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

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A B S T R A C T

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 ($\sim$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

[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.

extremely small (Hong & Mandel, 1986; Pittman, Jacobs, & Franson, 2005). A single-photon source based on this process can therefore produce light with dramatically different statistics than any classical light source; in particular, it can produce pulses that are guaranteed to contain no more than one photon. We have designed and constructed a source of this type which produces heralded single photons at 505 nm, essential to ongoing tests of whether the visual system can detect a single photon (Holmes, Christensen, Wang, & Kwiat, 2015). This source can also be used to generate semi-classical light pulses with reduced uncertainty in the number of photons, and we used this mode of operation for the present study of temporal summation.

We conducted two experiments to explore the duration and efficiency of temporal summation. Experiment 1 measured the duration of the integration window using a new paradigm that presented a stream of single photons at a constant rate with varying durations, both with a group of participants as well as three participants who completed multiple sessions to explore their individual summation behavior in more detail. Experiment 2 compared this integration (constant-rate) condition to constant-duration conditions in which the stream of photons was presented within a fixed, much shorter duration to determine the completeness of temporal summation, both at the group level and in two individual observers.

2. General methods

2.1. Participants

Participants were male and female university students between the ages of 20–28. Nearsighted participants were accepted if their prescription was less than 3.0 diopters (self-reported) and were permitted to wear their usual vision correction (contact lenses or eyeglasses, if non-tinted) during experimental sessions. The research protocol was approved by the University of Illinois Institutional Review Board. Informed consent was obtained from all participants, and we followed established guidelines on the use of human subjects in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Visual stimulus

In order to study temporal summation at lower light intensities, the visual targets were optimized to give participants the best chance of detection. The targets had a wavelength centered at 505 nm with a spectral bandwidth of 15 nm. The target beams emerged from two optical fibers and were collimated with 11-mm focal-length aspheric lenses; they were then imaged to approximately 50 μm on the retina (10 arcminutes, covering about 300 rod cells) with additional 150-mm focal-length lenses placed 36 cm from the observer's eye, and presented at approximately 16 degrees to the left or right of the fovea of the right eye and 5 degrees above the horizontal plane (see Fig. 1). This peripheral location was chosen to target the highest density of rod cells in the retina, with a vertical offset to help avoid the optic nerve. Note that the visual targets were narrow beams rather than point sources, so in principle all the photons emitted from the optical fiber can be delivered to the eye (rather than just the portion allowed by the solid angle of the pupil). The size of the beams at the pupil was 2.7 mm, and no mydriatic was used.

Participants fixated on a dim 700-nm (far red) LED positioned approximately 15 cm behind a small cross-shaped mask at a distance of 25 cm from the right eye. The power of the fixation cross was measured to be 11 nW through a 5-mm pupil at approximately the same location as the participant's eye, and the fixation cross covers approximately 1/3 degree in the visual field. Participants maintained their alignment during an experimental session by keeping the fixation LED centered behind the crosshairs mask such that the illuminated cross remained symmetrical (this method of alignment is analogous to a cross-hairs target or a rifle sight and is accurate to better than 0.5 mm at the pupil). Both the fixation cross and the stimulus presentation were monocular, and the right eye was used for all participants.

2.3. Apparatus

The visual targets were presented to participants via a viewing station (Fig. 1) located in a small room which could be made completely dark. The viewing station consisted of a chin rest and an optical breadboard. Motorized optical mounts for aligning the left and right visual targets were constructed on the breadboard. Light was delivered via optical fibers, which traveled through a channel in the wall from an adjacent room containing the single-photon source and the experimenter. A separate 505-nm LED was used as a bright source to align the viewing station to each participant.

The single-photon source (Fig. 2) was used to generate stimuli with variable mean photon numbers and durations. To produce a pulse of light, the pump laser was activated by computer control. A predetermined number of herald photons were then counted, and the laser was deactivated immediately after the target herald count was reached. Varying the pump laser power controls the rate at which photon pairs are generated, thus determining the duration of the stimulus for a given target herald count. Controlling the herald count H determines the mean number of photons in the pulse, $N = \eta H$, where η is the heralding efficiency of the single-photon source. Heralding efficiency is defined as the probability that a signal photon is emitted by the source when a herald photon is counted. In general, η is less than 1 due to optical loss (scattering, reflection, optical fiber collection efficiency, etc.) in the path of the signal photons. The herald photons also experience loss; however, the probability that a signal photon leaves the source without being heralded can be made extremely low (< 0.001) with a fast optical switch in the path of the signal photons, which only opens when a herald photon is counted (thus blocking any unheralded photons) (see Fig. 2). The single-photon heralding efficiency of our source at low pump laser power is 0.37 ± 0.01. (The heralding efficiency can increase at higher pump power due to the increased chance of multiple photon pairs created in the same laser pulse; however, this does not affect the accuracy with which the mean value of N can be determined.)

After a pulse of light is emitted by the source, it must enter the eye and be detected by a photoreceptor cell in the retina. A 500-nm photon that hits a rod cell end-on has about a 50% probability of being absorbed, and subsequently about a 60% probability of activating a rhodopsin molecule and initiating a cascade. The resulting total rod quantum efficiency of about 30% has been confirmed *in vitro* with both a classical source (Rieke & Baylor, 1998) and a single-photon source similar to the one used in this work (Phan, Cheng, Bessarab, & Krivitsky, 2014). The rest of the eye contributes additional loss. The total efficiency is difficult to measure accurately in the living eye, but there is thought to be at least 4% reflection loss at the cornea, about 50% loss in the vitreous humor of the eye at 500 nm, and additional loss and geometric fill factors in the retina (depending on the exact angular location of the stimulus) of perhaps 30–40% in the periphery, bringing the total efficiency of the eye down to about 10% at the peripheral location we studied (Rieke & Baylor, 1998). Thus, the estimated net efficiency of our single-photon source and the eye together is 3.7%, but there is significantly uncertainty in the efficiency of the eye.

Even when used to generate multiple photons, the single photon source produces light with binomial statistics (variance equal to $np(1-p)$ where n is the number of herald photons and p is

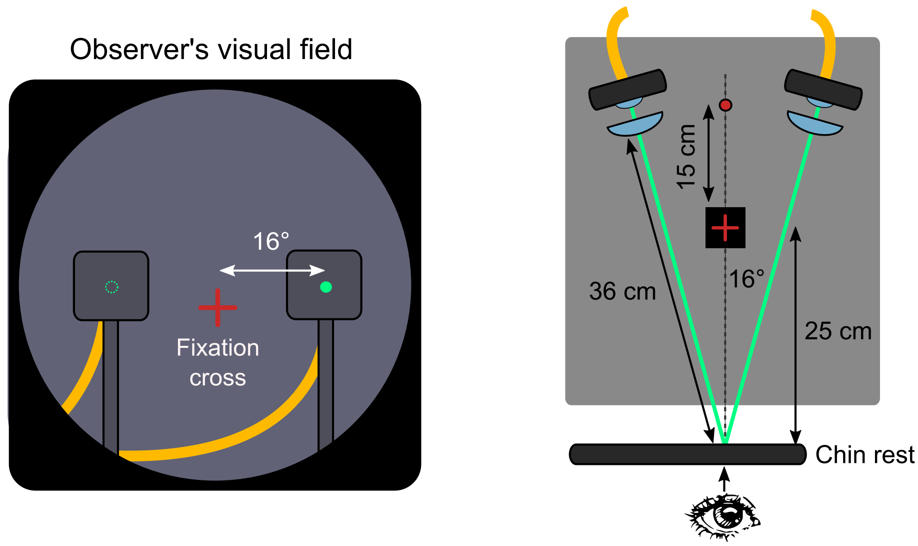

Fig. 1. Schematic of the observer viewing station and the observer's visual field. Visual targets and fixation cross are not to scale.

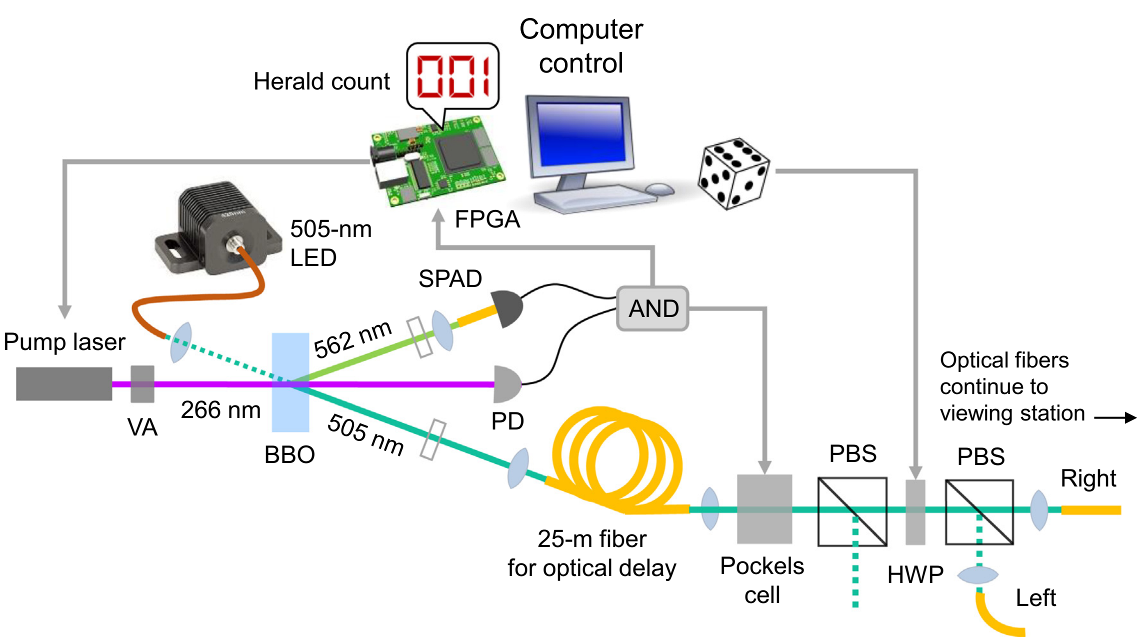

Fig. 2. The single-photon source. A 266-nm pulsed pump laser produces pairs of photons via spontaneous parametric downconversion. The laser power is controlled with a variable attenuator (VA). 562-nm herald photons are collected into optical fiber and detected by a single-photon avalanche photodiode (SPAD). Herald photons are counted in coincidence with a photodiode (PD) triggered on the pump laser pulses to reject dark noise and background photons. A fast field-programmable gate array (FPGA) counts herald photon detections and deactivates the pump laser when the desired count is reached. 505-nm signal photons are collected into few-mode optical fiber to be presented to the observer. A Pockels cell and polarizing beam splitter (PBS) act as a fast polarization-based optical switch to reject any unheralded signal photons. A half-wave plate (HWP) in a motorized computer-controlled mount and a second PBS direct signal photons to either a left or right optical fiber. Both fibers are connected to an observer viewing station. A 505-nm LED is also coupled into the optical path of the signal photons and can be used for alignment.

the total system efficiency) rather than classical Poisson statistics (variance equal to the mean N), which in general reduces the variance in photon number for a given mean. However, the reduction is on the order of the total efficiency of the system, and is therefore small in our experiment. The reduction in variance could be more significant in, e.g., *in vitro* studies with rod cells where losses can be significantly lower (Phan et al., 2014; Sim, Bessarab, Jones, & Krivitsky, 2011; Sim, Cheng, Bessarab, Jones, & Krivitsky, 2012).

2.4. Procedure

The viewing station was individually aligned to each participant using a 505-nm LED as an alignment source; the power of the alignment source (which was only used during the setup period, not during the experimental session itself) was measured to be less than 0.1 nW. Initial alignment took about 15 min for each participant and was conducted under dim lighting to avoid impacting later dark adaptation.

The experimental trials were self-paced (see Fig. 3). In each trial, the participant heard an alert tone indicating that the single-photon source was ready. The participant fixated on the dim red cross and pressed a key to trigger the stimulus, which began within 2 ms after the key press. The stimulus was randomly presented on either the left or the right side of the visual field in each trial. After the stimulus was delivered, the participant heard a tone indicating that the trial was complete. The participant was

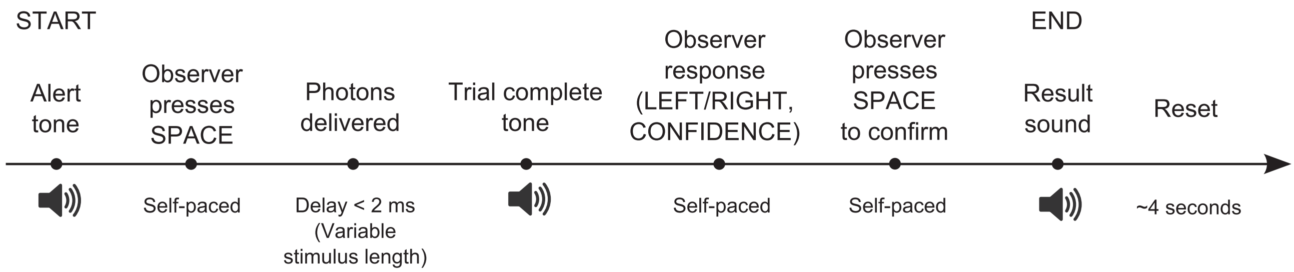

Fig. 3. Timeline of one experimental trial. The total time for each trial is about 10 s (depending on the length of the stimulus and the speed of the observer's response). The observer's response is not recorded until they press SPACE to confirm, allowing them to correct mistaken key presses.

then required to choose left or right, and to rate their confidence from 1 to 3, using a modified keyboard. To help maintain the participant's interest, after the response one of two result sounds was played to indicate whether the correct or incorrect answer was given. Each trial took approximately 10 s to complete.

Participants began each session with 30 min of dark adaptation. During the second half of the dark adaptation period, participants completed a series of self-paced practice trials. These trials were comparable to or brighter than the brightest experimental trials. Most sessions consisted of 300 self-paced experimental trials and took 1.5–2 h to complete, including dark adaptation time. The participants could take a break at any time by sitting back from the viewing station. After a break, accurate alignment could be easily re-established by visually centering the fixation cross (see Section 2.2). Participants were encouraged to rest if they experienced fatigue, and they were notified when half of the experimental trials had been completed.

3. Experiment 1a: mean integration time

Experiment 1a sought to measure the mean integration time by plotting accuracy as a function of the duration of the photon stream and estimating the turning point in a spline regression.

3.1. Method

Nine volunteers participated in this experiment (two were females). They each completed two experimental sessions.

Participants made forced-choice responses about the location of visual targets containing different mean photon numbers, with the photons in all trials presented at a constant rate of approximately 30 photons per 100 ms at the cornea. The two sessions were identical except for the choice of stimulus durations, and session 2 was conducted on a different day. The heralding efficiency in this experiment was 0.37. Trials were presented in a random order.

There were five duration conditions in each session and 60 trials in each condition, for a total of 300 trials in each session. In each trial, the position of the stimulus was determined randomly. As a result, the stimuli were presented on the left side in approximately half of the trials and on the right side in the other half.

3.2. Results and discussion

To estimate the temporal integration window during which incoming photons were combined for the detection of the signal, the mean accuracy across participants was plotted as a function of the stimulus duration (Fig. 4). Because the photons were presented at a constant rate, the total number of photons contained in the stimulus increased with the stimulus duration (Fig. 4, lower panel). If the duration fell within the temporal integration window, the additional photons should be included in the summation of the signal; therefore, performance should increase as a function of the stimulus duration, up to the point that the duration is equal to the integration window. When the duration exceeds the integration window, the additional photons should no longer be included in the summation process and will not contribute to the detection of the signal; therefore, performance should no longer improve even when the duration continues to increase and more photons are presented (a "boxcar" model of the integration window). Based on this assumption, performance should increase with duration until the duration reaches the temporal limit for summation, then remain constant afterward. The temporal integration window can be estimated as the turning point in performance as a function of the stimulus duration.

This turning point was estimated using a spline regression technique. First, the mean accuracy across participants was calculated for each stimulus duration. Then a spline regression model with three free parameters (the turning point, the intercept and slope of the first segment) was fitted to the data. The turning point value that generated the best fit (highest R^2) was taken as the estimated temporal integration window. [2]

The participant's accuracy is defined as the proportion of trials in which they chose left or right correctly. The spline regression analysis indicated that the mean integration time was 650 ms (Fig. 4, top panel). At long stimulus durations, the mean accuracy reached 0.76.

It should be noted that the spline regression analysis performed here used a simplified assumption that performance increases linearly as the photon number increases, up to the integration window limit. The actual function is likely to be non-linear, especially when the duration is closer to the turning point and the summation is only partially effective. It is possible to use a different function for the first portion of the curve in the spline regression analysis. However since we did not have an *a priori* assumption about what the best fitting function should be, we used the linear fit as the first order approximation. As a result, the estimation of 650 ms is likely a lower bound, conservative estimate, and the true integration window may be longer.

Experiment 1a estimated the temporal integration window using the group mean accuracy data. However, participants' performance seemed to vary significantly. Moreover, the apparent non-linearity in the temporal function of the group means may partly be due to the average of multiple people with different turning points. To get some estimate of the individual integration time, Experiment 1b recruited participants for multiple sessions to obtain sufficient data to estimate their individual integration window.

[2] The linear function appears to intersect with the x-axis at approximately 50 ms (instead of 0 ms) because the pump laser takes a short time to reach full power; therefore, the photons were generated at a lower rate initially, with the rate increasing during the initial ~50 ms, resulting in non-linearity in the initial portion of the function.

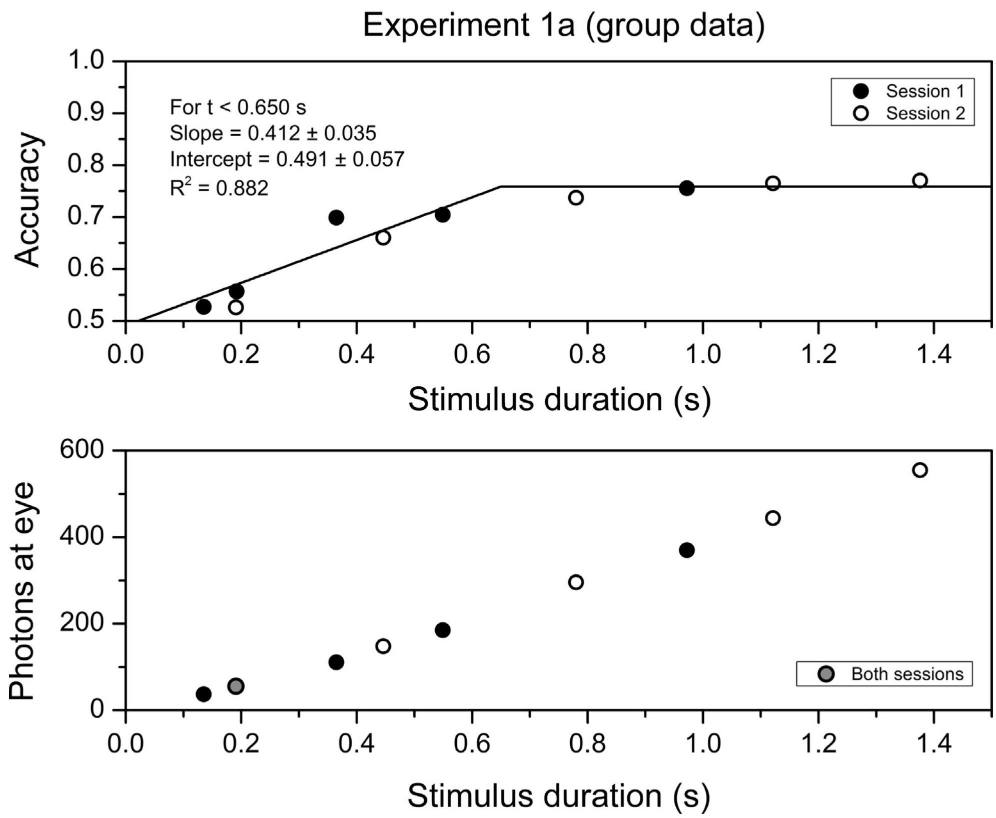

Fig. 4. Group results of Experiment 1a showing data from 9 participants. A spline regression was used to estimate the average integration time, t = 650 ms. Fit parameter uncertainties are the asymptotic standard error. The mean number of photons at the eye for each level is shown in the lower panel as a function of stimulus duration.

4. Experiment 1b: individual integration time

4.1. Methods

Three different participants, P1, P2, and P16 (two females; P1 is author RH), were recruited to complete 3 or 4 sessions each. The participants were tested with the same durations as session 1 of Experiment 1a. The methods were otherwise identical to Experiment 1a. P1 and P16 wore their usual eyeglasses during the experimental sessions, and P2 had no vision correction.

4.2. Results and discussion

We measured the individual integration window of the three participants (P1, P2, and P16) separately. P1 and P2 both completed 4 sessions, and P16 completed a total of 6 sessions (discussed below). A spline regression was fit to the mean accuracy data as a function of stimulus duration (Fig. 5) for each participant. The estimated integration window for P1 was found to be 600 ms, and the integration window of P2 was found to be 400 ms. P1 reached a higher maximum accuracy (0.95) compared to P2 (0.84). Unusually, P16 displayed no increase in accuracy with longer stimulus durations ($r = -0.83$, $t(3) = -2.53$, $p = 0.08$), and a low mean accuracy of 0.55; therefore, no spline regression analysis was performed for this participant.

These data suggest that the integration window does vary across participants. It is not clear why P16 showed no improvement in accuracy as the stimulus duration increased. One possibility is that this participant had an integration window shorter than the shortest duration tested in this study (~139 ms); therefore, what we observed was already the second half of the function. Given the overall low accuracy, it is also possible that the participant had a higher detection threshold, and the stimulus was too weak to reveal any change in accuracy as the duration increased, even if the integration window was comparable to other participants. To test these possibilities, we ran 3 new sessions for P16 in which the photon rate was approximately doubled (so that the total number of photons in each stimulus was also doubled, but each stimulus duration remained roughly the same as the in the original condition). The results showed a significant increase in accuracy as the duration increased (Logistic regression odds ratio = 0.999, $Z = 2.12$, $p < 0.05$), up to the longest duration tested (~960 ms). The spline regression analysis showed that at this increased light level P16 was indeed able to show integration, and the integration window was longer than 960 ms (Fig. 4).

It should be noted that the experimental paradigm used in the present study measures temporal summation at any level of efficiency. That is, performance can improve as the duration increases even if the summation is only performed partially; therefore, the temporal integration window estimated is the duration during which photons may be combined with any probability to enhance detection. To examine the efficiency of temporal summation within the temporal integration window, Experiments 2a and 2b compared visual detection of signals that contained the same number of photons but were presented at short vs. long durations.

5. Experiment 2a: efficiency of temporal summation

To investigate the efficiency of temporal summation, two conditions were tested in which similar numbers of photons as those in Experiment 1a were presented in a fixed, much shorter time window of either ~100 ms or <30 ms. These durations are equal to or

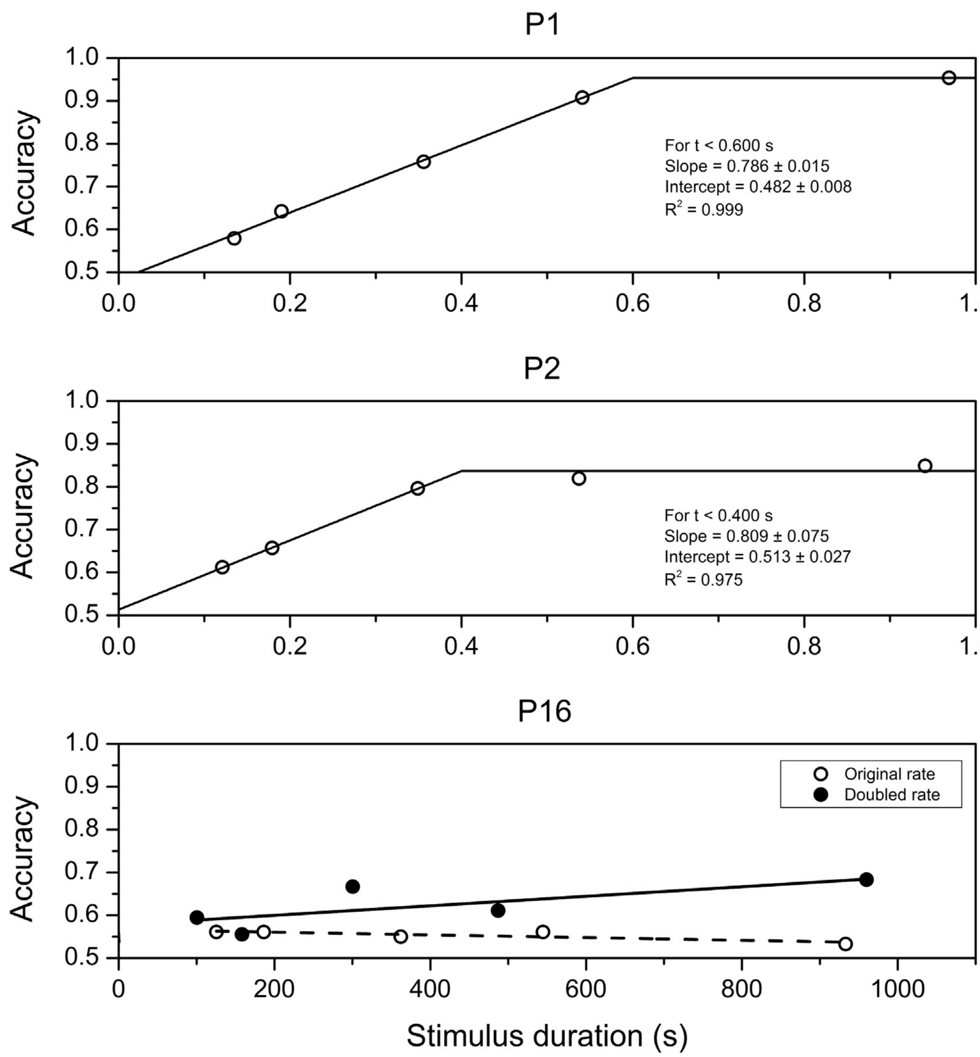

Fig. 5. Individual results of Experiment 1b. A spline regression was used to estimate the integration time for P1 and P2. Linear fits are shown for P16, as the integration time exceeded the longest stimulus. Fit parameter uncertainties are the asymptotic standard error.

shorter than the windows of complete summation measured in previous studies (e.g., Barlow, 1958; Sharpe et al., 1993), so these stimuli are likely to be fully integrated and could provide a measurement of the relationship between accuracy and photon number under complete summation. By comparing this function to that of Experiment 1a, we can determine whether the efficiency of summation remains constant over the entire integration window, or decreases/increases with time.

5.1. Method

A total of 18 participants (eight females) were recruited and each was tested in one of two Constant Duration conditions. Ten participants completed one session of the 100-ms condition, in which the photon numbers were similar to those in Experiment 1a, but the duration of the stimulus was kept constant at ~100 ms. Eight participants completed one session of the 30-ms condition, which had photon numbers comparable to the 100-ms condition, but the duration of the stimulus was less than ~30 ms. There were four photon levels of 75 trials each (shown in Fig. 6), for a total of 300 trials in each session. Again, the position (left vs. right) of the stimulus was determined randomly for each trial. The heralding efficiency in this experiment was 0.37 for the 100-ms condition and 0.54 for the 30-ms condition (which required a higher pump laser power). The method was otherwise the same as in Experiment 1a.

5.2. Results and discussion

We first tested whether detection performance differed in the 100-ms and 30-ms conditions. A General Linear Model on accuracy as a function of the photon number and duration condition showed a main effect of photon number ($r = 0.83$, $t(68) = 2.15$, $p < 0.05$), but no effect of the duration condition ($r = 0.07$, $t(68) = 0.32$, $p = 0.75$), nor any interaction between photon number and duration ($r = 0.25$, $t(68) = 0.53$, $p = 0.60$). These data suggest that the efficiency of temporal summation was comparable in the two Constant Duration conditions.

To further examine the efficiency of summation within the integration window, the data in Experiment 2a were compared to those in Experiment 1a (see Fig. 6) to see whether the temporal summation observed in Experiment 1a was as efficient as that in Experiment 2a. Only the data within the estimated temporal integration window (<600 ms) were included in the comparison. Since the photons were presented at a constant rate in Experiment 1a, the stimulus duration increased as the photon number increased.

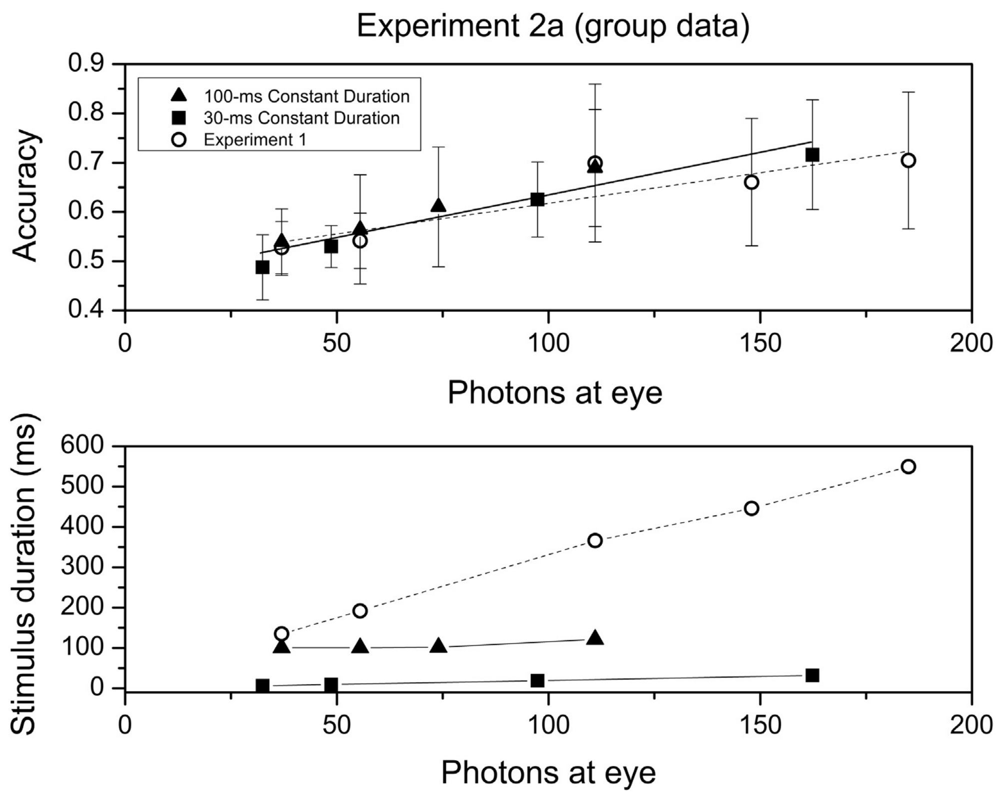

Fig. 6. Group results of Experiment 2a, comparing the 100-ms and 30-ms conditions with the integration condition of Experiment 1a. Linear fits are shown for the combined Constant Duration conditions (solid) and for Experiment 1a (dashed). Error bars are the standard deviation. Stimulus durations for each condition are shown in the bottom panel (lines are for clarity only).

If the temporal summation remains equally efficient throughout the integration window, then performance should be determined by the total number of photons only and unaffected by the stimulus duration; consequently, there should be no difference between Experiments 1a and 2a. In contrast, if the efficiency decreases for long durations, then performance should be lower for the longer durations in Experiment 1a comparing to that in Experiment 2a, leading to a shallower slope in Experiment 1a relative to 2a.

Since there was no difference in the two Constant Duration levels of Experiment 2a, they were combined and compared to the data in Experiment 1a to investigate the completeness of temporal summation. A General Linear Model on the detection accuracy as a function of the total photon number and experiment showed a significant effect of photon number ($r = 0.78$, $t(113) = 4.13$, $p < 0.001$), no main effect of experiment ($r = 0.12$, $t(113) = 0.70$, $p = 0.48$) or interaction between the photon number and experiment ($r = 0.32$, $t(113) = 1.18$, $p = 0.24$). These results showed that the mean accuracy increased with photon number in both experiments, but the slope was not significantly different in the constant duration condition than in the constant rate (i.e., increasing duration) condition (see Fig. 6), providing some indication that in the long durations the summation was fully efficient as in short durations.

Experiment 2a showed that at the group level, temporal summation remains efficient for at least 100 ms, and there was some indication that summation remained efficient in longer durations within the temporal integration window up to ~400 ms. However, given the individual difference observed in Experiment 1b, Experiment 2b further examined the efficiency of temporal summation at the individual level.

6. Experiment 2b: individual summation efficiency

6.1. Methods

Two participants from Experiment 2a (P37 and P41, one female) were recruited to complete multiple sessions in Experiment 2b in order to determine their individual summation efficiencies. These participants were chosen after a screening process which excluded participants with unusually low overall accuracy. Both completed three sessions each of the 30-ms Constant Duration condition and a Constant Rate condition (similar to Experiment 1; see Fig. 7). The order of the 30-ms Constant Duration and Constant Rate sessions was randomly determined. Trials were presented in random order, with 300 trials in each session. The heralding efficiency in the Constant Rate condition was 0.36. The methods were otherwise the same as Experiment 2a.

6.2. Results and discussion

A Logistic regression was performed for each participant on the scores as a function of photon-at-eye and duration condition. P37 showed a main effect of photon number (odds ratio = 1.004, $Z = 2.309$, $p < 0.05$), a main effect of duration condition (odds ratio = 0.659, $Z = 2.14$, $p < 0.05$), and an interaction between photon number and duration condition (odds ratio = 1.008, $Z = 3.663$, $p < 0.001$) (see Fig. 7).

P41 also showed a main effect of photon number (odds ratio = 1.013, $Z = 6.687$, $p < 0.001$), but no significant main effect of duration condition (odds ratio = 0.917, $Z = 0.431$, $p = 0.67$), nor

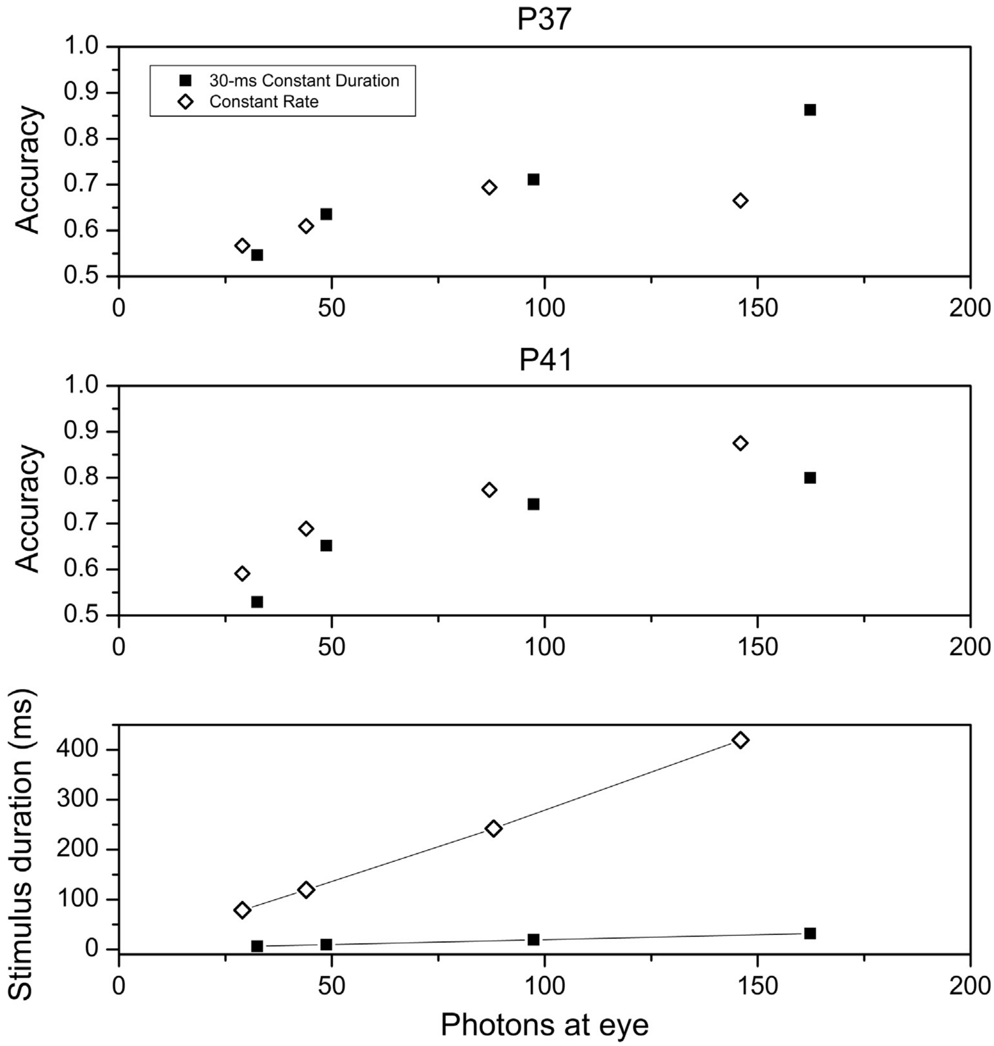

Fig. 7. Individual results of Experiment 2b, comparing 30-ms Constant Duration and Constant Rate conditions. Photon numbers in the two conditions are comparable but do not exactly match. Stimulus durations for each condition are shown in the bottom panel (lines are for clarity only).

an interaction between photon number and duration condition (odds ratio = 0.996, Z = 1.477, p = 0.14) (see Fig. 6).

Combined with results in Experiment 2a, these data suggest that in general temporal summation over a long duration remains efficient compared to summation within a short period of time, but there may be individual differences, and for some people the efficiency may decrease over the integration window.

7. General discussion

This study examined temporal summation at low light levels using a new experimental paradigm and a novel single photon light source. At the extreme, few-photon light level we were able to study (the weakest stimuli contained only 30–40 photons, of which only 3–4 are expected to be detected), we found that temporal summation continued for at least 650 ms on average. This summation is not necessarily perfectly efficient. Previous methods (e.g., Barlow) have measured the window of complete summation of relatively bright stimuli, and demonstrated the existence of partial summation that occurs after this window, but did not measure the length of partial summation. Here we measured the length of the whole range of summation for dimmer stimuli, including partial summation, and examined its completeness by comparing long visual stimuli (up to ~500 ms) to much shorter Constant Duration stimuli (100 ms or 30 ms) containing similar numbers of photons. We found some indication that summation remained efficient over longer durations within the temporal integration window, although there may be individual variations.

Although all participants exhibited some temporal summation, some participants had substantially higher or lower accuracy across all conditions than the average. Accuracy for the brightest trials varied between 0.56 and 0.95 for the nine participants in Experiment 1a. To account for the possibility that temporal summation varies with detection threshold/sensitivity level, we did a medium split of the participants according to their accuracy in the two longest durations, dividing them into low sensitivity (5 participants) and high sensitivity (4 participants) groups, and re-ran the spline regression analysis for each group separately. The integration window was 600 ms for the low sensitivity group and 700 ms for the high sensitivity group, both were quite similar to the all-participant analysis of 650 ms. Since we were not able to run statistical analysis between these integration window lengths, it is not clear whether the length of the integration window is actually affected by participants' visual sensitivity in our data. Similarly, we do not know whether P16's relatively long integration window was due to individual difference, or due to light level differences. Future research should examine variations in temporal integration window length and efficiency across participants more systematically.

There are a number of potential reasons for individual variations in their overall accuracy, including actual differences in visual sensitivity and the length/efficiency of summation, as well as differences in attention and skill at the task. Several factors in the experimental setting may also contribute to these variations. Participants were permitted to wear their usual vision correction (eyeglasses or contacts) during the experiment, which may have some impact on performance. Additionally, while the 30-min dark adaptation period was likely to be sufficient for most participants to reach their best performance, some participants could possibly have benefitted from a longer dark adaptation time if it were available (Davson, 1962). Nonetheless, in a post hoc analysis comparing participants' accuracy in the first and second half of the session combining data from all four experiments showed no significant difference (paired $t(29) = 0.105$, $p = 0.92$), suggesting performance did not improve from the first to the second half of the experiment and the potential effects of learning or improved dark adaption were minimal.

Because our measurement of the integration window includes partial summation, it is difficult to compare to previous measurements of complete summation with brighter stimuli (e.g., Barlow's value of ~100 ms), including direct measurements with rod cells which typically found shorter integration windows (Berntson, Smith, & Taylor, 2004; Cao, Zele, & Pokorny, 2007; Schmolesky et al., 1998; Schneeweis & Schnapf, 1995). Additionally, we note that our behavioral study cannot necessarily distinguish between the performance of the rods and higher-level processes. Our results do show that temporal summation persists for much longer than 100 ms for the weak, very small (50-μm diameter) stimuli we studied. This appears to be consistent with Barlow's finding that small stimuli in total darkness lead to the most significant partial summation outside the window of complete summation, although our stimuli were smaller and weaker than Barlow's.

We did not follow the traditional curve fitting in our analyses for several reasons. First, the relationship between detection rate and photon number in Hecht's study was based on the critical assumption of a Poisson distribution in photon number. Since our single-photon light source violates this assumption, the traditional function cannot be used to fit our data. Second, because our research goal was to find the temporal integration window, not the relationship between detection rate and photon number, Experiment 1 plotted accuracy as a function of duration, not photon number, so this is a completely different type of relation than the Hecht curve. Although the mean photon number is a linear function of duration, how many of those photons were integrated effectively may vary as duration increases and this efficiency function is unknown. Therefore the relationship between accuracy and duration is also unknown, and the traditional relation between accuracy and photon number does not apply to our experiment, even if we had used the classical light source. Finally, because the function is unknown *a priori*, we used the linear relationship as the first order approximation in the estimation of the temporal integration window. The actual data showed a very good fit (R^2=0.882 for the group data, 0.975–0.999 for the individual data), suggesting that the linear fit was reasonable for the current purpose.

The single-photon source itself was originally designed for ongoing studies of single-photon vision. In the multi-photon experiments reported here, it is mainly a useful tool for producing small numbers of photons which could also be produced with a classical source. Therefore, the use of the single-photon light source was not critical for the current study, in the sense that our study can also be carried out using a classical source. Nonetheless, this new type of light source has some properties that differ from the classical source, and these differences will likely affect visual perception. For example, the reduced variance in photon number compared to a classical source can potentially influence the detection rate. According to Hecht et al. (1942), the detection rate of very low lights depends on the probability of absorbed photon numbers exceeding a certain level due to variation in the stimuli. Therefore performance is primarily determined by the tail of the photon distribution, and even a small reduction in variance can be a potentially important factor. Moreover, the difference in the type of distribution can affect the detection function. Because this type of light source has never been used in psychophysics experiments, it's important to note any differences that can potentially affect performance.

The previous method of adjusting light intensity to a just-detectable level has an intrinsic limitation and can only be used to study temporal summation for stimuli at a particular subjective accuracy level. We developed a new paradigm that can study temporal summation with more flexibility in stimulus range by plotting detection accuracy as a function of the stimulus duration while holding photon rate constant. The temporal summation window was then estimated as the turning point when performance no longer increases as the stimulus duration increases. This paradigm can be used to test whether any arbitrary light source is within the temporal summation window by creating a sequence of stimuli that have the same photon rate but with varying durations and plotting the performance as a function of stimulus duration. This new method could be particularly useful for studying perception of lower intensity lights.

These results may have implications for studies of absolute visual threshold, e.g., whether people can see a single photon. Because summation was found to occur for at least 650 ms, an interesting conclusion is that the time delay needed for a stimulus to be truly considered a "single" photon appears to be quite long. The visual system may treat widely spaced single photons differently than photons arriving at the rates we studied, but the long integration time measured here suggests caution in treating photons that arrive even within a second of each other as separate.

8. Conclusion

We studied temporal summation in the visual system for few-photon stimuli generated by a single-photon source. In a group of nine participants, temporal summation was found to continue for at least 650 ms on average. Significant individual variation was observed, with two individuals found to have integration times of 600 ms and 400 ms respectively. The efficiency of the summation was also explored, both in a group of participants and in two individuals. The results give some indication that temporal summation remains efficient within the integration window, although there is individual variation. These results extend our understanding of how the visual system adapts to extremely low light levels with temporal summation, and demonstrate that a forced-choice experimental design and precise light source can be used to study behavior near the visual threshold where detection probabilities are low. The relatively long integration window measured in this study may also 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.

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