# Report

# Phase-of-Firing Coding of Natural Visual Stimuli in Primary Visual Cortex

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## Summary

We investigated the hypothesis that neurons encode rich naturalistic stimuli in terms of their spike times relative to the phase of ongoing network fluctuations rather than only in terms of their spike count. We recorded local field potentials (LFPs) and multiunit spikes from the primary visual cortex of anaesthetized macaques while binocularly presenting a color movie. We found that both the spike counts and the low-frequency LFP phase were reliably modulated by the movie and thus conveyed information about it. Moreover, movie periods eliciting higher firing rates also elicited a higher reliability of LFP phase across trials. To establish whether the LFP phase at which spikes were emitted conveyed visual information that could not be extracted by spike rates alone, we compared the Shannon information about the movie carried by spike counts to that carried by the phase of firing. We found that at low LFP frequencies, the phase of firing conveyed 54% additional information beyond that conveyed by spike counts. The extra information available in the phase of firing was crucial for the disambiguation between stimuli eliciting high spike rates of similar magnitude.

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Thus, phase coding may allow primary cortical neurons to represent several effective stimuli in an easily decodable format.

## Results

The most established hypothesis on how sensory information is represented in the brain is the spike-count-coding hypothesis [1], which suggests that neurons represent information by the number of spikes discharged over some relevant time window. However, the timing of spikes may add important information to that already carried by spike counts [2–9]. In particular, information may be encoded in the spike times relative to the phase of some concurrent network oscillation [2, 10–13]: This is called phase-of-firing coding. In this report, we investigated which of these coding strategies is used by the primary visual cortex (V1) during the presentation of rich naturalistic visual stimuli.

### Spike and LFP Responses to Natural Movies

We recorded neural signals with an array of extracellular electrodes from primary visual cortex of four anaesthetized macaques in response to a binocularly presented 3.5- to 6-min-long natural color movie. Each recording site corresponded to a well-defined V1 visual receptive field within the field of movie projection. From each electrode, we measured both spiking activity and local field potentials (LFPs). Spikes were detected by threshold-crossing of the 500–3500 Hz band-passed neural signal and represented the spiking activity of a small population of cells (i.e., multiunit activity) rather than well-separated spikes from a single neuron. LFPs, which were recorded as the 1–250 Hz band-passed neural signal, reflect the fluctuations in the input and the intracortical processing of the local cortical network, including the overall effect of population synaptic potentials [14, 15] and other types of slow activity, such as spike afterpotentials and voltage-dependent membrane oscillations [16–19]. We repeated each movie 12–40 times in order to sample the probability distribution of the neural responses to each part of the film. We obtained a dataset of 78 V1 recordings channels recorded during stimulation with a movie. Unless otherwise stated, we focused on the relationship between LFPs and multiunit spikes recorded from the same electrode.

Figure 1 reports responses recorded from one example recording site (electrode 2 in monkey A98) over repeated presentations of the same movie fragment. The presentation of the movie elicited patterns of spikes that were modulated over time in a reliable manner across trials (Figure 1D). As a consequence, and as summarized by the trial-averaged instantaneous spike rate (Figure 1F), some movie scenes elicited a high and reliable firing rate, and some other scenes elicited instead a low (but still reliable) firing rate. Thus, counting the number of spikes emitted within some time interval reduces the observer's uncertainty about which movie scene was being presented. This illustrates that spike counts encode movie scenes.

As for the spiking activity, the waveform of LFPs in single trials (Figure 1A) showed fluctuations that were reliable across
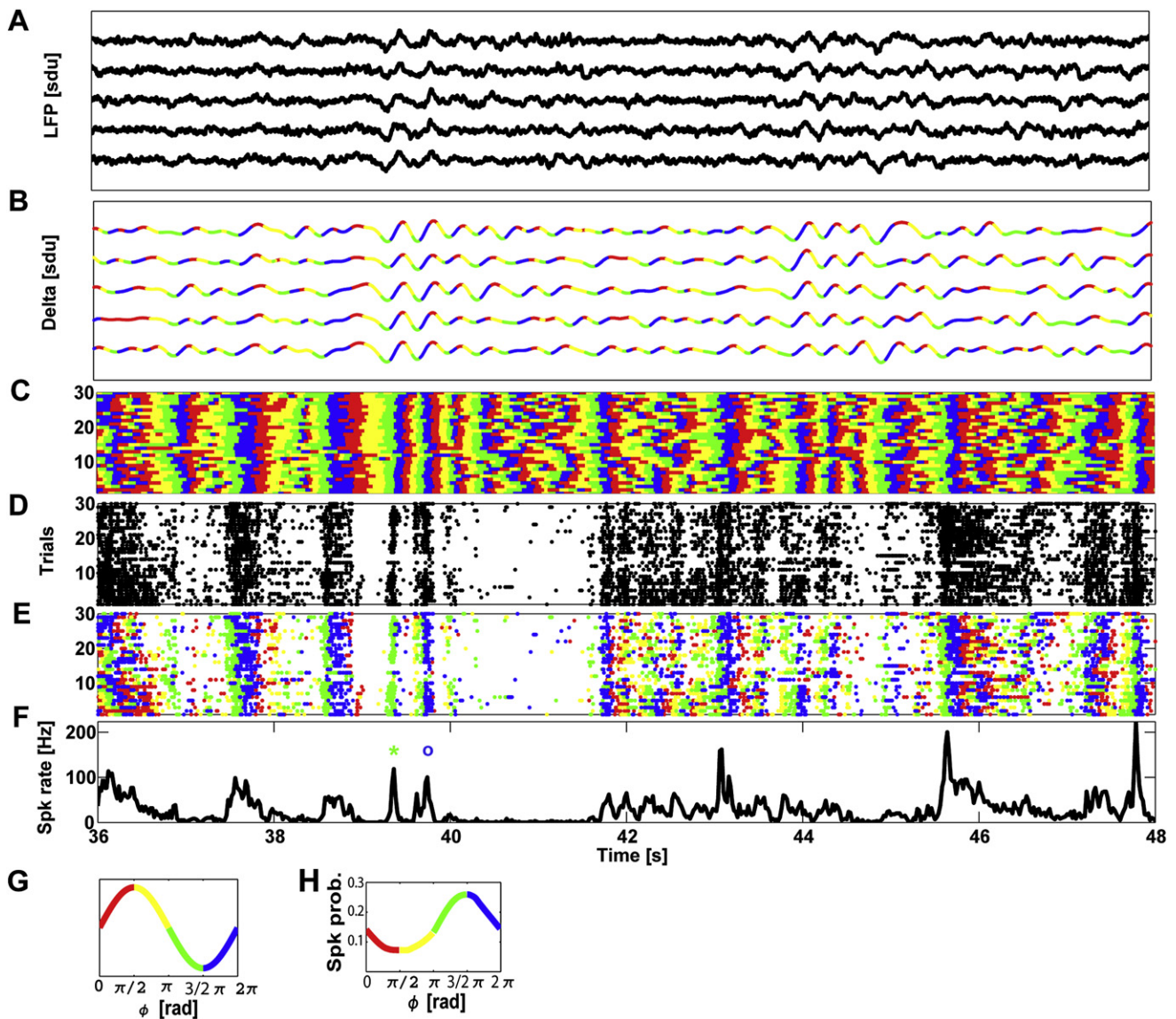
Figure 1. Illustration of the Time Course of the LFP Phase and of the Spikes, and of the Difference between the Spike Count and Phase-of-Firing Code

These data were recorded from electrode 2 in monkey A98 in response to a movie.

(A) LFP traces from five presentations of a 12-s-long movie extract. Traces were displaced on the vertical axis so that they could be made distinguishable.

(B) Time courses of the 1–4Hz (delta band) band-passed LFP to five presentations of the same 12-s-long movie extract as in (A). Traces were again displaced on the vertical axis. The color of the line at each time denotes to which of the four phase quadrants the instantaneous LFP phase belongs to (the color code for phase quadrants is shown in [G] and [H]).

(C) Time course of the phases of the 1–4Hz (delta) LFP over 30 repetitions of the movie extract. Phase values were color coded into quadrants as illustrated in (G). The bottom five trials in (C)–(E) correspond to the five trials in (A)–(B).

(D) Raster plot of spike times (indicated by dots) resulting from 30 repeated presentations of the selected 12 s movie extract.

(E) Raster plot of the same spike times as in (D) but with the dots representing the spikes color coded according to the 1–4Hz LFP phase quadrant at which they were emitted. These colored spike times illustrate the phase-of-firing code, whereas the colorless spike times in (D) illustrate the spike-count code.

(F) Spike rate, averaged over all 30 trials and computed in 4-ms-long sliding time bins, during the 12 s movie extract. The green star and the blue circle indicate movie points that elicit similar spike rate responses but different and reliable phase values. These two movie points can be much better discriminated from each other by consideration of the phase at which spikes were emitted rather than just the counting of spikes.

(G) The sinusoidal convention used for phase, plotted with the color code chosen to label phase quadrants. With this sinusoidal convention, the phase values $\pi/2$ and $3\pi/2$ correspond respectively to the peak and trough of the oscillation.

(H) The probability distribution of the LFP phases at spike times. The curve (plotted with the same color code as in [G]) is normalized as probability per unit angle (its integral across all angles equals one).

trials and modulated by the movie. During movie presentation, the power of the LFP spectrum was highest at low frequencies (<4 Hz) and then dropped with increasing frequency (Figure S1 available online). We thus started by considering the behavior of the phase of LFPs fluctuations in the highest-power band,

namely the 1–4 Hz frequency range (delta band). The single-trial 1–4 Hz band-passed LFP traces during movie presentation (Figure 1B) show that 1–4 Hz LFPs too were reliably modulated by the movie. To extract the instantaneous value of the phase of the LFP fluctuations in each trial and at each time

during the movie, we first computed the Hilbert transform of the band-passed traces in each trial, and we then computed the phase as the argument of the Hilbert transform (the resulting phase convention is plotted in Figure 1G).

To visualize how LFP phases were modulated by the movie, we divided the phase range into four equispaced quadrants and labeled each with a different color (Figure 1G). It was apparent that the 1–4 Hz LFP also encoded the movie, because the phase values were modulated by the movie time, and this modulation was extremely reliable across trials at several times during the movie (Figure 1C).

Moreover, there was a correspondence between spike rate (Figure 1F) and across-trial reliability of phase (Figure 1C): Scenes eliciting a high spike rate also elicited a highly repeatable phase. The distribution of 1–4 Hz LFP phases at spike times from this example channel during the presentation of the movie (Figure 1F) was nonuniform (Rayleigh test of nonuniform angular distribution [20], p < 0.01): The probability of spiking at the preferred phase ($3\pi/2$ rad) was twice the probability of spiking at the antipreferred phase ($\pi/2$ rad). The phase values around the preferred one for firing (coded as green and blue in Figure 1) appeared to be the ones encoding the movie more reliably during periods of firing (Figure 1C).

Because both spikes and LFP phases carry information about the movie, and because phases are particularly reliable in the presence of spikes, it is possible that, in addition to encoding information by spike count, neurons may encode extra information about the movie by the phase at which they fire. This hypothesis means that if we label the spikes with a color (as in Figure 1E) reporting the phase quadrant at which they were emitted (the phase-of-firing code), we can predict better which visual feature elicited the firing than if we just count the colorless spikes expressing the spike count code (Figure 1D). Figure 1F illustrates how phase may play a role in representing information about the visual scenes. Two scenes of the movie eliciting comparable firing rates (e.g., those occurring at times marked respectively by a green star and blue circle in Figure 1F) could not be discriminated by their colorless spike count (Figure 1D) but could be discriminated when their phase label was taken into account (green versus blue colored spikes in Figure 1E). The exact extent to which knowledge of the phase of firing helps stimulus discrimination will be determined below with information theory.

### LFP-Phase Reliability and Spike-Phase Relationships
Having illustrated the phase-of-firing coding with an example recording channel and a selected LFP-frequency range, we next characterized the behavior of the entire dataset over a wide range of LFP frequencies. To do so, we divided the LFP-frequency range into small frequency intervals (1–4 Hz; 4–8 Hz; and up to 124 Hz in 4-Hz-wide nonoverlapping intervals). We then computed band-passed LFPs in each such frequency interval, from which we extracted the instantaneous band-passed phase during the course of the movie.

A first fundamental condition for phase coding is that LFP phases are reliable and repeatable across different trials at fixed sensory input (i.e., at fixed time during the movie). We investigated phase reliability by computing the circular variance across trials of the phase at each time during the movie. Circular variance is a measure of angular dispersion (defined in [20] and in the Supplemental Data), and its values range from 0 (perfect reproducibility across trials) to 1 (total unreliability). To be useful for phase-of-firing stimulus coding, the reliable phase values must be observed during periods of firing: If the reliable
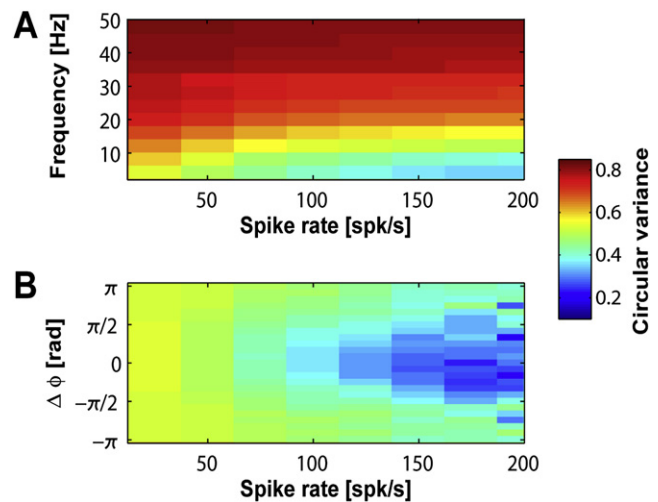


Figure 2. Phase Reliability of V1 LFPs under Natural Visual Stimulation

(A) The circular variance across trials at fixed time window of the phase of LFPs band passed in a given frequency range is plotted as function of the spike rate in the corresponding window. Results were averaged over all channels and time windows.

(B) The circular variance across trials of the phase of 1–4 Hz LFPs is plotted as function of the trial-averaged spike rate in the same window and of the angular distance $\Delta\Phi$ between the trial-averaged phase in the same time window and the channel's preferred phase. Results were averaged over all channels and time windows.

phases occur during silence, their information cannot be used to tag the spikes. Thus, in Figure 2A we examined how the circular variance of the LFP phase depends upon the spike rate observed in the same window. Figure 2A shows that, in the high-frequency LFP regions (>50 Hz), the circular variance is very high (population average: approximately 0.85) across all spike-rate levels. Thus, the phase in the high-LFP-frequency range is not reliable enough to support stimulus discrimination. In contrast, and for all spike-rate values, phase was far more reliable in the low LFP-frequency bands. In the LFP-frequency regions below 12 Hz, movie segments eliciting high firing rates also elicited substantially more reliable LFP phases: On average across the dataset, the circular variance across trials of the 1–4 Hz LFP phase was approximately 0.5 in low-spike-rate windows (<25 spk/s) and approximately 0.3 in high-spike-rate windows (>150 spk/s). A circular variance of 0.3 would be that achieved by a phase distributed uniformly over a $0.65\pi$-wide interval. This suggests that, in order to extract information from the phase of firing, we need to measure phases with a precision of approximately $\pi/2$ (i.e., a quarter of a phase cycle). A very similar dependence of phase reliability on rate was obtained with 4–8 Hz and 8–12 Hz phases (data not shown). The increase of phase reliability with firing strongly suggests that the role of phase-related spike times may be to discriminate between stimuli each eliciting similarly high spike rates.

A second crucial requirement for phase coding is that the different movie time windows elicit diverse reliable phase responses. For example, in Figure 1, we observed that several movie scenes elicited a reliable phase in the green-coded range, and other different movie scenes elicited a reliable phase in the blue-coded range; it is the color difference in the reliably colored phase ranges that makes it possible for us to use phase to tag successfully different movie parts. We found that the results obtained for the example channel
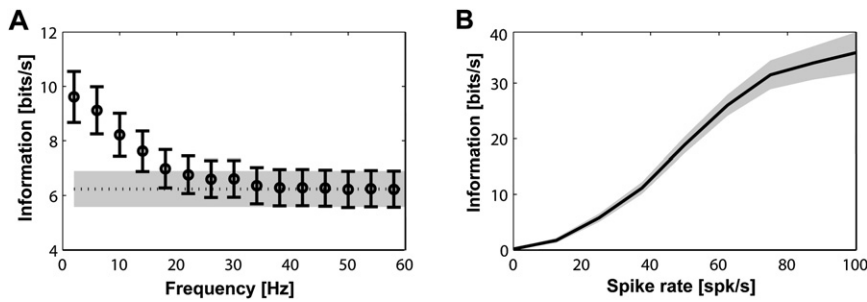
Figure 3. The Information about the Movie Conveyed by Spike Counts and by the Phase of Firing

(A) Black dots plot the information carried by the LFP phase at which spikes were emitted as function of the considered LFP frequency (mean ± SEM over the dataset). The black dashed line plots the mean over the dataset of the spike count information (SEM over dataset indicated as gray area).

(B) The information carried by the 1–4 Hz LFP phase of firing about movie scenes eliciting exactly the same spike rate is plotted as function of the elicited spike rate (mean ± SEM across the population are reported as full line and shaded area, respectively). For the purpose of plotting the line in Figure 3B, the phase-of-firing information about movie scenes eliciting exactly the same spike rate was averaged over 10-spk/s-wide spike-rate bins.

plotted in Figure 1 extended to the whole dataset. In particular, for the vast majority of all channels, the distribution of phases at spike times was significantly nonuniform (Figure S2A), and we could define a preferred phase of spike times for each channel. The preferred phase of the 1–4 Hz LFP varied from channel to channel and was located in most cases in the $3\pi i/2$ to $2\pi$ range (between the trough and the middle of the rising phase of the LFP oscillation). For the 1–4 Hz LFP, the average over the dataset of the preferred phase was $1.9\pi$ (Figure S2C). We qualitatively observed that for the vast majority of channels, phase values close to the preferred phase were more reliably during firing, much as for the example channel reported in Figure 1. Thus, to quantify which phase range is more reliable during firing at the population level, we realigned the 1–4 Hz LFP phase values for each channel so that the preferred phase was set to a zero reference value, and we expressed each phase value as $\Delta\Phi$, the difference between the phase value and the channel's preferred phase. We then examined how the circular variance of the phase depended upon the mean across trials of the phase (computed as angular mean; see [20] and the Supplemental Data) and upon the trial-averaged spike rate observed in the same window. Figure 2B reports the population average of the phase circular variance as a function of the value of the trial-averaged phase (expressed as $\Delta\Phi$) and the spike rate. We found that (Figure 2B) at high spike rates (>100 spk/s), all phase values within angular distance $\Delta\Phi$ of $\pi/2$ from each channel's preferred phase were reliable (with circular variation in the range 0.3–0.4). This makes it possible for us to disambiguate different stimuli eliciting an equally strong firing rate by tagging them with some of the different reliable phase values occurring within angular distance $\Delta\Phi$ of $\pi/2$ from the preferred phase. In this way, stimuli indistinguishable from firing rates alone may become distinguishable after being labeled by their phase of firing, and this permits the phase of firing to convey information about the movie that is genuinely novel with respect to the one provided by spike rates.

### The Sensory Information Conveyed by Spike Times Relative to LFP Phase

Finally, we used Shannon information [21] to address directly the issue of how much additional information, beyond that available in spike counts, is conveyed by the phase of firing. Shannon information (see Equation S1 in the Supplemental Data) between a set of stimuli and the neural responses is a principled measure of single-trial discriminability. It quantifies (in units of bits) the reduction of uncertainty about the stimulus that is gained by a single-trial observation of a neural response: One bit corresponds to a reduction of uncertainty of a factor of two. In the following, we computed the information

that the neural response conveys about which section of the movie was being presented. This characterization of information about the movie does not need any assumption about which features in the movie made the neuron respond [6]; thus, we are computing information about all possible visual attributes occurring in the movie. Information values were expressed in bits/s by division of the information value by the time window length (typically 4 ms wide; see the Supplemental Data) in which the neural response is computed.

The amount of information transmitted by a neural response depends on the way the response is quantified, which in turn reflects our assumption on what is the neural code. We considered and compared the information carried by the two candidate neural codes: the spike-count code (the neural response to a part of the movie was quantified as the total number of spikes emitted in the selected movie window) and the phase-of-firing code (the neural response is quantified as the LFP phase at which each spike was emitted). The latter was equivalent to computing information from the colored spikes as in Figure 1E, the former to computing information counting colorless spikes as in Figure 1D. We registered the phase of firing with a $\pi/2$ precision (i.e., phase divided into quadrants) because (consistently with the above phase-reliability analysis) using a precision finer than $\pi/2$ did not increase the information further (Figure S3).

We first investigated how well spike counts encode the movie. We found that, across the entire dataset, spike counts conveyed $6.23 \pm 0.66$ bits/s of information about the movie (mean ± standard error of the mean [SEM]). We then considered the information about the movie that is carried by the phase of firing. We found (Figure 3A) that there was considerably more information in the spike times relative to the LFP phase than in the spike counts alone and that the amount of phase-of-firing information strongly depended on the considered LFP-frequency range. The 1–4 Hz LFP phase of firing carried $9.6 \pm 0.94$ bits/s of information about the movie: Thus, the phase of firing in 1–4 Hz LFP band conveys 54% extra information that cannot be obtained in any way from spike counts. As reported in the Supplemental Data, the extra amount of information in the phase of firing did not change much when only spikes from well-isolated single neurons were considered. The phases of firing in the 4–8 Hz and 8–12 Hz LFPs were less informative than the 1–4 Hz LFP phase but still carried much more information than spike counts (46% and 32%, respectively). The amount of information in the phase of firing then rapidly decreased at higher LFP frequencies, and it became equal to the spike count information for LFP frequencies greater than 24 Hz. Further, additionally labeling the spikes with LFP amplitude instead of just with LFP phase did not lead to any increase of information (Figure S7).

Taken together, these results suggest that spike times are only informative with respect to the phase of low-frequency LFPs.

Can the phase-of-firing information still be accessed by decoders affected by limitations similar to that likely encountered by downstream neural networks? On the one hand, a neural decoder may not be able to finely filter the broad-band circuit fluctuations. To address this concern, we computed the phase-of-firing information obtained when the phase is extracted from LFPs filtered between 1 Hz and a low-pass frequency cutoff that was progressively varied between 4 and 250 Hz. We found that the amount of extra information in LFPs decreased from 54% for 1–4 Hz LFPs to 46%, 39%, and 38% for 1–25 Hz, 1–100 Hz, and 1–250 Hz LFPs, respectively (Figure S4). Thus, a substantial amount of phase-of-firing information was preserved even if the neural signal was filtered within very broad frequency bands containing the informative low-frequency components. On the other hand, although cortical low-frequency oscillations have high spatial coherence, a further-away decoder may not receive a perfect copy of the phase signal. To verify whether this leads to a loss of decoded information, we paired the spikes with 1–4 Hz LFPs recorded simultaneously from electrodes up to 4 mm away rather than pairing them with the same-electrode 1–4 Hz LFP. We found that there was less than 1% loss of information (not significant p > 0.2; bootstrap test) when we paired spikes with LFP phases at other electrodes, at all interelectrode distance considered ($\leq 2$ mm; $\leq 3$ mm; $\leq 4$ mm). Thus, the phase-of-firing information was robust to limitations of the downstream decoder.

Is some of phase-of-firing information genuinely novel with respect to that carried by spike counts? In the following, we demonstrate that this is the case by showing that the phase of firing enables to discern between stimuli that cannot be possibly distinguished on the basis of spike counts alone. For each recording channel, we took only movie parts eliciting exactly a certain spike rate. The spike count code conveys no information about these fixed-spike-rate movie parts. If the phase of firing is totally redundant to the spike rate, it will also convey zero information about fixed-spike-rate movie parts. If instead the phase of firing conveys significant information about the fixed-rate movie parts, then it must contain information that is novel and independent with respect to that provided by spike counts because stimuli undistinguishable from spike count alone become distinguishable from the phase of firing. Results for the 1–4 Hz LFP (reported in Figure 3B as population average) show that the phase-of-firing information about movie parts at fixed rate was small at low spike rates and steeply increased at higher spike rates: It reached a value of 30 bits/s at rates greater than 100 Hz. The phase-of-firing information about movie parts at fixed rate was significantly positive (p < 0.0001; bootstrap test) for all rates greater than 10 Hz. Similar results (although with an overall scaling down of the information value) were obtained for 4–8 Hz and 8–16 Hz LFPs. This proves our hypothesis that the phase of firing conveys information about the movie that is not redundant to that of spike rates, because it disambiguates stimuli that elicit equally high spike rates and thus cannot possibly be distinguished from spike counts alone. (See the Supplemental Data for further studies on the independence between spike count and phase-of-firing information.)

## Discussion

The hypothesis that neurons may encode information by the phase at which they fire has received renewed attention in recent years. Evidence has been reported that spatial-navigation- and memory-related structures encode some information by phase of firing [22–24]. However, the extent to which firing rate and phase encode genuinely different information, rather than just being produced by the same mechanism and thus reflecting largely redundant information, has remained debated [25, 26, 27]. Further, it has been unclear whether phase coding represents a fundamental currency for cortical information exchange right from the primary sensory representation and whether it is a robust enough coding mechanism to represent complex stimuli.

In this report, we have addressed some of these open questions about the nature of phase coding by demonstrating for the first time that, in primary visual cortex of anaesthetized monkeys, a substantial amount of information about natural stimuli is carried by the phase of firing and that some of this phase-of-firing information is genuinely different from the information carried by spike counts. In fact, phase of firing permits the discrimination of stimulus features that elicit an equally high spike rate and thus cannot be distinguished when firing rate alone is considered. This coding mechanism provides neurons in sensory cortex with a mean to represent more than one effective stimulus by tagging several effective stimuli with similar firing rates with different values of the phase of the network fluctuations.

We found that only low-frequency (<12 Hz) LFP phases were reliable enough during periods of firing to be useful for coding, whereas phases of LFPs with frequencies higher than 40 Hz (gamma range [13]) were not. Gamma-range oscillations were present in our data and were stimulus driven (the highest increase of LFP power from spontaneous activity to movie stimulation was in the gamma range; Figure S1), but they did not generate a reliable and informative spike-phase relationship. An interesting question is how the information-rich phase of low-frequency LFPs is generated. We hypothesize that it could be driven by the dynamics of natural movies, which contains the highest power in the low-frequency range (Supplemental Data). We suggest that a useful experimental paradigm that could help clarify the origin of the informative phase signal consists of changing the stimulus dynamics by using faster stimuli than natural movies and studying how this affects the phase-informative LFP-frequency range, as well the accompanying spiking precision [28].

Previous reports have documented that the timing of individual spikes with respect to the stimulus onset (such as latency codes [29–32]) is very informative. One objection to such individual-spike-timing codes is that their information may not be relevant because the brain does not have a separate representation of stimulus onset that could allow the interpretation of this spike timing code. Our results demonstrate that the timing of individual spikes is not only informative relative to stimulus onset but is also informative relative to slow fluctuations in the input and the intracortical processing of the local cortical network. Because the latter signal is presumably available to a downstream area decoding the stimulus attributes, our demonstration of phase-of-firing coding suggests that the visual cortex can access and use the information available in the timing of individual spikes. In this respect, one particular advantage of using low-frequency oscillations for phase coding is that such low-frequency oscillations are those with greater spatial coherence and can thus be made more widely available to decoding networks.

The type of biophysical mechanisms needed to decode the phase-of-firing information depends on the origin of the

informative phase signal. A simple scenario is that low-frequency LFP fluctuations reflect coherent membrane potential oscillations of populations of neurons (such as transition between up and down states). In this case, different phase-of-firing values may be decoded on the basis of their different postsynaptic responses. A more complex scenario is that the reliable LFP phase is the reflection of a very precise interaction of a large cell assembly [27]. In such case, a precisely wired circuit may be needed for the detection of assembly activation, but the information advantage offered by relative time of firing can be even more quantitatively prominent.

### Supplemental Data

Experimental Procedures, supplemental data analysis, and seven figures are available at http://www.current-biology.com/cgi/content/full/18/5/375/DC1/.

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