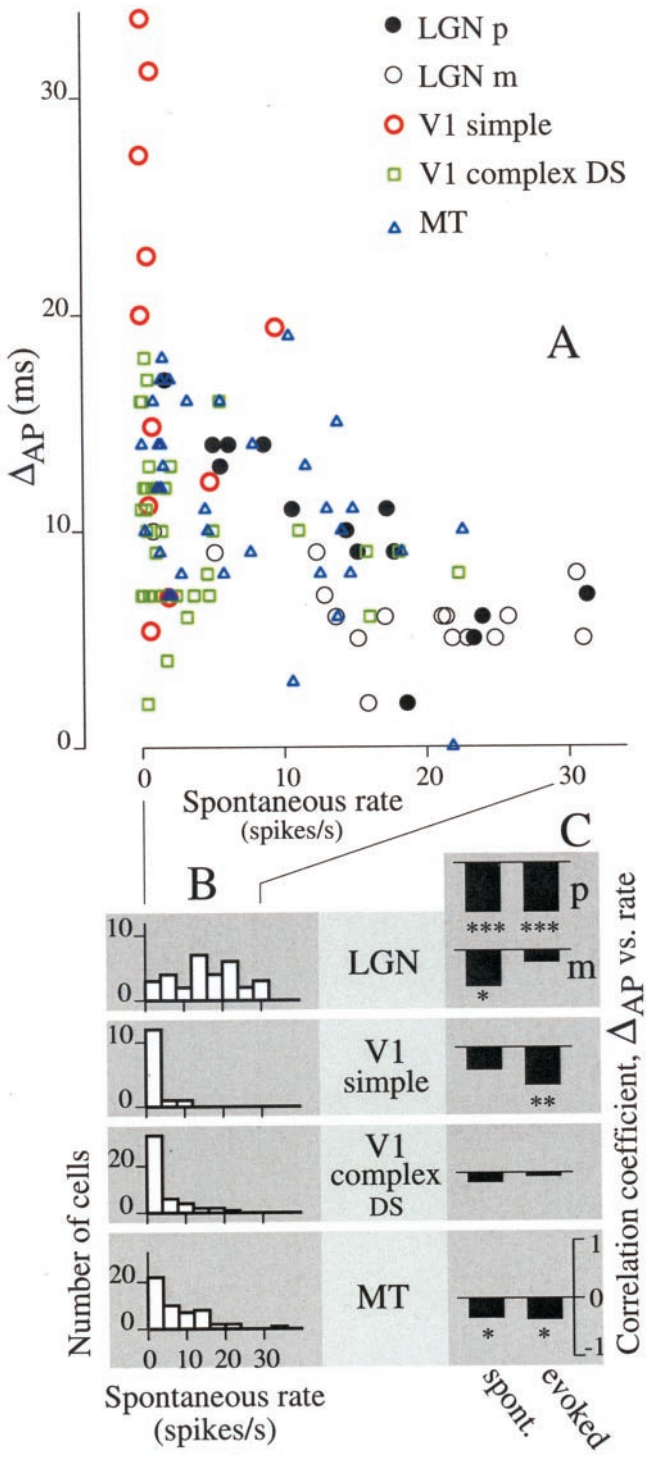

Figure 6. Firing rate is negatively correlated with Δ_{AP}. *A*, For five classes of neurons, Δ_{AP} is plotted as a function of spontaneous rate. LGN p- and m-cells and V1 simple cells were tested with the phase stimulus. V1 complex DS and MT cells were tested with the direction stimulus. *B*, The distribution of spontaneous rate varies across cell class. LGN p- and m-cell data were combined into one histogram because their distributions were statistically indistinguishable (*t* test for mean, $p = 0.34$; *F* test for variance, $p = 0.89$). LGN cells had high and varied spontaneous rates compared with cortical cells. *C*, Correlation coefficients computed between Δ_{AP} and spontaneous rate (*left column* of *bars*) and between Δ_{AP} and evoked rate (*right column*) were always negative. *Asterisks* indicate statistical significance: $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$. Evoked firing rate was computed in the 20 msec period after the onset of response to the AP transition.

response timing, then $\Delta_{NP} = \Delta_{AP}$. If the null stimulus caused no delay in response onset relative to offset, then $\Delta_{NP} = 0$.

A cell-by-cell comparison of Δ_{NP} and Δ_{AP} is provided by the scatterplot in Figure 7*G*. For all cells, $\Delta_{NP} < \Delta_{AP}$, and Δ_{NP} was near zero for many cells that had small Δ_{AP} (approximately $\Delta_{AP} < 10$ msec). For each cell, we computed the ratio Δ_{NP}:Δ_{AP} to asses the fraction of the delay, Δ_{AP}, that was present for the NP transition. We reasoned that a ratio measure would be justified if, as Figure 5*B* implies, Δ_{AP} primarily represents a neuronal integration time (as defined in Nowak and Bullier, 1997) and cannot be negative. Thus, if Δ_{AP} is small because a cell has an intrinsically short integration time, even a large effect of the null stimulus cannot cause a large absolute decrease in the already short integration time. The distributions of the ratio for all cell types fell mainly between 0 and 1, consistent with the scatter of points in *G*. Interestingly, for V1 simple cells, the ratio was significantly larger for the orientation stimulus (mean 0.71, SD 0.12, $n = 5$) than it was for the phase stimulus (mean 0.31, SD 0.14, $n = 4$; *t* test, $p = 0.005$). Taking the logarithm of the ratio, or using the absolute timing difference (because ratio measures are sensitive to noise in the denominator), did not destroy the significance of this result. This suggests that an orthogonal grating is more akin to mean gray than is a counterphase grating, and that the counterphase grating is the more appropriate antipreferred stimulus for V1 simple cells. It would be premature to draw any firm conclusion based on the low number of cells, but if this difference holds up, it provides quantitative evidence that afferent inhibition, associated with push–pull circuits (Ferster and Miller, 2000), is stronger than the recurrent inhibition associated with normalization and believed to underlie cross-orientation inhibition (Carandini et al., 1997).

We have just observed that responses to preferred stimuli were delayed more by A than by N stimuli, and we also observed that firing rate was related to response timing (Fig. 6). We will now examine the relationship between firing rate and delay for N and A stimuli. The mean firing rate in response to NP and AP transitions is plotted as a function of time in Figure 8*A* for a V1 complex DS cell. The firing rate just before the response to the AP transition (*black lines* below *arrow*) was lower than the rate just before the response to the NP transition (*gray lines* below *arrow*). This was typical across cell types, but a few counterexamples were present. Figure 8*B* shows a counterexample for which the firing rate just before the response to the AP transition was higher on average than the rate for the NP transition, yet the NP response still occurred sooner. For each cell, we computed the firing rates in the 10 msec period before the onset of response to the NP and AP transitions and subtracted the rate for the AP case from the rate for the NP case. Figure 8*C* shows the ratio of the timing measures, Δ_{NP}:Δ_{AP}, plotted against the firing rate difference (N-A) for cells marked by class and stimulus (for symbol legend, see Fig. 7*G*). There was a weak but significant correlation ($r = -0.43$) between these measures across all cells and a significant correlation for MT cells alone (*blue triangles*, $r = -0.66$; see legend for statistics). Points for the LGN (*black circles*) and V1 simple cells (*red circles*) contributed to the overall trend, whereas V1 complex DS cells (*green squares*) did not appear to follow the trend.

In summary, for the ternary sequences, antipreferred stimuli suppressed firing rate and delayed the onset of firing more than did null stimuli that were randomly interleaved with them. There was a mild tendency for cells with larger differences in firing rate to have larger timing differences in response to N and A stimuli by