and alert cats frequently respond with bursts. They show that the frequency of bursts (or "grouped spikes") varies strongly with the spatial frequency and orientation of sinusoidal drifting gratings, while the frequency of "isolated spikes" only weakly depends on these parameters, encoding rather the contrast of the stimulus. Bonds (1992) found in his analysis of cat striate neurons that the structure of spike trains—in his case the frequency and duration of bursts—can vary substantially on the basis of how the firing rate was generated. For instance, presentation of stimuli at nonoptimal orientations at high contrasts yields bursts that are shorter than those generated by lower-contrast stimuli at optimal orientations. Legéndy and Salcman (1985) hypothesized functional significance for burst-firing patterns in spontaneously active striate neurons of alert cats, but by their definition, bursts included mostly long periods (0.5–2.0 sec) of significant elevation in firing rate. Finally, Crick (1984) postulated that the neuronal expression of selective visual attention is the production of bursting in a subset of thalamic neurons. This bursting, in combination with a short-term and transient alteration in the synaptic strength (as proposed by von der Malsburg, 1981), could lead to the short-term formation of transient cell assemblies at the level of cortex (see also Crick and Koch, 1990, 1992).

Motivated by these findings and proposals, we investigated the temporal properties of cortical cells in the awake and behaving monkey. The data were obtained from an ongoing series of experiments linking the responses of neurons in extrastriate area MT (or V5) to the psychophysical performance of trained monkeys (Newsome et al., 1989a,b; Britten et al., 1992). MT is specialized for the analysis of visual motion, as indicated by its preponderance of directionally selective neurons (Zeki, 1974; Maunsell and Van Essen, 1983) and by the motion-specific effects of lesions and electrical microstimulation in MT (Newsome and Pare, 1988; Salzman et al., 1992). The monkeys were trained to discriminate the direction of motion in a stochastic visual display while the responses of MT neurons were simultaneously recorded. As reported previously, the responses of individual MT neurons, considered simply to be the total number of spikes occurring during the period of visual stimulation, can provide a remarkably accurate account of a monkey's performance on the near-threshold direction discrimination task. Single-neuron responses, analyzed by a method based in signal detection theory, provide a good description of psychophysical threshold and of the shape of the psychometric function relating performance to the strength of the motion signal (Newsome et al., 1989a; Britten et al., 1992). In addition, small trial-to-trial variations in the strength of a neuron's response to identical, weak motion stimuli can be significantly correlated with the directional judgements made by the monkey on the same trials (Newsome et al., 1989b). In all prior analyses of these data, however, the temporal characteristics of the spike train were ignored.

We now analyze this single-cell database with an eye toward describing the temporal structure of MT responses and uncovering any relationship between the temporal structure and the psychophysical performance of the animal. We only consider data from well-isolated single neurons, leaving the analysis of other data, including well-isolated pairs of simultaneously recorded neurons (Zohary et al., 1992) and multiunit data, to a future report. We find that the temporal structure of MT responses is characteristic for each neuron and does not change in a stimulus-specific manner. Spikes are distributed almost randomly in time for some neurons, but are highly nonrandom

for other neurons, being characterized by occasional "bursts" in which spikes are tightly clustered in time. Both firing patterns are well described by simple models that require no intrinsically oscillatory process. A signal detection analysis indicates that bursting neurons convey more information about the direction of motion in the stimulus if bursts are considered to be individual signaling events.

Some of these results are briefly described elsewhere (Bair et al., 1992, 1993).

Methods

We first summarize the methods used to obtain the spike trains and then describe the data analysis techniques. Given the importance of applying the underlying mathematical transformation correctly, we justify our analysis in detail.

Data collection

Experimental methods for the collection of the original data are described in detail by Britten et al. (1992). Three adult macaque monkeys were trained to report the direction of motion in a dynamic random dot display in which a certain fraction, c, of the dots moved coherently at a common speed in one direction, while the remaining dots moved in random directions and at random speeds. For $c = 0$ all dots moved randomly, for $c = 1$ all dots moved in a common direction, the neuron's preferred direction, and for $c = -1$ all dots moved in the opposite direction. For a given block of trials, the random dot stimuli were placed within the receptive field of a single MT neuron, and the coherent motion signal was randomly presented in the preferred direction of the MT neuron ($c \geq 0$) or in the direction 180° opposite (null direction, $c \leq 0$) and the fraction of dots, $|c|$, carrying the coherent signal was varied randomly from trial to trial to cover a prespecified range of coherence values near psychophysical threshold. For a typical experiment, at least 210 trials were performed: 15 trials at each of six preferred and six null direction motion coherence levels plus 30 trials at $c = 0$ (random noise). Far more data were obtained for some experiments since additional blocks of trials were run as long as the cell remained well isolated.

An individual trial began with the onset of a fixation point presented on an oscilloscope 57 cm distant from the animal. After the monkey directed its gaze toward the fixation point, the random pattern appeared within the receptive field of the MT neuron for 2 sec. The monkey attended to the random dot display and judged the direction of the coherent motion signal while maintaining its gaze on the fixation point. At the end of the viewing interval, the fixation point and the random dot stimulus were extinguished, and two light-emitting diodes (LEDs) appeared corresponding to the two possible directions of the coherent motion signal. The monkey indicated its decision regarding the direction of motion by making a saccadic eye movement to the appropriate LED; correct choices were rewarded with water or juice. The monkey's eye movements were monitored continuously throughout the experiment using a scleral search coil system (Robinson, 1963).

Action potentials were recorded extracellularly from 216 MT neurons while monkeys performed the direction discrimination task. Thus, physiological data and psychophysical data were obtained on the same trials. On each trial the physiological data consisted of a spike train recorded continuously during the fixation interval, the 2 sec visual stimulation interval, and the intertrial interval. The time of occurrence of each action potential was recorded with a resolution of 1 msec. In the previous analysis (Britten et al., 1992), psychophysical data were compiled into psychometric functions relating percentage of correct choices to the strength of the motion signal. A psychophysical threshold, c_{system}, was measured for each experiment, where threshold was considered to be the motion coherence level that supported 82% correct performance. This psychophysical threshold characterizes the perceptual sensitivity of the monkey to the motion signals under the specific conditions of each individual experiment. Neuronal sensitivity was measured from the responses to preferred and null direction motion obtained over a range of coherence levels; responses were considered to be the total number of spikes that occurred during the 2 sec visual stimulation interval. Using a method based on signal detection theory, a "neurometric function" was computed that expressed the theoretical performance of an ideal observer who judges the direction of motion in the visual stimulus based only on the responses of the MT neuron being