opposite in phase) was presented (Fig. 1, *Top*, *right* and *left icons*). We estimated the onset latency by comparing the response for the A-to-P (AP) transition with that for a reference stimulus that contained no transition to P. The AP transition was defined to be 30 msec of A followed by 20 msec of P, and the reference stimulus, lacking the transition, was 50 msec of A (Fig. 1*A, solid* and *dashed lines*, respectively; below abscissa). Because these 50 msec stimulus sequences appeared in an ongoing random sequence, the stimuli preceding and after them were random. In Figure 1*A*, the time at which the response to the AP transition (*solid line*) turns upward (*open arrow*) from the reference response (*dashed line*) is the onset latency. The latency is ~27 msec relative to the stimulus transition, which occurs at time 0. The upturn in the reference trace (*dashed line*) near 45 msec results from responses to random sequences that followed the trigger sequence and does not influence our timing measurements. We estimated the offset latency in a similar manner from the response to the P-to-A (PA) transition (30 msec of P followed by 20 msec of A) and its reference stimulus (50 msec of P) (Fig. 1*B*). The response to the PA transition diverges from the reference response ~25 msec after the stimulus transition (*B*, *open arrow*). To facilitate the comparison of onset and offset latencies, we plotted the AP response minus its reference response together with the PA response minus its reference. These response difference plots (Fig. 1*C*) make it apparent that the response decrease for the PA transition (*thick line*) occurred before the response increase for the AP transition (*thin line*) for this neuron.

Figure 2 shows response difference plots for cells from LGN, V1, and MT that were tested with random, binary sequences of P and A stimuli that were suited to the properties of the cells on the

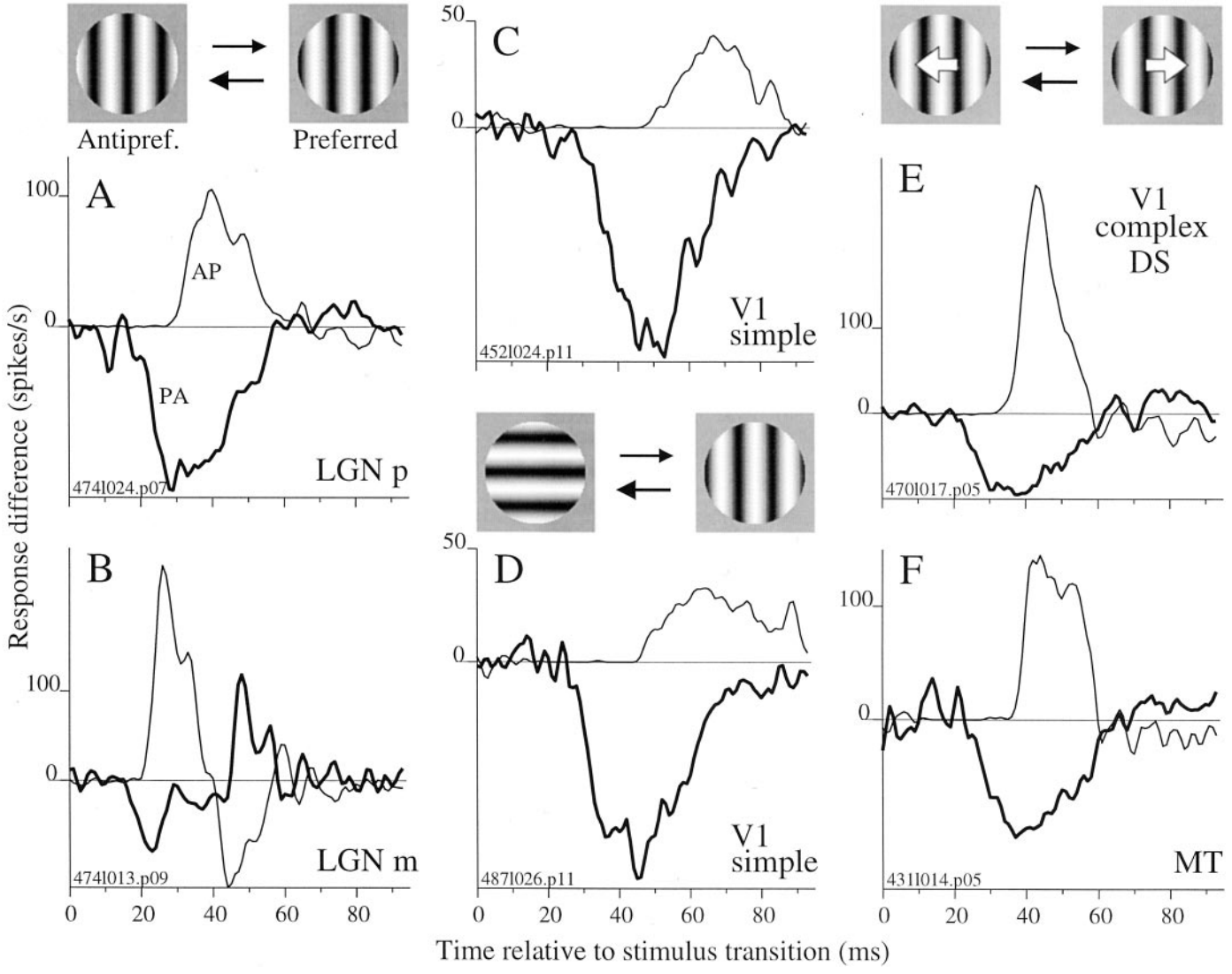

Figure 2. Response decreases occurred sooner than response increases when switching between P and A. For five classes of neurons, response difference plots (defined in Fig. 1) for PA and AP transitions (*thick* and *thin lines*, respectively) are shown for example cells responding to binary random sequences of optimized sinusoidal grating stimuli. *A*, Difference plots for an LGN p-cell responding to the phase stimulus (transitions between opposite phases, *icons*, *top* of *left column*) show that the PA response occurred before the AP response. *B*, For an LGN m-cell responding to the phase stimulus, a smaller timing asymmetry is present. The sign reversal at ~40 msec resulted from the combination of the transient nature of the m-cell response and the chance transitions that followed the reference stimuli (e.g., 50 msec of A was sometimes followed by P and vice versa). *C*, Difference plots for a V1 simple cell responding to the phase stimulus show a timing asymmetry larger than that observed for the LGN cells in *A* and *B*. *D*, Responses of a V1 cell to transitions between orthogonal orientations (*icons* in *center*) also show a large timing asymmetry. Responses of a V1 complex DS cell (*E*) and an MT cell (*F*) to transitions between opposite directions of motion (*icons*, *top* of *right column*) show a timing asymmetry as well.