Dynamics of the functional link between area MT LFPs and motion detection

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Recent efforts have focused on the local field potential (LFP) and suggest that distinct neurophysiological processes can be measured from different LFP frequency bands (Bastos et al. 2015; Katzner et al. 2009; Kopell et al. 2010; Siegel et al. 2012). Gamma-band LFPs are thought to carry stimulus information (Belitski et al. 2010) and reflect the synaptic inputs from earlier stages (Kawahaja et al. 2009) and the activity of local neurons (Ray and Maunsell 2011a), while beta-band LFPs may reflect intercortical feedback (Saalmann et al. 2007). Correspondingly, attention increases gamma LFP power in a manner similar to that of local spiking activity, while beta power is attenuated (Khayat et al. 2010). Although LFPs contain some components due to spike activity, they also allow us to observe nonspike components (e.g., postsynaptic potentials). Thus LFPs can provide useful insights into the functional link between neural activity and visually guided behavior.

A trial-by-trial neural-behavioral correlation between middle temporal area (MT) LFP power and perceptual performance [referred to as choice probability (CP)] was first shown in a motion discrimination task by Liu and Newsome (2006). They found that high-gamma LFP bands (>50 Hz) had a positive CP similar to the spiking rate of MT neurons while beta LFP power had a negative CP. Although they proposed a transfer in spectral power from the beta to gamma bands during the perceptual process, it is possible that this pattern of positive and negative CP could result if LFP bands reflected distinct neural processes.

We asked whether different neural processes reflected in LFPs could be resolved by the unique dynamics of their neural-behavioral correlations. For example, do certain MT LFP bands reflect fast, early, sensory-driven contributions to motion detection that would suggest a bottom-up link to behavior? Or are some LFP bands associated with slower, late, top-down signals from higher brain areas that originated after the perception of the motion had occurred? We examined LFP frequency bands during a detection task using a brief motion signal that was presented in a pair of spatially separate stimuli. Previously (Smith et al. 2011), we reported that the neural-behavioral correlation between MT spikes and performance [referred to as detect probability (DP)] had fast dynamics (early peak, Fig. 1A) that were accounted for by a causal, bottom-up, model.

In this study, we found that early high-gamma (100–200 Hz) LFP-DP had dynamics, stimulus, and reaction time (RT) de-
Three conditions:

1. RF 1: a single pulse in RF 1, RF 2: no pulse
2. RF 2: a single pulse in RF 2, RF 1: no pulse
3. RF 1 and RF 2: simultaneous pulses in both RFs

This was just prior to the motor response, when the LFP power in both bands peaked. Using the coherence of LFPs recorded from two different electrodes, we observed that the late LFP-DP was global across the two MT sensory pools. Although neural-behavioral correlations cannot directly reveal causality, these results demonstrate how DP dynamics provide insights for disentangling the causal and noncausal links between neural activity and behavior.

**METHODS**

**Data collection.** Two male monkeys (Macaca mulatta) performed a motion pulse detection task (Fig. 1B), as previously described (Smith et al., 2011). Area MT of visual cortex was located based on anatomical MRI scans, electrode depth, and electrophysiological responses. Data were collected from a pair of tungsten microelectrodes (0.5–1.5 MΩ), each monitoring a well-isolated MT neuron; each electrode was connected to its own BAK A1-B headstage and preamp with a frequency response of 5 Hz (cutoff slope 30 dB/decade) to 6 kHz (cutoff slope 12 dB/decade). Each electrode was loaded in its own guide tube 1–2 mm from the other and advanced with independent microdrives. Amplified neural signals were then low-pass filtered at 6 (or 8) kHz and 16-bit digitized at 20 (or 25) kHz. Eye position was sampled at 200 Hz with an infrared tracking system (ASL 6000, Applied Science Laboratories). Of the 50 experiments used in this study, 40 (80 recordings with 2 electrodes) came from one monkey. Because of problems that developed with the implants, only 10 (20 recordings) came from the other monkey. Analyzed individually, the key trends reported in this study were visible in each monkey (see Fig. 8).

**Visual stimulus.** During experiments, the receptive fields (RFs) of isolated neurons were mapped by hand to identify their size and location, using a computer mouse to control the position of a white bar on a CRT monitor that was 57 cm in front of the monkey (120-Hz refresh, 1,600 × 1,200 resolution). The direction, speed, and size tuning of each isolated RF were found with random dot patch (RDP) stimuli. Two RDP stimuli were shown during the experiment (Fig. 1B). Each consisted of a circular region of white dots (0.3° wide, density of 10 dots/°2) on a gray background. RDP stimuli were each placed within a separate, isolated RF. Dots moved randomly along the preferred-null axis of the overlapping RF. During 0% coherent motion, dots had a 0.5 probability of moving in the preferred direction of the neuron, independently of other dots. At 100% coherence, all of the dots moved in the preferred direction; only a short 50-ms pulse of coherent dot motion was ever shown during a trial. The speed of dot motion was set to that preferred by the neuron. Dot lifetime was infinite, but if a dot ran past the edge of the RDP then it was randomly replotted at the opposite side.

**Behavioral task.** The animals received daily care and observation from veterinarians and animal health technicians at the McGill University Animal Care Centre. All procedures were approved by the McGill University Animal Care Committee under guidelines set forth by the Canadian Council on Animal Care. Before training began, the animals were implanted with stainless steel posts to stabilize head position. After training, craniotomies were performed and fitted with recording chambers (Crist Instruments), allowing a dorsal approach to MT. The animals were anesthetized during surgical procedures, which were performed in sterile conditions.

Subjects performed a coherent motion detection task (Fig. 1B) after extensive training. Trials began when a fixation point and both static RDPs were presented. Once the monkey fixated and pressed a lever, the RDPs remained stationary for an additional ~200 ms before dots began moving with 0% coherence. The monkey had to maintain fixation and report the onset of a 50-ms pulse of coherent dot motion by releasing the lever. The length of 0% coherent motion was between 500 and 10,000 ms and randomly drawn on every trial from an exponential distribution (flat hazard function, 1-s time constant). Figure 1C shows the three stimulus conditions that were randomly presented during each block of trials.
chosen from trial to trial: 1) a motion pulse in RDP 1, 2) a motion pulse in RDP 2, or 3) simultaneous motion pulses in both RDPs. All dots returned to 0% coherent motion after the 50-ms coherent motion pulse.

Trials were scored as correct, and a juice reward was provided, if the monkey released the lever within a RT window lasting 200–800 ms after the motion pulse began. Note that for monkey F and a few early experiments for monkey W, a 100- to 700-ms RT window was used. The stimulus stopped as soon as the animal released the lever. Trials were failed, with no juice reward, if the monkey held the lever until the end of the RT window; a final 150 ms of 0% coherent motion was shown before the stimulus finally stopped. False-alarm trials happened when the monkey released the lever before the coherent motion pulse and were not rewarded. Trials were aborted and discarded from our analysis if the monkey failed to maintain fixation within 1.5° of the fixation point. The motion detection task was run as long as the two isolated neurons could be maintained on both electrodes.

RDP motion was designed to allow a change in dot coherence without a change in the apparent dot density. Therefore the animals had no cue that the motion pulse had occurred, other than coherent dot motion. Because dots moved in only the neuron’s preferred and null directions, motion energy was limited mainly to those two directions, and at the preferred speed. During the motion pulse, the fraction of dots moving coherently was set separately for each RDP to produce threshold performance (<50% correct) in the single-motion pulse condition (Smith et al. 2011).

Spectral estimation and signal processing. LFPs were computed from the raw, wide-band, 20 (or 25)-kHz sampled electrode recordings after the spikes were removed by downsampling the raw recordings to 1 kHz. Downsampling was implemented with the MATLAB function resample, using its default zero-phase antialiasing filter. Figure 2 outlines the steps for estimating LFP spectral power. To control for the spectral leakage of spike waveforms in the LFP results, we first removed the spike waveforms from the raw electrode recordings (Pesaran et al. 2002; Zanos et al. 2012). The same spikes analyzed in this and our previous study (Smith et al. 2011) were used to generate a spike-triggered average (STA) of the raw, wide-band electrode recordings for each neuron; a wide-band STA captured the full spectral content of the spike waveforms (Zanos et al. 2011). Each spike waveform was fit with a scaled version of the corresponding STA, which was then used to subtract away the spike. Note that our results were qualitatively the same whether or not spikes were removed.

After downsampling, we took measures to remove the 60-Hz noise and its harmonics from each LFP recording on each trial. This was done with a multitaper method (Mitra and Pesaran 1999) that modeled the oscillations of the artifact and subtracted them (Chronux function rmllinesc). Note that our results were qualitatively the same whether or not 60-Hz noise was removed.

We next used a short-time Fourier transform (STFT) to compute spectral power as a function of time (Fig. 2). Power spectra were estimated separately for every trial and for each of our two electrodes. A 200-ms analysis window was moved incrementally at 1-ms steps over the raw neural signal, from the start to finish of a trial. At each step, the stretch of neural signal contained within the analysis window was weighted through multiplication with a 200-ms Hamming window, to reduce spectral leakage, before computing the discrete Fourier transform. A 200-ms window was chosen because it allowed us to capture the dynamics of the 50-ms motion pulse while still retaining a reasonable level of resolution in the frequency domain; in a control analysis, a 100-ms window produced qualitatively similar results.

Zero-padding was used to interpolate the Fourier transform to 1,000 frequency bins (0–999 Hz) in the main analysis. But for the data shown in Figs. 3–5, we used enough zero-padding to interpolate 601 frequency bins from 5 to 200 Hz; as this matched the 601 time bins in the −300 to 300 ms epoch around the start of the motion pulse. This was done to achieve the same density of data points along both axes. Spectral power was computed from each Fourier transform by taking its squared absolute value and dividing by the width of the time window.

Finally, the 1/f relationship in the spectrum was normalized. The least-squares linear regression between spectral power and frequency was estimated on a log-log plot in which the slope (α) became the power coefficient describing the 1/fα relationship between the spectral power and frequency on linear axes. 1/f bias was then attenuated by multiplying the spectral power with 1/fα. Note that our results were qualitatively the same whether or not 1/f normalization was performed.

Because of the frequency response of our amplifiers, we only used frequency components between 5 and 200 Hz for our analyses. To compare the dynamics of LFP spectral power over time using only the recorded spike response (see Fig. 7), we convolved all spike trains (represented numerically as a string of 1s and 0s) with the same 200-ms Hamming window. A 200-ms moving window was also used to compute the magnitude-squared coherence between all pairs of LFP recordings and all pairs of spike trains using Welch’s averaged, modified periodogram method (200-ms signal broken into eight 44-ms segments with 50% overlap, 44-ms Hamming window applied to each segment). The neural signals were first z-scored, before windowing and computing coherence. Subtracting the mean was necessary to center the signals to 0, in order to obtain coherence measures without a baseline shift, and normalizing the variance to 1 brought the signals on both electrodes into a similar numeric range, which helped to avoid computer round-off errors. As with the STFT analysis, the moving 200-ms window provided measurements of coherence at each position over time. It should be noted that any multiplicative scaling that is applied to the LFP Fourier transform will be normalized away, simply by computing coherence. This is due to the denominator term that contains the multiple of the two autocorrelation spectra. Thus the 1/f effect is also normalized in the coherence measures.

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We adopted a convention of plotting all data over time by placing each data point at the center of the moving 200-ms Hamming analysis window, so that each point represented the neural signal from 100 ms before to 100 ms after that point. For example, all data points shown at 100 ms following the start of coherent motion include Hamming-weighted signals from 1 to 200 ms after the start of coherent motion.

Data analysis. Standard area under the receiver operating characteristic curve (aROC) was used to measure the neural-behavioral correlations between spectral power (or spike rate) with the animal’s detection performance; this measurement is called detect probability (DP; Cook and Maunsell 2002). To calculate the DP of spectral power (referred to as LFP-DP) at time \( t \) and frequency \( f \), we computed the aROC using the distribution of power at \( f \) Hz for correct trials (hits) and the distribution of power at \( f \) Hz for failed trials (misses) computed from the Fourier transform of neural signals within the 200-ms Hamming window centered at time \( t \). The same procedure was used, substituting spectral power with coherence, to compute the DP of the coherence between the two electrodes (referred to as LFP-DPcoh). A similar procedure used distributions of spike rates taken at 100 ms following the start of coherent motion include coherence, to compute the DP of the coherence between the two electrodes (referred to as LFP-DPcoh). The lever-aligned results in Fig. 12 are compared with distributions of the 50-ms coherent motion pulse. This is the distribution of time that coherent motion was shown, rather than onset times. It was computed by finding the distribution of motion pulse onset times plus 25 ms and then convolving with a 50-ms square window.

We used bootstrapping for some of our analyses to compute confidence intervals reported in the text. A bias-corrected accelerated method was employed (bootci function, MATLAB, MathWorks) using 10⁴ bootstrap samples; bias correction and acceleration is a standard technique for improving the accuracy of bootstrap confidence intervals (Efron and Tibshirani 1993).

Spectral and signal processing controls. Spectral estimation depends on several parameters, such as windowing, zero-padding, and preprocessing to reduce the effects of noise. We wanted to verify that our results obtained from the STFT methods described above were robust against any specific parameters or techniques. Thus we performed numerous control analyses using different spectral and signal processing methods, which are outlined here. All control analyses produced results nearly identical to those reported using the STFT method described above.

We began by using a second method to quantify the spectral-temporal dynamics of our LFP signals. Each LFP recording was fed into a bank of fifth-order Butterworth filters with 20-Hz wide pass bands that increased in 10-Hz steps and one low-pass filter with a cutoff of 20 Hz. To quantify the amplitude for each filtered copy of the LFP recording, we computed the root mean square (RMS) in a 100-ms boxcar analysis window moving over time. Thus the amplitude of each LFP recording was measured over time for a series of its underlying frequency components. RMS was substituted for LFP power to compute LFP-DP. These data produced the same qualitative LFP-DP dynamics as the STFT-based data (results not shown).

To further ensure that our results were robust, we repeated our analysis, using the multitaper spectral methods of the Chronux software package (www.chronux.org; Mitra and Bokil 2008) to quantify spectral dynamics. Increasing the number of tapers can provide more accurate estimates of the Fourier transform at the expense of resolution in the time or frequency domain, because the maximum number of tapers that can be used is \( 2TW - 1 \). We used a time constant \( T \) of 0.1 s and a frequency bandwidth \( W \) of 20 Hz to get 3 tapers while maintaining a sufficiently narrow bandwidth to resolve beta LFPs, and improve temporal accuracy. The resulting LFP spectral power was used to compute DP. Again, we found that the LFP-DP (and LFP-DPcoh) computed using multitapers reproduced all the important dynamical trends for the beta and high-gamma bands (data not shown).

We further examined whether different frequency-dependent phase shifts in our recording equipment or analysis could have delayed the peak in beta LFP-DP, relative to high-gamma LFP-DP. We did so by using the same equipment and software to record and analyze synthetic sinusoidal LFPs (5–200 Hz). The synthetic LFPs were made with a signal generator, which was triggered by the stimulus-generating computer at the same instant as the motion pulse began; the simulator’s output went straight into the recording amplifier headstages. Our analysis of the synthetic data produced LFP-DPs with no phase delay across our frequency bands (data not shown). Therefore, the delayed occurrence of the peak beta LFP-DP was a genuine feature of cortical activity.

Finally, we used a simple bootstrap analysis to ask how much of the empirical LFP-DPcoh was explained by independent changes in the electrodes (see Fig. 10). Only one electrode at a time was allowed to predict the behavioral outcome for each bootstrap repetition (predictive electrode). This was accomplished by sampling (with replacement) correct trials from correct trial data and failed trials from failed trial data for the predictive electrode—while always sampling from both correct and failed data for the other, uncorrelated electrode. Ten thousand repetitions were generated and the average LFP-DPcoh was computed each time, which yielded a bootstrap distribution of the average LFP-DPcoh. Two bootstrap distributions were formed, one for beta LFP-DPcoh at 230 ms after the motion pulse and another for high-gamma LFP-DPcoh at 275 ms. Both distributions were significantly gaussian in shape (Lilliefors test \( P > 0.184 \)). Thus the more powerful bias-corrected and accelerated method was not required (Efron and Tibshirani 1993). Statistical significance was simply computed by finding the fraction of bootstrap samples that were less than (beta) or greater than (high gamma) the empirical LFP-DPcoh values.

RESULTS

When and how do different neural processes contribute to a visually guided decision? We addressed this question by analyzing MT spike and LFP recordings from two monkey subjects performing a two-patch, coherent motion detection task (Fig. 1, B and C). Isolated spikes and LFPs were recorded at the same time from two electrodes positioned 1–2 mm apart in the same hemisphere. Fifty experiments yielded 100 LFP recordings (50 pairs) and 124 isolated neurons (89 pairs). The spike data were previously used to show that the neural-behavioral correlations between MT spike activity and the detection of a brief motion pulse are well described by a causal, bottom-up model in which fluctuations in sensory responses are likely responsible for fluctuations in behavior (Smith et al. 2011). Importantly, the dynamics of the spike-based neural-behavioral correlation peaked soon after the motion pulse (reproduced in Fig. 1A).
In this study, we wanted to know whether other distinct neural processes were at play during the animals’ perception of the motion stimulus, and whether these processes could be revealed in the dynamics of the functional link between LFP bands and behavior. For example, LFP bands with neural-behavioral correlations that peaked early and mimicked the dynamics of the spike neural-behavioral correlations would suggest a similar causal, bottom-up, functional link to behavior. On the other hand, LFP bands with neural-behavioral correlations that had slow dynamics and peaked long after the motion stimulus occurred would suggest a noncausal, top-down, functional link with behavior. This is because late-occurring fluctuations in LFPs would likely have originated after the perception of the motion had already occurred. Thus our approach was to compare the dynamics of spike and LFP neural-behavioral correlations during the motion pulse detection task.

Our results are presented as follows. First we report how different LFP frequency bands were correlated with the detection of the motion signal and compare the dynamics of these correlations with those computed using the spike activity. Second, we grouped LFPs into low (beta) and high (high gamma) frequency bands in order to compare how the temporal dynamics between LFPs, spikes, and behavior changed for our different stimulus conditions, RTs, and alignment to the behavioral response. We also examined how the neural-behavioral correlations in the LFPs were correlated with each other, using a coherence measure.

Two-patch motion detection task. Experiments began when two MT neurons were isolated (1 on each electrode; Fig. 1B) and the classic RF (white dashed circles) of each neuron was mapped. The stimuli consisted of two RDPs (white dots), and each patch overlapped only one of the two RFs. We deliberately recorded from neurons with nonoverlapping RFs in order to minimize the amount of common stimulus information present at both recording sites (the relative RF locations are illustrated in Fig. 1B of Smith et al. 2011). Importantly, the coherent motion pulse in each RDP moved in the preferred direction and speed of the corresponding recording site. This has been shown to increase the chances that the neural signals we recorded would be functionally linked to the monkeys’ perceptual decisions (Bosking and Maunsell 2011).

A trial began when the monkey simultaneously fixated a target while holding down a lever. Both RDPs remained static for 200 ms before moving randomly (0% coherent, Fig. 1C); 0% motion continued for a random duration (0.5–10 s, flat hazard function), followed by a 50-ms pulse of coherent dot motion in the preferred direction of each RF. The 50-ms motion pulse was the signal that the monkey had to report by releasing the lever within a RT window.

With respect to a single RF, there were three randomly interleaved stimulus conditions (Fig. 1C): 1) Two coherent motion pulses occurred simultaneously, one in each RDP (2-pulse condition). 2) The coherent motion pulse occurred in the RDP overlapping the RF while 0% coherent motion continued in the other RDP (1 pulse in the RF). 3) 0% coherent motion occurred in the RDP overlapping the RF while the other RDP contained the motion pulse (1 pulse in the other RF). The strength of the coherent motion in each RDP was adjusted to obtain threshold performance on trials with one motion pulse. Random dot motion resumed immediately after the motion pulse signal and lasted for at most 950 ms or until the monkey released the lever. If the monkey released a lever within a RT window after the motion pulse began, then the trial was marked correct and the monkey was rewarded. Trials with lever releases before the RT window were considered false alarms (36% of trials) and terminated without reward.

As previously reported in Smith et al. (2011), average detection performance was better when two motion pulses occurred (35% correct) versus a single motion pulse (29% correct), and the RT was faster (median 2-pulse RT = 404 ms, 1-pulse RT = 419 ms). In addition, we computed the probability of a random lever release within the RT window and found that correct guesses were relatively infrequent (~15%). Relative to the start of 0% coherent motion, the distributions of correct and false-alarm lever release times were similar for each monkey (data not shown). Both peaked around 1.5 s with long tails skewed to the right—approximating the exponential probability distribution (1-s time constant + 0.5-s delay) of the motion pulse onset plus the variability in the RT distribution.

In other words, the monkeys raised their false alarm rates when a motion pulse was more likely to occur, as reported for other similar tasks (Harrison et al. 2013). Taken together, these results indicate that our monkey subjects actively performed the detection task.

Our experimental design contained uncertainty in both time and space, which was crucial for separating the contribution of different neural processes. Because the coherent motion pulse was a short 50 ms in duration, its sensory representation in MT was equivalently short and easy to isolate from potential top-down neural processes with slower temporal dynamics. Thus we were in a relatively good position to examine whether spiking activity and LFP frequency bands exhibited similar (or different) dynamics in their neural-behavioral correlations, for changes in both time and stimulus location.

LFP power spectra as function of time. A relatively large body of evidence suggests that different neural processes can be distinguished through spectral analysis of LFP recordings (Asher et al. 2007; Belitski et al. 2008, 2010; Buschman and Miller 2007, 2009; Harris and Thiele 2011; Kayser et al. 2007; Khawaja et al. 2009; Liu 2006; Liu and Newsome 2006; Monosov et al. 2008; Rasch et al. 2008; Ray et al. 2008a, 2008b; Ray and Maunsell 2011a; Rotermund et al. 2009; Saalmann et al. 2007). We wanted to know whether these neural processes, as defined by their LFP frequency bands, could be further characterized by their unique temporal dynamics. Given the temporal nature of our task design, and that we usually recorded many trials per experiment (average 638), we used a simple STFT analysis to estimate LFP spectral power for each trial as a function of time (illustrated in Fig. 2).

Raw electrode voltage recordings had spike waveforms subtracted out before they were low-pass filtered and down-sampled into 1-kHz LFPs. Afterwards, 60-Hz electrical noise was removed. For each electrode on each trial, a 200-ms analysis window was moved over the entire trial. At each window position, the LFP segment was weighted by a 200-ms Hamming window to reduce spectral leakage. The Fourier transform of the weighted segment was found and its power spectrum computed and normalized by 1/f from 5 Hz to 200 Hz.

Color maps illustrate the mean of 5- to 200-Hz LFP power, averaged across all experiments, in Fig. 3. Power is aligned to
either the initial onset of 0% coherent motion (Fig. 3A) or to the start of the coherent motion pulse (Fig. 3, B–D). There was a responsive modulation visible in the LFP power at the start of the 0% coherent motion (Fig. 3A) and when the motion pulse occurred inside the RF (Fig. 3, B and C) but not when the motion pulse occurred outside the RF (Fig. 3D). This is set against the MT spike rate (plotted above each color map in Fig. 3), which was computed with the same 200-ms Hamming window and averaged over all neurons. In agreement with previous work (Britten et al. 1992), MT neurons in our recordings responded to the motion pulse with a transient increase in their spike rate but usually maintained the same relative spike rate when the motion pulse occurred outside their RF.

Comparison of MT spiking and LFP power reveals that the modulation in LFP power occurred at the same time as the transient increase in spike rate. Thus LFP spectral power contained some stimulus information that was also present in the MT spike response. We next quantified the neural-behavioral correlation between the LFP spectral power and the detection of the motion pulse.

**Dynamics of functional link between LFP spectra and behavior.** We calculated the neural-behavioral correlation between LFP spectral power and motion detection using a common trial-by-trial ROC-based metric, referred to as detect probability (DP) (Cook and Maunsell 2002). At each time point throughout a trial, we computed DP by comparing two distributions of LFP power, corresponding to trials when the motion pulse was detected (correct trials) and trials when it was not detected (failed trials). A LFP-DP value of 0.5 indicates no difference between the correct and failed distributions of LFP power, and thus no correlation between detection performance and the underlying neural process. When LFP power becomes greater on correct trials than on failed trials, the LFP-DP approaches a value of 1 and suggests a positive correlation. On the other hand, when LFP power becomes smaller on correct trials than on failed trials, then the LFP-DP approaches a value of 0 and suggests a negative correlation.

The color maps in Fig. 4 show the mean LFP-DP (averaged across recording sessions) for the same conditions and alignments as in Fig. 3. LFP-DP is aligned to the initial onset of 0% motion using all conditions in Fig. 4A, while Fig. 4, B–D, show LFP-DP aligned to the start of the motion pulse for trials grouped by the stimulus conditions with two motion pulses in both RFs, one motion pulse in the RF, and one motion pulse in the other RF, respectively. For comparison, the corresponding average DP of the MT spike rate (spike-DP) is shown above each color map in Fig. 4, computed with the same sliding Hamming window.
A qualitative comparison of the LFP-DP in Fig. 4 shows several distinguishing features. Early in the trial, during the onset of the 0% coherent dot motion, there was no correlation between LFP power and detection performance (LFP-DP ≈ 0.5; Fig. 4A). Because the stimulus conditions were the same at the beginning of a trial, LFP-DP estimates in Fig. 4A used all trials and thus showed less variability. When the motion pulse occurred in the recording site’s RF, two distinct regions of correlation were visible, separated by time and frequency (Fig. 4, B and C). One was a high-frequency (>50 Hz) band of positive correlation (LFP-DP > 0.5) that peaked ~100 ms after the start of the coherent-motion pulse. As this is part of the upper- to high-gamma range, we refer to this functional correlation as high-gamma LFP-DP for convenience (see Fig. 5 for more details concerning our working definition of high gamma). Although high-gamma LFP-DP peaked when a motion pulse was in the RF (Fig. 4, B and C), it remained relatively flat when the motion pulse occurred in the other RF (Fig. 4D). As also shown by Liu and Newsome (2006), there was little neural-behavioral correlation in the low- to mid-gamma (~30–50 Hz) range.

The other distinguishing feature of the LFP-DP was a band of low-frequency, negative correlation (LFP-DP < 0.5) that grew strongest 200 ms or more after the start of the motion pulse. The neural-behavioral correlation at these low frequencies (~10–30 Hz) roughly coincides with the beta band (for convenience referred to as beta LFP-DP). Curiously, beta LFP-DP appeared whether there was a motion pulse in the RF (Fig. 4, B and C) or not (Fig. 4D), although it was slightly weaker in the absence of the motion pulse.

As reported previously (Smith et al. 2011) and reproduced here, the spike activity of MT neurons had no initial correlation with detection performance (spike-DP = 0.5, Fig. 4A) but later showed a strong transient spike-DP that peaked in unison with the response to the coherent-motion pulse (compare Fig. 3, B and C, and Fig. 4, B and C). Other trends include a stronger spike-DP during the one-pulse condition compared with the two-pulse condition, an early rise in spike-DP just before coherent motion began, and a small but significant spike-DP when there was no motion pulse in the RF (Fig. 4D). A causal, feedforward model suggested that these trends in spike-DP reflected a bottom-up functional link between sensory-related activity and detection of the motion pulses (Smith et al. 2011). Thus we can shed light on the nature of the MT LFPs by comparing the dynamics of the LFP-DP to the spike-DP.

Comparison of LFP-DPs with spike-DP in Fig. 4 suggests that the temporal evolution and stimulus condition dependence of high-gamma LFP-DP and spike-DP were fairly well...
cies of the LFP-DP. It is important to first address whether our data collection or analysis procedures biased the frequency and temporal dependencies of the LFP-DP.

**Potential LFP spectral detect probability confounds.** The first study to examine the trial-by-trial correlation between MT LFP frequency bands and behavior during a motion-based task was by Liu and Newsome (2006). In that study, the functional link was described by the ROC metric choice probability (CP; Britten et al. 1996), which is similar to DP. In their study, CP described the correlation between LFP power and the choice that a subject made during a speed discrimination task. Because their task used a long, fixed-length, stimulus presentation interval, the authors did not report the temporal dynamics of LFP-CP. Across the entire stimulus presentation interval, they found a positive correlation with behavioral choice (LFP-CP > 0.5) for high-gamma LFP frequencies and negative correlations with behavioral choice (LFP-CP < 0.5) for beta LFP frequencies. In addition, the dynamics and frequency range of our high-gamma LFP-DP are similar to the LFP-CP recorded from the temporoparietal junction of humans during the detection of a brief microstimulation at another location in visual cortex (Beauchamp et al. 2012). Thus the frequency dependence and dynamics of the LFP-DPs in our study are in agreement with these previous results.

We wanted to confirm that our LFP estimates were accurate and unbiased. First, we observed similar changes in LFP-DP as a function of frequency when we estimated LFP power using either multitaper spectral methods (Chronux) or band-pass filtering in the time domain (see METHODS). We also observed the same LFP-DP results whether or not we first removed spike waveforms and the strong 60-Hz noise from our raw electrode signals before computing LFP spectra (see METHODS).

Finally, we examined whether spectral leakage from the burst of MT action potentials, fired in response to the motion pulse, could have produced the LFP-DPs. For example, if neurons became fatigued or underwent rapid adaptation then they may have produced fewer spikes or a different pattern of spikes in the period immediately following the transient response. We applied the same time-frequency analysis as shown in Fig. 2 to each spike train, which was represented numerically as a series of 0s (no spike) and 1s (spike). This produced the spectral power of our spike trains from 5 to 200 Hz, as a function of time. We used this data to compute DP for our spikes as a function of both time and frequency, in the same manner as the LFP-DP.

This analysis revealed that the spike-based time-frequency DP was similar across all frequencies to the high-gamma LFP-DP and had the same dynamics as the spike-DP shown in Fig. 4 (data not shown). This would be expected, as the power spectrum of a spike train is similar across frequencies (Belitski et al. 2008). Thus spike trains could recreate high-gamma LFP-DP but not beta LFP-DP. We present the results of this particular analysis in more detail below when quantifying the differences between LFP- and spike-DP (see Fig. 7). Thus we were confident that the LFP-DP results shown in Fig. 4, especially in the beta band, were physiologically based signals that were not related to the spike activity.

**Early and late LFP spectral DP.** The results presented so far suggest that the high-gamma LFP power in MT had dynamics similar to the local spike rate during motion detection—while the beta-band LFP power did not. Beta LFPs appear to have reflected a neural process that was different from the bottom-up sensory processing of the motion pulse. We further quantified this result by taking a detailed look at the LFP-DP over all frequencies at an early (100 ms) and a late (275 ms) time point after the motion pulse began, when high-gamma and beta LFP power were the most correlated with detection performance, respectively.

Figure 5 shows the population average LFP-DP (±SE) over frequencies for the two time points (100 ms and 275 ms) when there were two pulses in both RFs (Fig. 5A), one motion pulse in the RF (Fig. 5B), or one motion pulse in the other RF (Fig. 5C). The LFP-DPs in these plots were smoothed over the frequency domain with a 15-Hz window. At both time points, and during all stimulus conditions, LFP power was negatively correlated with detection performance from ~10 to 30 Hz. It was also positively correlated from ~70 to 200 Hz, reaching a plateau by 100 Hz. The negative correlation under 30 Hz was stronger at 275 ms than at 100 ms for all stimulus conditions. On the other hand, the positive correlation above 100 Hz was stronger at 100 ms than at 275 ms for all stimulus conditions.
stronger at 100 ms than at 275 ms, but only when a motion pulse signal was in the RF (Fig. 5, A and B). Finally, a key observation is that the same positive correlation always appeared stronger when there was a signal in the RF (compare Fig. 5, A and B, with Fig. 5C).

To confirm these observations statistically, we computed the mean LFP-DP for the two frequency bands in Fig. 5: 10–30 Hz (beta LFP-DP) and 100–200 Hz (high-gamma LFP-DP). We used 100–200 Hz because the LFP-DP plateaued above chance around 100 Hz, for both time points. It is important to note, however, that this high-gamma band is usually associated with nonrhythmic activity and has a much different interpretation than lower gamma frequency bands commonly referenced in the oscillations literature.

For each band, the average LFP-DP was first taken across frequency components, for each electrode recording. The population response was then assessed by averaging the LFP-DP across all electrodes. In all stimulus conditions and for both time points, the mean beta LFP-DP was <0.5 (1-sample, left-sided t-test) for two pulses in both RFs (100 ms DP = 0.484, P < 0.0001; 275 ms DP = 0.480, P < 1 × 10⁻⁵), one pulse in the RF (100 ms DP = 0.482, P < 0.001; 275 ms DP = 0.470, P < 1 × 10⁻⁵), and one pulse in the other RF (100 ms DP = 0.490, P = 0.012; 275 ms DP = 0.482, P = 0.002) while the mean high-gamma LFP-DP was >0.5 (1-sample, right-sided t-test) for two pulses in both RFs (100 ms DP = 0.526, P < 1 × 10⁻⁷; 275 ms DP = 0.522, P < 1 × 10⁻¹⁵), one pulse in the RF (100 ms DP = 0.530, P < 1 × 10⁻⁶; 275 ms DP = 0.525, P < 1 × 10⁻¹⁵), and one pulse in the other RF (100 ms DP = 0.510, P < 0.001; 275 ms DP = 0.517, P < 1 × 10⁻⁷). Only high-gamma LFP-DP differed with stimulus condition, at 100 ms (one-way ANOVA, P < 1 × 10⁻⁶) but not at 275 ms (P = 0.18). At 100 ms, high-gamma LFP-DP with two motion pulses in both RFs was not different from when one motion pulse was in the RF (Tukey-Kramer P = 0.64) but LFP-DP with one motion pulse in the other RF was less than either condition with a motion pulse in the RF (P < 0.001). Although the mean beta LFP-DP at 275 ms was less with one pulse in the RF than two pulses, and less with two pulses than one pulse in the other RF, there was no significant difference in beta LFP-DP between stimulus conditions (100 ms, 1-way ANOVA P = 0.38; 275 ms, P = 0.21).

To test whether LFP-DP changed over time, we pooled our LFP-DP data over the two stimulus conditions that contained a motion pulse in the RF (1 and 2 pulses). Beta LFP-DP was found to be slightly stronger at 275 ms (mean = 0.475) than at 100 ms (mean = 0.483, paired t-test, P = 0.043), while high-gamma LFP-DP was found to be slightly stronger at 100 ms (mean = 0.528) than at 275 ms (mean = 0.523, paired t-test, P = 0.026).

Comparing dynamics of spike-DP, high-gamma and beta LFP-DP. Although the color maps of Fig. 4 provide a good snapshot of how LFP-DP changed over time, differences can be difficult to discern with precision. Thus we computed the time course of LFP-DP for the 10–30 Hz beta and 100–200 Hz high-gamma frequency bands (Fig. 5). Figure 6 shows the average population DP (±SE) dynamics aligned to the start of the motion pulse for spiking responses (Fig. 6A), the high-gamma LFP band (Fig. 6B), and the beta LFP band (Fig. 6C). DP was computed separately for trials grouped by stimulus condition (Fig. 6, left; 2 pulses, 1 pulse in the RF, and 1 pulse in the other RF) or RT (Fig. 6, right; fast RTs and slow RTs).

The average spike-DP (Fig. 6A) showed a strong dependence on stimulus condition and RT. The effects of stimulus condition on spike-DP (Fig. 6A, left) were previously shown to be well accounted for by a feedforward model of the detection process (Smith et al. 2011) but were recomputed here with the same sliding 200-ms Hamming window as used for the LFP-DP. As we have shown previously, spike-DP peaked around 100 ms after the motion pulse began (Fig. 6A, arrow a) and was stronger in magnitude for the one pulse in RF condition compared with the two-pulse condition. When no motion pulse occurred in the RF, spike-DP was weak but significantly above chance. In addition, the feedforward model showed that the integration of MT activity by downstream
areas could produce a spike-DP that began to increase above 0.5 shortly before the coherent motion (Fig. 6A, arrow b), which was not an artifact of temporal smearing by our analysis window (Smith et al. 2011).

We also divided correct trials into fast RTs (median, Fig. 6, right) and slow RTs (median), as it has been shown that MT responses are correlated with RT during motion detection (Bosking and Maunsell 2011; Cook and Maunsell 2002). For the grouping by RT, we combined all trials in which the motion pulse occurred in the neuron’s RF (2- and 1-pulse conditions). Over all experiments, the median RT of fast trials was 425 ms (95% bootstrap CI [402, 436]) and the median RT of slow trials was 505 ms (CI [492, 528]). We found that spike-DP was much stronger and peaked earlier for fast RTs (Fig. 6A, right, arrow c) compared with slow RTs. This result indicates that MT neurons responded more robustly and with a shorter latency in fast RT trials compared with slow RT trials.

The average high-gamma LFP-DP had early dynamics similar to spike-DP but grew distinct as the trial approached the behavioral response (Fig. 6B). When the motion pulse occurred in the RF, high-gamma LFP-DP showed a strong transient (Fig. 6B, arrows d) similar to spike-DP with a similar dependence on RT. Although there was no appreciable difference in high-gamma LFP-DP between the one- and two-pulse conditions, there was a slight increase in high-gamma LFP-DP above chance when the motion occurred in the other RF. Thus, early after the motion pulse, high-gamma LFPs exhibited a functional link with behavior similar to the MT spike activity.

At ~200 ms after the motion pulse began, the high-gamma LFP-DP began to increase (Fig. 6B, arrows e). This upward deflection was present in all high-gamma LFP-DP groups in Fig. 6B, although when the motion pulse occurred outside the RF the upward deflection seems to have occurred earlier (~150 ms). Thus, as the trial approached the time of the behavioral response (lever release by the monkey), the dynamics of the high-gamma LFP-DP became distinct from that of the spike-DP. Unfortunately, we were not able to reliably estimate LFP-DP any further than 300 ms after the motion pulse began (which corresponds to the center of the last 200-ms Hamming window), because correct trials were dropped once the behavioral response entered the sliding analysis window and not enough correct trials remained.

In contrast to the transient dynamics of the spike- and high-gamma LFP-DP, the dynamics of the beta LFP-DP showed a slow decay that began at the onset of the motion pulse (Fig. 6C). Notably, as beta LFP-DP decreased during the first 200 ms, it exhibited little appreciable difference between stimulus and RT groups. In addition, beta LFP-DP tended to be slightly below 0.5 before the motion pulse (Fig. 6C, arrow g) compared with the spike- and high-gamma LFP-DP, which tended to be slightly above 0.5. One feature that beta and high-gamma LFP-DP had in common, however, was the deflection just after 200 ms (Fig. 6, B and C, arrows e and f). Beta LFP-DP began to rise at around this time, or plateaued in the case of the one-pulse and slow RT conditions.

The comparison of the DP dynamics in Fig. 6 suggests four broad conclusions regarding the functional link between MT signals and the subjects’ ability to perceive the motion pulse. First, LFP high-gamma and spike responses shared a similar functional link to behavior soon after the behaviorally relevant stimulus began. If we assume that the early spike-DP is driven primarily by bottom-up fluctuations in sensory input (Smith et al. 2011), then early high-gamma LFP-DPs also share this bottom-up link to behavioral outcome.

Second, the late (~200 ms) departure between spike- and high-gamma LFP-DP dynamics reveals slower modulations in the high-gamma band that are potentially top-down (e.g., attentional or associated with the impending motor response). This late modulation is also present in the beta LFP-DP.

Third, beta LFP-DP differed in both its sign and dynamics from spike- and high-gamma LFP-DP. Thus the beta-band signals may have had a unique functional link with behavior, with little contribution from bottom-up sensory components. Earlier in the trial, however, beta LFP-DP was significantly less than chance (0.5) at ~100 ms before the start of the motion pulse (Fig. 6C, arrows g) on trials with two pulses (mean = 0.487, 95% CI [0.481, 0.494]; t-test, P < 1 × 10^-4) and at ~35 ms before the motion pulse on trials with one pulse in the RF (mean = 0.482, CI [0.472, 0.491]; P < 0.001). Trials with one pulse in the other RF had no beta LFP-DP under 0.5 at either ~100 ms (mean = 0.499, CI [0.491, 0.510]; P = 0.45) or ~35 ms (mean = 0.498, CI [0.490, 0.508]; P = 0.35) before the start of the motion pulse. Beta LFP-DP at ~100 ms before two pulses was no different than at ~35 ms before one pulse in the RF (mean 1 pulse in RF − 2 pulse = 0.005, CI [0.015, 0.005]; paired t-test, P = 0.36). The same kind of trends appeared at ~25 ms before the motion pulse in high-gamma LFP-DP (2 pulses, mean = 0.505, CI [0.501, 0.510], t-test, P = 0.01; 1 pulse in RF, mean = 0.507, CI [0.502, 0.512], P = 0.004; 1 pulse in other RF, mean = 0.502, CI [0.498, 0.507], P = 0.23), including no significant difference on trials with two pulses or one pulse in the RF (mean difference = 0.002, CI [−0.004, 0.008]; paired t-test, P = 0.48).

Except for the sign of beta LFP-DP before the motion pulse, it had a timing and stimulus dependence that was reminiscent of a local, bottom-up sensory response (Smith et al. 2011). This contrasts with beta LFP-DP at 100 ms after the motion pulse, which was invariant to the stimulus configuration. Nevertheless, it is difficult to disentangle a feedforward sensory influence from a top-down effect at ~100 and ~35 ms before the motion pulse, particularly because of the ~200-ms width of the analysis window. With a narrower analysis window of 100 ms, beta LFP-DP maintains the same trends (~100 ms before 2 pulses, mean = 0.488, 95% CI [0.481, 0.495], t-test, P < 0.001; ~35 ms before 1 pulse in RF, mean = 0.477, CI [0.467, 0.488], P = 7.475 × 10^-5, ~100 ms before 1 pulse in other RF, mean = 0.495, CI [0.485, 0.505], P = 0.150; ~35 ms before 1 pulse in other RF, mean = 0.496, CI [0.485, 0.507], P = 0.258; ~35 ms before 1 pulse in RF − 100 ms before 2 pulses, mean = −0.010, CI [−0.023, 0.0019], P = 0.12), making it less likely to have resulted from the local sensory response to the coherent motion pulse.

Finally, the weak modulations in DP ~200 ms before the motion pulse deserve further comment. Attentional signals in MT could explain why spike-DP (mean = 0.510, 95% CI [0.503, 0.517], P = 0.005) and high-gamma LFP-DP (mean = 0.505, CI [0.502, 0.508], P < 0.001) were above chance at ~200 ms before the motion pulse when the RT was short but not when the RT was long (mean spike-DP = 0.502, CI [0.495, 0.509], P = 0.31; mean high-gamma LFP-DP = 0.501, CI [0.498, 0.505], P = 0.18). In contrast, the beta LFP-DP was not
appreciably different from chance at this time, regardless of RT
(short RT mean = 0.495, CI [0.489, 0.501], P = 0.07; long RT
mean = 0.498, CI [0.492, 0.504], P = 0.25).

Increased attentional allocation would have increased the
signal-to-noise ratio of MT’s response to the motion pulse,
leading to a faster rise in pooled output and thus a faster
response from the subject. At the same time, increasing atten-
tion could have increased the baseline spike rate and high-
gamma LFP power, leading to a rise in DP when RTs were
short. Obviously, the purely bottom-up sensory model of Smith
et al. (2011) does not account for the modulations in spike- and
high-gamma LFP-DP —200 ms before the motion pulse. Thus
small fluctuations in top-down attentional modulation, before
the motion pulse began, appear to have contributed to the
detection of the motion pulse. These fluctuations seem to have
been captured in the spike- and high-gamma LFP-DP but not
the beta LFP-DP and further suggest that beta LFPs reflected a
distinct part of the detection, and possibly also attention pro-
cess. It should be noted, however, that this experiment was not
designed to control for the possible alternatives to attention.

\textit{Using spike trains to compute high-gamma and beta DP.}
The comparison of spike-DP and LFP-DP dynamics in Fig. 6
revealed several similarities in the high-gamma band. It is
important to investigate whether these similarities arose inde-
pendently, or whether high-gamma LFP-DP was linked to the
presence of spikes in the recorded waveforms (Zanos et al.
2011) despite our attempt to remove them. To examine this, we
performed the same time-frequency analysis on spiking re-
sponses as we did on the LFPs. Thus we produced high-gamma
and beta spike-DP dynamics (Fig. 7, A and B, respectively)
using the spike trains (0s and 1s).

As in the LFP-DP data in Fig. 6, we show beta and high-
gamma spike-DP dynamics for trials grouped either by motion
pulse location (Fig. 7, \textit{left}) or by RT (Fig. 7, \textit{right}). It is clear
that both the high-gamma and beta-band spike-DP dynamics in
Fig. 7 resemble an attenuated version of the spike-DP in Fig.
6A. From this, one might conclude that the high-gamma
LFP-DP reflects a filtered copy of spike-DP. However, we do
not think this fully accounts for high-gamma LFP-DP because
the high-gamma spike-DP in Fig. 7A did not reproduce the late
deflection in high-gamma LFP-DP (Fig. 6B, arrows \textit{e}). Thus
late-occurring (after 200 ms) high-gamma LFP-DP may reflect
neural processes that are not present in the spike response.

Importantly, the beta LFP-DP (Fig. 6C) bears no resem-
blance to DP calculated from a filtered copy of spikes in the
same beta frequency band (Fig. 7B). This also includes the
late-trial deflection of beta LFP-DP (Fig. 6C, arrows \textit{f}), which
was not present in the beta spike-DP. Thus beta LFP-DP and
late high-gamma LFP-DP have components that are indepen-
dent of MT spike activity.

\textit{LFP-DP dynamics were similar for each subject.} Figure 8
breaks out the LFP-DP for the beta and high-gamma bands
shown in Fig. 6 for each subject. In this analysis, plots are
grouped by stimulus condition and the mean LFP-DP (\pm SE) is
shown for each animal. Monkey \textit{W} had the most recordings
(\(n = 80\)) and thus showed the least variability compared with
monkey \textit{F} (\(n = 20\)). When a pulse occurred in one or both RFs,
both animals demonstrated high-gamma LFP-DPs that tended
to have an early positive peak, followed by a later negative
peak in the beta LFP-DP (Fig. 8, A and B). When no motion
pulse occurred in the RF (Fig. 8C), the beta band still demon-
strated a late negative LFP-DP peak for both subjects.

\textit{Correlations between spike-DP, beta and high-gamma LFP-DP.}
If the fluctuations in power of different LFP bands reflected the
same neural mechanism, then the LFP-DP should
have been correlated across bands. For example, if high-
gamma LFP-DP (\(>0.5\)) and beta LFP-DP (\(<0.5\)) had the same
underlying source, then a negative correlation in power might
be expected between those bands (Liu and Newsome 2006).
However, any correlation could be masked by broadband
noise.

To observe the correlation between high-gamma and beta
power while minimizing the effects of broadband noise, we
computed the partial Spearman’s correlation coefficient by
using power in the intermediate gamma LFP band (40–80 Hz)
as the control variable. This partial correlation was found
across trials in each session using the same moving 200-ms
Hamming window. There was no significant correlation in LFP
power at any point in time until \(>200\) ms after the motion
pulse, and only on correct trials. Although significant, this
trial-by-trial correlation between high-gamma and beta was
weak and thus not appreciable (275 ms after motion pulse; 2
pulses mean partial correlation = 0.040, \(t\)-test \(P = 0.006\); 1
pulse in RF mean = 0.042, \(P = 0.026\); 1 pulse in other RF
mean = 0.071, \(P < 0.001\)).

To better explore correlations between beta and high-gamma
LFP power, we performed a different partial-correlation anal-
ysis of DP values, in this case across experimental sessions.
The early beta LFP-DP was correlated with the early high-gamma LFP-DP ($\rho = 0.22$, $P < 0.001$) but not the early spike-DP (Fig. 9C; $\rho = -0.03$, $P = 0.590$), while the late beta LFP-DP was not significantly correlated with either late 

(Fig. 9). The goal of this analysis was to see whether DP values computed from spikes or the two LFP bands covaried across experiments, which would suggest a common neural mechanism. Figure 9A illustrates the spike- and LFP-DPs at two time points, 100 ms (early) and 275 ms (late) after the start of coherent motion. The size of the six circles in Fig. 9A is scaled to reflect the relative mean DP, while filled circles represent positive DPs ($>0.5$) and open circles negative DPs ($<0.5$). The size and thickness of the arrows between the circles represent the strength of significant ($P < 0.05$) partial correlations. As before, we averaged LFP-DP over the beta ($10–30$ Hz) and high-gamma ($100–200$ Hz) bands. We also took the spike-DP at the same time points. To increase the power of our correlation analysis, we converted DPs to $z$ scores before pooling the data over all three stimulus conditions. The Spearman partial correlation ($\rho$) was computed between every pair of the six $z$-scored DPs (only significant correlations are reported above the arrows in Fig. 9A), while controlling for the other four DPs. Two example DP pairings are highlighted for the early high-gamma LFP-DP versus early spike-DP (Fig. 9B) and early beta LFP-DP versus early spike-DP (Fig. 9C).

As suggested above, high-gamma LFP-DP and spike-DP were relatively well correlated across experimental sessions, both early (Fig. 9, A and B; $\rho = 0.25$, $P < 0.001$) and late (Fig. 9A; $\rho = 0.16$, $P = 0.002$) in the trial. In addition, significant autocorrelations were found across time for each individual neural signal (Fig. 9A, horizontal arrows; early spike-DP vs. late spike-DP $\rho = 0.26$, $P < 0.001$; early high-gamma LFP-DP vs. late high-gamma LFP-DP $\rho = 0.28$, $P < 0.001$; and early beta LFP-DP vs. late beta LFP-DP $\rho = 0.13$, $P < 0.017$). This again suggests that some of the correlated fluctuations of high-gamma LFPs came from motion-driven spiking activity.
spike-DP ($\rho = -0.02, P = 0.655$) or late high-gamma LFP-DP ($\rho = 0.07, P = 0.176$). The analysis shown in Fig. 9 was repeated using only the two stimulus conditions with a pulse in the RF, and the same qualitative results were obtained (data not shown). Importantly, the lack of any significant correlation between the early beta LFP-DP and spike-DP or the late beta LFP-DP and the other two late DPs supports the hypothesis that beta LFPs had a unique functional link with behavior that was independent from the high-gamma LFPs or spike rates.

A final comparison of DP correlations was made by performing the same paired analysis of z-scored DPs computed −200 ms before the motion pulse, as both beta LFP-DP and spike-DP were different from chance at this time (see Fig. 6). We found that beta LFP-DP was significantly correlated with high-gamma LFP-DP ($\rho = 0.19, P < 0.001$) but not with spike-DP ($\rho = 0.07, P = 0.22$). However, high-gamma LFP-DP was significantly correlated with spike-DP ($\rho = 0.14, P = 0.01$). This correlation analysis further strengthens the argument that beta and high-gamma LFP-DP did not carry information about the same bottom-up detection processes, while high-gamma LFP- and spike-DP appear to have shared some of the same neural origins. This is in line with the observation that the spike- and high-gamma LFP-DP changed with RT, while beta LFP-DP did not (see Fig. 6).

**LFP coherence reveals late global functional link in both beta and high-gamma bands.** Our high-gamma and beta-band results suggest that later, top-down signals originating after the perception of the motion pulse arrived in MT near the end of correct trials. There is also the suggestion that these late top-down signals were global because they are present in the LFP-DP whether or not a motion pulse was in the RF (see Fig. 6, B and C, arrows e and f). However, the LFPs from individual electrodes cannot reveal whether a late, top-down signal arrived at just one recording site at a time or both at once. The invariance of late changes in LFP-DPs to the motion pulse location (see Fig. 6, B and C) suggests that the top-down signal was globally distributed. If this was the case, then one would predict that the pairs of LFPs recorded at the same time from separate electrodes should have become correlated near the end of the trial.

The magnitude-squared coherence can detect simultaneous changes in the LFP power on both electrodes. Therefore, to examine whether the two electrodes were correlated at the end of the trial, we computed the magnitude-squared coherence of paired LFP signals (after first z-scoring the data) over time in a moving 200-ms analysis window (see METHODS). Thus a coherence trace was obtained for every correct and failed trial. The average LFP coherence ($\pm SE$) is shown in Fig. 10A, aligned with the start of the motion pulse, for high-gamma and beta frequencies, on correct and failed trials. We pooled trials with one or two motion pulses together, to improve our coherence estimates; however, we also verified the following results for trials grouped separately by motion pulse location (data not shown).

While beta LFP coherence was greater than high-gamma coherence, there was little difference in the correct and failed coherence from either band until late in the trial. Beta LFP coherence grew significantly weaker on correct trials 230 ms after the motion pulse (mean correct – failed = −0.012, 95% CI [−0.019, −0.006], paired t-test, $P < 0.001$), while correct high-gamma coherence grew stronger by 275 ms (mean difference = 0.010, CI [0.006, 0.017], $P < 0.001$). This suggests that the MT LFP coherence was correlated with the monkeys’ responses.

Since LFP coherence was available on every trial, we were able to ask whether the trial-to-trial fluctuations in LFP coherence could predict detection performance. We computed ROC curves that compared the distribution of correct-trial coherence (hits) versus the distribution of failed-trial coherence (misses). The area under each curve was the probability that an ideal observer could predict the monkey’s performance given the level of LFP coherence, so this metric was called the LFP-coherence detect probability (LFP-DP$_{coh}$). The average LFP-DP$_{coh}$ ($\pm SE$) is shown in Fig. 10B for the beta and high-gamma frequency bands and compared against the average spike-DP.

The mean LFP-DP$_{coh}$ of both bandwidths fluctuated randomly around 0.5 until late in the trial. Beta LFP-DP$_{coh}$ peaked significantly below 0.5 at 230 ms after the coherent motion pulse began (mean = 0.483, 95% CI [0.472, 0.493], left-tailed t-test $P = 0.001$). Thus beta LFPs were less coherent prior to correct detections. By comparison, the high-gamma LFP-DP$_{coh}$...
rose slightly later in the trial and climbed significantly above 0.5 by 275 ms after the motion pulse began (mean = 0.515, CI [0.509, 0.523], P < 0.001). Thus high-gamma LFPs were more coherent prior to correct detections. It is worth noting that the late changes in LFP-DP$_{coh}$ occurred at about the same time as the late changes in LFP-DP (compare with Fig. 6, B and C, arrows a and f). The LFP-DP$_{coh}$ of both LFP bands peaked well after the corresponding spike-DP (Fig. 10B). Also, an analysis of coherence computed using only the spikes did not reproduce the late surge in LFP-DP$_{coh}$ (data not shown). Altogether, these results suggest that LFPs just prior to the lever response reflected a top-down, global, input signal that arrived simultaneously at both MT recording sites.

One potential confound of this analysis is that coherence can change even if there is an independent change in LFP power on just one electrode—although it is most sensitive to correlated changes on both. Therefore, it is possible that the LFP power on only one electrode was correlated with the behavior at a time, and that the correlated electrode switched between trials; the same changes in LFP-DP and LFP-DP$_{coh}$ could have resulted in this case. Therefore, we used a simple bootstrap test (see Methods) to ask how much of the measured LFP-DP$_{coh}$ was explained by independent changes on the electrodes. The average empirical LFP-DP$_{coh}$ was significantly different from what would be expected if the LFPs from only one electrode predicted the behavior at a time—for beta LFPs (230 ms after motion pulse onset, P < 0.002) and high-gamma LFPs (275 ms after pulse onset, P < 0.001). This can be accounted for by changes in the LFPs that predicted the behavior simultaneously on both electrodes—which altogether bolsters the conclusion that there was a late, top-down, source of DP that arrived at both electrodes regardless of where the motion pulse occurred.

**Behavioral response-aligned spikes and LFPs.** The results so far suggest that after the perception of the motion pulse had occurred there was a nonsensory, global, top-down signal that affected the LFP-DP. We hypothesized that such a late-occurring top-down modulation in LFP-DP would also be observed, and might even be more prominent, when the data were aligned to the animals’ behavioral response. Thus we examined the average spike response, LFP power, and the associated DPs aligned to the lever release event.

The average spike response and LFP power were aligned to the lever release for correct and false-alarm trials (Fig. 11). For correct trials, we combined all trials where the motion pulse occurred in the RF. During false-alarm trials, the animals responded with a lever release before the motion pulse occurred. To aid in comparing the data shown in Fig. 11, responses were normalized by the average spike rate (or LFP power) from −700 to −650 ms over correct and false-alarm trials. The lever-aligned spike response and high-gamma power (Fig. 11, A and B, respectively) had qualitatively similar dynamics for both correct and false-alarm trials. The spike response peaked around −260 ms before the lever release, while the high-gamma power peaked soon after. However, the high-gamma LFPs showed a late deflection approximately −180 ms before the lever release (Fig. 11B, arrow a) that was not in the spike response. Beta LFPs had different dynamics compared with high-gamma and spikes, and also showed a strong deflection around −180 ms before the lever release (Fig. 11B). Interestingly, the beta LFPs had almost identical correct and false-alarm dynamics and amplitudes (Spearman’s correlation = 0.93, P < 0.001). In comparison, the similarity between correct and false-alarm trials contained no motion pulse, the MT neurons still exhibited a relatively robust spike response (Fig. 11A). This is likely due to the stochastic nature of the 0% coherent random dot stimuli, which produced a weak motion signal by chance, triggering the animals’ response. Overall, the lever-aligned results in Fig. 11 bolster the observation that high-gamma LFPs initially had dynamics similar to the sensory response of the MT spikes. At about −180 ms before the lever response, however, a clear change in both the beta and high-gamma dynamics occurred that was likely not due to the sensory response.

**Behavioral response-aligned spike-DP, LFP-DP, and LFP-DP$_{coh}$** We next examined how LFP neural-behavioral correlations aligned to the behavioral response compared with those aligned to the stimulus onset. Figure 12 illustrates the neural-behavioral correlations for the spike response, and our two LFP bands, aligned to the lever release. Because failed trials contained no lever release, we estimated a pseudo-lever event for each failed trial by randomly drawing from the RT distribution of each experiment (see Methods). Spike- and
LFP-DPs in Fig. 12, A and B, are grouped by stimulus condition in order to compare how they aligned with the distribution of the 50-ms motion pulses (Fig. 12, A and B, top). The colors correspond to the stimulus condition and are the same as those of the motion-pulse aligned DPs in Fig. 6. The two vertical dashed lines in Fig. 12, A and B, are aligned to the peaks of the motion pulse distribution and spike-DP, respectively.

Overall, the dynamics for the lever-aligned DPs in Fig. 12, A and B, are relatively similar to those aligned to the motion pulse in Fig. 6. The similarities between spike- and high-gamma-DP dynamics, as well as the unique negative beta LFP-DP, were preserved in the lever-aligned analysis. For the spike-DP, one qualitative difference is that the lever-aligned analysis shows a more prominent peak when the pulse was in the other RF (compare Fig. 12A and Fig. 6A). Another qualitative difference is that both the high-gamma and beta LFP-DP show somewhat more prominent late deflections (Fig. 12A, arrows a) in the lever-aligned versus pulse-aligned plots. Importantly, in Fig. 12, A and B, there is no suggestion of a late-occurring deflection in any of the lever-aligned spike-DPs.

The neural-behavioral correlations of the lever-aligned coherence are shown in Fig. 12C and can be compared to the motion pulse-aligned plots in Fig. 10B. As in the previous LFP-DPcoh analysis, coherence between the two electrodes becomes more predictive of behavior as time approaches the lever release. Interestingly, the beta LFP-DPcoh aligned to the lever release does not exhibit a late jump as seen in the motion pulse-aligned plots at ~250 ms in Fig. 10B. Taken together, the lever-aligned LFP-DP and LFP-DPcoh support the hypothesis that a distinct, nonsensory, late-occurring signal is present in the LFPs but not in the MT spike activity.

DISCUSSION

To understand the simultaneous contribution of bottom-up (fluctuations due to sensory input) and top-down (fluctuations due to changes in attention, arousal, expectation, etc.) neural processes linked to motion perception, we analyzed the correlation between MT LFPs and behavior (LFP-DP) in both the time and frequency domains and compared them to the correlations between MT spiking activity and behavior (spike-DP). Since the spikes and LFPs were derived from the same wideband electrode recordings, there was little chance that differences observed between the spike-DP and LFP-DP were due to experimental artifacts.

We found that LFP-DP had two distinct functional bands (beta and high gamma) with a gradual transition from one to the other from 40 to 90 Hz. High-gamma LFP-DP at first resembled early, bottom-up spike-DP but later exhibited unique dynamics that likely reflected top-down processes. In comparison, the beta LFP-DP dynamics were different from the spike-DP dynamics, peaking later in the trial, just before the behavioral response. This suggests that beta LFP-DP reflects a top-down functional link with behavior, such as a change in attention, that occurred after the decision to respond was made. Furthermore, late LFPs in both bands were correlated between MT locations, suggesting a global signal just before the behavioral response. Finally, the small spike- and LFP-DPs before the coherent motion pulse occurred suggest a weak top-down, attentional contribution throughout the detection processes. These results were also present when data were aligned to the behavioral response.

Although neural-behavioral correlations cannot directly reveal causality, these results suggest a hypothesis for how the different DP dynamics may reflect the causal and noncausal
links between neural activity and behavior. The fast, early peak in spike- and high-gamma LFP-DP likely represents a causal functional link to the motion detection. This conclusion is supported by our previous study of the spike-DP (Smith et al. 2011) and the similar dynamics between early LFP-DP and spike-DP. In comparison, the slow, late peak in both LFP-DP bands just before the lever response likely represents a non-causal link to behavior due to changes in the internal state (e.g., changes in attention, reward expectation, or motor preparation) after the perception of the motion pulse had occurred. This conclusion is further bolstered by the fact that neural-behavioral correlations just before the animal’s response were not dependent on any one stimulus location or (for beta LFP-DP) RT, and likely did not have enough time to causally influence the perceptual decision.

Sources of LFP perceptual fluctuations. LFP power in the high-gamma band predicted detection performance in a manner similar to local spiking activity. The correlation was positive, with a transient peak shortly after a motion pulse signal occurred in the recording site’s RF—but not when a motion pulse was absent. Furthermore, we could reconstruct the early peak in high-gamma LFP-DP from spike trains, and there was significant correlation between the early high-gamma LFP-DP and early spike-DP measured simultaneously from the same electrode. The early peak in high-gamma LFP activity was likely reflective of local motion processing in MT with a bottom-up, sensory-driven, link to behavior. This is consistent with a diversity of previous work showing a link between gamma oscillations and local spiking activity (Borgers et al. 2012; Cardin et al. 2009; Whittington et al. 1997).

After the motion pulse, activity in the LFP beta band was not correlated with detection performance in a bottom-up way. Beta LFP-DP was negative and peaked late in the trial, after the initial bottom-up sensory response to the motion pulse signal. Importantly, beta-band LFP power was equally correlated with detection performance whether or not the motion pulse was in the RF. The beta LFP-DP had different dynamic, sign, and stimulus dependence from either spike-DP or high-gamma LFP-DP. Neither was the spectral power of beta and high-gamma LFPs negatively correlated. Finally, we could not reconstruct beta LFP-DP using spike trains, and there was no significant correlation of beta LFP-DP with high-gamma LFP-DP or spike-DP from the same electrode. A correlation between the spike times and the beta LFPs might have been present, as the coherence between spikes and the mid-gamma band LFPs (40–70 Hz) can be modulated by attention (Womelsdorf et al. 2006). Nevertheless, the present study cannot attribute the perceptual fluctuations of beta LFPs to local bottom-up sensory processes in MT, or a shift in power from one band to another.

The differences with spiking and high-gamma LFP activity could be explained if beta LFPs contained signals from other areas. Horizontal connections can transmit spiking activity to cortex within a radius of several millimeters (Nauhaus et al. 2009, 2012; but see Ray and Maunsell 2011b)—while MT has clusters of connected neurons that are several millimeters apart on average, which was the approximate separation between our recording electrodes (Ahmed et al. 2012). Therefore, if one recording location in MT responded to a motion pulse in its RF, then horizontal connections could have passed that response to the other recording location. This could account for the presence and latency of beta LFP-DP when no motion pulse was in the RF. However, this does not explain beta LFP-DP on one-pulse trials when a motion pulse was in the RF and the other RF contained no motion pulse.

Alternatively, LFP activity could have reflected top-down signals from downstream areas (Gilbert and Li 2013). MT neurons can show a direction-selective response to coherent motion far outside of the classic RF—even when the motion is located in the ipsilateral hemifield (Zaksas and Pasternak 2005). It is thought that this information arrives in MT through feedback connections, likely from prefrontal cortex (Hussar and Pasternak 2010; Lui and Pasternak 2011; Zaksas and Pasternak 2006). The same mechanism could explain why LFP power was correlated with the subject’s detection performance when there was no coherent motion pulse in the RF.

Contribution of attention signals. A recent study (Khayat et al. 2010) showed that LFP spectral power in the beta band is attenuated when attention is directed to MT (see also Harris and Thiele 2011; Lee et al. 2013). It could account for several DP trends if, after detecting the motion pulse, the monkey focused more attention on the visual stimulus. For example, this would have caused beta LFP power to be lower on correct trials than it was on failed trials when there was no detection and thus no change in attentional state. Since beta LFP-DP was independent of the stimulus condition, global attention signals would have reached both recording locations. The functional link of the LFP coherence near the end of correct trials, regardless of stimulus condition, supports this hypothesis. Indeed, changes in LFP coherence may accompany changes in attentional state (Buscchia and Miller 2007; Saalmann et al. 2007; Siegel et al. 2012).

A change in attention could also explain why high-gamma LFP-DP increased late in the trial, as this band is known to respond to changes in attention (Fries et al. 2001; Khayat et al. 2010; Rotermund et al. 2009; Womelsdorf et al. 2006; but see Ray and Maunsell 2011a) and possibly perceptual state (Panganagotaropoulos et al. 2012). Since the beta and gamma bands respond differently to attention signals in MT (Khayat et al. 2010) and because late beta LFP-DP had no pairwise correlation with high-gamma LFP-DP (Fig. 9), the two bands may have carried independent information (Siegel et al. 2012) about incoming attention signals. Near the end of correct trials, LFPs may have responded to attention signals independently of local spiking—as suggested by the late increase in LFP-DP and LFP-DPcoh that was concurrent with a decay in spike-DP.

If late LFP activity reflected attention signals, then we can place constraints on a bottom-up, causal model that links MT spiking activity with detection (Smith et al. 2011). A key assumption of the model is that MT’s noisy representation of the motion pulse was primarily responsible for the trial-to-trial variations in detection performance. If it is given that late beta LFP-DP reflects top-down attention signals in MT, then we can argue that top-down attention was not the major source of sensory noise before detection occurred. However, it may have been a minor source. For example, we observed that spike rates and high-gamma LFPs could weakly predict the subject’s behavior well before the motion pulse began, when the subject responded quickly (Fig. 6, fast RT). Similarly, recent multi-electrode studies found that variation in trial-to-trial estimates of attention in V4 could predict the subject’s perceptual behavior, before neurons responded to the stimulus (Cohen and...
Maunsell 2010, 2011). To see when the effect of RT on the spike-DP dynamics could have resulted from bottom-up processing, we reanalyzed a simulated data set from a purely causal, bottom-up model that explained the stimulus dependence of spike-DP (Smith et al. 2011). The simulations showed that the correlation of RT and spike-DP was well accounted for by the model after the motion pulse, but not before (data not shown). This suggests a small, top-down contribution to the spike- and LFP-DP activity of MT from at least ~200 ms before the coherent motion pulse. It is likely that there was an ongoing interplay between bottom-up and top-down mechanisms.

Previous studies suggest that subjects favor early sensory information when making perceptual decisions (Nienborg and Cumming 2007, 2009) but that visual neurons reach a maximum correlation with the perceptual decision later, if the stimulus duration is long (Dodd et al. 2001; Nienborg and Cumming 2009; Uka and DeAngelis 2004). Taken together with our results, it is likely that there was a sequential activation of perceptual mechanisms (Smith et al. 2012): a bottom-up mechanism during the transient response to the stimulus, followed by a top-down mechanism as neurons settled to a sustained response. Because the subject’s performance on this task was mostly accounted for by a bottom-up model (Smith et al. 2011), it is likely that the perceptual decision was made some time between the activation of the two mechanisms, between the peak in spike-DP 100 ms after the motion pulse began and the peak in beta LFP-DP ~120–160 ms later.

Finally, we found relatively weak LFP neural-behavioral correlations in the lower- to mid-gamma range (~30–50 Hz), which agrees with the results of Liu and Newsome (2006). Changes in this gamma-band power have been the focus of many studies that show it is linked to cortical network function (Fries et al. 2008; Gray and Singer 1989; Gregoriou et al. 2009; Pesaran et al. 2002; Whittington et al. 2011). Recently, increased gamma power has been linked to improved coupling between two visual cortical areas (Jia et al. 2013). Why our neural-behavioral correlations in this range of the gamma band are weak is not known but may be the result of the transition from positive to negative neural-behavioral correlations as one moves from the high-gamma to beta bands, respectively.

Although attention provides a useful explanation of the late LFP-DP dynamics, it should be noted that the experiment was not designed to properly control for attention effects. For example, a change in the animals’ state of arousal from trial to trial might have contributed to the common changes in RT and spike- or high-gamma LFP-DP. However, arousal does not account for the rapid modulations in LFP-DP and LFP-DP_coh later in the trial. Alternatively, these later changes could result from some other top-down signals (Gilbert and Li 2013), like reward expectation or the expected value of the stimulus.

**Contribution of decision or motor signals.** Another possibility could explain the dynamics of LFP-DP near the end of the trial. It bears resemblance to a decision variable in the process of accumulation toward a threshold (Gold and Shadlen 2007; Smith and Ratcliff 2004)—particularly the dynamics of late high-gamma LFP-DP, which varied with the speed of the subject’s response (Fig. 6B). Activity resembling accumulation has been observed in the firing rates of neurons in areas such as LIP (Shadlen and Newsome 2001), and there is evidence of communication between areas MT and LIP during a perceptual task (Saalmann et al. 2007) that might serve to transfer information about the ongoing accumulation of sensory evidence back to MT.

However, the resemblance of beta and high-gamma LFP-DP to accumulators could have been artifactual. If the top-down activity of LFPs was brief and discrete—but always the same time before lever releases—then the analysis window width and the variations in RT would have had a smearing effect on LFP-DP over time, even in a response-aligned analysis (Fig. 12). A different analysis, such as matching pursuit (Ray and Maunsell 2011a) that aims to provide better temporal resolution at all frequencies, could dispel this potential artifact.

On the other hand, MT LFPs may have reflected the upcoming motor response, as the dynamics of LFP power were similar on correct and false-alarm trials (Fig. 11). This is unlikely to have resulted from a preparatory remapping of the RFs in MT, which do not change with eye movements (Hartmann et al. 2011; Inaba and Kawano 2014; Ong and Bisley 2011), but the RF in other areas can shift before eye movements (Duhame et al. 1992). Thus, as LFP activity can resemble the input to an area, late MT LFPs may have reflected the preparatory activity in downstream areas prior to the lever release. Nevertheless, our results suggest that the dynamics of MT LFP-DPs reflect different perceptual signals in the different frequency bands.

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**DISCLOSURES**

No conflicts of interest, financial or otherwise, are declared by the author(s).

**AUTHOR CONTRIBUTIONS**

Author contributions: J.E.T.S., C.A.Z., and E.P.C. conceived and designed the experiments; J.E.T.S. and C.A.Z. performed the experiments; J.E.T.S., V.B., A.S., J.R., C.A.Z., and E.P.C. analyzed the data; J.E.T.S. and E.P.C. interpreted the results of the experiments; J.E.T.S. and C.A.Z. drafted the manuscript; J.E.T.S., V.B., A.S., and J.R. revised the manuscript for important intellectual content.

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