

SHORT REPORT**Shape recognition elicited by microsecond flashes is not based on photon quantity****Ernest Greene**Laboratory for Neurometric Research, Department of Psychology, University of Southern California, Los Angeles, CA, 90089 USA; e-mail: egreene@usc.edu

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Abstract. It is generally thought that the perceptual impact of a brief flash of light is determined by the quantity of photons the flash delivers. This means that only the total quantity of photons is important below a critical duration of about 30–100 ms. Recent findings have challenged this concept and the present work provides additional evidence that it is not correct. The first experiment reported here delivered a given quantity of photons in under 200 μs , either as a single threshold-intensity flash or as multiple flashes at the same intensity. The single flash was ineffective at eliciting recognition, but multiple flashes became progressively more effective as the number of flashes was increased. A second experiment varied the number of 10 μs flashes. The effectiveness of multiple flashes was far higher than would be expected on the basis of the total quantity of photons being delivered. The results of both experiments suggest that the brief transitions of intensity provided by the flashes are far more important than the quantity of photons. A final experiment examined the combined impact from two threshold-intensity flashes as the interstimulus interval was increased. The pair members were able to combine their influence for at least 100 ms. These results call for more attention to how very brief light flashes generate signals that convey image content.

Keywords: shape recognition, brief flashes, Bloch's Law, information persistence.**1 Introduction**

Bloch's Law specifies that the absolute threshold for detecting a brief flash is determined by the quantity of photons being delivered (Barlow, 1958; Bloch, 1885; Graham & Margaria, 1935; Karn, 1936), and there have been a number of claims that it also applies to other perceptual and neuronal responses (Adrian, 1927; Graham & Cook, 1937; Hartline, 1934; Kahneman & Norman, 1964). The time interval across which the photons are summed has been reported to be in the 30 to 100-ms range (Barlow, 1958; Graham & Margaria, 1935). However, recent work that displayed shape patterns with an LED array found minimal summation of photons across durations in the low microsecond range. For example, with photon quantity held constant, displays that elicited shape recognition with 3- μs flashes were ineffective with flash durations of 8 μs (Greene & Ogden, 2013). Further, Greene (2013) found no evidence for summation with durations that ranged from 10 μs to 100 ms. Clearly, more work is needed to examine summation of brief flash influence.

Respondents were asked to name shapes patterns from a 360 inventory, each being briefly displayed on an LED array as one or more simultaneous flashes of all the dots forming the pattern. For convenience, the term "flash" will be used to describe each event in which all the pattern dots were activated simultaneously. The respondent either successfully identified (named) the shape or did not, and the proportion of successes for a given treatment constituted the hit rate. Examples from the inventory of shapes are provided in [Figure 1](#).

Experiment 1 evaluated the relative salience of multiple flashes wherein the summed duration of the emitted light was 100 μs . For this experiment, the luminance intensity was set at a level that was previously found to be the threshold needed for eliciting recognition when delivered as a single 100- μs flash. There was an expectation, supported by pilot data, that multiple flashes would be more effective than a single flash, therefore a threshold intensity was chosen to allow ample room to register multiple-flash effects.

A logistic model was used to evaluate treatment effects, the specifics being provided in the Method. The raw data consisted of binary decisions, i.e., recognize shape or not. A suitable statistical treatment of such categorical data makes use of a logistic regression wherein the possible outcomes of a single trial are specified as a function of the explanatory (predictor) variable. The logistic regression

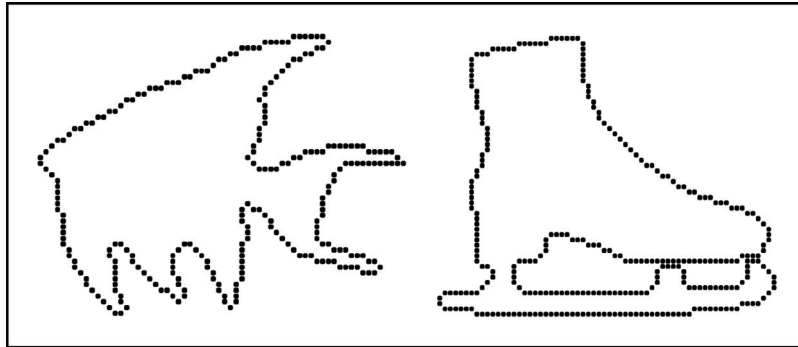


Figure 1. Shape examples: Two examples from the 360 inventory of shape patterns are illustrated. All the dots in a given pattern were briefly flashed simultaneously. The three experiments that were conducted varied duration of the flashed display, or the light intensity, and/or the number of times the pattern was displayed on a given trial.

applied here measured the relationship between a categorical dependent variable (hit rate) against the independent variable (intensity), predicting the probability of hit rate as a continuous value across the range of intensities. This provided for smooth plots of predicted hit rates rather than plots of mean hit rate at each treatment level. The plots in [Figure 2](#) show individual models and a group model as well as a confidence band around the group model. Consistent with what was found previously (Greene & Ogden, 2013), the single flashes with durations of 100 μs elicited minimal recognition. However, multiple flashes delivering the same total quantity of photons provided for high hit rates. The interval between the first and last flash was less than 200 μs , which is far lower than the interval across which Bloch's Law should apply. Therefore, the rise in hit rates as a function of the number of flashes cannot be attributed to a process that sums the quantity of photons being delivered. Rather, it is reasonable to infer that the fast transitions of light level provided by the flashes are critical for triggering responses from retinal neurons, thus generating signals that allow for perception. Providing 10 of these transitions in less than 200 μs allowed an intensity that was at threshold for the one-flash condition to be very effective at eliciting shape recognition.

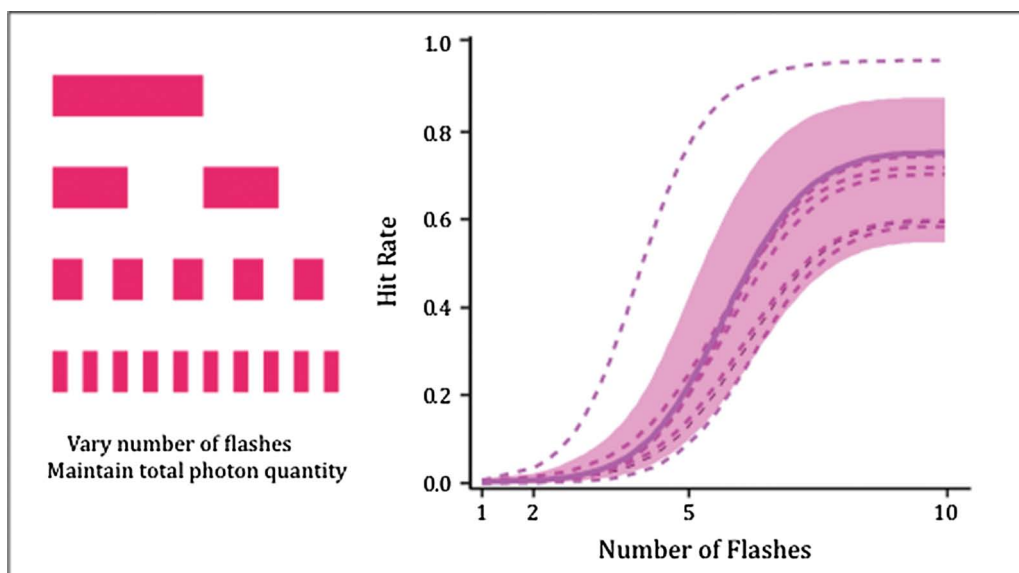


Figure 2. Single and multiple flashes with constant photon quantity: Each shape pattern was randomly assigned to single- and multiple-flash conditions. The goal was to see if breaking a fixed quantity of photons into multiple flashes would be more effective at eliciting shape recognition. Models for individual subjects are plotted with dashed lines, and the combined model for the group is plotted with a solid line. A 95% confidence band is provided for the group model. The single 100 μs flash and the two 50 μs flashes were ineffective. One begins to see an increase in hit rate with five flashes, and a substantial proportion of the shapes could be identified when the photon quantity was broken into a 10-flash train.

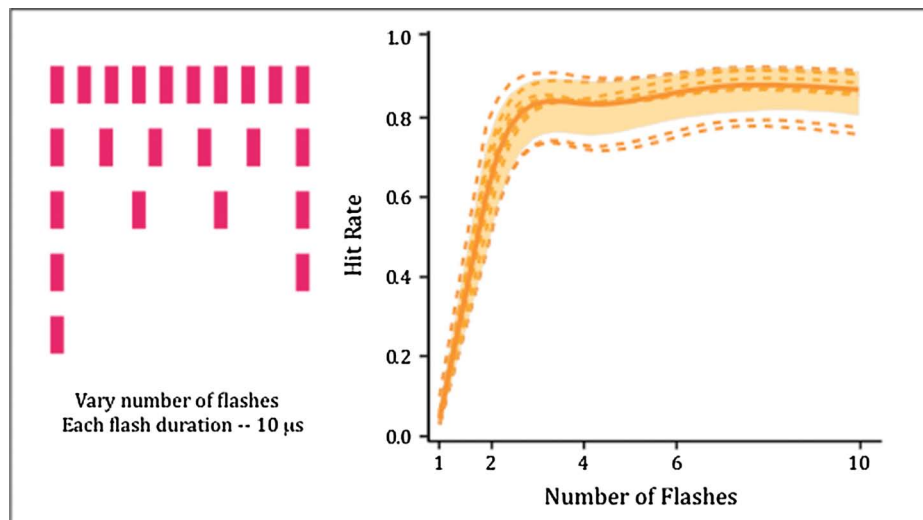


Figure 3. One versus multiple 10- μ s flashes: Single and multiple flash conditions were again tested with each flash lasting 10 μ s. Flash intensity for all treatments was at threshold for the one-flash condition. For multiple flashes, the interval between flashes was adjusted so that the time from onset of the first flash to offset of the last flash was the same, i.e., 190 μ s. Here again, individual subject models are presented as dashed lines and the group model is shown as a solid line. As expected, the single flash was not effective at eliciting recognition of the shape patterns. However, each of the multiple flash conditions was able to elicit a high hit rate.

Experiment 2 further examined the effectiveness of multiple brief flashes by comparing the hit rate from a single flash with that produced by 2, 4, 6, or 10 flashes—each at 10 μ s. Luminance intensity for a given flash was set at the shape-recognition threshold for 10- μ s flashes (Greene & Ogden, 2013). For multiple flashes, the separation was adjusted to provide the same total time between the beginning of the first flash and the end of the last flash.

The individual and group models are shown in Figure 3. Consistent with prior findings (Greene & Ogden, 2013), the single flash elicited minimal recognition for each of the respondents. All the multiple-flash conditions produced hit rates that were well above the shape-recognition threshold; indeed even the two-flash condition was able to elicit recognition not far from the top of the range.

Here again, the level of effectiveness of the flashes cannot be attributed to the quantity of photons being delivered. The two-flash condition provided only a fifth the amount of light in the 10-flash sequence, yet was only a little less effective at eliciting recognition of shape patterns. More telling was the 59% hit rate produced by two 10-ms flashes compared with a 1% hit rate for the two 50- μ s flashes of Experiment 1. This differential in flash effectiveness raises the possibility that activation of retinal neurons involves competing excitatory and inhibitory influences, and the prolonged duration of Experiment 1 flashes may actually impair signaling that conveys the locations of pattern dots.

Experiment 3 examined the interval across which two successive 10- μ s flashes can combine their influence, with flash separations ranging from 50 μ s to over 800 ms. Each flash used an intensity that was at threshold for a single 10- μ s flash. A one-flash condition was also included in the experiment to serve as a baseline.

The models showing changes in hit rate as a function of flash separation have been plotted in Figure 4. The means for the one-flash condition are shown as a band that allows a visual comparison for how much the hit rate was boosted by the second flash across the range of separations. The two-flash models manifested fairly constant levels of recognition for flash separations up through about 10 ms. This was followed by a decline in the aggregate influence of the two flashes, with overlap of the confidence bands at about 100 ms. The decline for the group model appears to reach a minimum at 400 ms, not quite at the mean hit rate with a single flash. One would need additional data to determine if this represents a significant difference.

One may infer that the first flash generates a neural response that last for 100 ms or more, in that a second flash that is delivered during that interval can sum or otherwise amplify the retinal activation, resulting in visual signals that are remarkably effective at eliciting shape recognition. This mechanism has been variously described as visual persistence (see Long, 1980), visible persistence (see Coltheart,

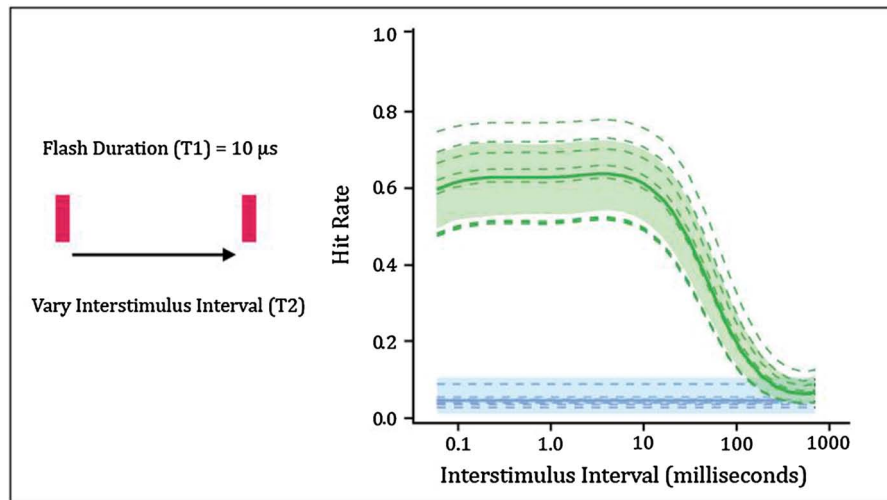


Figure 4. Persistence of flash influence: Two 10- μ s flashes were displayed, varying the interval between them to examine how long the pattern information would persist and allow for activity summation. The individual and group models for the two-flash condition are shown in green. The one-flash condition is shown as horizontal lines (in blue) to facilitate comparison with the two-flash condition across the range of interstimulus intervals. One can see that the influence of the first flash persisted and combined with the second flash without any sign of decline for about 10 ms. With longer separations, the net effect slowly dropped and reached one-flash levels after 100 ms.

1980), visual information store (Sperling, 1960), iconic memory (Neisser, 1967), and short-term visual storage (Haber & Standing, 1969). The persistence provides for shape information in successive displays to be combined, as demonstrated by Eriksen & Collins (1967, 1968). These investigators briefly displayed two dot patterns that were complementary samplings of three-letter trigrams. Persistence allowed the cues provided by the first dot pattern to be combined with those from the second dot pattern for up to 100 ms, allowing identification of the trigram message. These and related studies are discussed at length in an earlier paper (Greene, 2007a); see also Greene (2007b) and Greene & Ogden, 2012). One might hypothesize that a given dot-flash serves to activate one or more ganglion cells at a given retinal location, providing a sustained signal that specifies the dot's location. The present results indicate that activation is generated and sustained even when a pattern flash does not have sufficient intensity to elicit recognition, but a second threshold flash can boost activity to a level that is effective.

It is striking that as few as two 10- μ s flashes can combine their influence across such long time intervals, and can do so where each flash is at a threshold level of intensity. Prior work has found that the intensities needed for flash detection are only a little lower than those needed for shape recognition (Greene, 2013). At each level of intensity that produces a given probability of recognition, one only has to drop the intensity a small amount to get the same probability of flash detection. Therefore, failure to identify a shape could mean that a visual signal is not being delivered from the retina. This supports the possibility that recognition thresholds reflect whether or not the retina has delivered a visual signal. However, based on current data one cannot rule out the possibility that ganglion cells are being activated by flash intensities that are below the perceptual threshold, with the resulting signals being summed by cortical neurons.

The current work clearly shows that the effectiveness of brief flashes is not determined by the quantity of light being delivered. Bloch's Law may only apply to the lowest levels of light sensitivity, such as the impulse response of fully adapted rods where special photochemical mechanisms and pooling of rod responses provides for detection of single photons (Baylor, Nunn, & Schnapf, 1984; Field, Sampath & Rieke, 2005). Neurophysiologists had already provided abundant evidence that Bloch's Law does not preclude rapid neuronal response and retinal neurons are not limited to summing the light across many tens of milliseconds. For example, neighboring ganglion cells manifest synchrony of firing with precision in the millisecond range (Ackert et al., 2006; Amthor, Tootle, & Grzywacz, 2005; Baden, Esposti, Nikolaev, & Lagnado, 2011; Chatterjee, Merwind, Amthor & Grzywacz, 2007; Mastrorarde, 1989; Shlens et al., 2009). Retinal fibers are designed with differentials of travel time that compensate for distance, thus allowing spikes that were elicited at the same moment to arrive at

the head of the optic nerve simultaneously (Stanford, 1987; Zeck, Lambacher & Fromherz, 2011). Theios & Morgan (1989) found that with near simultaneous display of two incompatible images, one can be made dominant by increasing its duration by as little as 250 μ s. Neural mechanisms could not operate with such high temporal precision if they were required to sum photon quantity across many tens of milliseconds.

The present experiments, in combination with earlier work from this laboratory (Greene, 2013; Greene & Ogden, 2013), are at odds with our current understanding of how visual signals are generated. The challenge is not only to the principle that the strength of activation from brief flashes is determined by the total quantity of photons being delivered—Bloch's Law. Additionally, the findings call for a mechanism for registering flash intensity and/or duration within microseconds. Greene and Ogden (2013) found that fewer photons were required to elicit a given level of shape recognition when shorter flash durations were used. Specifically, the photon quantity needed to produce a full activation curve, from threshold to high levels of shape recognition, was less for 3 μ s flashes than for 10 μ s flashes, and progressively more light was required to produce activation curves at longer flash durations. Further, if one used a quantity of photons that could elicit recognition of 90% of the shapes with a 3- μ s flash, none of the shapes could be identified if that quantity was spread across a duration of 8 μ s. These results call for a new principle for generating a visual signal that operates with a temporal precision of just a few microseconds. It does not, however, operate only in the microsecond range. Greene (2013) tested recognition with constant-photon flashes across a range from 10 μ s to 100 ms; brief flashes were more effective than were the longer ones. Further, both for recognition and for flash detection, a photon quantity that was very effective when delivered in 1 ms was completely ineffective when delivered in 1.4 ms.

The classic photoreceptor impulse response may be too slow to explain these findings. With a 10-ms dim flash, the time for the impulse to reach peak voltage is 32–35 ms in monkey cones (Schneeweis & Schnapf, 1995, 1999). In human cones, it rises to a peak in about 20 ms (van Hateren & Lamb, 2006). Studies in other species using flashes in the microsecond range have not found that ultrashort flash durations produce faster rise times (Cobbs & Pugh, 1987; Nikonov, Kholodenko, Lem, & Pugh, 2006).

Brown & Murakami (1964) used a 20- μ s flash and observed what they called an “early receptor potential” that rose with no detectable latency. This finding has been confirmed by others (see Cone, 1967; Pak & Cone, 1964; Pak & Boes, 1967). Brown and Murakami (1964) suggested that this fast potential was generated by displacement of electric charges (electrons, ions, or charge groups) as the photopigment changed its conformation, a process that takes place within femtoseconds (Bownds, 1967; Cone, 1967). The early receptor potential seems an attractive candidate for a new high temporal precision signaling mechanism, but we will need definitive physiological evidence that it can directly control synaptic transmission. As a further caution, thus far it has been observed in vertebrate photoreceptors only with flash intensities that are beyond the physiological range.

An alternative possibility is for flash duration to be registered by mechanisms similar to those used to detect microsecond differentials in sound and object localization by bats, owls, and electric fish (see, e.g., Fay, 1988; Knudsen & Konishi, 1979; Heiligenberg, 1991; Rose & Heiligenberg, 1985; Payne, 1971). Temporal delays of the ON and OFF bipolar cells might register onset and offset of the flash, thus providing high-resolution temporal discrimination of its duration. Wooten et al. (2004) have provided a formal model of how neurons can combine input from cells having low temporal resolution to provide for high-precision temporal responses. See the Supplemental Discussion in Greene and Ogden (2013) for a more comprehensive evaluation of physiological options.

2 Method

Three experiments were conducted, each with 8 respondents (24 total). For a given respondent, shape patterns were randomly assigned to the treatment conditions, without replacement, requiring also the allocation of an equal number of shapes to each condition. Flash durations are designated as T1 and T2 specifies the interval between flashes.

For Experiment 1, luminance intensity of each LED emission was 0.23 Cd. A given shape pattern was displayed as: (1) a single flash with T1 = 100 μ s; (2) two flashes, T1 and T2 = 50 μ s; (3) five flashes, T1 and T2 = 20 μ s; (4) ten flashes, T1 and T2 = 10 μ s. Note that the aggregate of T1 durations for each condition was 100 μ s, so the total quantity of photons delivered by each condition was the same.

For Experiment 2, each flash was displayed at an intensity of 0.36 Cd. Five treatment conditions were provided, wherein each flash was 10 μ s and the shapes were displayed with 1, 2, 4, 6, or 10

flashes. The multiple flashes were equally spaced, with total time for display of the flash sequence being 190 μ s.

For Experiment 3, flash intensities were again set at 0.36 Cd. Eight levels of flash separation were used for the two-flash displays, spaced exponentially using the formula $50 \mu\text{s} \times 4^x$; $X = 0$ to 7. The ninth treatment condition displayed a single 10- μ s flash.

Logistic regression models were used to evaluate timing or number of flash with the response curve modeled with a cubic-spline with two equally spaced internal knots. The within-subject effect consisted of a random intercept and a penalized spline. For each group model of this report the treatment effects were significant at $p < 0.0001$. Analyses were performed using SAS version 9.3 (The SAS Institute, Cary, NC). See Greene and Ogden (2013) for more complete details on equipment, shape inventory, and test protocols.

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