



**Figure 7.** A comparison of neuronal threshold to the shape of the power spectrum. There is no significant correlation ( $r = 0.045$ ,  $p = 0.61$ ) between  $\log(c_{\text{cell}})$  and  $\log(P)$ . Neuronal threshold,  $c_{\text{cell}}$ , is the coherence level that supports 82% correct decisions by an ideal observer counting total number of spikes.  $P$  is the ratio of the height of the peak (dip) in the 40 Hz band of  $S'(f)$  to the baseline level for burst (nonburst) cells. We obtain similar results when correlating  $P$  against measures of the animal's psychophysical performance on motion discrimination (not shown).

monkey's intent to make a discrimination had no effect on the spectral peak. There was a significant change in  $P$  between the choice and background conditions (paired  $t$  test,  $p < 0.05$ ), but the effect was quite small:  $P$  decreased by an average of 3% for burst cells ( $n = 122$ ) and increased by an average of 8% for nonburst cells ( $n = 59$ ). We therefore infer that  $P$  is substantially independent of behavioral state, a conclusion that is supported by visual inspection of power spectra like those illustrated at the bottom of Figure 5.

We next inquired whether the spectral peak developed or changed with time during the course of a 2 sec trial. Analyzing the evolution of the shape of the power spectrum is difficult due to the small amount of data that most spike trains contain in a period as short as a few hundred milliseconds. The average spike rate over our entire database is 19 Hz (with an SD of 18 Hz), so the exact placement of any one spike will have a large contribution toward the overall shape of the power spectrum for short windows. Because of this, we address a special case of this question that allows averaging over trials. This method is therefore limited to detecting changes that are locked to the stimulus onset.

We divided each trial (starting 336 msec after the onset of the stimulus to eliminate initial transients) into six equal time windows that overlapped by one-third of their width. The average value of  $P$  was computed from individual spectra for all windows of similar time lags that fulfilled a minimum spike criterion of five spikes per window. Only 10% of burst cells and 21% of nonburst cells showed a significant correlation between  $P$  and time (Spearman rank-order correlation coefficient,  $p < 0.05$ ). Of those cells,  $P$  increased by an average of 11% and 14% for burst and nonburst cells, respectively. Because  $P$  shows no correlation with time during the trial for 86% of cells and changes little for the other cells, we compute only one spectrum per trial in other analyses.

In a prior analysis of this data set, signal detection theory was

used to compute a neuronal "threshold" that expressed the sensitivity of each neuron to motion signals in the display (Britten, et al., 1992; see Methods). Threshold was defined to be the coherence value at which the neuron signaled the direction of motion with a criterion level of reliability. Thresholds varied widely among neurons in the data set, and we therefore tested for the hypothesis that burstiness as measured in the present analysis could be systematically related to the measure of sensitivity computed in the prior study. Figure 7 shows cell threshold plotted against the index of burstiness,  $P$ , for all neurons that yielded a reliable estimate of  $P$ . The scatterplot contains no structure signifying a relationship between the two measures, an impression that is confirmed by calculation of a correlation coefficient ( $r = 0.045$ ,  $p = 0.61$ ).

Psychophysical threshold also varied across these experiments since the testing conditions were changed to match the preferences of each cell (Britten et al., 1992). For some purposes, therefore, it is useful to express the sensitivity of each neuron relative to psychophysical sensitivity by calculating for each experiment the ratio of neuronal to psychophysical threshold. To determine whether  $P$  is related to cell sensitivity expressed in this manner, we calculated a correlation coefficient between the log of the "threshold ratio" and  $\log(P)$ , but again we found no relationship ( $r = 0.097$ ,  $p = 0.28$ ). Thus, the prominence of a peak in the 40 Hz region of the power spectrum does not correlate with prior measures of cell sensitivity.

Finally, we asked whether the prominence of the peak varied in a systematic way with the decision made by the monkey on successive presentations of a given motion condition. Previous analyses have demonstrated a trial-to-trial covariation between neuronal response and psychophysical decision when the response is considered to be the integrated spike count (Newsome et al., 1989b; K. H. Britten, W. T. Newsome, M. N. Shadlen, S. Celebrini, J. A. Movshon, unpublished observations). We therefore wondered whether a measure of temporal structure in