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Measuring temporal summation in visual detection with a single-photon source

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ABSTRACT

Temporal summation is an important feature of the visual system which combines visual signals that arrive at different times. Previous research estimated complete summation to last for 100 ms for stimuli judged “just detectable.” We measured the full range of temporal summation for much weaker stimuli using a new paradigm and a novel light source, developed in the field of quantum optics for generating small numbers of photons with precise timing characteristics and reduced variance in photon number. Dark-adapted participants judged whether a light was presented to the left or right of their fixation in each trial. In Experiment 1, stimuli contained a stream of photons delivered at a constant rate while the duration was systematically varied. Accuracy should increase with duration as long as the later photons can be integrated with the proceeding ones into a single signal. The temporal integration window was estimated as the point that performance no longer improved, and was found to be 650 ms on average. In Experiment 2, the duration of the visual stimuli was kept short (100 ms or <30 ms) while the number of photons was varied to explore the efficiency of summation over the integration window compared to Experiment 1. There was some indication that temporal summation remains efficient over the integration window, although there is variation between individuals. The relatively long integration window measured in this study may be relevant to studies of the absolute visual threshold, i.e., tests of single-photon vision, where “single” photons should be separated by greater than the integration window to avoid summation.

1. Introduction

A key feature of visual processing is the integration of signals that arrive at different times (temporal summation) or at different nearby locations on the retina (spatial summation). Summation combines the responses of individual photoreceptor cells, which aids in visual detection and, along with physical changes (e.g., pupil dilation) and chemical changes (e.g., increased sensitivity of the rod pathway), contributes to the wide dynamic range of the visual system. At a higher level, summation helps combine visual signals into persistent information that is used in decision-making (Huk & Shadlen, 2005). Many aspects of summation have been studied in detail, but measurements at very low light levels such as those near the absolute limit of the visual system—which may be as low as a single photon (Rieke & Baylor, 1998; Sakitt, 1972; Tinsley et al., 2016)—have been limited by technical constraints. Moreover, most studies focused on the estimation of complete summation windows. The present study uses a new experimental paradigm and a unique quantum light source to measure the full range of temporal summation at fewer-photon levels.

Temporal summation can be characterized by an integration window, the length of time over which incoming visual signals are summed. This integration window is usually taken to be the range of stimulus durations for which the threshold intensity is inversely proportional to the duration, i.e., where Bloch’s law holds (Bloch, 1885). The typical estimate for the length of temporal summation in previous research was about 100 ms. However, summation is complex and dynamic, and many factors can affect both its length and completeness. The durations of previous visual stimuli affect the detection of new stimuli (di Lollo, 1980), and integration has been shown to occur between visual images and on-going percepts (Brockmole, Wang, & Irwin, 2002). Colors and forms can also be integrated when visual stimuli are presented close together in time, with the integration lasting much longer than the stimuli themselves (Pilz, Zimmermann, Scholz, & Herzog, 2013).

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For simple flashes of light, the temporal summation window increases for smaller stimulus areas and lower background illumination (Barlow, 1958), although background illumination primarily affects the cones (Sharpe, Stockman, Fach, & Markstahler, 1993). Barlow studied the effects of stimulus size and background light in detail by presenting observers with flashes of varying durations, sizes, and intensities against a range of background illuminations. The observer adjusted the intensity of a repeated stimulus "until he considered that it was usually just visible," equivalent to about 80% detection probability. For a small stimulus (0.011 degree^2) presented with no background light, the slope of the log-threshold vs. log-duration relationship was found to diverge from Bloch's law at a stimulus duration of about 100 ms, marking the end of complete summation. Significant partial summation (indicated by a negative slope greater than -1) continued after the window of complete summation, and this partial summation was reduced with added background light. A much larger stimulus (27.6 degree^2) resulted in both a shorter window of complete summation (30 ms) and reduced partial summation outside this window.

The method of Barlow, in which the intensity of a stimulus is adjusted to maintain a constant probability of detection, has some advantages. It is quick, because the observer makes judgements about a stimulus with a high probability of detection. It also provides information about the completeness of summation via the slope of the threshold vs. duration relationship at constant detection probability. However, this method is only useful for studying relatively bright stimuli at a fixed level (e.g., "just detectable" according to the observer's subjective criteria). It is difficult to use this method to test whether an arbitrary stimuli is within the temporal summation window. For example, in order to measure whether a much less detectable light is fully integrated, this method would require the observers to adjust the light intensity to match the same arbitrary detectability rate to obtain the constant-detectability curve, which can be difficult and unreliable. Therefore, a different, more flexible paradigm is needed to examine the range of temporal summation at various light intensity levels, e.g., for low light intensities such as single photons presented successively, which have previously been considered "below threshold." [1]

Our new method differs from previous research in several aspects. First, unlike some of the classical studies (e.g., Hecht et al., 1942), we used a discrimination task instead of a detection task. Experimental designs that rely on the observer's subjective seeing criterion are vulnerable to noise and bias against false positives. Such designs have been used since the earliest studies (e.g., also, van der Velden, 1946), which has contributed to uncertainty about the visual threshold. Instead, we use a two-alternative forced-choice (2AFC) design, in which participants' accuracy (proportion of correct responses) at a task in which they are forced to choose the location of a stimulus (left or right) in many trials is used as a measure of how often they perceive the stimulus. The 2AFC design is particularly suitable for our study because it can measure responses to stimuli so weak that observers will almost never report seeing them in a detection task. For example, Hecht et al. (1942) did test stimuli with 24–47 photons at the cornea (comparable to our shortest stimuli), and none of the three observers ever reported seeing them. However, stimuli at this level can be examined using the 2AFC method. A preliminary study showed that participants were able to detect a visual stimulus containing just 30 photons at the cornea (~3 at the retina), choosing left or right significantly above chance with an accuracy of 0.54 ± 0.01 (Holmes et al., 2014). While a detection task could probably be used to study the longer stimuli we used (closer to the integration window), the 2AFC design allows us to study the entire range of responses.

Second, we measured the temporal integration window in two steps to estimate both the length of any temporal summation and the length of complete summation. Since the temporal integration window we sought to measure includes all levels of summation, Bloch's law does not apply. Moreover, since we were interested in integration at any light intensity level (much lower than the typical threshold of 60% detection), we developed a new two-step paradigm that does not require the constant threshold curve used by Barlow (1958). The first step (Experiment 1) measured the entire range of temporal summation (including the complete integration that follows the Bloch's law, and the subsequent partial integration that does not) using a spline regression analysis on the constant-rate curve. The second step (Experiment 2) measured the efficiency of integration to estimate the complete integration window by comparing the constant-rate condition to the constant-duration condition. Experiment 2 was essentially a test of the Bloch's law, which measured whether the two different stimulus durations produced the same observer response for a given mean photon number (similar to Barlow, 1958). The combination of the two steps provides estimation of both the entire range of temporal summation and the length of complete summation.

The spline regression analysis method consists of systematically varying the length of a visual stimulus while single photons were presented at a constant rate. Because the intensity is constant, the total number of photons contained in the stimulus increases with the stimulus duration. If the duration falls within the temporal integration window, the additional photons should be included in the summation of the signal; therefore, performance in the 2AFC task should increase as a function of the stimulus duration, up to the point that the duration is equal to the integration window. The temporal integration window can therefore be estimated as the turning point in performance as a function of the stimulus duration. Again, this method measures the length of all levels of summation, including partial summation.

Finally, we used a single-photon light source rather than a classical source. Research on the lower limit of the visual system has been limited by the availability of light sources with ideal photon statistics. Virtually all available light sources—bulbs, LEDs, lasers, sunlight, etc.—emit photons randomly in time, with each photon emitted independently from the previous photon. This produces a Poisson distribution in the number of photons contained in a given pulse of light, characterized by a mean photon number and a variance equal to the mean. With any such classical light source, it is impossible to know how many photons are in any given pulse, or even to put an upper limit on the number of photons that may be present.

In the last three decades, the field of quantum optics has developed new, more precise methods of generating photons with quantum light sources. One such method is based on the nonlinear optical process of spontaneous parametric downconversion, in which a single high-energy laser photon splits into a pair of lower-energy daughter photons inside a crystal. Although this process occurs with low probability (approximately 1 in 10^9), a laser can easily supply enough pump photons to produce thousands of downconverted pairs per second. One photon from each pair can be separated and detected with a single-photon detector, thus "heralding" the presence of its undetected partner, the "signal" photon. This allows each signal photon to be counted and its arrival time to be precisely known. If H herald photons are counted, the chance that more than N signal photons are produced can be made

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[1] For example, the average accuracy in our Experiment 1a (discussed in Section 3) reached only 76% for the longest stimuli. If this accuracy is converted to a detection rate it is just barely above 50%. Therefore by the conventional definition of threshold level, our stimuli were generally below threshold.