in real-time with an EyeLink 1000 (SR Research) video-based system. Improper fixation—defined as gaze deviation from the fixation cross of more than 2° of visual angle—or blinks—defined as when no eye position signal was available because the pupil was occluded by the lid—resulted in an aborted trial and random reinsertion of the trial type into the trial sequence. To prevent adaptation across trials, the comparator was randomly positioned 8° of visual angle to either the left or the right of the fixation cross in either the upper or the lower quadrant of the screen, and the standard was positioned in the opposite quadrant. Stimulus position (up–down versus left–right) was counterbalanced. The comparator and the standard were presented sequentially to ensure that their relative durations could not be directly compared. Presentation order of the comparator and standard within each 2-s trial, as well as each Gabor's orientation, were randomized. Each subject was tested for 10 trials per condition. In the single-flash experiments, each subject was tested in each of the 1,056 experimental conditions once per session for 10 sessions (1 per day), resulting in 10 trials per condition tested over a total of 10 sessions for each experiment (20 sessions total for both the unblocked and the blocked single-flash experiments). Experiments were carried out under the guidelines of the Barrow Neurological Institute's Institutional Review Board (protocol 04BN039), and written informed consent was obtained from each participant.

Each subject was tested first in the unblocked and then in the blocked experiment (see *Results* for description of unblocked versus blocked experiments). The order of the blocks in the blocked experiment was as follows: (i) 50-ms long standard, 40% contrast comparator; (ii) 50-ms long standard, 60% contrast comparator; (iii) 500-ms long standard, 40% contrast comparator; and (iv) 500-ms long standard, 60% contrast comparator.

Flicker Experiment: Stimulus and Task. A different set of subjects ($n = 6$) participated in the flicker experiment. Comparator and standard stimuli flickered simultaneously on the screen for 2 s, with a flicker structure that varied as a function of stimulus on- and off-time (Fig. 3A). The possible contrasts for both stimuli were the same as in the single-flash experiment. For the temporal parameters, we chose durations for the on-periods of the stimuli that were the same as in the single-flash experiment, whereas the off-time (interstimulus interval) was kept constant at 17 ms to ensure flicker fusion of the stimuli. Therefore, this experiment had the same number of conditions as the single-flash experiment. The ordering of conditions in this experiment was completely randomized, as in the unblocked single-flash experiment. Each subject participated in 10 sessions of the experiment.

Data Analysis. We collapsed the subjects' reports across the different stimuli positions on the screen, resulting in a total of 40 trials per condition for each subject. To create psychometric functions, we fit a logistic regression (one fit per comparator duration) to the comparator choice probability versus standard contrast plots (Figs. S1–S3). The 50% crossing point of each psychometric curve indicated the standard contrast necessary to achieve the equivalent perceived contrast of the comparator (i.e., the PSE). To average the PSEs across the different condition sets, we normalized the PSEs across the different groups of conditions to control for the fact that different conditions crossed the 50% point at different standard contrasts. We used the average PSE for the three longest comparator durations on each condition set as the baseline and calculated the percentage increase over this baseline before averaging across subjects (Figs. 2B and 3C).

Statistical Analysis. The differences between PSEs in the blocked and unblocked experiments, and between the PSEs from these two experimental designs and the baseline, were tested using a two-tailed *t* test, with multiple hypothesis testing controlled for using the FDR (14) ($q = 0.05$). We used a binomial test to compare the between-subject variability in the blocked and unblocked designs.

ACKNOWLEDGMENTS. We thank M. Ledo, M. Stewart, and I. Gomez-Caraballo for their technical support and assistance. H.R. was funded by Fundación Ibercaja. J.L.P.-V. was funded by the Spanish Ministry of Education. The project was funded by grants from the Barrow Neurological Foundation to S.L.M. and S.M.-C.; Catholic Healthcare West SEED awards; Science Foundation Arizona (CAA 0091-07); and National Science Foundation Grant 0726113 (to S.L.M.).

- Williams PE, Mechler F, Gordon J, Shapley R, Hawken MJ (2004) Entrainment to video displays in primary visual cortex of macaque and humans. *J Neurosci* 24(38):8278–8288.
- U.S. Department of Energy (2002) *U.S. Lighting Market Characterization. Vol. I: National Lighting Inventory and Energy Consumption Estimate*. http://apps1.eere.energy.gov/buildings/publications/pdfs/ssl/lmc_vol1_final.pdf.
- Macknik SL, Livingstone MS (1998) Neuronal correlates of visibility and invisibility in the primate visual system. *Nat Neurosci* 1(2):144–149.
- Macknik SL, Haglund MM (1999) Optical images of visible and invisible percepts in the primary visual cortex of primates. *Proc Natl Acad Sci USA* 96(26):15208–15210.
- Macknik SL, Martinez-Conde S, Haglund MM (2000) The role of spatiotemporal edges in visibility and visual masking. *Proc Natl Acad Sci USA* 97(13):7556–7560.
- Macknik SL, Martinez-Conde S (2004) Dichoptic visual masking reveals that early binocular neurons exhibit weak interocular suppression: Implications for binocular vision and visual awareness. *J Cogn Neurosci* 16(6):1049–1059.
- Bloch AM (1885) Experience sur la vision. *Comptes Rendus de Seances de la Societe de Biologie, Paris* 37:493–495.
- Broca A, Sulzer D (1902) La sensation lumineuse en fonction du temps. *J. Physiol (Paris)* 4:632.
- Blondel A, Rey J (1911) Sur la perception des lumières brèves à la limite de leur portée. *J Phys Theor Appl* 1:530–550.
- Gorea A, Tyler CW (1986) New look at Bloch's law for contrast. *J Opt Soc Am A* 3(1):52–61.
- Georgeson MA (1987) Temporal properties of spatial contrast vision. *Vision Res* 27(5):765–780.
- Goldiamond I (1958) Indicators of perception. I. Subliminal perception, subception, unconscious perception: An analysis in terms of psychophysical indicator methodology. *Psychol Bull* 55(6):373–411.
- Watanabe T, Náñez JE, Sasaki Y (2001) Perceptual learning without perception. *Nature* 413(6858):844–848.
- Gori S, Spillmann L (2010) Detection vs. grouping thresholds for elements differing in spacing, size and luminance. An alternative approach towards the psychophysics of Gestalten. *Vision Res* 50(12):1194–1202.
- Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: A practical and powerful approach to multiple testing. *J R Stat Soc, B* 57(1):289–300.
- Macknik SL, Martinez-Conde S (2007) The role of feedback in visual masking and visual processing. *Adv Cogn Psychol* 3(1–2):125–152.
- Spillmann L, Wolf E, Nowlan AT (1971) Dark and light adaptation with opposite time courses. *J Opt Soc Am* 61(8):1122–1123.
- Fukuda T (1979) Relation between flicker fusion threshold and retinal positions. *Percept Mot Skills* 49(1):3–17.
- Brücke E (1864) Über den Nutzeffect intermittierender Netzhautreizungen. *Sitzungsber k Akad Wissensch Math-naturw Cl, Wien* 49:128–153.
- Bartley SH (1939) Some effects of intermittent photic stimulation. *J Exp Psychol* 25(5):462–480.
- Troncoso XG, Macknik SL, Martinez-Conde S (2009) Corner salience varies parametrically with corner angle during flicker-augmented contrast: Further predictions on corner perception from Vasarely's artworks. *Spat Vis* 22(3):211–224.
- Anstis S, Ho A (1998) Nonlinear combination of luminance excursions during flicker, simultaneous contrast, afterimages and binocular fusion. *Vision Res* 38(4):523–539.
- Wu S, Burns SA, Reeves A, Elsner AE (1996) Flicker brightness enhancement and visual nonlinearity. *Vision Res* 36(11):1573–1583.
- Roufs JAJ (1972) Dynamic properties of vision. I. Experimental relationships between flicker and flash thresholds. *Vision Res* 12(2):261–278.
- Kelly DH, Savoie RE (1978) Theory of flicker and transient responses. III. An essential nonlinearity. *J Opt Soc Am* 68(11):1481–1490.
- Kitterle FL, Corwin TR (1979) Enhancement of apparent contrast in flashed sinusoidal gratings. *Vision Res* 19(1):33–39.
- Bowen RW, Markell KA (1980) Temporal brightness enhancement studied with a large sample of observers: Evidence for individual differences in brightness perception. *Percept Psychophys* 27(5):465–476.
- Gilchrist A, et al. (1999) An anchoring theory of lightness perception. *Psychol Rev* 106(4):795–834.
- Lotto RB, Purves D (1999) The effects of color on brightness. *Nat Neurosci* 2(11):1010–1014.

Supporting Information

Rieiro et al. 10.1073/pnas.1213170109

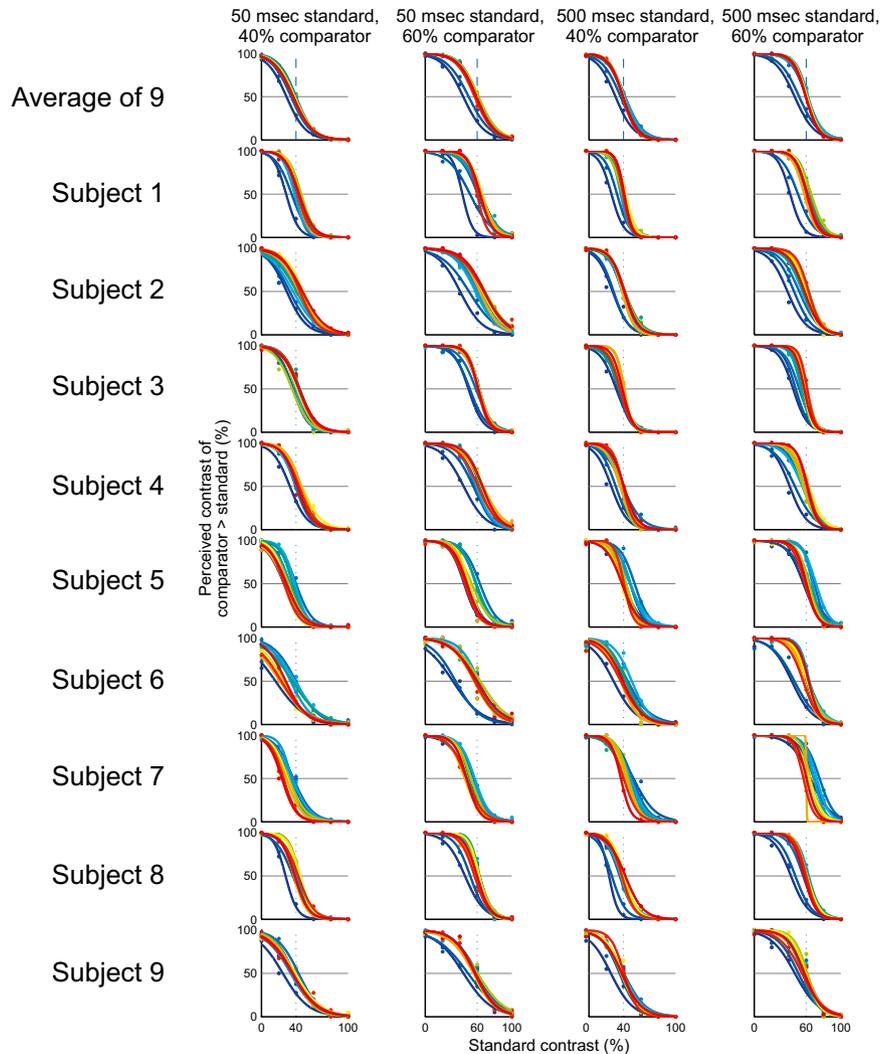


Fig. S1. Psychometric curves for the unblocked experiment. Top row shows psychometric curves for the subject average. Subsequent rows show psychometric curves for individual subjects. Columns show the four different combinations of standard duration and comparator contrast. All psychometric curves present a similar pattern, shifting initially to the right and then translating to the left with increasing stimulus durations, in agreement with the Broca-Sulzer effect. Color coding as in Figs. 1–3.

