Local Computation of Decision-Relevant Net Sensory Evidence in Parietal Cortex

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To investigate the contribution of parietal cortex to perceptual decisions, we trained monkeys on a perceptual decision task that allowed simultaneous experimental control over how much sensory evidence was provided for each of 3 possible alternative choices and recorded single unit activity and local field potentials (LFPs) from the lateral intraparietal area (LIP). While both the behavior and the spiking activity were largely determined by the difference between how much supporting sensory evidence was provided for a particular choice (pro evidence) and how much sensory evidence was provided for the other alternatives (anti evidence), the LFP reflected roughly the sum of these 2 components. Furthermore, the firing rates showed an earlier influence of the anti evidence than the pro evidence. These observations indicate that LIP does not simply receive already precomputed decision signals but that it plays an active role in computing the decision-relevant net sensory evidence and that this local computation is reflected in the LFP. The results further demonstrate that the competition between the different alternatives cannot solely be mediated by lateral or feedback inhibition, as proposed by a major class of decision models but that feedforward inhibition makes an important contribution.

Keywords: decision mechanism, feedforward inhibition, LIP, local field potential, perceptual decision making

Introduction

Making a decision based on sensory information typically requires multiple decision-relevant sensory evidence signals to be integrated and to be converted into a categorical choice. Previous recordings of neural activity from monkeys performing perceptual decision tasks have revealed several brain areas that carry decision-related activity (Freedman and Assad 2006; Hernandez et al. 2010). One such task that has been studied in great detail is the random-dot motion direction discrimination task. In this task, the monkey has to identify the net direction of motion in a random-dot display and to make a goal-directed eye movement to a target that is associated with the identified direction of motion. One cortical area that has been shown to carry decision-related activity in the context of this task is lateral intraparietal area (LIP) (Shadlen and Newsome 2001; Roitman and Shadlen 2002; Churchland et al. 2008). However, other areas carry similar activity, including (pre)frontal areas (Kim and Shadlen 1999) and the superior colliculus (Horwitz and Newsome 1999). The specific contributions of each of these areas to the decision process are still unknown. Furthermore, while it is generally agreed that integration-to-threshold mechanisms play an important role in the decision process, the actual structure of the decision mechanism and its biophysical implementation are still a matter of debate (Ditterich 2010).

Using a random-dot motion discrimination task that requires subjects to identify the strongest of multiple embedded coherent motion components (Niwa and Ditterich 2008), which provides simultaneous experimental control over how much sensory evidence is provided for each alternative, we simultaneously recorded spiking activity and local field potentials (LFPs) from LIP. Our data provide evidence for parietal association cortex calculating net sensory evidence signals for each alternative through a local combination of multiple decision-relevant sensory evidence signals. This conclusion is based on the observation that both spiking activity and LFPs carry information about the sensory stimulus but in a “nonredundant” way. Whereas the spiking of neurons that are selective for one of the choices reflects the net sensory evidence, that is, the “difference” between the sensory evidence supporting this choice (pro evidence) and the sensory evidence against this choice (anti evidence), the LFPs, recorded from the same electrodes, reflect roughly the “sum” of the pro and anti evidence. This suggests that the decision-relevant sensory signals arrive individually at parietal cortex and are combined into a net evidence signal through a local computation, which is reflected in the LFP. The interpretation that pro and anti evidence arrive independently at LIP is further supported by the observation of a significant delay between pro and anti evidence affecting the firing rate of LIP neurons with, surprisingly, the anti evidence showing an earlier effect. Thus, unlike suggested by a major class of decision models (Usher and McClelland 2001; Wang 2002; Furman and Wang 2008; Albantakis and Deco 2009; Ditterich 2010), the inhibitory effect of the anti evidence cannot solely be mediated through lateral or feedback inhibition, which would require an earlier effect of the excitatory pro evidence. Our results therefore indicate that feedforward inhibition makes a substantial contribution to the competition between different choice alternatives.

Materials and Methods

Animal Preparation and Neural Recordings

Three adult rhesus monkeys (Macaca mulatta) were prepared for chronic recordings of neural signals from LIP. In sterile surgery, under general anesthesia, they received a head implant built from dental acrylic that was attached to the skull using ceramic screws (Thomas Recording, Germany). Embedded into the implant were a head holder and a recording chamber (both made from CILUX; Griss Instrument, Hagerstown, MA) sitting on top of a craniotomy over the right intraparietal sulcus. After implantation, a structural magnetic resonance imaging was obtained from each animal for guiding the physiological recordings. All procedures were approved by the Institutional Animal Care and Use Committee and were in accordance with the US National Institutes of Health Guide for the Care and Use of Laboratory Animals.
A multielectrode drive with 5 independently movable elec trodes (Mini Matrix; electrode impedance: 1–3 MΩ Thomas Recording) was used for obtaining the neural recordings. After being preamplified in the drive, each signal was split and one copy was sent to a Plexon MAP processor (Plexon, Dallas, TX) for spike recordings. The other copy was sent to an amplifier with programmable filters, set to allow signals between 1 and 300 Hz to pass (Alpha Omega, Israel), and digitized with a sampling rate of 1 kHz for LFP recordings. All signals, including time stamps for critical experimental events (see below), were stored by a computer running the Windows operating system (Microsoft, Redmond, WA) and the Plexon RASPUTIN software.

The electrodes were lowered into the lateral bank of the intraparietal sulcus. Single units (SUs) were isolated using Plexon’s Sort Client and matched with a memory-guided saccade task. We recorded only neurons with spatially selective persistent activity during the 1-s memory period of the task. The spike counts during the memory period in response to approximately 50 (more if necessary to reveal the response field [RF] structure) randomly placed saccade targets (spatial range determined by the experimenter to cover the RFs of all isolated neurons) were used to construct RF maps. LFPs were recorded from a sampling rate of 1 kHz for LFP recordings. All signals, including time stamps for critical experimental events (see below), were stored by a computer running the Windows operating system (Microsoft, Redmond, WA) and the Plexon RASPUTIN software.

The monkeys were allowed to watch the stimulus for as long as they wanted before making a decision (up to 5 s, but they always responded well before this time limit). They were trained to make a decision about the direction of the strongest motion component. The answer was provided by making a saccade to 1 of the 3 targets, each of them being associated with the closest direction of motion. The time when leaving the central fixation window was taken as the saccade onset time, and the time difference between this time and the time when the motion stimulus appeared on the screen was registered as the response time (RT). For a valid trial, the eye position had to be within 2° of a target location, not later than 150 ms after leaving the central fixation window, and stay there for at least 250 ms. The monkeys received a fluid reward for choosing the target associated with the strongest motion component. In the case of all 3 coherences being equal, the monkeys were randomly rewarded with a probability of 1/3.

For each session, the locations of the 3 targets, the location of the motion stimulus, as well as the 3 motion directions were chosen such that, if possible, each of the isolated SUs had exactly one of the targets in its RF, the monkey could reliably associate each of the targets with one of the motion directions, and there was no overlap between the RFs of the recorded neurons and the motion stimulus. Thus, across sessions, the motion stimulus was placed at various locations with eccentricities ranging from 0 to 4.2°.

The experiment was controlled by a computer running the QNX operating system (QNX Software Systems, Ottawa, Ontario, Canada) and the REX software (Laboratory of Sensorimotor Research, NEI), which sent information about critical events to the Plexon MAP processor. Graphical stimuli were created by a computer running Mac OS (Apple, Cupertino, CA), MATLAB (MathWorks, Natick, MA), and the Psychophysics Toolbox (Brainard 1997; Pelli 1997) at a frame rate of 75 Hz and displayed on a CRT monitor (ViewSonic P225FB) at a viewing distance of 60 cm.

Data Analysis

Error bars and confidence bands consistently reflect 95% confidence intervals. Confidence intervals for the probabilities of making a particular choice are based on the method proposed by Goodman (1965). The confidence intervals for the mean RTs (MRTs) are based on the standard error of the mean (SEM).

All neural analyses are performed at the population level by pooling trials across experimental sessions. Our results therefore reflect the best possible estimate of the average overall population response together with the associated confidence interval. Firing rate plots were created by counting spikes in 40 ms wide time windows, centered on the indicated time, which were moved in 20 ms steps. Confidence intervals are based on the SEM. For estimating the slope of the firing rate, spikes were counted in nonoverlapping 20-ms bins and linear regression applied.

For isolating the effect of one variable of interest (Veffective), for example, pro coherence, on some measurement (e.g., firing rate) while controlling for another variable (Vcontrol), for example, average anti coherence, that could also affect the measurement, we applied a histogram-matching algorithm. The goal was to compare the measurements from 2 subsets of trials with very different distributions of Veffective but identical distributions of Vcontrol to eliminate the effect of Vcontrol on the measurement. To achieve this on a session-by-session basis, trials were first sorted by Veffective and split into 2 groups of equal size. The histogram of Vcontrol was then calculated for each of the 2 groups (Vcontrol always had a discrete distribution). Subsequently, the count in each of the bins of the first histogram was compared with the count in the corresponding bin of the second histogram. Whenever there was a mismatch, trials contributing to the larger count were randomly removed until the counts were identical. This process
continued until the 2 histograms were identical, leaving 2 groups of trials with a clear difference in \( V_{\text{effect}} \) but no difference in \( V_{\text{control}} \). This procedure ensures that, after pooling across sessions, each group is identical in the number of trials that are contributed by each cell and also in the distribution of \( V_{\text{control}} \) but with a clear difference in \( V_{\text{effect}} \).

When isolating the effects of pro and average anti coherence on firing rate, the 2 required histogram-matching procedures were linked to obtain identical numbers of trials in both cases (for equating the statistical power of the tests used for determining when the firing rates separate; see below) and to make the difference between the means of \( V_{\text{effect}} \) of the larger groups was smaller than the difference between the means of \( V_{\text{effect}} \) of the smaller groups (the goal), a matched pair with the smallest possible difference in \( V_{\text{effect}} \) was removed, resulting in an increased difference. If the current difference between the means of \( V_{\text{effect}} \) of the larger groups was larger than the difference between the means of \( V_{\text{effect}} \) of the smaller groups, a matched pair with the largest possible difference in \( V_{\text{effect}} \) was removed, resulting in a decreased difference.

We performed a residual analysis to determine when firing rates were significantly influenced by pro or average anti coherence. Since LFP neurons can have quite different firing rate response profiles, we first calculated each neuron’s average response profile by collapsing across all trials. This average response profile was subtracted from each trial that had been recorded from this particular neuron, and the remaining residuals were pooled across neurons. These residuals have zero means as long as there is no difference between the neural responses under both compared conditions (e.g., high vs. low pro coherence), but the means deviate from zero as soon as the neural responses separate. \( t \)-tests were used for comparing residuals across conditions as they were roughly normally distributed.

Time-resolved power spectra of the LFPs were created by, on a trial-by-trial basis, taking the LFP signal in a 200-ms wide time window centered on the indicated time, which was moved in 50-ms steps, subtracting its mean to remove the DC component, and calculating the power spectrum using the Chronux toolbox (http://chronux.org. Last accessed: 16 June 2011). Only a single taper was used to maximize the spectral resolution (5 Hz). To be robust against outliers and artifacts, power spectra for a particular experimental condition were calculated as the median power across trials at each time-frequency point.

To determine whether LFP power spectra were significantly different between experimental conditions, a \( P \) value was obtained for each time-frequency point in each difference map by comparing the 2 distributions of powers at this time-frequency point using a Mann–Whitney \( U \) test. Since we wanted to know whether there were any significant differences between any of the analyzed conditions, in any frequency band, and in any time window, we had to correct for multiple testing. To this end, we applied the false discovery rate (FDR) algorithm suggested by Benjamini and Hochberg (1995), which, as Benjamini and Yekutieli (2001) have shown, can also be applied when the individual tests are not statistically independent but positively correlated. This is the case here since neighboring time windows overlap, and the spectral power is calculated at frequencies that are closer than the spectral resolution of the estimation technique. (Note that statistical independence assumptions by individual tests still need to be met.) Since we are comparing 4 experimental conditions, 6 possible pairs of conditions can be formed for direct comparison. Each difference map has 286 time-frequency points, resulting in a total of 1716 tests. To keep the FDR under 0.05, at least one of the \( P \) values has to be smaller than \( \frac{0.05}{286} = 2.9 \cdot 10^{-5} \). The algorithm sorts all \( P \) values in ascending order. If the smallest \( P \) value is less than \( \alpha_{\text{corrected}} \) the corresponding test is marked as significant and the algorithm continues with the second smallest \( P \) value. If this \( P \) value is less than 2 \( \cdot \alpha_{\text{corrected}} \), the corresponding test is marked as significant. If not, the algorithm stops. If the algorithm has not stopped yet, the third smallest \( P \) value is compared with 3 \( \cdot \alpha_{\text{corrected}} \) and so on. Compared with Bonferroni correction, the FDR procedure provides the same Type 1 error rate without, after the null hypothesis has been rejected, being overly conservative when determining which individual tests indicate a significant contribution to the difference between the compared data sets.

To estimate the LFP power in a time-frequency range of interest, the power estimates of all trials at all time-frequency points within the range of interest were pooled and the median of this distribution was calculated. To obtain a confidence interval for this estimate, we applied a bootstrap technique with 1000 repetitions. The smallest 25 and the largest 25 values were removed, and the minimum and the maximum of the remaining 950 values were reported as the 95% confidence interval.

### Selection of Cells

To be included for detailed analysis an SU had to fulfill the following criteria:

1. Exactly one of the targets had to be located inside the mapped RF.
2. Locations eliciting a response of at least 20% of the peak response above baseline (\( FR > \text{baseline} + 0.2 \times (\text{peak-baseline}) \)) during the memory-guided saccade mapping task were defined as inside the RF.
3. No positive response to the onset of the motion stimulus to make sure that the motion stimulus did not overlap with the RF. To this end, the spike count in the last 100 ms before motion stimulus onset was compared with the spike count in the time window from 50 to 150 ms after motion stimulus onset on a trial-by-trial basis. (A positive response to the motion stimulus onset tends to peak around 100 ms after stimulus onset; see Fig. 4) A significantly higher spike count in the later time window (Wilcoxon signed-rank test; \( P < 0.05 \)) led to the exclusion of the cell.

4. Choice selectivity for the target in the RF: The spike count during the last 100 ms before saccade onset had to be significantly larger for trials in which the monkey chose the target in the RF compared with each of the alternatives (Mann–Whitney \( U \) test; \( P < 0.05 \)).

5. If multiple SUs were recorded from the same electrode, they all had to have the same target in the RF. Otherwise we would not have been able to unambiguously determine the motion component providing the pro evidence for the LFP recorded from this electrode. However, it was very rare that neurons that were recorded from the same electrode had different targets in their RFs. In fact, we had only a single occurrence in our data set.

### Criteria 1, 2, and 3 were also applied when analyzing the selectivity of MUA.

For analyzing the choice selectivity of LFP signals, we first determined an LFP choice signature. We did so by, on a session-by-session basis, splitting all trials in 2 groups: target inside the RFs of the isolated SUs chosen versus target outside the RFs of the isolated SUs. To remove any effects of motion coherence, we applied our histogram-matching technique and equated the distributions of the combinations of pro and average anti coherence in both groups. The resulting differences in the LFP power are shown in Supplementary Figure S4 m. White stars mark significant differences according to the FDR algorithm (FDR < 0.05). The plot reveals 3 major differences for frequencies below 50 Hz: higher power at very low frequencies (<10 Hz) but mainly after saccade onset, lower power in the same frequency band that also carries our coherence-driven effect, and higher power in the gamma band, mainly in a frequency band between 30 and 40 Hz and mainly during the last 100 ms before saccade onset. Since the choice selectivity of SUs and MUA was determined on the basis of spike counts during the last 100 ms before saccade onset, we chose this difference in the gamma band for evaluating the choice selectivity of LFPs recorded in individual sessions. To this end, the median power in the time-frequency range of interest (black box in Supplementary Fig. S4 m) was estimated for each trial, and the power distributions for the 3 possible choices were subjected to pairwise comparisons (Mann–Whitney \( U \) test; \( P < 0.05 \)). If the power for choosing the target in the RFs of the isolated SUs was significantly different from the power for not choosing that target, the selection criteria were noted.
larger than each of the powers associated with the other 2 choices, the LFP was said to have the same choice selectivity as the SUs.

For the control analysis of units with part of the motion stimulus in the RF, cells were selected according to the following criteria:

1. The RF map, as obtained from the memory-guided saccade task, had to show an overlap between the motion stimulus and the RF.
2. The spike count in the time window from 50 to 150 ms after motion stimulus onset had to be significantly higher than the one during the last 100 ms before motion stimulus onset (see above).
3. The neuron also had to have exactly one target in its RF (in addition to part of the motion stimulus).

Results

Behavior

Three adult rhesus monkeys were trained to make decisions about the direction of the strongest motion component in a 3-component random-dot stimulus. The directions of the 3 motion components were always separated by 120°, and, on any given trial, a randomly selected proportion of dots moved coherently in the first direction (motion strength or coherence of the first component), a randomly selected proportion moved coherently in the second direction (motion strength of the second component), a randomly selected proportion moved coherently in the third direction (motion strength of the third component), and the remaining dots flickered randomly. The monkeys had control over the viewing duration of the stimulus and terminated its display by making a goal-directed eye movement to 1 of 3 choice targets, each associated with 1 of the 3 motion directions. Thus, the strength of motion in a particular direction controls how much sensory evidence is provided for choosing the associated target. The monkeys received a fluid reward for choosing the target associated with the strongest motion component. If all motion components had identical strength, reward was given randomly with a probability of 1/3. The task design is illustrated in Figure 1a.

Here, we focus on the results obtained from analyzing the pooled data across animals. The Supplementary Material shows that the results that are discussed in the main paper were consistent across animals (Supplementary Figs S1–S3). The average behavior from 44 experimental sessions (21,009 trials), during which the selected neural signals have been recorded, is shown in Figure 1b,c. The distribution of the monkeys’ choices was almost completely determined by a single experimental variable: the difference between the strength of the strongest motion component and the average motion strength of the other 2 components (Fig. 1b). We refer to this variable as target-collapsed net motion strength. The relative frequency of a particular choice as a function of net motion strength is shown in Figure 1b. Circles indicate the proportion of correct choices, squares represent choices of the target associated with the motion component with intermediate strength, and diamonds represent choices of the target associated with the weakest motion component. The color represents the combination of the 2 weaker motion components (see key). For example, the 3 leftmost data points in Figure 1b all correspond to a net motion strength of zero, but they originate from different combinations of coherences: the blue point represents stimuli without any coherent motion, the red point represents stimuli with 10% coherent motion in each of the 3 directions, and the green point represents stimuli with 20% coherent motion in each direction. Accuracy ranged from pure guessing performance (33%; dashed line) for zero net motion strength to almost perfect for 40% net motion strength. Data points for different motion strength combinations (different colors), but identical net motion strength (located in the same gray bar; data points are slightly shifted horizontally to improve visibility), superimpose almost perfectly. To quantify this overlap, we performed an analysis of variance of the relative frequencies of correct choices for net motion strengths of 0%, 10%, and 20%, indicating that net motion strength accounts for 99% of the variance.

Like the distribution of choices, the MRTs (time between appearance of the motion stimulus and saccade onset) were already almost completely determined by target-collapsed net motion strength (Fig. 1c). MRTs ranged from approximately 850 ms for trials with zero net motion strength to approximately 600 ms for trials with 40% net motion strength. An analysis of variance of the MRTs for net motion strengths of 0%, 10%, and 20% indicated that net motion strength accounts for 95% of the variance. Taken together, the monkeys’ behavior, including choices and RTs, was almost completely determined by a single experimental variable: the difference between the coherence of the strongest motion component and the average coherence of the other 2 components, or, in other words, the difference between the sensory evidence for selecting the target associated with the strongest motion component and the average sensory evidence against making this choice.

Spiking Activity in LIP

While the monkeys were performing the decision task, we recorded from 133 SUs in LIP with spatially selective persistent activity during the delay period of a memory-guided saccade task. These are the type of neuron that has been analyzed by Shadlen and colleagues in other versions of the random-dot motion discrimination task (Shadlen and Newsome 2001; Roitman and Shadlen 2002; Churchland et al. 2008). We set up the task geometry such that 1 of the 3 choice targets was located inside the RF of a recorded neuron, whereas the other 2 targets as well as the motion stimulus were located outside the RF. This is not always easy to accomplish, especially when recording from multiple neurons simultaneously, as we often did. To ensure that the analyzed neurons had the intended properties, we defined a set of inclusion criteria: The neuron had to have exactly one of the targets in its RF according to the map obtained during the memory-guided saccade task, the neuron also had to be choice selective for exactly this target during the decision task, and the neuron was not allowed to show a positive response to the onset of the motion stimulus, which would suggest some overlap between the neuron’s RF and the motion stimulus (for further details, see Materials and Methods). Applying these selection criteria left us with a set of 58 neurons for further analysis.

The average response of these neurons time locked to the onset of the saccade (dashed vertical line) to one of the choice targets as a function of whether the monkey chose the target inside the RF (red; 9474 trials) or one of the targets outside the RF (blue; 16,531 trials) is shown in Figure 2a. Like all other neural measures that are presented in this paper, the graph reflects our best possible estimates of the average overall population activity given all available measurements together with the associated 95% confidence intervals. Similar to earlier
studies, the neurons were continuously increasing their firing rate during the last 400 ms prior to a saccade to the target inside the RF, with the activity peaking roughly 40 ms prior to the saccade onset, whereas the firing rate was substantially lower and decreasing during the last 400 ms prior to a saccade to a target outside the RF. Also similar to previous observations, the neurons showed a stereotyped response during the first 200 ms after motion stimulus onset (Fig. 2b) before an effect of the sensory evidence could be observed.

In contrast to previous monkey experiments, we were using a multicomponent motion stimulus, which allowed us to experimentally control sensory evidence in favor of choosing the target inside the RF, the strength of the motion component toward this target (pro coherence), as well as sensory evidence for choosing a target outside the RF, the strengths of the motion components toward these alternative targets (anti coherences). The neural activity in LIP could therefore be influenced by the combination of sensory evidence supporting the target in the RF as well as sensory evidence supporting the other alternatives and, therefore, evidence against choosing the target in the RF. To quantify this effect, we created 4 groups of trials with roughly equal size: 4114 (Hpro/Lanti) trials with high pro coherence (≥20%) and low anti coherences (≤15%), 4055 (Lpro/Lanti) trials with low pro coherence (<20%) and low anti coherences (≤15%), 3574 (Hpro/Hanti) trials with high pro coherence (≥20%) and high anti coherences (≥20%), and 4057 (Lpro/Hanti) trials with low pro coherence (<20%) and high anti coherences (≥15%). The LIP activity between 200 and 400 ms after motion stimulus onset was significantly different for these 4 groups (Fig. 2b). The overall strongest activity was seen for (Hpro/Lanti) trials (red) and the weakest for (Lpro/Hanti) trials (black), with (Lpro/Lanti) trials (green) and (Hpro/Hanti) trials (blue) in between. This suggests that the LIP firing rate is influenced by both the strength of the sensory evidence in favor of choosing the target in the RF (pro coherence) as well as by the sensory evidence against doing so (anti coherences). To further quantify this effect, since the firing rates were roughly linear functions of time during the time window between 250 and 400 ms after motion stimulus onset (shaded area in Fig. 2b), we estimated the slopes of the firing rate functions for all 31 used combinations of coherences (see Materials and Methods).

The estimated firing rate slopes turned out to be approximately a linear function of target-specific net motion strength, the difference between pro coherence and average anti coherence, the mean of both anti coherences (Fig. 2c). Between 497 and 1058 trials were available for estimating each of the 31 slopes. The correlation between the slope and net motion strength is highly significant (P < 0.0001) and the linear function captures 94% of the variance in the slope estimates. Thus, the target-specific equivalent of the variable that captures most of the decision behavior (see Fig. 1b,c) captures most of the variance in the average slope of the LIP firing rate across stimulus conditions. In contrast to the
Figure 2. Firing rate of decision-related neurons in LIP. (a) Average firing rate of 58 neurons with exactly one target in their RF as a function of whether the monkey chose the target in the RF (red) or one of the targets outside the RF (blue), aligned with the time of saccade onset (vertical dashed line). The shaded areas indicate 95% confidence bands. (b) Average firing rate as a function of the combination of the strength of the pro and the anti sensory evidence, aligned with the time of motion stimulus onset (dashed vertical line). After 250 ms, the highest firing rate is observed for trials with high pro evidence and low anti evidence (Hpro/Lanti, red), whereas the lowest firing rate is observed for trials with low pro evidence and high anti evidence (Lpro/Hanti, black). The colored shaded areas indicate 95% confidence bands, the gray shaded area marks the time interval that was used for estimating the slope of the firing rate function. (c) Firing rate slope as a function of target-specific net motion strength, the difference between pro coherence and average anti coherence. The red dashed line shows the linear regression, accounting for 94% of the variance in the data. The error bars again reflect 95% confidence intervals. (d) Isolated effect of pro coherence on firing rate (matched for average anti coherence). The shaded areas indicate 95% confidence bands. (e) Isolated effect of average anti coherence on the deviation of the firing rate from each neuron’s average response profile (matched for pro coherence). The shaded areas indicate 95% confidence bands. (g) Isolated effect of pro coherence on the deviation of the firing rate from each neuron’s average response profile. The gray shaded area as well as the triangles at the bottom mark time bins with a significant difference ($P < 0.05$). The first significant difference is observed 200 ms after motion stimulus onset.

The analysis of behavior where we can collapse across targets since it is only important whether the target associated with the strongest, intermediate, or weakest motion component is chosen, we cannot collapse across targets when analyzing the neural data since LIP neurons are selective for the particular target in their RF.

A linear regression estimating separate coefficients for the impact of pro coherence and average anti coherence on firing rate slope provides a 95% confidence interval of [3.0 ± 3.6] for the pro coherence and [-3.1 ± -2.3] for the average anti coherence, with both individual correlations being significant ($P < 0.05$). Thus, the 2 components of sensory evidence have effects on the firing rate of roughly similar size but "opposite sign": stronger pro evidence increases the slope of the firing rate, whereas stronger anti evidence decreases the slope. A control analysis that will be of relevance later is shown in Figure 2d: the firing rate slope is not well explained by the sum of pro coherence and average anti coherence. The correlation
is only borderline significant ($P = 0.05$) and the linear function captures only 12% of the variance.

A closer look at Figure 2b reveals another interesting feature of the firing rate data: The group formed by the red and the green trace ($H_{pro}^g/\text{anti}^g$ and $I_{pro}^g/\text{anti}^g$) separates from the group formed by the blue and the black trace ($H_{pro}^b/\text{anti}^b$ and $I_{pro}^b/\text{anti}^b$) before red separates from green ($H_{pro}^g/\text{anti}^g$ vs. $I_{pro}^g/\text{anti}^g$) and before blue separates from black ($H_{pro}^b/\text{anti}^b$ vs. $I_{pro}^b/\text{anti}^b$). This seems to suggest that how much evidence there is against choosing the target in the RF might have an earlier effect on the LIP firing rate than how much evidence there is in favor of choosing the target in the RF. To further quantify this phenomenon and to isolate the effects of pro coherence and average anti coherence, we performed a histogram-matching analysis (for details, see Materials and Methods). The idea is to analyze the effect of pro coherence on firing rate, while eliminating the effect of average anti coherence and vice versa. This is achieved by sorting the trials by pro coherence, splitting them into 2 halves with low and high pro coherence and performing a subselection such that the distributions of average anti coherence are identical in both groups.

The isolated effect of the motion component supporting the target in the RF on the LIP firing rate, as a result of this analysis, is shown in Figure 2e. The average pro coherence in the high pro coherence group was 26.5%, the one in the low pro coherence group 6.6% (7321 remaining trials per group). To isolate the effect of the motion components supporting the other alternatives, we sorted the trials by average anti coherence and matched for pro coherence. The result of this analysis is shown in Figure 2f. Each group had again 7321 trials (forced to be identical; see Materials and Methods) and the average anti coherence in the high average anti coherence group was 24.2%. The average anti coherence in the low average anti coherence group was 8.0%. Since a substantial proportion of variability in the pooled data is due to different neurons having different firing rate response profiles, we first removed this systematic variability by calculating each neuron’s average response profile and subtracting it from all trials that had been recorded from this particular neuron (for details, see Materials and Methods). To identify the time when the pro coherence first had a significant effect on the firing rate, we performed an analysis on the residuals (shown in Fig. 2g) and identified the first time bin (with a resolution of 20 ms) where the firing rates were significantly different according to a t-test ($P < 0.05$), with all following time bins up to 400 ms after motion stimulus onset also showing a significant difference. This first time bin was determined to be located at 280 ms after motion stimulus onset. The shaded area in Figure 2g indicates the time range with significantly different firing rates. The first time bin to show a significant difference in the LIP firing rates due to average anti coherence was located at 200 ms after motion stimulus onset (Fig. 2b). Thus, surprisingly, the inhibitory sensory evidence against choosing the target in the RF showed an earlier effect on the LIP firing rate than the excitatory sensory evidence in favor of choosing the target in the RF (by ca. 80 ms).

Local Field Potentials in LIP

In addition to recording the spiking activity of single neurons in LIP, we also recorded the LFPs from the same electrodes. To address the question whether the LFPs also carry information about the sensory evidence and in what way they are modulated by it, we performed a time-resolved spectral analysis. In the following, we will focus on the frequencies below 50 Hz, since the information carried by the higher frequencies seemed largely redundant with the information carried by the firing rate (data not shown). The average power spectrum relative to the time of motion stimulus onset is shown in Figure 3a (15 800 trials). The spectrum essentially shows a fall off in power with both increasing frequency and time. The DC component of the signal was removed before calculating the spectrum, causing the power to also fall off for frequencies near 0 Hz. To test whether the sensory evidence had a significant effect on the power spectrum, we calculated the average spectra for the same 4 groups of trials ($H_{pro}^g/\text{anti}^g$, $I_{pro}^g/\text{anti}^g$, $H_{pro}^b/\text{anti}^b$, and $I_{pro}^b/\text{anti}^b$) that had already been used for analyzing the firing rate in Figure 2b. The motion component that had been determined to support the target in the RFs of the single neurons recorded from the same electrode was also used as the supporting motion component for the LFP analysis. We then calculated the differences between all possible combinations of these 4 spectra. Being agnostic as to what times and frequencies and between which conditions a difference might be expected, we had to take a cautious statistical approach. Each power spectrum is composed of 286 time-frequency points and there are 6 possible combinations of experimental conditions, meaning that a total of 1716 time-frequency points had to be tested for statistical significance. We calculated the individual $P$ values based on Mann–Whitney U tests and then applied the FDR approach proposed by Benjamini and Hochberg (1995). As has been shown by Benjamini and Yekutieli (2001), this approach is still valid when the individual tests are not statistically independent, but positively correlated, which is the case here due to overlapping time windows and the limited spectral resolution of the analysis. To keep the FDR under 0.05, at least one individual $P$ value has to be smaller than $1716 	imes 0.05 / 6 = 2.85 	imes 10^{-5}$.

The differences between the LFP power spectra for the 4 sensory evidence conditions are shown in Figure 3b–g. All significant differences surviving the FDR procedure are marked with white stars. Three of the difference maps (Fig. 3c,d,f) show significant differences between 300 and 400 ms after motion stimulus onset and in a frequency band between 9 and 20 Hz, whereas 3 others (Fig. 3b,e,g) do not. This time-frequency range is marked with black boxes in Figure 3b–g. The interesting observation is that Figure 3g, the difference between the ($H_{pro}^g/\text{anti}^g$) and the ($I_{pro}^g/\text{anti}^g$) conditions, the conditions that showed the largest difference in firing rate, does not show any significant LFP differences in this time-frequency range, whereas Figure 3d, the difference between the ($H_{pro}^b/\text{anti}^b$) and ($I_{pro}^b/\text{anti}^b$) conditions, the conditions that showed the smallest difference in firing rate, does show a clearly significant LFP difference in this time-frequency range. The only significant differences between ($H_{pro}^g/\text{anti}^g$) and ($I_{pro}^g/\text{anti}^g$) are seen late (400 ms after motion stimulus onset) and for frequencies above 44 Hz. This is probably a first manifestation of firing rate-related effects that reliably show up at higher frequencies. However, the lower LFP frequencies apparently also carry information about the sensory evidence signals but in a format that is not redundant with what is coded in the firing rates.

To further quantify the effect of the sensory evidence signals on the LFP, we extracted the average LFP power in the time-
Figure 3. LFPs. (a) Average time-resolved power spectrum, aligned with the time of motion stimulus onset (dashed vertical line). (b–g) Differences between the power spectra associated with different combinations of pro and anti sensory evidence. White stars mark significant differences according to an algorithm proposed by Benjamini and Hochberg (1995), which keeps the FDR under 0.05. The black boxes mark the time-frequency range that was used for estimating the LFP power for the following analysis. (h) LFP power as a function of the sum of pro coherence and average anti coherence. The red dashed line shows the linear regression, accounting for 59% of the variance in the data. The error bars reflect 95% confidence intervals. (i) LFP power as a function of target-specific net motion strength, the difference between pro coherence and average anti coherence. No significant correlation was found between these 2 variables. Error bars again reflect 95% confidence intervals.
frequency range of interest (black boxes in Fig. 3b–g) for all 31 combinations of coherences. The resulting estimates as a function of the sum of pro coherence and average anti coherence are plotted in Figure 3h. As can be seen, the LFP power is well correlated with this sum \( (P < 0.0001) \), with a linear function being able to capture 59% of the observed variance in the power estimates. In contrast, as shown in Figure 3i, the LFP power is not significantly correlated with target-specific net motion strength, the difference between pro coherence and average anti coherence \( (P = 0.21) \), and a linear function would only capture 5% of the observed variance. A linear regression analysis estimating separate coefficients for the pro coherence and the average anti coherence provides a 95% confidence interval of \([-1.3 \ldots -0.5]\) for the pro coherence and \([-1.3 \ldots -0.3]\) for the average anti coherence, with both individual correlations being significant \( (P < 0.05) \). Thus, the 2 components of the sensory evidence have effects of the “same sign” and roughly the same size on the LFP power. This is in stark contrast to what had been observed for the firing rate slopes, which were well explained by target-specific net motion strength but only marginally correlated with the sum of pro coherence and average anti coherence. Thus, whereas the firing rate slopes reflect the difference between the sensory evidence in favor of choosing the target in the RF and the sensory evidence against doing so, the LFP power roughly reflects the sum of the excitatory and inhibitory sensory evidence components.

**Controls for Potential Differences in the Choice Selectivity of the Single Unit and the LFP Data Due to Different Spatial Resolutions**

One concern one might have in interpreting these findings is that the spatial resolution of an SU recording is different from the spatial resolution of an LFP recording (Katzner et al. 2009; Xing et al. 2009; Gawne 2010). Whereas our SUs had a clear choice selectivity for the target in their RF, the recorded LFPs could have potentially been influenced by neurons with different choice selectivity due to their lower spatial selectivity. As the firing rate slopes were a linear function of target-specific net motion strength, we first demonstrated that any weighted average of net motion strength signals associated with different alternatives, which could result from a linear superposition of signals originating from different pools of neurons, could never have the properties of the described LFP effect (for details, see Supplementary Material).

We still have to consider the possibility of other potentially nonlinear interactions of neural signals originating from neurons with different choice selectivity. To address this concern, we have performed a number of control analyses of our LFP data. The details of these analyses can be found in the Supplementary Material. First, in a subset of our experimental sessions (34%), the task geometry was such that only one of the targets was located in the hemisphere contralateral to the cortical hemisphere from which we recorded, whereas the other 2 targets were located in the ipsilateral hemisphere. Since LIP neurons have RFs that mainly cover the contralateral visual hemisphere (Blatt et al. 1990), with such a task geometry, no major subpopulation of LIP neurons in the recorded hemisphere should be selective for a target other than the one in the RFs of the recorded single neurons. Thus, if the pattern of our LFP effect were due to nonlinear interactions between subpopulations of LIP neurons with different choice selectivity, the pattern should change when analyzing only these sessions, but the pattern of results remained unchanged (Supplementary Fig. S4a–f).

The second control was based on analyzing the MUA that was recorded from the same electrode as the SU and LFP data. The idea behind this analysis is that the spatial resolution of the MUA should be more similar to the spatial resolution of the LFP than the spatial resolution of the SU data (Xing et al. 2009). Fifty-nine percent of our recordings had quantifiable MUA with identical selectivity properties as the SU data. Restricting the analysis to only these recordings again did not change the pattern of results (Supplementary Fig. S4g–h).

The third control was based on an attempt to quantify the choice selectivity of the LFP itself. As explained in the Supplementary Material, the power in the low-gamma range just before saccade onset was used to assess the choice selectivity of individual LFP signals (Supplementary Fig. S4m). According to this criterion, 50% of the recorded LFP signals had a choice selectivity that was identical to that of the recorded SUs. Restricting the analysis to only these recordings again did not change the pattern of results (Supplementary Fig. S4n–s).

To summarize, we have performed 3 controls to address the issue of the LFP being less local than our SU recordings and therefore potentially less selective. None of the controls has revealed a substantial change in the pattern of the LFP result, suggesting that our results show a robust and probably relatively local phenomenon.

**Control for a Potential Contribution of LIP Neurons Responding to the Motion Stimulus Itself to the Observed LFP Effect**

We have demonstrated so far that it is unlikely that the observed LFP effect could have resulted from pooling neural signals originating from subpopulations of LIP neurons with different choice selectivity (different target in the RF). However, there are not only LIP neurons with targets in their RFs but also neurons with the motion stimulus in their RFs. If these neurons’ firing rates were modulated by the sum of coherences, we would have to be worried about a possible contamination of the recorded LFP signals. Since we were not always successful in avoiding any overlap between the RFs of the recorded LIP neurons and the motion stimulus, we were able to identify 16 neurons that did not only have a target in their RF, but whose RF, according to the memory-guided saccade mapping, also overlapped with the motion stimulus, and which actually showed a significant increase in their firing rate in response to the motion stimulus onset (for further details, see Materials and Methods). We demonstrate in the Supplementary Material that, while these neurons showed a strong response to the motion stimulus onset, their response was neither significantly modulated by the sum of all coherences (Supplementary Fig. S5a) nor by the sum of pro coherence and average anti coherence (Supplementary Fig. S5c), the variable that strongly modulated the LFP power. Thus, since LIP neurons responding to the motion stimulus are apparently not sensitive to sums of coherences, it is unlikely that they have contributed to the observed LFP modulation by the sum of pro and anti evidence.

Having recorded from neurons with only a target in the RF, as in previous studies, as well as from neurons with part of the...
motion stimulus in the RF allows us to address another question that has been raised on the basis of previous LIP recordings during the random-dot motion direction discrimination task: the origin of the dip in the firing rate of neurons with a target in their RF after motion stimulus onset. An overlay of the average firing rate of neurons with only a target in the RF (solid yellow line) and the average firing rate of neurons with part of the motion stimulus in their RF (dashed yellow line) is shown in Figure 4. The other colors represent the same 4 stimulus conditions as in Figure 2b. The dashed vertical line (110 ms after motion stimulus onset) marks the approximate time of the peak of the response of the neurons being excited by the motion stimulus onset. The lowest firing rate of the neurons with only a target in the RF occurs shortly after this peak, approximately 10 ms later. While this observation does not prove a causal relationship, it is consistent with the possibility that the dip in the firing rate is either caused by lateral inhibition provided by neurons with the motion stimulus in their RF or by a more general normalization mechanism in LIP.

Discussion
In a perceptual decision task that requires the evaluation of multiple components of sensory evidence, we have shown that different neural signals in parietal cortex reflect different combinations of these evidence signals. Changes in firing rate of decision-related LIP neurons were primarily driven by the difference between sensory evidence supporting a particular alternative (pro evidence) and sensory evidence against this alternative (anti evidence). This difference, the "net evidence" in favor of a particular choice, also largely determined the decision behavior. In contrast, LFPs in the 10–20 Hz band reflect particular combinations of pro and anti coherence (see Fig. 2a). Shaded areas reflect 95% confidence bands. The dashed vertical line marks the approximate time of the peak of the response of neurons with part of the motion stimulus in the RF. This peak is closely followed by the lowest firing rate of the neurons with only a target in the RF approximately 10 ms later.

Figure 4. Overlay of the firing rate of neurons with only a target in the RF (solid lines) and the firing rate of neurons with part of the motion stimulus in the RF (dashed lines). The yellow lines reflect the average activity across stimuli, the other colors reflect particular combinations of pro and anti coherence (see Fig. 2b). Shaded areas reflect 95% confidence bands. The dashed vertical line marks the approximate time of the peak of the response of neurons with part of the motion stimulus in the RF. This peak is closely followed by the lowest firing rate of the neurons with only a target in the RF approximately 10 ms later.

Implications for the Decision Mechanism
While it is generally agreed that perceptual decision making involves integration of sensory evidence to a decision threshold, models of the decision process disagree considerably how such a mechanism is implemented. One of these aspects is how the competition between the different choice alternatives, each of them being represented by an associated decision pool, is mediated. On one extreme, there are models that assume that this competition is solely mediated by feedforward inhibition: individual sensory evidence signals excite one pool of decision neurons and inhibit the remaining pools of decision neurons; the decision pools themselves do not interact (Mazurek et al. 2003; Ditterich 2006; Niwa and Ditterich 2008). Such a model has been shown to be able to account for human decision behavior in the same task as the one that has been studied here (Niwa and Ditterich 2008) and is illustrated in the Supplementary Figure S6a. The key feature of such a model is that an increase in the sensory evidence for one particular direction leads to an immediate increase in the input signal to its associated decision pool and to an immediate decrease of the input signals to the competing decision pools.

On the other extreme, there are models that assume that the competition between choice alternatives is solely mediated by lateral or feedback inhibition: individual sensory evidence signals excite only one pool of decision neurons; the decision pools interact by inhibiting each other (Usher and McClelland 2001; Wang 2002; Furman and Wang 2008; Albantakis and Deco 2009; Ditterich 2010). Such a model has also been shown to be able to account for human decision behavior in the same task as the one that has been studied here (Ditterich 2010) and is also depicted in the Supplementary Figure S6b. The chain of action in this class of models is very different from what we have discussed above. Initially, an increase in the sensory evidence for one particular direction leads only to an increase of the input signal to its associated decision pool. The input signals to the competing decision pools are unchanged. It is only the increased activity of the supported decision pool due to its increased input that, via the feedback inhibition, leads to reduced input signals to the competing decision pools. Thus, the inhibitory action of the anti evidence is a consequence of the excitatory action of the pro evidence.

The timing of events in our LIP recordings is inconsistent with such a view. Surprisingly, the strength of the inhibitory (anti) sensory evidence showed an earlier impact on the LIP firing rate than the strength of the excitatory (pro) sensory evidence. Thus, a change in the strength of the inhibition cannot have resulted from a change in the firing rate of decision-related neurons due to excitatory sensory evidence. This observation indicates the presence of a feedforward inhibition component that is driven by sensory evidence, and mechanisms that solely rely on lateral/feedback inhibition can be ruled out. However, it does not rule out the presence of feedback inhibition. In fact, the observation that the dip in the firing rate of decision-related neurons with a target in their RF
follows shortly after the peak in the firing rate of neurons with the motion stimulus in their RF suggests the presence of lateral/feedback inhibition in the circuitry, which could also be present between pools of neurons with different targets in their RFs. Thus, we have to consider the possibility of a hybrid mechanism involving both feedforward as well as feedback inhibition for mediating the competition between the alternatives. A decision mechanism that would be consistent with our experimental observations is illustrated in Figure 5. It relies on feedforward inhibition (dashed colored arrows pointing to the right) but does not rule out the presence of feedback inhibition (dashed colored arrows pointing to the left).

Why Does the Inhibitory Sensory Evidence Show an Earlier Impact on the Firing Rate?

We have just discussed that the inhibitory evidence showing an earlier effect on the firing rate of decision-related neurons rules out the possibility that the inhibition is only driven by the activity of the decision pools, but why is the inhibition able to act earlier? One could think of 2 possible answers: either the inhibitory evidence arrives indeed earlier at parietal cortex or the pro and the anti evidence arrive at roughly the same time, but the effect of the excitatory evidence is delayed or transiently masked. Both of these alternatives seem puzzling at first. If both components were mediated by similar pathways, one would expect them to arrive at similar times or, perhaps, the inhibitory component slightly delayed because it has to pass through inhibitory interneurons. In principle, such a delay could be compensated by stronger synaptic efficacy in the inhibitory pathway. Consistent with this, the delayed effects of excitation have been reported in a mouse somatosensory cortex preparation (Cruikshank et al. 2007). However, the reported delays are in the single millisecond range and therefore at least an order of magnitude smaller than the delay of approximately 80 ms reported here.

While our data cannot provide a definitive answer to the question “why” the excitatory effect of the pro evidence is delayed and future work is clearly necessary to address this issue, there is weak evidence that the excitation might transiently be masked by feedforward inhibition that is also driven by the pro evidence. A transient inhibitory effect of the pro coherence approximately 180 ms after motion stimulus onset is suggested by Figure 2e (red line below blue line; the t-tests at 160 and 180 ms after motion stimulus onset have P values of 0.04 and 0.01, respectively). Consistent with this, the red line in Figure 2b transiently drops below the green line before crossing back approximately 250 ms after motion stimulus onset. Likewise, the blue line transiently drops below the black line before crossing back at roughly the same time. This phenomenon has some similarities with lagged cells in the lateral geniculate nucleus, which were originally described in the anesthetized cat (Mastronarde 1987; Saul and Humphrey 1990) and later also in the awake monkey (Saul 2008b). The delayed response of the lagged cells is believed to be caused by feedforward inhibition in combination with a slow-acting excitation mechanism, potentially mediated via NMDA receptors (Heggelund and Hartveit 1990; Saul 2008a). As a side note, this could have interesting implications for the implementation of the temporal integration mechanism. Whereas Wang (2002) decision model relies on NMDA-mediated excitatory recurrent feedback for temporal integration, the sensory inputs are mediated via faster AMPA receptors. A major contribution of an NMDA pathway to mediating the sensory evidence would raise

Figure 5. Potential decision mechanism and the role of LIP. A decision mechanism that would be consistent with our data. LIP receives independent sensory evidence signals providing information about the strength of motion in each direction. The broken colored lines indicate that these signals do not necessarily have to be provided directly by extrastriate visual areas. LIP combines these signals into net evidence signals through local computations, which are reflected in the LFP (left purple electrode), involving feedforward inhibition for incorporating the anti evidence. The Δt boxes indicate the delayed effect of the (excitatory) pro evidence compared with the (inhibitory) anti evidence. The diagram further indicates the possibility of a feedforward inhibitory effect of the pro evidence, which shows up transiently before the delayed excitation kicks in. Due to the limited space, it is only drawn for the red signal but should be there for the green and blue signals as well. The diagram also indicates the potential presence of lateral/feedback inhibition as suggested by the temporal alignment of the motion stimulus onset response and the dip in the FR of decision-related neurons (see Fig. 4).
the question to what extent such a mechanism, due to its relatively long time constant, would already be able to account for temporal integration of the sensory evidence.

The delayed effect of the feedforward excitation is illustrated in Figure 5 with the ”At” boxes. The possibility of the pro evidence not only causing feedforward excitation but also feedforward inhibition is indicated by the dashed red arrow pointing to the summation point for the first net evidence signal. Due to the limited space, this arrow has been omitted from the second and third net evidence signals.

**Is the Observed Modulation a Local Property of the LFP Signal?**

In addition to the spiking activity that we have discussed so far, we have also recorded LFPs from LIP. Rather than being modulated by the difference between pro and anti evidence like the firing rates, the LFPs were modulated by roughly the sum of pro and anti evidence. This raises the question whether we have recorded 2 local neural signals with different properties or whether the LFP has different properties because it is not a local signal but rather the result of a superposition of signals originating from subpopulations of neurons with quite different properties. There is still uncertainty about the spatial spread of the LFP. Estimates range from a few hundred microns to a few millimeters (Katzner et al. 2009; Xing et al. 2009). We were therefore concerned that the observed modulation of the LFP might have originated from contributions by or interactions with nonlocal populations of neurons with either different choice selectivity or with the motion stimulus in their RF. However, none of our controls for narrowing down the choice selectivity, one based on the task geometry, one based on the selectivity of the multiunit (MU) activity, and one based on the choice selectivity of the LFP itself, led to a substantial change in the LFP results, and the response of neurons with the motion stimulus in their RF proved not to be significantly modulated by sums of coherences. Thus, it appears that the observed modulation of the LFP power by the sum of pro and average anti coherence is a robust and relatively local phenomenon. This is consistent with recent comparisons between the selectivity of SU, MU, and LFP recordings for visual stimulus parameters, which suggest that the tuning properties of the different signals are more similar than one might expect based on the larger estimates of the spatial spread of the LFP, suggesting a substantial local contribution (Liu and Newsome 2006; Katzner et al. 2009; Xing et al. 2009; Gawne 2010).

**Implications for the Role of Parietal Cortex in Perceptual Decision Making**

Previous recordings from parietal cortex during perceptual decision tasks had shown decision-related neural activity (Shadlen and Newsome 2001; Roitman and Shadlen 2002; Freedman and Assad 2006; Churchland et al. 2008). Furthermore, microstimulation in parietal cortex during a perceptual decision task had demonstrated that parietal cortex is part of the causal chain determining the choice (Hanks et al. 2006). However, the specific contributions of parietal cortex to the decision process are still unclear.

In contrast to previous decision tasks, we have used a design that allowed us to simultaneously control how much sensory evidence is provided for each of the alternatives the monkey could choose from. This allowed us to reveal neural signatures of these evidence signals being combined. Just like the behavior, changes in the firing rate of decision-related LIP neurons were primarily driven by the net sensory evidence, the difference between pro and anti evidence. This relationship was remarkably linear, meaning that the individual sensory evidence signals carried by the firing rate of direction-tuned motion-responsive neurons in extrastriate visual cortex have to be roughly a linear function of motion coherence (Britten et al. 1993) and that these individual evidence signals are combined roughly linearly. LIP neurons must have access to the resulting net evidence signals, since this is what is reflected in their firing rate. These net evidence signals could either be computed locally or they could be computed elsewhere and then sent to LIP. In the following, we will explain why our results argue for the net sensory evidence signals being computed locally in LIP rather than LIP just performing a passive readout of net evidence signals that have been computed elsewhere.

The LFPs, recorded from the same electrodes as the SUs, showed a modulation in the 10–20 Hz band, which roughly reflected the sum of pro and anti evidence rather than the difference. In the previous section, we have discussed why such a signal is unlikely to result from an interaction of multiple subpopulations of LIP neurons with different choice selectivity or from contributions of an LIP subpopulation that is directly driven by the motion stimulus. Thus, if the net evidence signals were computed elsewhere and sent to LIP, the resulting excitatory drive should also be reflected in the LFP, meaning that it should also be modulated by the difference between pro and anti evidence. This, however, was not the case. Two such hypothetical situations that can be ruled out based on our data are illustrated in the Supplementary Figure S6a.

In contrast, if LIP had access to the individual sensory evidence signals as they are carried by different subpopulations of MT or MST neurons with different preferred directions (Salzman et al. 1992; Celebrini and Newsome 1995; Ditterich et al. 2003), the net sensory evidence signals could be computed locally by, in our case, having one of the individual evidence signals excite a particular subpopulation of LIP neurons and the other 2 inhibit the same subpopulation. Why, then, would LIP also compute a signal that reflects the sum of individual evidence signals as reflected in the LFPs? We believe that the LFPs are a by-product of the local computation of net evidence signals. We will return to this issue in the section Implications for interpreting the LFP. The view that individual sensory evidence signals arrive independently at LIP is further supported by our observation of a substantial delay between pro and anti evidence affecting the firing rate. If LIP simply performed a readout of already precomputed net evidence signals such a delay would not be expected.

The most likely explanation for our findings is therefore that LIP performs local computations to obtain the decision-relevant net sensory evidence signals. This view assigns parietal cortex a relatively early position in the processing chain, right after the representation of the sensory evidence. The expected entry point to LIP is illustrated by the dotted line in Figure 5. However, the firing rate of decision-related LIP neurons does not directly reflect the net evidence signal, but a signal resulting from integrating such a net evidence signal over time, as it is the change in the firing rate or the slope that is determined by the net evidence. This is indicated by the right
purple arrow in Figure 5. Thus, LIP also reflects the result of the integration process, which makes it likely that it is also actively involved in accumulating the sensory evidence.

Implications for Interpreting the LFP

There is still considerable debate about what the LFP actually reflects. Up to this point in the paper, we have made an argument that was solely dependent on the observation that a particular frequency band of the LFP was modulated by the sum of different sensory evidence components but did not rely on any particular interpretation of the LFP. Further pursuing the idea that LIP might compute the required net evidence signals locally, could the observed LFP modulation simply be a by-product of this local computation? It has been suggested that the LFP is strongly influenced by dendritic activation and therefore reflects mainly input to a cortical area (Mitzdorf 1985; Scherberger et al. 2005; Einevoll et al. 2007; Khawaja et al. 2009). In our case, to compute the net evidence signal locally, excitatory pro evidence as well as inhibitory anti evidence would have to arrive in LIP. We have seen that an increase in the strength of either component caused a reduction in the LFP power in the 10–20 Hz band. Thus, if this signal reflected the overall dendritic activation of a local pool of neurons, regardless of whether the input is excitatory or inhibitory, an LFP signal reflecting the sum of the evidence components could result from a local calculation of the difference between pro and anti evidence. This is indicated by the shaded area and the left purple arrow in Figure 5. How do the observed frequency, the reduction of LFP power with stronger sensory evidence, as well as the idea of an additive effect of excitation and inhibition relate to the existing LFP literature?

We have observed a modulation that was centered on a frequency of 14–15 Hz. Pesaran et al. (2008) reported a peak in coherence at the same frequency when analyzing activity in premotor cortex and parietal reach region during a free choice task. According to the electroencephalography (EEG) literature, this frequency is thought of as being close to the lower "boundary" of the beta band (Shackman et al. 2010). There is still considerable debate about what activity in the beta band reflects, but it has been suggested that, in contrast to gamma rhythms, which are thought to originate from the more superficial layers of cortex, beta rhythms are generated in the deeper layers (Wang 2010). Since cortical bottom-up projections arise from the more superficial layers, whereas top-down projections arise from the deeper layers, some authors have linked gamma activity to bottom-up input and beta activity to top-down input (Wang 2010). LIP receives input from a variety of other cortical areas. Among those are extrastriate visual areas like, for example, MT but also frontal areas like the frontal eye field or lateral prefrontal cortex (Cavada and Goldman-Rakic 1989; Blatt et al. 1990; Lewis and Van Essen 2000). It has been shown anatomically that the input from extrastriate visual areas is of the "bottom-up" type, whereas input from frontal areas is of the "top-down" type (Andersen et al. 1990; Neal et al. 1990). Thus, the observed LFP activity in LIP that is modulated by the sensory evidence could potentially be driven by these inputs from frontal areas. It would be an interesting thought to consider that the individual sensory evidence signals are not provided by direct inputs from area MT or MST but are routed through frontal areas first. This could explain why the sensory evidence does not have a major impact on the LIP firing rate until approximately 200 ms after motion stimulus onset, whereas areas MT and MST carry reliable signals about the strength and direction of motion already approximately 100 ms after motion stimulus onset. The broken lines in Figure 5 between pools of MT neurons and LIP illustrate the possibility of these signals being provided by routes other than a direct feedforward connection. However, we clearly need a much better understanding of the generation of cortical LFPs before we are able to pinpoint the origin of our recorded signal.

It might at first seem surprising that we have observed a reduction in LFP power with stronger pro or anti evidence rather than an increase. However, in contrast to LFP power in the gamma band, which tends to increase with stronger sensory stimulation, the power at lower frequencies tends to be reduced by stronger stimulation, which has been observed in both EEG (Pfurtscheller and Lopes da Silva 1999; Bauer et al. 2006) and LFP recordings (Ray et al. 2008; Zhang et al. 2008). It is generally thought that the suppression of power at low frequencies is a consequence of cortical activation causing a desynchronization of low-frequency synchronous activity in an "idling" state (Pfurtscheller and Lopes da Silva 1999). Based on our data, we would have to postulate that both excitatory and inhibitory input cause such a desynchronization. To our knowledge, the specific contributions of excitation and inhibition to the desynchronization of LFPs have not been addressed in the literature. However, regarding the contributions of excitation and inhibition to the active generation of field potentials, there is mounting evidence that excitatory and inhibitory dendritic events can have similar effects (Ellender and Paulsen 2010). Consequently, Mazzoni et al. (2008) modeled the LFP as being driven by the sum of the absolute excitatory and inhibitory currents and were very successful in explaining LFP recordings from primary visual cortex. Thus, it seems reasonable that LFPs can reflect the sum of excitatory and inhibitory input.

In summary, our findings show that the observed LFP modulation in parietal cortex during perceptual decision making reflects a local computation of net sensory evidence for a particular choice alternative (see also Rainer [2008] for a discussion of the idea that simultaneous recordings of spikes and LFPs provide information about local processing). This net evidence signal is generated by combining excitatory evidence supporting a particular choice with inhibitory evidence against doing so. These individual evidence signals arrive independently at parietal cortex, which is also supported by the observation of a significant delay between when the firing rate of decision-related neurons is first reliably modulated by each of the evidence components. Since the inhibitory component showed an earlier effect than the excitatory component, it cannot exclusively be mediated by lateral or feedback inhibition, which has important consequences for the structure of the decision circuitry, namely the presence of feedforward inhibition that is driven by sensory input.

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Supplementary Material
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References


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