

Are transient spikes special? An information study of the MT response to the onset of visual motion

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A transient peak in the firing rate following a step change in input is a general property of sensory systems. We investigated the information structure of this transient in visual cortex area MT. We found spike counts in the transient to be more reliable than those in the sustained response; this appears to be due to relative refractory effects. We analysed the temporal information available from transient spikes, finding brief periods at onset with synergy or redundancy between spikes. We also varied the spatial structure of the motion stimulus, finding more coherent inputs to give rise to a stronger transient.

Introduction

A prominent feature of neuronal dynamics in sensory systems is a transient peak in the firing rate following a step change in input, followed by a prolonged but lower sustained response. The properties of this characteristic transient response have been investigated in a number of systems including the fly visual system (Egelhaaf and Borst, 1989), the monkey primary visual cortex (Muller et al., 2001, e.g.), and monkey visual area MT (Lisberger and Movshon, 1999; Priebe, 2001).

Is the onset transient simply the inevitable consequence of the necessary filter properties of the visual system, or do transient spikes possess special information properties as a consequence of optimisation to a rapidly changing environment? The perceptual importance of transient spikes in V1 cells has been hypothesised by (Muller et al., 2001), on the basis that fixation durations in everyday tasks leave insufficient time to integrate substantially beyond the transient response. Similar arguments apply to neuronal responses in area MT, in that the times used to process motion occurring in the visual environment during natural fixation behaviour must be bounded by the inter-saccade interval. Furthermore, in human visual motion perception, measured thresholds for speed discrimination asymptote quite rapidly (100-200 ms) as a function of presentation time at the velocities preferred by typical MT cells (McKee and Welch, 1985; De Bruyn and Orban, 1988; Snowden and Braddick, 1991). It thus seems plausible that the motion system might be optimised to make special use of transient spikes.

In this paper, we therefore compare the transient and sustained responses of MT cells to the onset of visual motion, to determine whether transient spikes have any special information-bearing properties.

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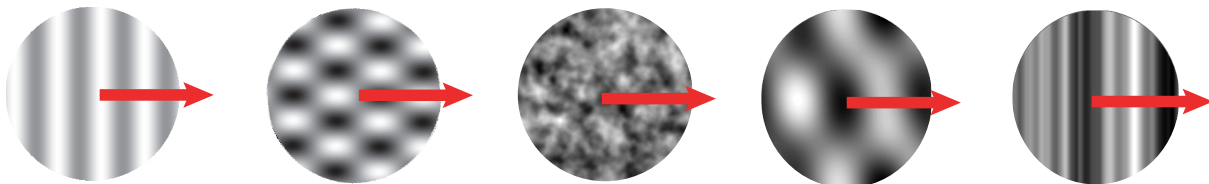


Figure 1: Instances of the drifting motion stimuli used to probe the transient response. Left to right: grating; plaid; texture formed by bandpass filtering white noise with the spatial frequency tuning function of an MT cell; narrower bandpass filter; 1D version of the previous texture.

Experimental Methods

We recorded activity extracellularly from 117 single units in area MT (V5) of the visual cortex of anaesthetised, paralysed macaque monkeys; see Cavanaugh et al. (2002) for detailed methods. The optimal orientation, spatial frequency, temporal frequency and receptive field size of each cell were determined using drifting grating stimuli. The information properties of the transient response to drifting grating and plaid stimuli were assessed by presenting brief (320 ms) epochs of motion in immediate succession; gratings and plaids of 12 different directions of motion were randomly interleaved, together with some blank epochs. Additional experiments were performed in order to examine the effect on the response transient of altering the spatial structure of the motion stimulus: a texture motion stimulus was generated by filtering drifting white noise with the spatial frequency tuning function of the cell, thus concentrating power within the bandwidth to which each cell was most responsive. Variations upon this stimulus were made by progressively narrowing the passband of the filter and by removing one of the spatial dimensions. These stimuli are shown in Fig. 1.

Results

Spike count reliability and information

The response of a typical MT cell to a step change in a visual motion stimulus (in this case a grating) is shown in Fig. 2. The reliability of spike counts in a narrow (20 ms) window was examined by computing the Fano factor (spike count variance to mean ratio) at various onset asynchronies. The Fano factor was noticeably lower during the period of the transient firing peak, compared to later in the response. Similarly, the Shannon mutual information conveyed by 20 ms spike counts about stimulus motion direction was higher in the transient, as would be expected given the higher firing rate. For this cell, however, the efficiency with which the response entropy was made use of for conveying stimulus direction information was actually lower in the transient than in the sustained response.

Across the entire dataset, the Fano factor tended to be slightly lower in the transient than in the sustained response ($P < 0.001$ by a one-sided K-S test; see Fig. 3). Despite this, transient information efficiencies were no higher (in fact, slightly lower on average). On a cell-by-cell basis, the lower transient Fano factors appeared to be well accounted for

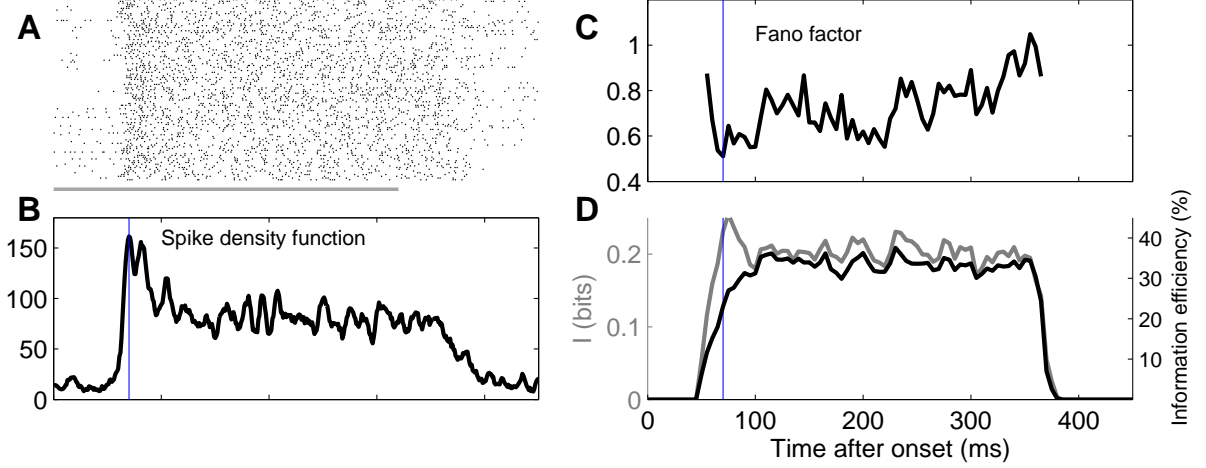


Figure 2: The transient response of an MT cell. **A** Rasters for the response to the preferred direction. **B** The spike density function for the preferred direction. Note that because of the stimulus paradigm, spikes prior to the response onset (stimulus onset + cell latency) are to “random” stimuli, rather than a blank screen (which was a separate control stimulus). **C** The Fano factor in each 20 ms time bins during the period beginning at response onset. **D** Left axis (grey): mutual information conveyed by spike counts in the same 20 ms windows about motion direction; right axis (black): information efficiency (mutual information normalised by the spike count entropy used to convey it).

by regularisation of the spike counts due to relative refractory effects occurring during brief periods of high firing rate.

Spike timing information during the onset transient

Might there be differences in the temporal structure (beyond those dictated by the spike counts) of the spike train during the onset transient? We utilised the procedure developed in Panzeri and Schultz (2001) to address this question. For the time windows used in this study, the mutual information may be broken up into several components,

$$I(\text{Responses}; \text{Stimuli}) \approx I_{PSTH} + I_{COR,IND} + I_{COR,DEP}. \quad (1)$$

I_{PSTH} contains the terms which depend only upon moments of the dynamic instantaneous firing rate, and consists of a positive first order term with linear time dependence and a negative second order correction. The latter two components reflect the effect of correlations between spike occurrences - the average level of correlation and the stimulus-dependence of that correlation respectively. In practice, we found $I_{COR,DEP}$ to be zero for all cells in this dataset. The values of the other two components are shown in Fig. 4 A and B for two example cells. The first of these cells shows a negative value of $I_{COR,IND}$ during the transient, despite remaining around zero during the sustained response. The implication of this is that there is a redundant interaction between the timing information available from spikes in the onset transient. In contrast, the second example cell shows synergistic interaction between spikes in the onset transient. Independence of temporal information from sustained spikes was a

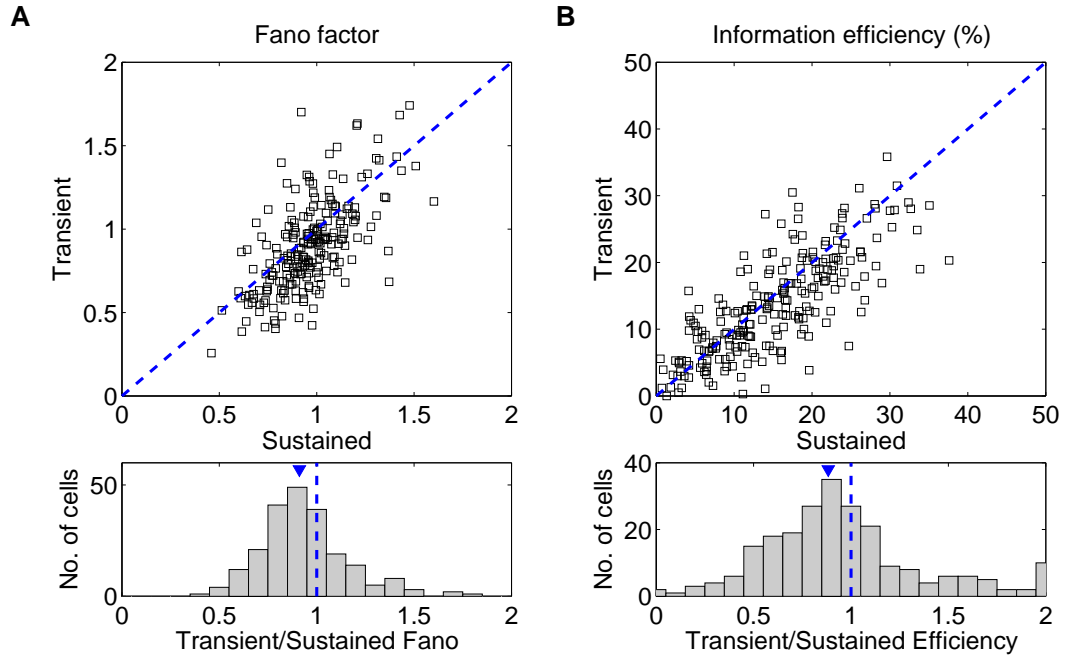


Figure 3: Comparison of transient and sustained properties. **A** 20 ms Fano factor for the peak transient response for each cell, compared to the average of 20 ms epochs within the sustained period. **B** Information efficiency in the same time windows. While transient responses tend to have lower Fano factors, particularly at low variance, the overall information efficiency of the transient and sustained responses is very similar.

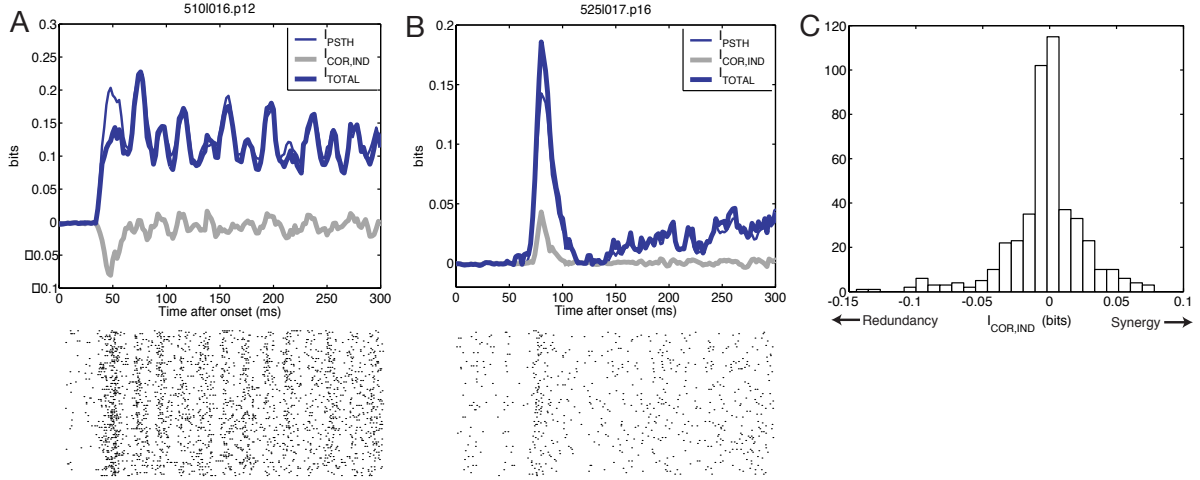


Figure 4: Components of spike timing information in 10 ms epochs following motion onset. **A** A cell showing a brief period of redundancy between spikes in the transient. **B** Another cell showing a synergistic pattern of spikes. Below: spike rasters for the most effective stimulus for these cells. **C** The distribution across cells of the effect of correlations on the temporal information content.

uniform feature throughout the dataset, however the amount of synergy or redundancy in the onset transient varied widely from cell to cell (Fig. 4C).

Spatial structure and response dynamics

The previous results were obtained with both grating and plaid stimuli - in other words, motion stimuli comprised of one and two velocity vectors respectively. Real-life motion stimuli are constrained by more than two velocity vectors, and so we investigated whether the onset transient was affected by different extents (and dimensionality) of motion integration resulting in the same overall vector. The stimuli presented were similar to those shown in Fig. 1, lasted for 320 ms, and were typically separated by a 320 ms period of static display of the same texture. The texture was optimised for each cell, by making careful measurements of its spatial frequency tuning curve (tested with gratings) at the optimal temporal frequency, and fitting this with a lognormal function. This lognormal curve was then used to filter drifting white noise. The resulting texture would optimally drive the cell if it linearly combined responses to different spatial frequencies within its bandwidth; however, in practice it resulted in similar firing rates to those for grating and plaid stimuli.

In general, texture stimuli seemed *less* likely than grating and plaid stimuli to give rise to a prominent onset transient when tested with stimuli that resulted in a similar sustained response. We tested this explicitly by performing two operations upon the stimulus. The first was to narrow the bandwidth of the spatial filter (keeping power constant), resulting in a stimulus not dissimilar to a random plaid (i.e. with only a small range of spatial frequency content). The second manipulation was to turn the texture into a 1D spatial structure. In both cases, the result was an increase in the height of the transient peak, while preserving the same sustained activity. One way to understand this is as evidence that the transient

peak is dependent upon the amount of coherence in the input (from e.g. V1) to the MT cell, whether that coherence is in the dimension of orientation or of spatial frequency.

Summary

Spikes in the transient had a small, but statistically significant decrease in Fano factor (and thus increase in reliability) compared to the sustained response. Even though this could be accounted for by relative refractory effects at high firing rates, the improvement in mutual information is still “there” to be used by any receiver. However, both noise entropy and total entropy (of spike counts) were affected in the same way by this regularisation, and thus the information efficiency of spikes in the transient was very similar to that of sustained spiking activity. There was a qualitative difference in the spike timing information available during the onset transient, with the appearance of synergistic or redundant interactions between spikes that were not present in the sustained response - the sign and magnitude varying widely across cells. These interaction terms were contributed by a component of the information due to stimulus-independent correlations - and bound the performance of even a “Poisson” decoder of these spike trains which knows nothing about correlations. We suspect that they are due to characteristic, and stimulus-independent, temporal structure in the onset transient for each cell.

References

- Cavanaugh, J. R., Bair, W., and Movshon, J. A. (2002). Nature and interaction of signals from the receptive field center and surround in macaque V1 neurons. *J Neurophysiol*, 88(5):2530–2546.
- De Bruyn, B. and Orban, G. A. (1988). Human velocity and direction discrimination measured with random dot patterns. *Vision Res*, 28(12):1323–1335.
- Egelhaaf, M. and Borst, A. (1989). Transient and steady-state response properties of movement detectors. *J. Opt. Soc. Am.*, 6(1):116–127.
- Lisberger, S. G. and Movshon, J. A. (1999). Visual motion analysis for pursuit eye movements in area MT of macaque monkeys. *J. Neurosci.*, 19(6):2224–2246.
- McKee, S. P. and Welch, L. (1985). Sequential recruitment in the discrimination of velocity. *J Opt Soc Am A*, 2(2):243–251.
- Muller, J. R., Metha, A. B., Krauskopf, J., and Lennie, P. (2001). Information conveyed by onset transients in responses of striate cortical neurons. *J. Neurosci.*, 21(17):6978–6990.
- Panzeri, S. and Schultz, S. R. (2001). A unified approach to the study of temporal, correlational and rate coding. *Neural Computation*, 13(6):1311–1349.
- Priebe, N. J. (2001). *Constraints on the mechanism of short-term adaptation in area MT*. PhD thesis, University of California San Francisco.
- Snowden, R. J. and Braddick, O. J. (1991). The temporal integration and resolution of velocity signals. *Vision Res*, 31(5):907–914.