LETTERS

Gamma-band synchronization in visual cortex predicts speed of change detection

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Our capacity to process and respond behaviourally to multiple incoming stimuli is very limited. To optimize the use of this limited capacity, attentional mechanisms give priority to behaviourally relevant stimuli at the expense of irrelevant distractors. In visual areas, attended stimuli induce enhanced responses and an improved synchronization of rhythmic neuronal activity in the gamma frequency band (40–70 Hz)[1–11]. Both effects probably improve the neuronal signalling of attended stimuli within and among brain areas[1,12–16]. Attention also results in improved behavioural performance and shortened reaction times. However, it is not known how reaction times are related to either response strength or gamma-band synchronization in visual areas. Here we show that behavioural response times to a stimulus change can be predicted specifically by the degree of gamma-band synchronization among those neurons in monkey visual area V4 that are activated by the behaviourally relevant stimulus. When there are two visual stimuli and monkeys have to detect a change in one stimulus while ignoring the other, their reactions are fastest when the relevant stimulus induces strong gamma-band synchronization before and after the change in stimulus. This enhanced gamma-band synchronization is also followed by shorter neuronal response latencies on the fast trials. Conversely, the monkeys' reactions are slowest when gamma-band synchronization is high in response to the irrelevant distractor. Thus, enhanced neuronal gamma-band synchronization and shortened neuronal response latencies to an attended stimulus seem to have direct effects on visually triggered behaviour, reflecting an early neuronal correlate of efficient visuo-motor integration.

Two monkeys were trained to perform a change detection task while spikes and local field potentials (LFPs) were recorded from several electrodes in area V4 (Fig. 1a, b; see Methods for details), an area that is strongly modulated by attention[3–5]. Local synchronization was assessed by the coherence spectrum between spike trains and LFPs, as well as the power spectrum of the LFPs. We previously found that visual stimuli induced gamma-band synchronization in V4, which was enhanced when the stimulus was attended[4] (Fig. 1c). Here we use data from our previous study in a new analysis that focuses on the behavioural reaction times to the stimulus change and on any associated changes in power, coherence and firing rates, time resolved in successive 10-ms steps with a sliding analysis window of ±125 ms.

We first calculated LFP power ($n = 64$ recording sites) and spike–LFP coherence ($n = 244$ pairs of recordings sites) in the gamma frequency band (40–72 Hz), as well as firing rates ($n = 61$ recording sites) separately for the 25% trials with the slowest behavioural reactions and the 25% trials with the fastest reactions. Spike–field coherence from one pair of recording sites is shown in Fig. 2. Both in this example and across the set of recordings, we found that trials

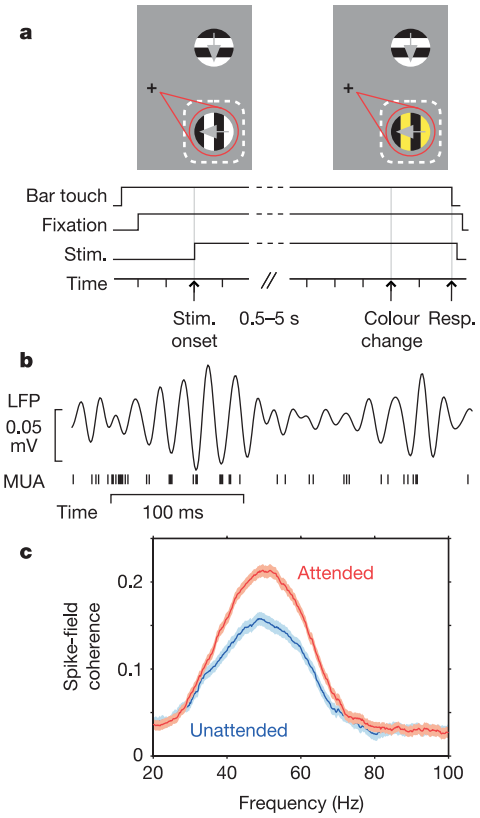

Figure 1 | Stimuli, behavioural model and examples of gamma-band synchronization and its modulation by attention. a, Monkeys started a trial by touching the bar and directing gaze to the fixation point. After a baseline period, two stimuli were presented, one inside the receptive field of the recorded neurons (broken rectangle) and one outside. On separate trials and before stimulus presentation, monkeys were cued to attend to one of the stimulus locations (red spotlight) and ignore the other. They were rewarded for releasing the bar on a subtle colour change in the cued stimulus while ignoring equally likely changes of the uncued stimulus. Changes could occur at any moment between 0.5 and 5 s after stimulus onset. **b**, Example of rhythmic multiunit activity (MUA) that is synchronized to gamma-band oscillations in the LFP. Multiunit activity and LFP were recorded from two separate electrodes. **c**, Example of spike–field coherence as a function of frequency for one pair of recording sites. The red (blue) lines show data recorded when the monkey directed attention into (away from) the receptive field of the recorded neurons. Shaded regions indicate ±1 s.e.m.

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leading to fast reaction times contained more gamma-band power (Fig. 3a) and gamma-band spike–field coherence (Fig. 3b) during epochs before and after the stimulus change event. The earliest significant change was found for spike–field coherence at 350 ms preceding the change event, whereas gamma-band power in the LFP was significantly enhanced ~125 ms before the stimulus change. Because of the ±125-ms width of the analysis window, we cannot precisely localize the beginning of these effects in time, although it is clear that they begin before the change event itself. Thus, enhanced gamma-band synchrony seems to lead to faster behavioural responses. Spike rates analysed with the same ±125-ms analysis window that was used for the spectral analysis showed a significant increase beginning 50 ms before the change event in trials leading to fast reaction times (Fig. 3c). Given the width of the analysis window, this could be an enhanced visual response to the change event itself.

In addition to these neuronal effects before the change event, all measures showed stronger gamma-band synchrony and spike rates in response to the change event on fast trials. On average, fast reactions were associated with a relative gamma-band power enhancement of 14.1% in the analysis windows centred between 0 and 75 ms after the change event, and an average spike rate enhancement of 8%. We did not consider effects beyond 75 ms after the change event, because the ±125-ms analysis window in this case would include the time of the earliest behavioural responses, which could be as fast as 200 ms (see Supplementary Fig. 1). We also computed spike rates on the basis of a narrower analysis window (gaussian with s.d. of 10 ms) and found that trials with fast reactions had shorter response onset latencies to the change event (~10–20 ms), and an enhanced evoked response to the stimulus in the period from 40 to 130 ms after the stimulus change (Fig. 3d).

The response and coherence differences found on fast versus slow trials could be selective to the attended stimulus, or they could be due to a general increase in arousal, or alertness, on trials with fast reaction times[17]. If the latter is true, we would expect enhanced gamma-band power and coherence also on trials with rapid behavioural responses to the stimulus outside the receptive field of the recorded neurons. We therefore computed power, coherence and firing rates in response to the stimulus inside the receptive field when the monkey was attending to a stimulus outside the receptive field and around the time of the change of this attended stimulus outside the receptive field. In contrast to the results when the monkey responded to the stimulus change inside the receptive field, gamma-band power and coherence at the unattended location were significantly reduced throughout most of the pre-change period when the monkeys responded quickly to the stimulus outside the receptive field (Fig. 3e, f). Spike rates were only marginally reduced for fast versus slow trials (Fig. 3g). Thus, the effects of attention on LFP power and coherence inside the receptive field were approximately reversed for fast versus slow responses to attended stimuli outside the receptive field (Fig. 3h), which is inconsistent with a general change in arousal.

These results suggest that when the monkey attends to one stimulus and ignores a distractor, the relative gamma-band coherence differences in response to the attended and ignored stimulus will, on average, predict fast versus slow reaction times well before the change event occurs. When the change event occurs, neuronal responses have a shorter latency and stronger gamma-band coherence on the faster trials. Some of the observed effects became apparent already in the first analysis window, 500 ms before the change event—that is, the time of stimulus onset for the shortest

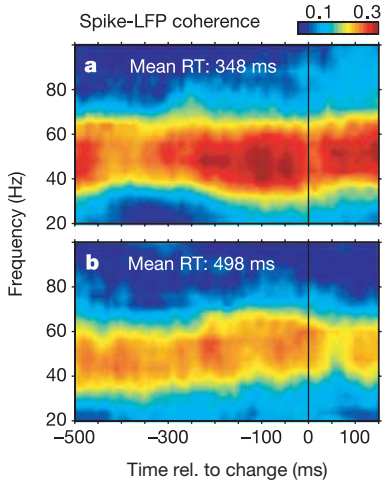

Figure 2 | Spike–field coherence from one pair of recording sites. Shown are averages over the 25% of trials with the fastest (**a**) and the slowest (**b**) reaction times.

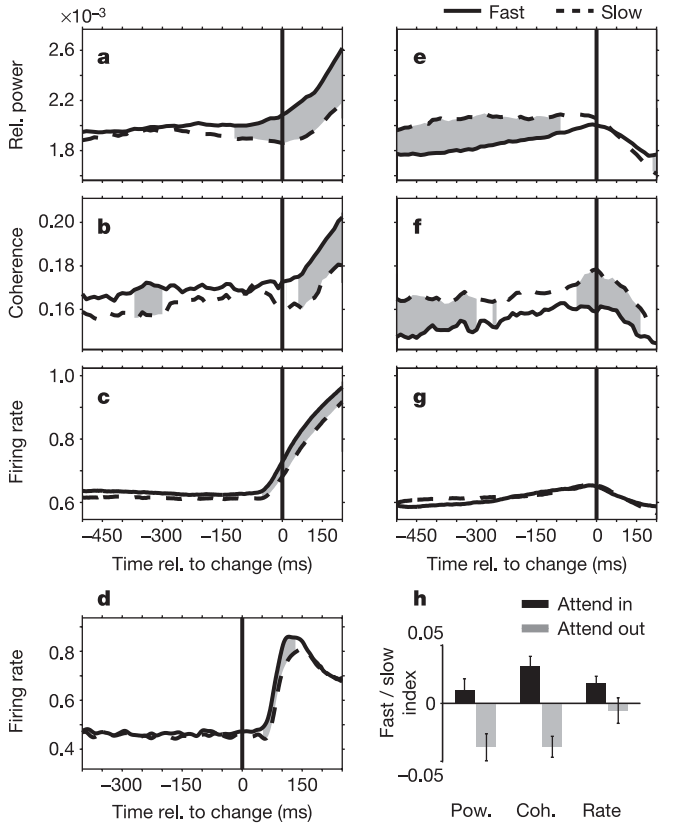

Figure 3 | Neuronal activity parameters in trials with fast and slow change detection. **a**–**d**, Time course of neuronal activity parameters induced by the attended stimulus inside the receptive fields around the change of the attended stimulus. **a**, Relative LFP power in the gamma band (40–72 Hz). **b**, Spike–field coherence in the gamma band. **c**, **d**, Firing rate. In **a**–**c**, analysis windows of ±125 ms were used; in **d**, a gaussian kernel of 10-ms s.d. was used. Shown are grand averages calculated separately for the 25% of trials with the fastest (unbroken lines) and slowest (broken lines) behavioural responses. Grey shading indicates significance (two-sided paired *t*-test, $P < 0.05$ after multiple comparison correction). **e**–**g**, As **a**–**c**, but showing the time course of neuronal activity parameters induced by the ignored distractor, around the change of the attended stimulus that was outside the receptive fields. **h**, Comparison of neuronal activity parameters for fast versus slow trials (average over −500 to −125 ms preceding the change) when behavioural reports were in response to changes inside (black bars) or outside (grey bars) the receptive fields. Shown is the modulation index defined as $(P_{fast} - P_{slow})/(P_{fast} + P_{slow})$, where P_{fast} is one of the parameters investigated for trials with fast responses and P_{slow} is one for trials with slow responses. Error bars denote ±1 s.e.m. Pow., power; Coh., coherence.

trials. To determine the earliest neural effects on reaction time, we therefore repeated the above analyses for a 250-ms window before stimulus onset, but we found no significant effects in that interval.

To test directly whether trial-by-trial fluctuations of synchrony could predict the speed of change detection on a single-trial basis, we performed a correlation analysis. For this, we correlated trial-by-trial variations in reaction time with trial-by-trial variations in coherence or power and firing rate (see Methods). To obtain an overview of the spectral specificity of the neuronal response changes, we extended the time-resolved analysis to frequencies of 8–100 Hz. Consistent with the preceding analysis, we found that short reaction times were predicted by enhanced power and coherence in the gamma-frequency band (40–72 Hz) in time epochs preceding the stimulus change by several hundred milliseconds (Fig. 4a, b). Also shortly before and after the change event, behavioural response times were predicted by the degree of synchrony and neuronal response magnitude. Correlations of firing rate (analysed within the same sliding ±125-ms analysis window used above) and reaction time were significant from 40 ms before the change and onwards (Fig. 4c). In contrast to firing rate and gamma-band modulation, we observed reduced power in the alpha (10 Hz) and beta (15 Hz) frequency bands for fast trials in a restricted time window starting 80 ms before the stimulus change (Fig. 4a).

Across measures, the strongest correlations with reaction times were evident at a time immediately after the stimulus change. To analyse this effect for single recording sites, we calculated *Z*-scores of the correlation of reaction time with gamma-band power and spike rate averaged over the analysis windows centred between 0 and 75 ms after the change event. The distribution of *Z*-scores for LFP power and firing rate is strongly biased towards negative values (see Supplementary Fig. 2 and Supplementary Table). Moreover, the negative reaction time correlations are clearly evident in both monkeys, which is noteworthy because the two monkeys showed a different trend in reaction time speed as a function of time in trial (namely, a slightly increasing/decreasing response speed with time in trial; see Supplementary Fig. 1 and Supplementary Note). Thus, while the two monkeys showed weak but opposite trends in reaction times across the trial, they both showed the same patterns of correlation between reaction times and spectral power, firing rate and coherence.

Our results show that the degree of neuronal synchrony in the gamma-frequency band in time intervals preceding and following a behaviourally relevant sensory change can predict the speed of behavioural responses to that change. These effects are reversed for responses to stimulus changes outside the receptive field.

The neuronal processes in visual area V4, studied here, constitute only one link in the processing chain from the stimulus change event to its behavioural report. Oscillatory synchronization within and between other structures along this way has been described and probably also has a functional role[16,18–24]. Enhanced gamma-band synchronization in V4 could be directly involved in the detection process and/or in the signalling of the detection achieved in V4 or a preceding area. In both cases, enhanced gamma-band synchronization among the recorded neurons probably subserves rapid and reliable signalling mechanistically, because it results in efficient summation of postsynaptic potentials[13,25,26].

A reported effect of gamma-band synchronization during the onset of visual stimuli is enhanced synchronization and shortened response latencies of the first spikes on stimulus presentation[27]. If this finding is extended to stimulus changes, in addition to stimulus onsets, it suggests that there is a mechanistic link between enhanced gamma-band synchrony around the time of the sensory change and the more rapid, shifted response latency that we observe. Taken together, our results suggest that the enhanced precise synchronization is instrumental in subserving a rapid and reliable transmission of information about sensory changes to the postsynaptic targets and thus ultimately triggers enhanced detection efficiency.

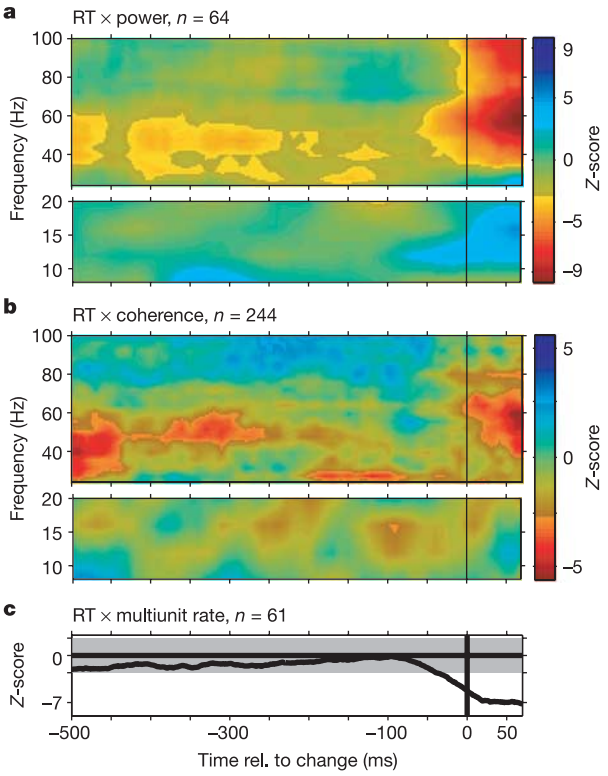

Figure 4 | Trial-by-trial prediction of reaction times by neuronal activity. Shown are *Z*-scores of correlation coefficients pooled across monkeys and recordings sites (**a**, **c**) or pairs of recording sites (**b**) on the basis of analysis windows of ±125 ms. Note inverted colour scale. Grey shading highlights significance (99% confidence). Results are shown separately for lower and higher frequencies because different spectral concentrations were used (see Methods). **a**, LFP power versus reaction times. **b**, Spike–field coherence versus reaction times. **c**, Firing rates versus reaction times.

METHODS

Procedures were done in accordance with NIH guidelines and were approved by the National Institute of Mental Health (NIMH) Intramural Animal Care and Use Committee. Simultaneous recordings of spikes and local field potentials were made from four to eight electrodes in visual areas V4 in two hemispheres of two monkeys. In total, multiunit recordings were obtained from 61 sites (39 and 22 in monkey A and B, respectively) and LFP recordings from 64 sites (40 and 24, respectively). Power and coherence spectra were assessed for windows of ±125 ms, moved over the data in steps of 10 ms from 500 ms before to 150 ms after the stimulus change. Neuronal activity parameters were compared between trials with the 25% fastest and trials with the 25% slowest response times of individual recording sessions. The mean reaction time for the fast and slow trials was 346 ms and 490 ms, respectively (median, 359 and 485 ms, respectively). To determine the predictive capability of neuronal activity parameters for reaction time, we calculated the Pearson correlation coefficient between the trial-by-trial variations in reaction times and the trial-by-trial variations in power, coherence and spike rate. See Supplementary Methods for more information.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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