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Visual Responses in V1 of Freely Viewing Monkeys

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We have developed techniques to study the response properties of single units in V1 of alert non-fixating macaque monkeys. We map the orientation preference and the receptive field of each single unit using stimuli that do not require the animal to fixate. We then allow the animal to freely view simple and complex images while we record from these units. For each spike, we record the position of the eyes at a given interval preceding its occurrence; this should reveal the parts of the image that lead to the cell's firing. V1 cells in the alert monkey tend to have higher spontaneous activity than in the anesthetized monkey, and this high background firing usually obscured the spontaneous activity than in the anesthetized monkey, and this high background firing usually obscured the specific responses in activity maps for complex images. We found that the response patterns of neurons gave surprisingly poor reflections of what the animal had been viewing, unless we restricted the analysis to bursts of spikes or short intervals of very fast firing.

METHODS

We recorded 31 units from V1 of an alert male macaque monkey. We have recently obtained similar results from a second monkey.

Stimulus Presentation and Data Collection

We first mapped the orientation tuning and receptive-field location using stimuli that did not require the animal to fixate.

Orientation tuning. To determine the orientation selectivity of a unit, the monkey was presented with a series of images such as that of panel a in Figure 1, consisting of 40-60 randomly positioned parallel bars. All orientations, in 10-degree increments, were presented at a rate of 5 or 10 Hz. In a given cycle, each orientation was presented once, in random order. Because many bars were presented in each frame, it did not matter precisely where the monkey looked, but because we were recording from the left hemisphere (and therefore the right visual field), we encouraged the monkey to keep his gaze in the left half of the screen by rewarding him with a drop of water or juice whenever he kept his gaze for 3-4 seconds within 5-15 degrees of a 2- to 5-degree spot on the left side of the monitor. On different days different fixation requirements were used, depending on the monkey's willingness to fixate; the goal was simply to keep his gaze in the left half of the screen. Total spikes were recorded for all except the first 35 msec of each presentation. Tuning curves show polar plots of firing rate versus orientation angle (0 degrees = vertical). For simplicity in viewing the plots, the data points were reflected through the origin. Each curve represents at least 7 cycles of each orientation. At least two tuning curves showing approximately the same optimal orientation curves were required before we went on to the next step with a given cell. Error bars indicate the standard error of the mean.

Receptive-field mapping: Flashing bar stimulus. A single bar of optimal orientation was flashed at random positions on the screen at 10 Hz (for a few cells the stimulus rate was 20 Hz) while the monkey was encouraged to keep his gaze in the left half of the screen (because the electrode was in the right hemisphere) as described above. For each spike, a 200-msec history was recorded of bar positions, eye positions, and preceding interspike intervals. After recording this information for 2000 or more spikes, usually over a period of 10-60 minutes, the record was analyzed by reading back the information for each spike as eye position relative to bar position at various times before the spike occurred (the “delay time”). We could also read back either all spikes in the record or only those events that consisted of two, or more, spikes within a specified time interval (the “burst filter”). When using the burst filter, a dot is plotted at each eye position at a given delay before the first spike in each burst that passed the burst filter. Each panel in the figures represents the entire video monitor, which covered 60 by 45 degrees of visual angle. For each flashing bar record, the bar position is shown only once, plotted at the same location, and the foveal position relative to the bar position is calculated for each spike or burst.

In the gray-scale maps, the number of spikes assigned to each 10 pixel x 10 pixel area was calculated; these values were scaled linearly to fall into seven value ranges and assigned a corresponding gray level (darker corresponds to more spikes per unit area). For each cell studied, we used the flashing bar data to determine the optimum burst filter and delay time for data collection during free viewing.

Free-viewing recording. Static stimuli were put on the video monitor screen and remained there continuously for up to 3 hours; for cells recorded in the left hemisphere calcarine sulcus whose receptive fields were 15-30 degrees to the right of the center of gaze,
Figure 1. Panel a shows one frame of a series of stimuli used to generate the orientation-tuning curve shown in the inset from a single unit from Area V1 in the roof of the calcarine sulcus of the left hemisphere. The inset shows a polar plot of bar orientation vs. average firing rate; error bars indicate standard error of the mean. Panel b shows the foveal positions relative to the bar for every spike recorded during the flashing bar stimulus, using a delay time of 35 msec. Total spike number = 2400. There was no clear positional specificity in the response pattern, and it did not become any clearer at any delay time tested between 0 and 100 msec. (We show this particular delay time for the total spike train because a delay of around 35 msec gave the clearest receptive-field maps using the burst filter.) Panel c shows the same data, after eliminating all spikes that occurred within 50 msec of an eye movement of more than one-half degree. Panel d shows the same data as panel b, but with the number of spikes assigned to each unit area represented by a linear gray-scale value. The total spike data, as well as the total minus eye-movement spikes, also showed no clear evidence for a receptive-field structure. Panels e and f show responses to a flashing white bar stimulus using different burst filters for the same unit. From the clear enhancement of the receptive-field map, such a burst filter enables us to restrict data collection predominantly to spikes that occurred in response to the bar stimulus. The receptive field map corresponds to an eccentricity of 30 degrees.

Guided scanning recording. Similar stimuli and data collection as for the free-viewing experiments were used. A fixation spot appeared for 2 seconds at random locations over the image within a designated region, which was sized and positioned so that as the animal's center of gaze followed the fixation spot, the cell's receptive field would be positioned over all parts of the

the stimulus was placed on the right half of the screen, and the left half of the screen was left completely blank. A 200 msec-long running buffer of eye position was continuously updated, and whenever an event (spike burst) occurred that satisfied the burst filter, the foveal position at a preset time before the first spike in the burst was recorded, and a pixel was plotted there.
image. The animal was rewarded for following the spot.

**Interspike interval distribution calculations.** Using a receptive-field map from a flashing bar stimulus set, a rectangle was drawn around an area on the map—either the area that represented the response to the bar, or an area outside the response region. All spikes in the rectangle were tagged, and the time was determined between each tagged spike and the next spike in the train (this second spike did not have to be tagged). Predicted interspike interval distributions for random spike trains having a given rate were predicted using the exponential function:

\[ f(t) = \lambda e^{-\lambda t} \]

In this expression, \( t \) = time, and \( \lambda \) = the rate of firing (Ash 1993). All histograms and curves were calculated for a bin size of 1 msec up to a total maximum interval of 35 msec; all results were normalized to give percentages of the total number of intervals up to 35 msec.

**Alert monkey recording methods.** Before recording began, under general anesthesia (1.5-2% halothane in 1:1 oxygen in air) and using sterile techniques, we implanted a head post, a scleral search coil, and a recording chamber (Wurtz 1969; Judge et al. 1980). The monkey was given analgesics for 2 days postoperatively (Torbutrol, 0.25 mg/kg, q12 hr) and prophylactic antibiotics 10 days postoperatively (2.5 mg/kg Baytril, bid). The monkey was allowed to recuperate for 2 weeks before recording began.

During recording we took extensive precautions to prevent infections. Anything that came in contact with the inside of the recording chamber, such as instruments, electrodes, guide tubes, and the electrode advance, was either sterilized or disinfected with Nolvasan before use. The chamber was rinsed daily with sterile saline, and drops of antibiotic/anti-inflammatory solution (Neodecadron) were applied daily. The skin margins around the implants were painted with Nitrofurazone ointment daily.

The monkey was trained to sit in a primate chair with his head fixed, and, during the orientation tuning and receptive-field-mapping parts of the experiment, was rewarded with a drop of water or fruit juice when he kept his gaze within 5-10 degrees of a 1- to 5-degree-diameter spot for 3-4 seconds. Eye position was sampled at 250 Hz. The monitor was 34 cm from the monkey’s eyes. Single units were recorded with lacquer-coated electropolished tungsten electrodes. All procedures conformed to National Institutes of Health guidelines for the care and use of laboratory animals.

**RESULTS**

Figure 1a shows one frame of the stimulus used to determine a cell’s orientation preference, and the inset shows the orientation tuning of a typical unit. After the optimal orientation was determined, the unit’s receptive-field location was determined by flashing an optimally oriented bar at various positions on the monitor screen, while storing a continuously updated buffer of eye position and bar location for the previous 200 msec. The bar was flashed in a different random position every 100 msec. Every time a spike occurred, the eye positions, bar positions, and preceding interspike intervals for the previous 200 msec were recorded. To analyze these spike trains, the bar was plotted at one position on the screen, and then a dot was plotted at the position the monkey’s center of gaze had occupied, relative to the bar, at a designated time before the spike occurred (the delay time). This procedure is similar to a reverse correlation calculation (Jones and Palmer 1987). When all the spikes recorded were mapped in this manner, we could seldom see a very clear reflection of receptive-field organization at any delay time for a narrow bar stimulus (Fig. 1b).

We considered several possible explanations for this unexpected difficulty in seeing the effects of an appropriate visual stimulus on a V1 cell. We thought perhaps that eye movements might result in erroneously assigned eye positions. We therefore programmed the computer to eliminate from the plot all spikes that occurred within 50 msec of an eye movement of more than one-half degree. As shown in panel c, only a very few spikes were eliminated by this procedure, and the receptive field became no clearer.

Next we asked whether increases in firing might be concealed if points from more than one spike were plotted on top of each other during rapid firing. To test this possibility we converted the same spike data to a gray-scale map, assigning a gray level to each 10 pixel x 10 pixel area depending on the number of spikes assigned to that area (darker areas represent the highest spike counts). As shown in panel d, the cell of Figure 1 showed a hint of a receptive field in this gray-scale map, reflecting the fact that on average the cell fired 3 times faster when the bar was somewhere in the cell’s receptive field (average rate = 53 spikes/sec) than when it was outside (average rate = 17 spikes/sec). The response was clearer than in the map in panel b, but not nearly as clear as we would have expected from listening to the neuronal activity on the audio monitor, or from our experience with anesthetized animals.

Our failure to produce a clear response map corresponding to the presence of the stimulus in the cell’s receptive field surprised us, since we could often hear, and see on the oscilloscope trace, that cells did respond to the flashing bar, often in bursts of action potentials. We therefore tried analyzing the spike trains to display only those events when spikes occurred in bursts of a given number of spikes within a given interval. A clear response map then usually emerged. After collecting several thousand spikes for a particular unit, we could display the data using various burst filters (varying the number of spikes required within a variable time...
window) and using different delay times. Panels e and f show two maps, using different burst filters, for the same spike train. Restricting the display to responses consisting of 2 or 4 spikes within 10 msec shows an increasingly clear picture of the response to the flashing bar. Different cells showed the clearest maps using different filters, but the optimal delay time was usually between 35 and 50 msec.

For each unit, having first determined the optimal orientation, we used the flashing bar stimulus to determine the receptive-field location and optimal burst filter and delay. We then allowed the monkey to freely view simple black and white images or to scan the images by following a fixation spot that appeared at various positions, while recording spikes and keeping track of eye position. Figure 2 shows results for one cell. The flashing bar stimulus reveals a response map with the unfiltered spike train, but the map is much clearer when only those events where 2 spikes occurred within 10 msec were plotted. The right panels show the cell's responses while the animal viewed a simple circular white spot on a black background with and without this same burst filter. We positioned the white circle as shown, near the right edge of the monitor; thus, for the receptive field of the cell to be over part of the circle, the animal had to be looking at the lower left part of the screen. The animal was encouraged to explore the entire lower left part of the screen by rewarding him for following a fixation spot that appeared at various locations in that part of the screen.

![Figure 2](image-url)

**Figure 2.** Responses of a cell located in the roof of the calcarine sulcus of the left hemisphere. The inset at the top left shows the cell's orientation tuning. Panel a shows the responses to the flashing bar stimulus (a white bar on a black background presented at 20 Hz), using no burst filter, but with spikes that occurred within 50 msec of a one-half degree eye movement eliminated. Total spike number for the flashing bar stimulus = 6300 spikes. Panel b shows the same spike train, filtered to show only those events when 2 spikes occurred within 10 msec. In this experiment, the monkey did not freely view the static stimuli, because we wanted to compare the responses with a burst filter to responses without a burst filter, and for technical reasons the two sets of spike trains had to be collected separately. Therefore, we programmed a fixation spot to appear at random locations, changing positions every 2 sec, in the otherwise blank lower left part of the screen, and the monkey was rewarded for following the spot. Panel c shows the spikes recorded in response to the white disk, while the monkey followed the fixation spot, without using any burst filter. Panel d shows the responses to the same stimulus, but recording only those events when 2 spikes occurred within 10 msec, and no eye movements of more than one-half degree occurred within 50 msec.
the right panels, each dot indicates the foveal position 35 msec before each spike (c), or before each pair of spikes occurring within 10 msec (d). This cell had a spontaneous firing rate of 20 spikes/sec and a visually evoked firing rate of 60 spikes/sec, but this difference in rate was not enough to produce a clear picture of what the animal had been viewing using the total spike record (c). When we filtered the spike train, however, it became clear that the cell tended to fire bursts of action potentials most frequently when its receptive field lay on or near contours of the same orientation as its preferred orientation.

Responses from a different cell are shown in Figure 3. This cell showed a poor response map to the flashing bar stimulus with no filter, even after eliminating spikes that occurred within 50 msec of an eye movement of more than one degree. A clearer response map emerged when we mapped only those events in which 5 spikes occurred within 40 msec. Then the monkey was allowed to freely view the monitor screen with a stationary white spot in the upper right corner. The cell fired bursts predominantly when the eyes were in such a position that the receptive field lay over contours of the preferred orientation. Unlike the cell of the preceding figure, this experiment was done without any guiding fixation spot, although the monkey was encouraged to keep his gaze in the (completely blank) left part of the screen by being rewarded for keeping his gaze in that half of the screen.

We also used slightly more complicated figures to see how cells would respond and how accurately the responses reflected the image the animal had been viewing. For several cells we let the monkey freely view images with multiple contours, without using any fixation spot (Fig. 4). The cells fired bursts not only to the parts of the arcs that had the same orientation as

Figure 3. Responses of another cell recorded from V1 in the roof of the calcarine sulcus. Panel a shows the responses to the flashing bar stimulus (a white bar on a black background presented at 10 Hz), using no burst filter, but with spikes that occurred within 50 msec of a one-half degree eye movement eliminated. Panel b shows the same data, displayed using a gray scale to represent the density of events at each location. Panel c shows the same spike train filtered to show only those events when 5 spikes occurred within 40 msec. Panel d shows eye positions corresponding to events of 5 spikes within 40 msec while the animal freely viewed a large white spot on a black background. There was no fixation spot; the animal was encouraged to keep his gaze in the blank left half of the screen by juice rewards.
Figure 4. The inset in the upper right panel shows the orientation tuning of a cell recorded in the roof of the calcarine sulcus of the left hemisphere. Panels a and b show responses to the flashing bar stimulus, without and with a burst filter, as indicated (total spikes = 9600). Panel c shows the stimulus used during the free-viewing recording. In this experiment, there was no fixation spot; the animal was rewarded only for keeping his gaze in the blank left half of the screen. Panel d shows the foveal positions 35 msec before each event that passed the burst filter during the free viewing. All stimuli for this cell were white on a black background.

the cell's preferred orientation, but also usually to the short terminations of the arcs, which were also of the appropriate orientation. Figure 5 shows responses of another cell, using guided scanning with a similar stimulus.

One could ask whether the burst filter revealed the cells' responses simply because it acted as a temporal cutoff, indicating when cells fired faster than some baseline rate, or whether the responses were characterized by bursts of action potentials, as was our impression from listening to the cells and from looking at the oscilloscope trace. If we define a burst as a pair of spikes occurring within a given interval, \( t \), for a theoretical random spike train, we can calculate the predicted burst rate. The average burst rate will be equal to the average firing rate times the probability that any spike in the train will be followed by a second spike within an interval, \( t \). The probability that a second spike will occur within \( t \) is roughly proportional to the rate, as long as the average number of spikes per interval \( t \) is small. That is, for low spike rates and short intervals, the ratio of the burst rates is predicted to be approximately the square of the ratio of the two spike rates. For bursts of three events within a short interval, the ratio of burst rates will be roughly the cube of the ratio of the spike rates. For most of the cells we looked at, the average firing rate in response to the flashing bar stimulus was less than 100 spikes/sec. For spike rates below 100 spikes/sec, a burst filter of 2 spikes in 5 msec roughly squares the ratio of evoked to spontaneous firing (see Appendix). The effectiveness of the filter is less for higher rates or longer intervals.

This power relationship at least partly explains how our burst filter increases the evoked-to-spontaneous event ratio. That is, the fact that the burst filter increases the ratio of the rates of evoked-to-spontaneous events does not necessarily mean that a cell would have to show a change in firing pattern, such as an increase in burstiness, during evoked responses. Nevertheless, we do think that for some cells the firing
pattern may differ in more than simply rate between spontaneous and visually evoked firing. For all 31 cells in this study, we calculated the predicted rate for events of 2 spikes per 10 msec as \( \lambda (1-e^{-2T}) \), where \( \lambda \) is the rate in spikes/sec and \( T = 0.01 \) sec. Of this population of 31 cells, one third showed evoked-to-spontaneous event ratios that exceeded the prediction by more than 20%, suggesting a difference in firing pattern between evoked and spontaneous activity.

To get some idea of what this difference might be, we looked at raw spike records and calculated interspike-interval histograms for visually evoked and spontaneous firing. Figure 6 shows raster plots of individual responses for the cells illustrated in Figures 1 and 2. The responses of the cell of Figure 1, shown in the top panel of Figure 6, are characterized by a transient increase in firing rate, followed by a sustained response of about twice the background rate, lasting for the length of the stimulus presentation (100 msec). By inspection, there are frequent clusters of two or more spikes in both the transient and the sustained parts of the response, as well as occasionally in the spontaneous firing, shown to the left of time = 0. Interspike interval histograms for visually evoked and spontaneous firing for these two cells are shown in the bottom half of Figure 6. The interspike interval histogram for the first cell indicates that half the spikes in the visually evoked response occurred within 6 msec of another spike, yet the average rate during the visually evoked response was only 53 spikes/sec. For a random spike train with a rate of 53 spikes/sec, only a third of the interspike intervals should be less than 6 msec. This suggests that this cell does tend to respond with pairs or bursts of spikes. Of course, the initial response transient will contribute to the proportion of short intervals in the histogram. We do not know whether there is also a contribution from sustained bursty firing. The second cell responded to visual stimulation with a sustained increase in firing rate that lasted for about 50 msec, which was the duration of the
Figure 6. Raster plots and spike interval histograms for the cells shown in Figs. 1 and 2. The top panels show raster plots for a series of consecutive responses aligned so that 0 represents the appearance of the flashing bar in the cell's receptive field. For the cell of Fig. 1 (top panel) the stimulus duration was 100 msec; for the second cell it was 50 msec. The bursts do not show any relationship to the refresh rate of the monitor. The lower panels show interspike interval histograms for the same cells. The dark upward-going bars indicate interspike intervals for visually evoked firing, and the white downward-going bars indicate interspike intervals for spontaneous activity. The curves indicate the predicted interspike interval distribution for random spike trains having the same rate as the spontaneous firing (dotted downward-going curves) or the same rate as the average firing rate for that cell during the visual response (solid upward-going curves).

For the 31 cells in this study, the receptive field shape and size did not differ qualitatively with different filter settings; the only differences were in the ratio of visually evoked to background signal. Cells varied in how clear the receptive field was without using any filter; the average ratio of evoked-to-background firing was 4. However, all the cells showed an increase (on average a fivefold increase) in the ratio of visually evoked versus background events using a filter of 2 spikes/5 msec. All cells studied showed interspike interval histograms that were shifted to the left of what would be predicted for a random process, with, on
average, twice as many intervals in the 2 to 6 msec bins as would be predicted, for visually evoked firing, and 1.5 times as many short intervals as predicted for spontaneous firing.

**DISCUSSION**

We find that looking selectively at 2 or more spikes within a short interval greatly increases the evoked-to-spontaneous event ratio. There are at least four contributing factors to the effectiveness of the burst filter in revealing visually evoked responses: (1) Any increase in firing rate is selectively enhanced because of the power relationship of the rate ratios; (2) many cells tend to fire in a bursty pattern, and the burstiness is increased during visual stimulation; (3) most cells show a transient period of very fast firing at the beginning of the response, which is selectively passed by the burst filter; (4) during free viewing or guided scanning, we suspect that small eye movements (Ditchburn and Foley-Fisher 1967) tend to bring the stimulus repeatedly into and out of the receptive field, producing a series of transient responses.

It is not surprising that the firing patterns of cells in V1 of alert, freely viewing macaque monkeys showed position- and orientation-specificity, as these properties have been well documented in anesthetized macaques (Hubel and Wiesel 1968) and in alert fixating macaques (Wurtz 1969; Dow 1974; Schiller et al. 1976; Maunsell and Gibson 1992; Snodderly and Gur 1995). Previous studies on alert fixating macaques of course found that cells do show an overall increase in firing rate to specific stimuli, but in these studies responses are averaged over many identical presentation repetitions, time-locked to stimulus presentation, so even a small increase in overall rate can be clearly distinguished as a specific response. In our experiments, for both the free-viewing situation and with the flashing bar stimulus, the appropriate stimulus falls on the cell's receptive field only a small proportion of the recording time, giving a much lower ratio of signal to noise. Moreover, the response is spatially distributed depending on the geometry of the stimulus. Gallant et al. (1994) recently reported that in V1 and V2 of freely viewing macaque monkeys, neuronal responses were poorly correlated with the cells' receptive-field properties, just as we found for most cells when no burst filter was used.

Our results suggest that, in the freely viewing animal, bursts of spikes, or episodes of very rapid firing, convey more information about the environment than single spikes or overall firing rate. We cannot yet distinguish between the contribution of transient high firing rate at the beginning of a response and genuine bursty firing, although both bursty firing and response transients may be very common in V1: Figures 6 and 7 of Wurtz (1969) show two cells in alert macaque V1 with very bursty responses; in the alert and the anesthetized cat, cells in area 17 frequently respond with bursts (Cattaneo et al., 1981); and responses in more than half the cells of a population of MT cells in the alert macaque showed bursty firing (Bair et al. 1994). In the present study, most of the cells showed transient high firing rates, with elevated average firing rates lasting 30 msec or less, and this transient response is essentially a single burst of spikes.

One might question our assumption that the burst-filtered response patterns, which more accurately reflect the image the animal had been viewing, carry more information than the noisier unfiltered maps. It is not sensible to assume that the function of a cell in the visual cortex is to reproduce as clearly as possible the image the animal was viewing, because this generates the homunculus problem, by implicitly assuming that some (one?) must be viewing this internal image. We do not assume that there is more information in the burst-filtered records because of the clarity of the images, but rather simply because the burst filter increases by severalfold the ratio of evoked-to-spontaneous events.

It seems reasonable to ask whether a method of looking just at bursts of spikes or transient rapid firing may be useful, not only as a technique for the neurophysiologist, but also to the brain. That is, if we find that the information carried by cortical cells (in V1) is carried more by bursts of spikes (or episodes of very fast firing) than by overall firing rate, it would make sense for the brain region receiving inputs from these cells to respond preferentially to bursts of spikes. Indeed, because of synaptic facilitation (Koch and Crick 1994), a postsynaptic cell is more likely to reach threshold when it is bombarded by bursts of spikes than when its input is evenly spaced spikes of the same overall rate. Moreover, if afferent neurons not only burst, but also burst in synchrony (Kreiter and Singer 1992; Softky and Koch 1993; Livingstone 1996), both temporal and spatial summation would make those signals carried by simultaneous bursts of spikes particularly potent at the next stage.

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**APPENDIX**

**Prediction of Rate Ratios for Two or Three Events within a Short Interval**

We will define a burst as two events occurring within a given interval. \( t \). For a Poisson process, the predicted burst rate is equal to the product of the single event rate times the probability that at least one other event will occur within an interval \( t \). For each single event, the probability of at least one other event
occurring within an interval $t$ of the first event is equal to $1$ minus the probability that no event will occur within $t$.

Given a random spike train (Poisson process), the probability of $k$ events occurring in an interval $t$ is

$$e^{-\lambda t} \frac{(\lambda t)^k}{k!}$$

where $\lambda$ = the average rate for the process (Ash 1993). From the above equation, the probability that no event will occur within a given interval ($k = 0$) is

$$e^{-\lambda t}$$

The probability that at least one event will occur within an interval $t$ is

$$1 - e^{-\lambda t}$$

So the predicted (2 spike) burst rate will be

$$\lambda \left(1 - e^{-\lambda t}\right)$$

For small $\lambda t$, the function $1 - e^{-\lambda t}$ is approximated by the function $\lambda t$ as $\lambda t$ approaches 0. The ratio of these functions, as $\lambda t$ approaches 0, is $1$.

$$\lim_{\lambda t \to 0} \frac{1 - e^{-\lambda t}}{\lambda t} = 1$$

So, for low rates and short intervals, the burst rate for bursts of two events within a given interval approaches $\lambda^2$. Therefore, the ratio of burst rates for two different spike trains should be the square of the ratio of their rates.

In Figure 7 we have graphed the values of $1 - e^{-\lambda t}$ for rates from $\lambda = 0$ to 200 spikes per second for two intervals, $t = 5$ msec and $t = 10$ msec. Figure 7 shows that for an interval of 5 msec, the probability of a second spike occurring within 5 msec of another spike is proportional to the rate for low firing rates, but falls below proportionality above rates around 100 spikes/sec. For a 10-msec interval, the proportionality falls off at lower rates. Thus, for evoked spike rates below 100 spikes/sec, a burst filter of 2 spikes in 5 msec will roughly square the ratio of evoked-to-spontaneous firing. The effectiveness of the filter will be less for higher rates or longer intervals.

By a similar argument, for bursts of three events within a given interval, the ratio of the burst rates will be approximately the cube of the ratio of the spike rates, for low rates and short intervals.

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V1 RESPONSES IN FREELY VIEWING MONKEYS

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