



Figure 3. A comparison of onset and offset latencies across cell types and stimulus categories. The latency of the response to the transition from antipreferred to preferred (*onset latency*) is plotted against the latency of the response to the opposite stimulus transition (preferred to antipreferred, *offset latency*). Nearly all points fell above the diagonal line of equality, indicating that onset latency is longer than offset latency. The mean onset and offset latencies for each cell class and stimulus type are reported in Table 1.

basis of initial characterization with sinusoidal stimuli. The phase stimulus, presented to LGN p- and m-cells and to V1 simple cells (*A–C*, respectively), covered the classical center and surround of the LGN RF and was restricted to the CRF for V1 cells. V1 simple cells were also tested with the orientation stimulus (*D*), which differed from the phase stimulus only by a 90° rotation of the antipreferred sinusoid. V1 complex DS cells (*E*) and MT cells (*F*) were tested with the direction stimulus (*icon above E*), which was an optimally oriented grating that moved in either the preferred or opposite direction every 10 msec. For each example in Figure 2, the response difference trace for the PA transition (*thick lines*) dropped from zero before the trace for the AP transition

rose (*thin lines*). We quantified the offset and onset times for each cell from the respective response difference plots as the time to reach 5% of the maximum excursion from zero (see Materials and Methods).

Onset latency is plotted against offset latency for all cells in Figure 3. The points fell mainly above the *diagonal line* of equality, indicating that offset time was less than onset time. For each cell class, onset and offset times were significantly correlated (Pearson's r ranged from 0.60 to 0.97, $p < 0.004$, for each cell class). Our median LGN onset latencies (24 and 34 msec for m- and p-cells, respectively) fell within the range of medians reported by Maunsell et al. (1999), and our minimum onset latency (20 msec) was larger than theirs (16–18 msec). In V1, our shortest onset latencies (26–30 msec) were consistent with the shortest reported in the literature (Bartlett and Doty, 1974; Maunsell and Gibson, 1992; Nowak et al., 1995). For MT, however, 5 of 39 cells responded before 35 msec, which was faster than most published minimum latencies for MT (Raiguel et al., 1989, 1999; Lagae et al., 1993; Schmolesky et al., 1998; Raiguel et al., 1989, 1999; Lisberger and Movshon, 1999) but was consistent with a report of responses from 30 to 40 msec in area MST (Kawano et al., 1994). Overall, our mean onset latencies (Table 1) were smaller than most published mean values but were not inconsistent with published minimum latencies. This was expected for our rapidly changing stimulus because visual responses are known to be faster for rapid and broadband temporal stimuli (Shapley and Victor, 1978; Sestokas and Lehmkuhle, 1986; Movshon et al., 1990; Reid et al., 1992; Lagae et al., 1993; Kawano et al., 1994; Bair et al., 1997; Lisberger and Movshon, 1999).

Our offset latencies, being consistently smaller than onset latencies, were smaller than the minimum latency values reported in nearly all previous extracellular studies of these visual areas in the macaque monkey. Specifically, our earliest offset latencies were between 15 and 20 msec in the LGN and between 20 and 25 msec in V1 and MT (Fig. 3, *horizontal axis*; see Table 1 for mean values). This is not inconsistent with physical limitations of the circuitry, and, given early responses in the LGN, is consistent with there being only several milliseconds of delay from LGN to cortex (Reid and Alonso, 1995, reported 1–4.5 msec for cat) and a 1–2 msec conduction delay from V1 to MT (Movshon and Newsome, 1996). Thus, offset latencies for our dynamic stimuli indicate that the flow of information through visual cortex can be faster than revealed by most extracellular studies of onset latency.

To quantify the difference between onset and offset latency for each cell, we defined Δ_{AP} (Fig. 1C, *thick bar*) to be onset time minus offset time. Measurements of Δ_{AP} across cell types and stimuli are summarized in Figure 4. For the LGN, in addition to the sinusoidal stimuli just described, cells were also tested with a constant-luminance disk in the center of the RF (*A*) and an

Table 1. Average response offset and onset latencies for the data plotted in Figure 3

Cell type	Stimulus	Offset (msec)		Onset (msec)		<i>n</i>
		Mean	SD	Mean	SD	
LGN m-cell	Phase	18	3.5	24	2.9	17
LGN p-cell	Phase	27	12	37	14	14
V1 simple	Phase	31	8.5	52	16	11
V1 simple	Orientation	29	8.9	52	18	16
V1 complex DS	Direction	28	6.6	38	6.1	34
MT	Direction	29	5.2	40	4.8	39