

# SCHOOL OF MEDICINE

## Objective

Prior expectations can alter judgements of upcoming sensory stimuli. Previous studies argue that the evolution of LIP activity reflects the formation of these decisions. Therefore, we hypothesize that LIP activity should reflect the prior probability of a task-relevant sensory stimulus.

#### Methods

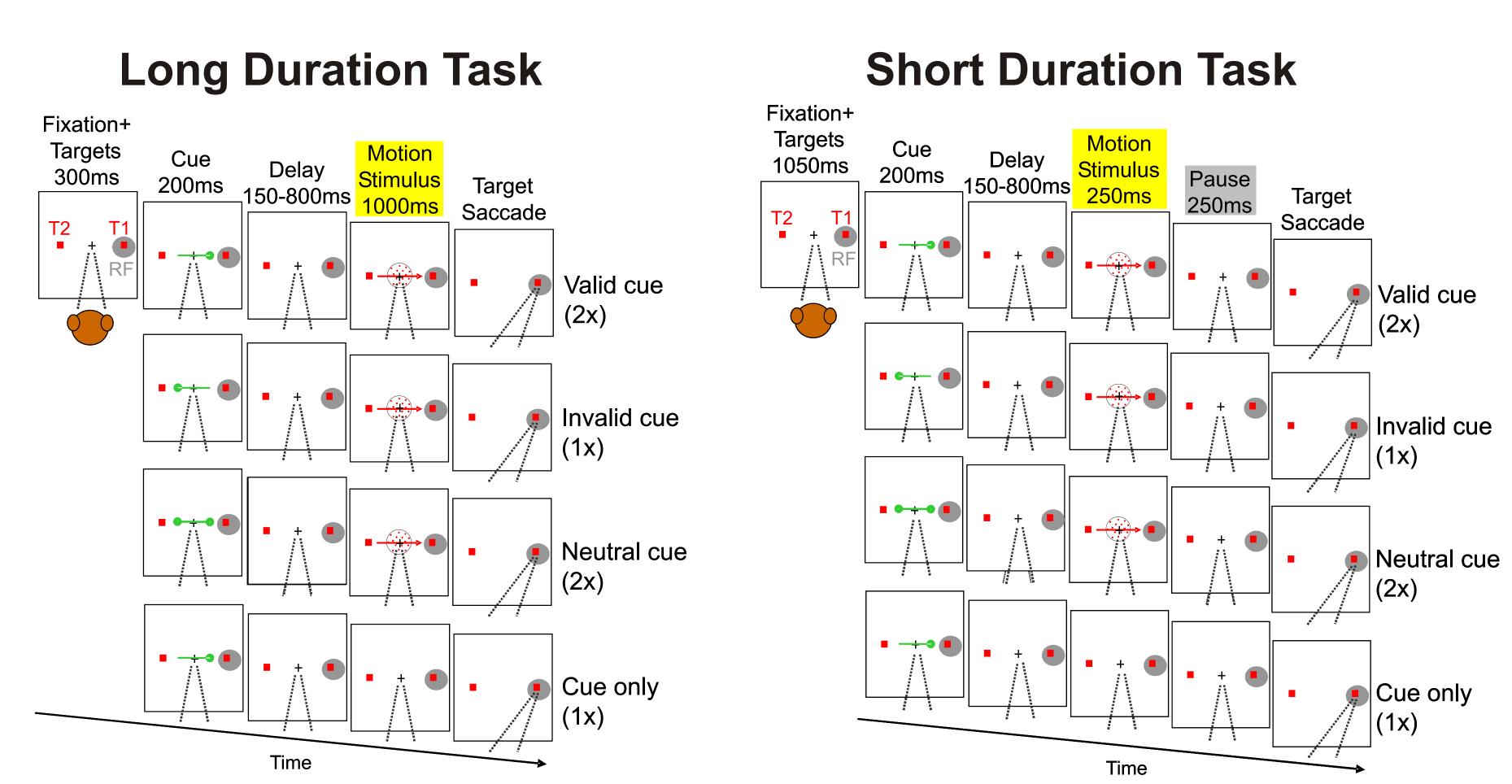
Subject: One rhesus monkey (Macaca mulatta) has been used so far in these experiments. Eye positions were monitored using scleral search coils.

**Behavioral Task:** Extensive work from the Newsome and Shadlen labs has revealed the importance of LIP neurons in decision formation based on visual motion stimuli. We examined the effects of prior knowledge using a Newsome-style direction discrimination task (below). The cue and a random-dot motion stimulus were presented foveally. Two targets appeared at the start of the trial: T1 within the LIP cell's response field (RF), and T2 at a location 180deg opposite T1. The monkey is rewarded for making a saccade to the target in the same direction as the motion in the random-dot stimulus.

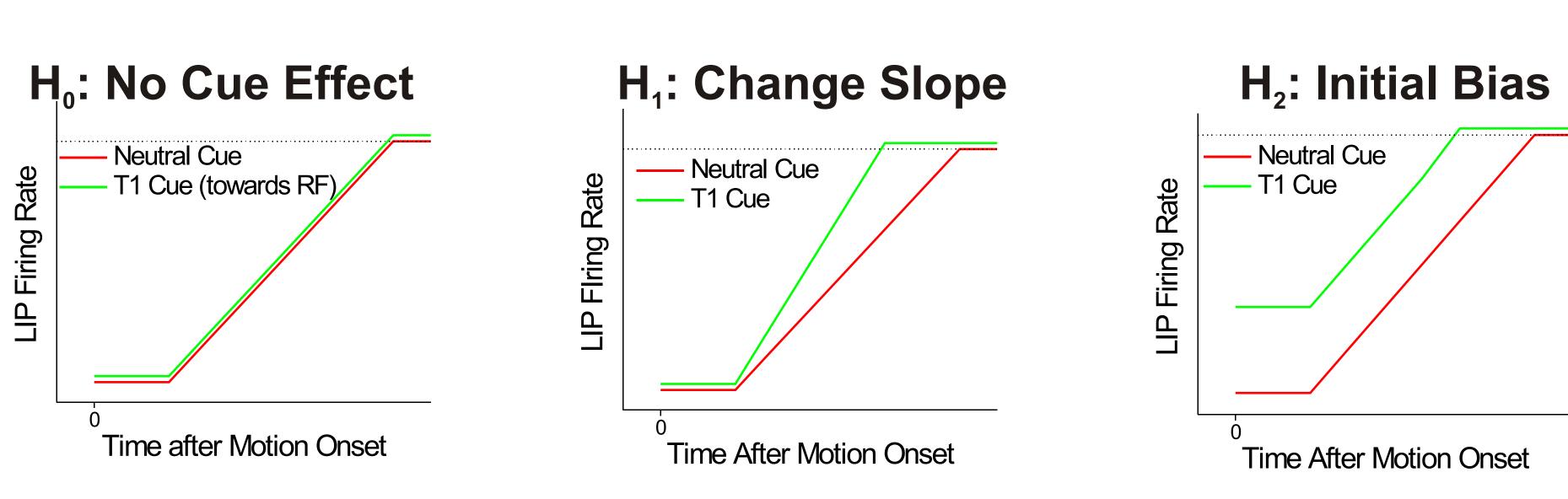
Four cue conditions were presented: Valid cue, Invalid cue, Neutral cue, and Cue Only (see below). Trials were presented at a ratio of 2 Valid: 1 Invalid: 2 Neutral: 1 Cue Only, each at five levels of motion coherence in both directions. *The 2:1* ratio of valid to invalid trials means the cue is a partially reliable predictor of motion direction.

The monkey performed two versions of the task. In one version, referred to as the Long Duration task (below, left), the motion stimulus is presented for a fixed duration of 1000ms and is immediately followed by the 'go-signal.' In the Short **Duration task** (below, right), the motion stimulus is presented for 250ms, followed by a 250ms pause before the 'go'-signal.

**Physiology:** Single-units were isolated from area LIP, shown to have maintained activity in a memory-saccade task, and recorded during performance of the cued direction discrimination task. A minimum of 5 repetitions of the task were recorded



### Predictions



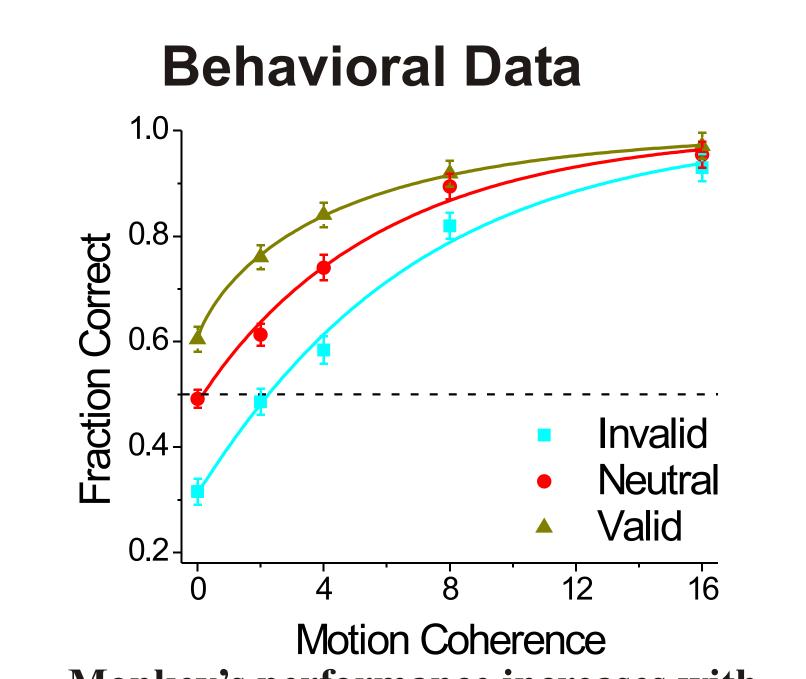
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# Prior Probabilities and Decision Formation in LIP

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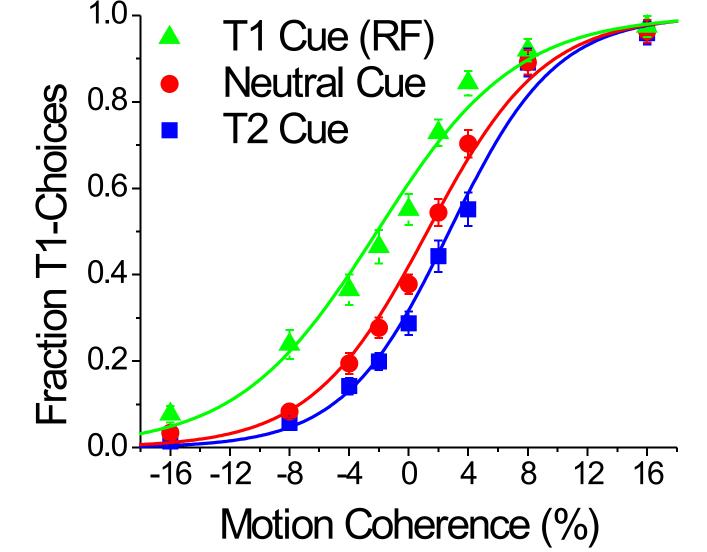


# Long Duration Task



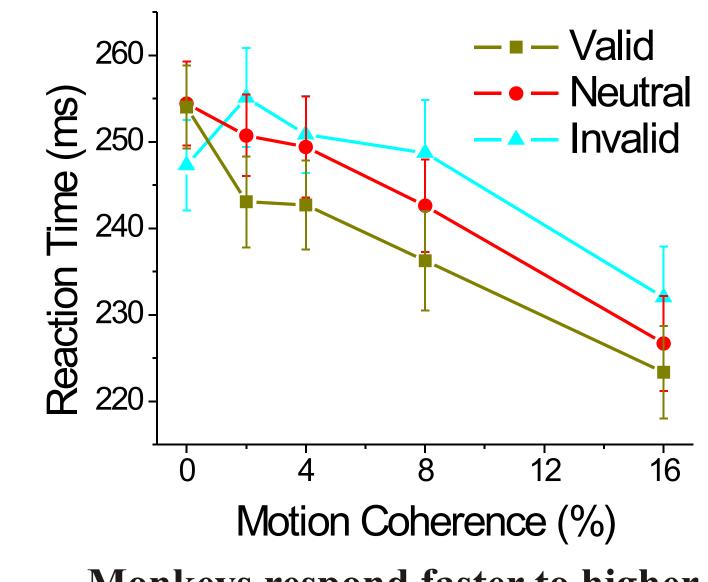
Monkey's performance increases with coherence and validity of cue. Average psychophysical performance during multiple recording sessions

(N=48). Error bars are standard errors across sessions. Data are fit to a modified cumulative Weibull distribution.



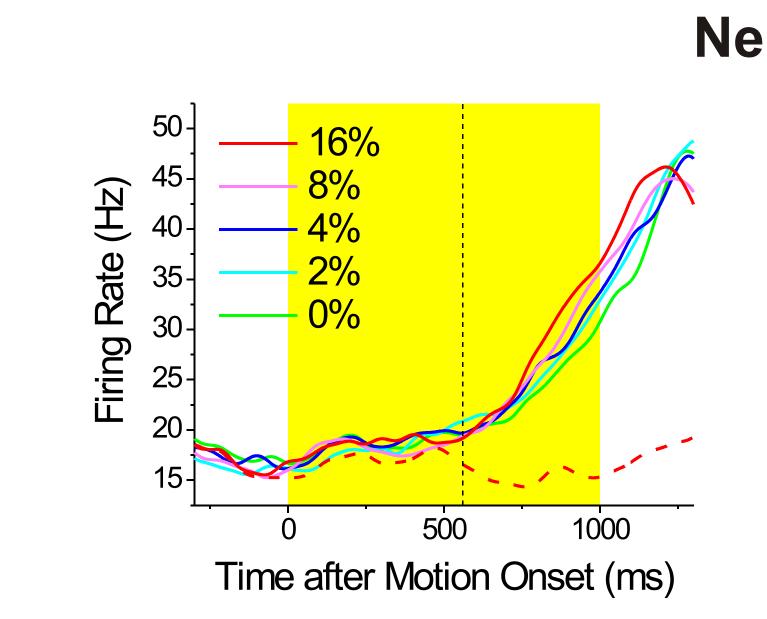
Cues bias the monkey's distribution of choices.

Data from the previous panel are plotted as fraction choices to the T1 target, as a function of signed motion strength (positive is motion towards T1). Data are sorted by cue-direction (not validity) and fit to logistic functions. The data are significantly biased ( $p < 10^{-9}$ ) by logistic regression.



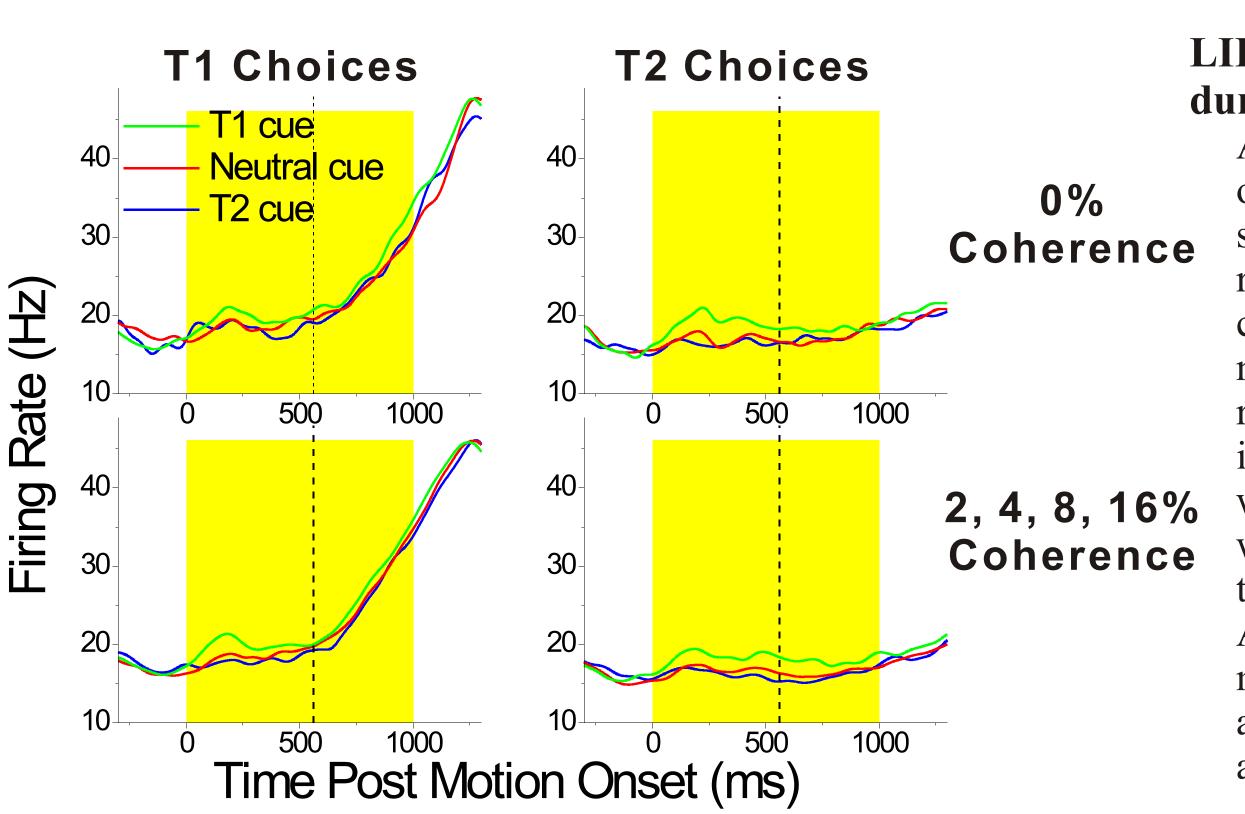
Monkeys respond faster to higher coherences and slower to invalid cue trials.

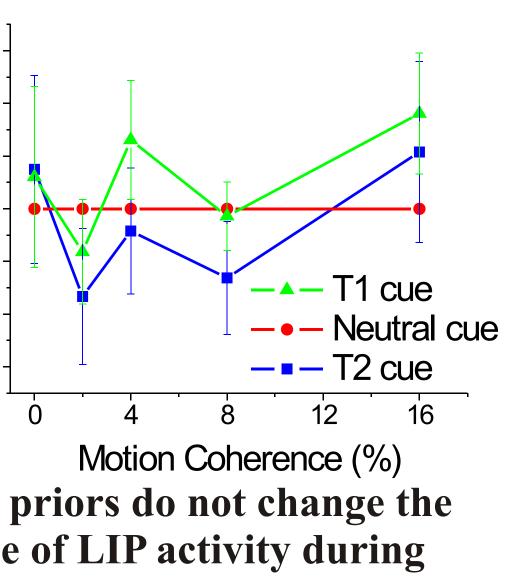
Effects of coherence (p≈0) and validity (p<10<sup>-4</sup>) are significant by repeated-measures ANOVA. Note that the monkey had to wait for the 'go'-signal before responding.



LIP activity reflects motion integration in long duration task.

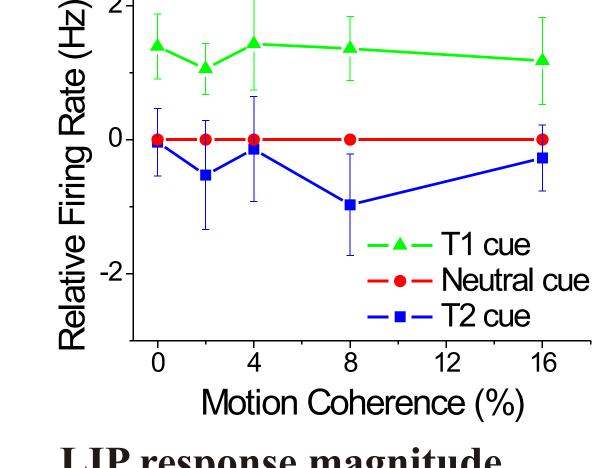
Average PSTHs for neutral-cue, T1-choice trials (solid) at each coherence. Red dashed curve is the average PSTH for T2-choice trials at 32% coherence motion. Yellow bar indicates motion period. Vertical dashed line indicates first detectable directional signal in LIP (~560ms).





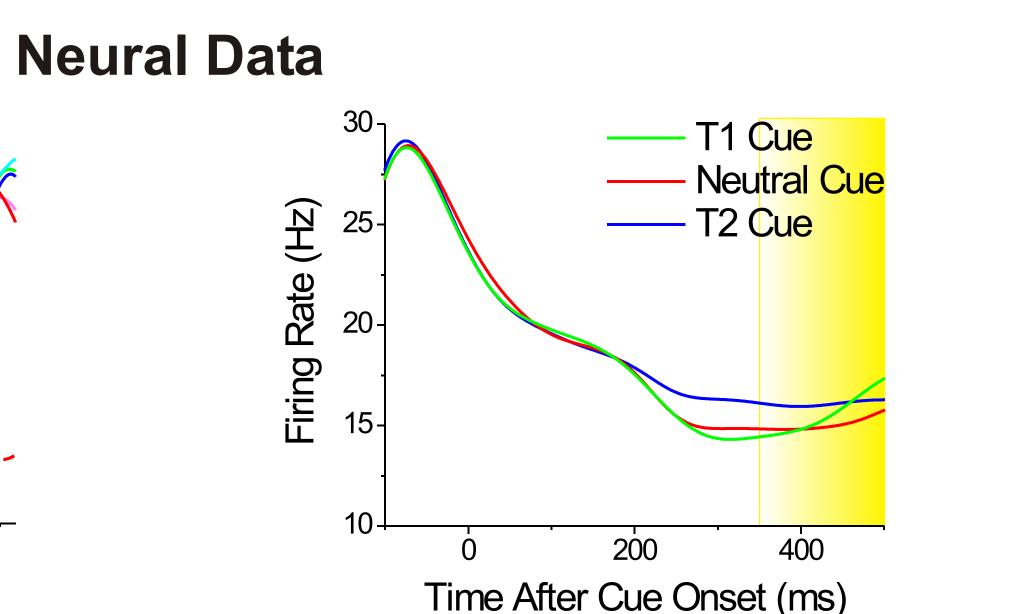
The priors do not change the slope of LIP activity during motion integration.

For each cue direction and motion coherence, the slope of the LIP activity is estimated from 560-1000ms after motion onset. Slopes fail to reach significance for either T1- or T2-cue trials (p=0.14 and p =0.69, respectively, paired t-



LIP response magnitude during motion integration is modified by a prior T1 cue.

Relative to neutral cues, the mean firing rate on cued trials from 560-1000ms after motion onset is plotted as a function of coherence. T1-cues elicit a significantly greater response (p=10<sup>-4</sup>, paired t-test), but T2cues fail to elicit a significantly lower response (p=0.13).

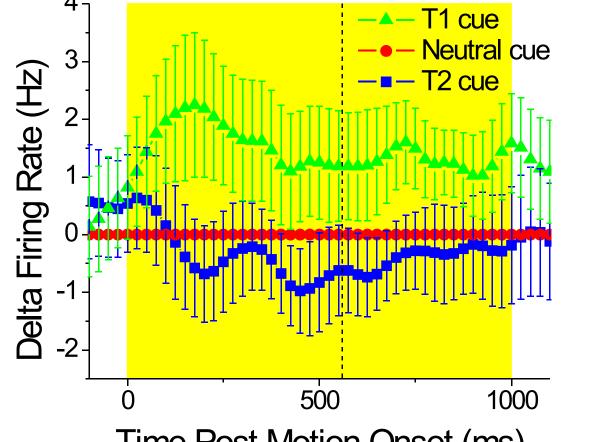


Cues have paradoxical effect on activity prior to motion onset.

Average PSTHs for each cue direction, aligned to start of cue. Yellow shaded bar indicates period in which motion may occur, with the earliest possible motion onset at 350ms after the cue. Target onset caused early transient.

LIP activity is modified by the cue during the motion presentation.

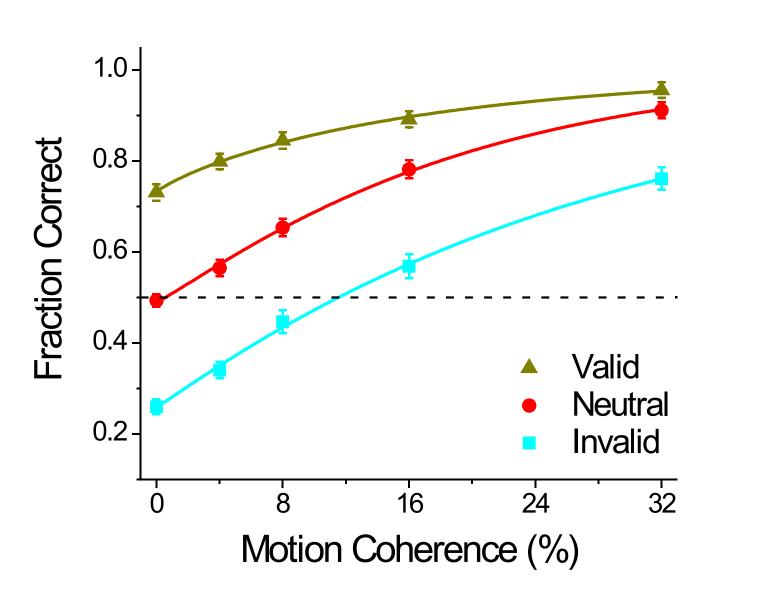
Average PSTHs aligned to the onset of motion across multiple recording sessions (n=48). Top and bottom rows reflect averages from 0% coherence motion trials and from all non-0% coherence trials, respectively. The left column indicates responses from trials where the monkey chooses T1, whereas the right column represents trials where the monkey chooses T2. Activity increases coincident with motion onset on T1-trials. Note absence of cue-direction-related activity prior to motion onset.



Time Post Motion Onset (ms) **Cue-related firing rate** differences wane at arrival of directional motion signals.

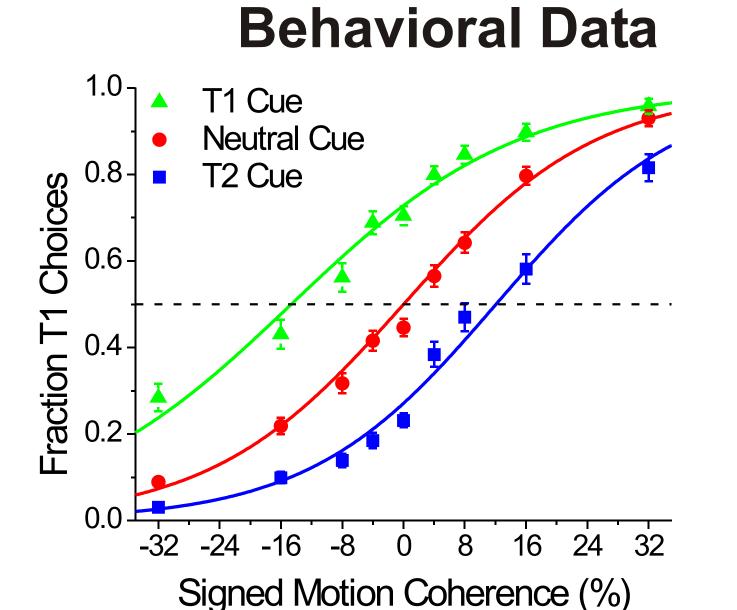
The relative firing rate is computed in 50ms bins stepping at 25ms. Error bars are 95% confidence intervals. By the end of the motion integration window in T1-cue trials, LIP responses remain





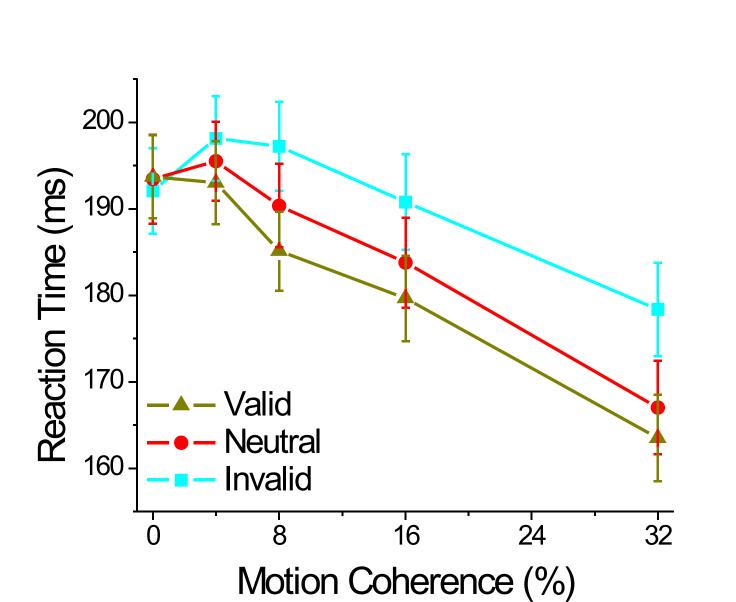
Monkey's performance increases with coherence and validity of cue. Average psychophysical performance during

multiple recording sessions (N=60). Note different range of tested coherences.

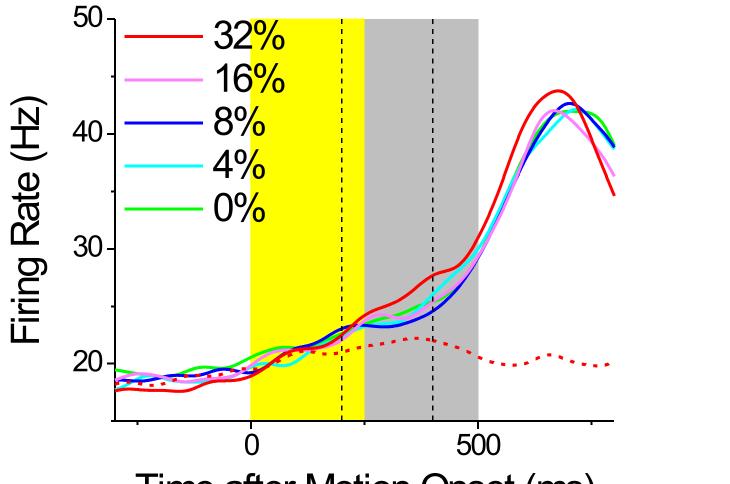


Priors bias the monkey's distribution of choices. Data are sorted by cue direction. Bias is

significant (p<10<sup>-36</sup>, logistic regression).

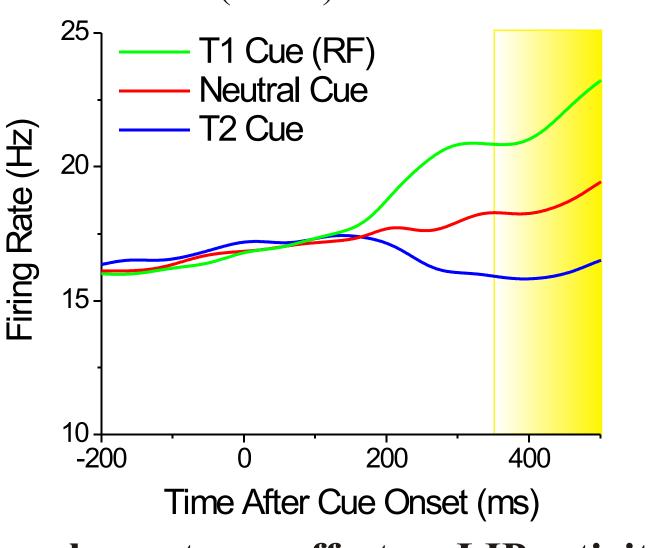


Monkeys respond faster to higher coherences and slower to invalid cue trials. Effects of coherence (p≈0) and validity (p<10<sup>-4</sup>) are significant by repeated-measures



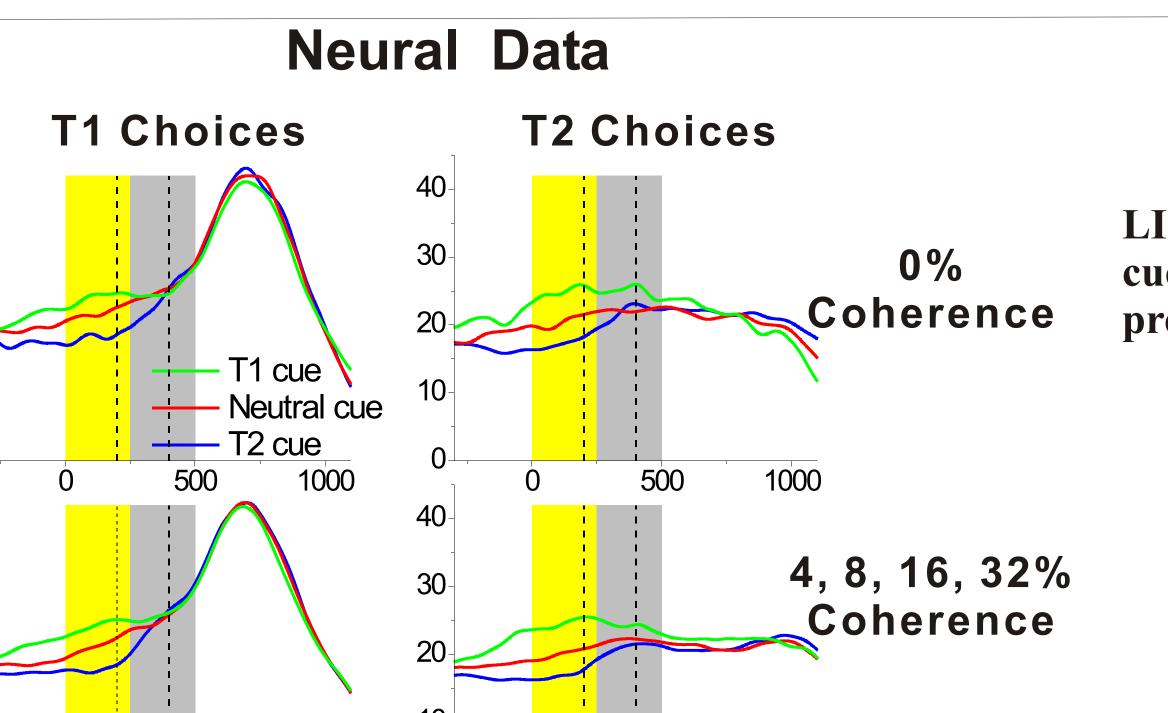
Time after Motion Onset (ms) Partial sorting of PSTHs by motion strength. Yellow and gray bars indicate motion and

pause periods, respectively. Vertical dashed line indicates first detectable directional signal in LIP (200ms), and the second line follows after 200ms. (N=60)



Cues have strong effect on LIP activity in short duration task.

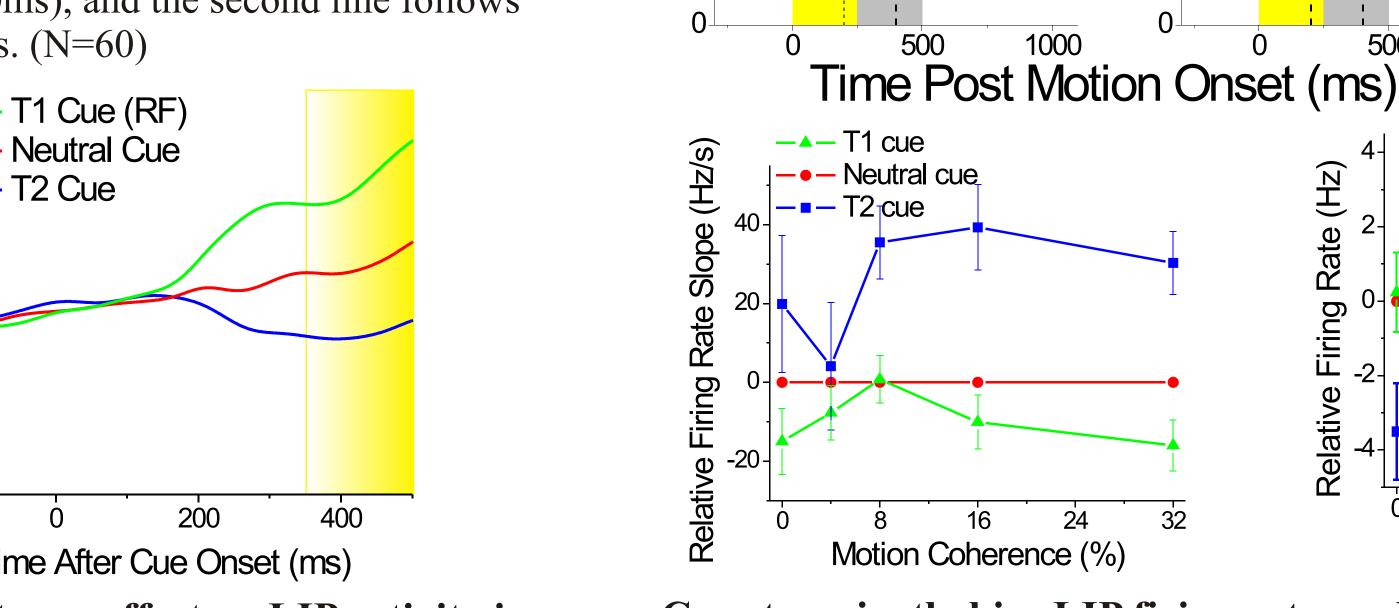
LIP activity is increased in response to the cue in T1cue -trials, and is suppressed relative to neutral on T1-cue trials.



LIP activity is modified by the cue during the motion presentation. Average PSTHs aligned to the

onset of motion across multiple recording sessions.. Note similar course of activity before the saccadic peak in T1-choice trials.

Time Post Motion Onset (ms)



Motion Coherence (%) Cues transiently bias LIP firing rate, and this is reflected in the slope.

Although the changes in slope reach significance during motion integration (200-400ms) for both T1-cue (p=0.02) and T2-cue trials (p<10<sup>-4</sup>), the signs of the changes are *opposite* the slope-change hypothesis. Coupled with the significant firing rate differences ( $p=10^{-4}$  and  $10^{-7}$ , respectively), these imply that there exist early firing rate differences which are gradually diminished during motion integration, as seen in the time-course graph.

\_**\_** \_ T1 cue

-**-** T2 cue

- ● – Neutral cue

## Summary

•The animal's choices are influenced by a partially reliable cue. Cue validity also influences the animal's reaction times.

•These data offer mixed support for motion integration in LIP. Good separation of neutral cue responses by coherence in the long duration task (albeit with long latencies) is balanced by poor separation of low-coherence motion PSTHs in the short duration task.

•The two versions of the task show differing effects of the cue direction on LIP activity:

- -The long duration task shows a minimal early effect of cue, followed by a weak, but maintained increase in activity during and beyond the motion.
- -The short duration task has a strong early effect of the cue, which disappears after directional motion signals begin to arrive in LIP. •The long duration task data supports the notion that prior expectations change behavior by selectively amplifying LIP activity. The short duration task has a stronger, earlier modulation by cue direction, although it is puzzling why LIP does not sustain this modulation through the motion integration period.