

SHORT COMMUNICATION

Stimulus locking and feature selectivity prevail in complementary frequency ranges of V1 local field potentials

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Abstract

The local field potential (LFP) is a population measure of neuronal activity complementary to spike trains. Whereas the response properties of the spiking activity in the visual cortex have been characterized extensively, the responses of the LFP have not been well explored. No coherent picture exists about which frequency ranges exhibit feature tuning or show stimulus locked activity. Addressing this, we recorded LFP in the primary visual cortex of alert cats and calculated the tuning indices for orientation, spatial and temporal frequency. Furthermore, we quantified the locking of the power in different LFP frequency bands to the velocity profile of artificial and natural stimuli. We found that the LFP in alert animals is well tuned with similar specificity to orientation, spatial frequency and temporal frequency. Tuning to these features is most prominent in two frequency bands (8–23 Hz and 39–109 Hz). In two complementary frequency bands (23–39 Hz and above 109 Hz) the dynamics of the LFP power is locked tightly to the temporal structure of the stimulus. This locking is furthermore independent of the spatial structure of the stimulus. Together these four frequency bands cover the whole frequency range investigated. In contrast to previous studies, which often reported correlates of visual processing only in a limited frequency range of the LFP, the present results suggest that the entire frequency range of the LFP can be assigned a role in visual processing.

Introduction

Local field potentials (LFP) are a measure of neuronal activity complementary to spike trains. Whereas the LFP represents the low frequency component of the electrical signal recorded using microelectrodes, the spike trains are extracted from the high frequency range. The LFP is influenced by currents originating from axons, somata and dendrites around the electrode, and thus mainly reflects the input to a local brain region (Freeman, 1975; Mitzdorf, 1985, 1987; Logothetis, 2003). As a continuous signal the LFP is well suited to investigate the temporal structure of neuronal activity. Indeed, the temporal structure of the LFP is directly related to the processing of sensory stimuli in a variety of paradigms (Gray *et al.*, 1989; Eckhorn *et al.*, 1993; König & Engel, 1995; König *et al.*, 1995; Rols *et al.*, 2001; Brosch *et al.*, 2002; Fries *et al.*, 2002; Woelbern *et al.*, 2002; Barth, 2003). In analogy to seminal work on the tuning properties of spiking activity in visual cortex (Hubel & Wiesel, 1962), the LFP has been shown to be selective to the orientation of a bar or a grating in the anaesthetized and awake condition (Gray & Singer, 1989; Fries & Eckhorn, 2000; Siegel & König, 2003). According to these studies, only selected frequency bands of the LFP are tuned to orientation. In contrast, tuning to other stimulus features, such as spatial and temporal frequency, has been explored poorly in the awake preparation. Further-

more, few studies exist which investigate tuning to several features in the same animal.

The phase of the LFP can lock to the temporal structure of a stimulus. This has been demonstrated using either flickering full field stimuli (Rager & Singer, 1998) or randomly moving gratings (Kruse & Eckhorn, 1996). Furthermore, the modulation of the LFP amplitude is locked to dynamic stimuli (Kayser *et al.*, 2003). This can occur upon stimulation with gratings as well as with natural movies, and thus is a property of everyday sensory processing. However, different frequency ranges have been reported to exhibit locking, but no systematic investigation exists.

Here we address the two phenomena of feature tuning and stimulus locking simultaneously in the awake cat. We study in which frequency ranges the LFP shows tuning to the features of visual stimuli and in which frequency ranges amplitude locking to the stimulus motion is observed.

Materials and methods

Subjects and recording procedures

Data were obtained from eight adult cats using chronically implanted electrodes. A microdrive was implanted in five animals (for details see Kayser *et al.*, 2003) and floating electrodes were used in three animals (for details see Siegel & König, 2003). Implantations were performed using Isoflurane anaesthesia (0.4–1.5%) and analgesics were delivered during and after surgery. For recordings, the animals were head-fixed.

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The animals were habituated to this restraint by starting with short fixations (<1 min) and by increasing this time by 1 min every day until the length of a typical recording session (20 min) was reached. The stimuli were presented on a 19-inch Hitachi monitor (120 Hz refresh, 8-bit grey scale, 57 cm in front of the animal). In part of the recording sessions, eye movements were measured using a Dual Purkinje Imaging system (Fourward Optical Technologies Inc., Clute, TX, USA; see Körding *et al.*, 2001 for further details). The signals of the electrodes were passed through a preamplifier (Neurotrack, Ltd) and digitized at 20 000 Hz using a Synamp system (Neuroscan Ltd, El Paso, TX, USA) using a 5 Hz analogue high-pass filter. During recording the state of alertness of the animal was checked continuously using an infrared camera and by examining the LFP online. All procedures were approved by the local ethics committee and conformed to NIH guidelines.

Stimuli

Tuning properties were measured using drifting sine-wave gratings (SF, spatial frequency; TF, temporal frequency). For SF tuning we used horizontal gratings including both directions of drift (TF = 2 Hz and SF = 0.1, 0.2, 0.4, 0.8, 1.6, 3.2 cycles per degree, c.p.d.). For TF tuning we used horizontal gratings including both directions of drift (TF = 0.8, 1, 1.6, 2, 2.5, 4 Hz and SF = 0.2 c.p.d.). For a subset of the recording sites we used also TF = 8 and 12 Hz. For orientation tuning we used 12 equally spaced directions of drift between 0 and 360° (SF = 0.2 c.p.d. and TF = 2 Hz). Stimuli were shown in a pseudorandom sequence and repeated 20 times.

Locking of the power in a given frequency band of the LFP to the stimulus motion has two consequences: first, changes of the LFP power are correlated with changes of the stimulus velocity; and second, changes of the LFP power are correlated across trials when the same stimulus is repeated. Following this, we first used two types of stimuli with known irregular motion to directly demonstrate locking of the LFP to the stimulus motion: (i) natural movie clips recorded using a camera mounted to the head of a freely moving cat; and (ii), jittering gratings (SF = 0.2 c.p.d.) moving according to the velocity profile extracted from a natural movie. Then we computed cross-correlations across trials upon stimulation with: (i) the same natural movie clips; and (ii), pink pixel noise that had the same spatial and temporal frequency content as a natural movie but lacked the higher order structure. The latter stimulus was used to demonstrate that locking occurs also for stimuli with smoothly changing structure. The velocity profiles of the natural movies were estimated using standard techniques described elsewhere (see Kayser *et al.*, 2003).

All stimuli had the same mean luminance and RMS contrast. Stimuli lasted for 2 s and were separated by uniform blank screens of the same length and same mean luminance.

Data analysis

The LFP was extracted by low-pass filtering the raw data at 500 Hz using a third-order Butterworth filter and was resampled at 1000 Hz. To quantify the activity in different frequency bands, a time-localized Fourier spectrum was computed using data windows of 160 ms, overlaid with a Hanning window and zero padded to 256 ms. This results in a resolution of 3.9 Hz and 8 ms in the frequency and temporal domain, respectively. In the stimulus paradigm used, the initial 200 ms following stimulus onset are dominated by the evoked potential arising from the sharp transition between blank and stimulus. Although this evoked potential conveys information about the stimulus, e.g. its orientation (Bonds, 1982), it is characterized by much higher power than the activity later in the trial. Because of this difference in power the evoked part cannot be mixed with the rest of the trial for analysis.

We thus excluded the first 200 ms of each trial from the analysis and our results pertain only to the so-called steady state of the trial.

Tuning curves were computed for each recording site and LFP frequency separately. First, the power at a given frequency was averaged over the time course of the stimulus presentation. To obtain the tuning curve, the power was further averaged across repeats of the same stimulus and across the two opposite drift directions. The selectivity of the tuning curve was quantified using a tuning index: $(\max - \min)/(\max + \min)$; max and min denote the maximal and minimal value of the tuning curve. For each recording site this results in a curve describing the selectivity index as a function of the LFP frequency. The results in Fig. 1B were obtained by averaging these curves across recording sites.

The significance of each tuning curve was assessed using a Wilcoxon rank test. The test compared the power of individual repeats of the stimulus at the optimal orientation with the power at the orientation with the lowest average response (similar for spatial and temporal frequency). This yielded one *P*-value for each LFP frequency. For a given recording site, we thus obtained two curves: the selectivity index and the *P*-value, both as a function of the LFP frequency. A high selectivity index implies a low *P*-value and vice versa. Tuning was taken to be significant if the *P*-value was <0.05. By averaging the selectivity indices of those LFP frequencies where the *P*-value curve crossed this threshold, we obtained the average selectivity index corresponding to a threshold of *P* = 0.05. These thresholds were used to determine frequency ranges with significant tuning and are indicated in Fig. 1B. To visualize the selectivity of the LFP, we also computed tuning curves from the average power in the frequency range from 30 Hz to 100 Hz (Fig. 1A, upper panels).

The correlation between stimulus motion and LFP activity was estimated for each repeat of a stimulus and LFP frequency separately. The normalized cross-correlation between the time course of the stimulus velocity and the time course of the LFP power at this LFP frequency was computed. These cross-correlations were then averaged across stimulus repeats and recording sites (see Fig. 2A for an example). Note that a correlation value of +1 implies perfect correlation whereas a value of 0 implies completely uncorrelated signals. The significance of these correlations was estimated using a bootstrap technique (Press *et al.*, 1992). We computed 1000 cross-correlations between a velocity profile from one stimulus and the LFP power recorded using a different stimulus. From this population the 95% confidence levels were obtained. These confidence intervals are indicated in Fig. 2. The correlation of LFP power across trials and animals for a given stimulus was computed as follows. First, random trials from two different recording sites in the same or different animals were chosen. Then, for each LFP frequency, the cross-correlation of the time course describing the LFP power in the two trials was computed. These correlations were averaged over 3000 random pairs. The significance of these correlations was estimated using a bootstrap as above. A total of 1000 cross-correlations using trials obtained with two different stimuli were computed and from these the 95% confidence levels were obtained.

Results

The LFP power in a broad frequency range is clearly tuned to orientation, spatial frequency and temporal frequency (Fig. 1A, upper panel). From the tuning curves calculated at individual LFP frequencies and recording sites we computed the average tuning-index characterizing the strength of the tuning as a function of LFP frequency (Fig. 1A, lower panel). Tuning to orientation is prominent between 8 and 16 Hz and in a broad range of frequencies between 43 and 102 Hz.

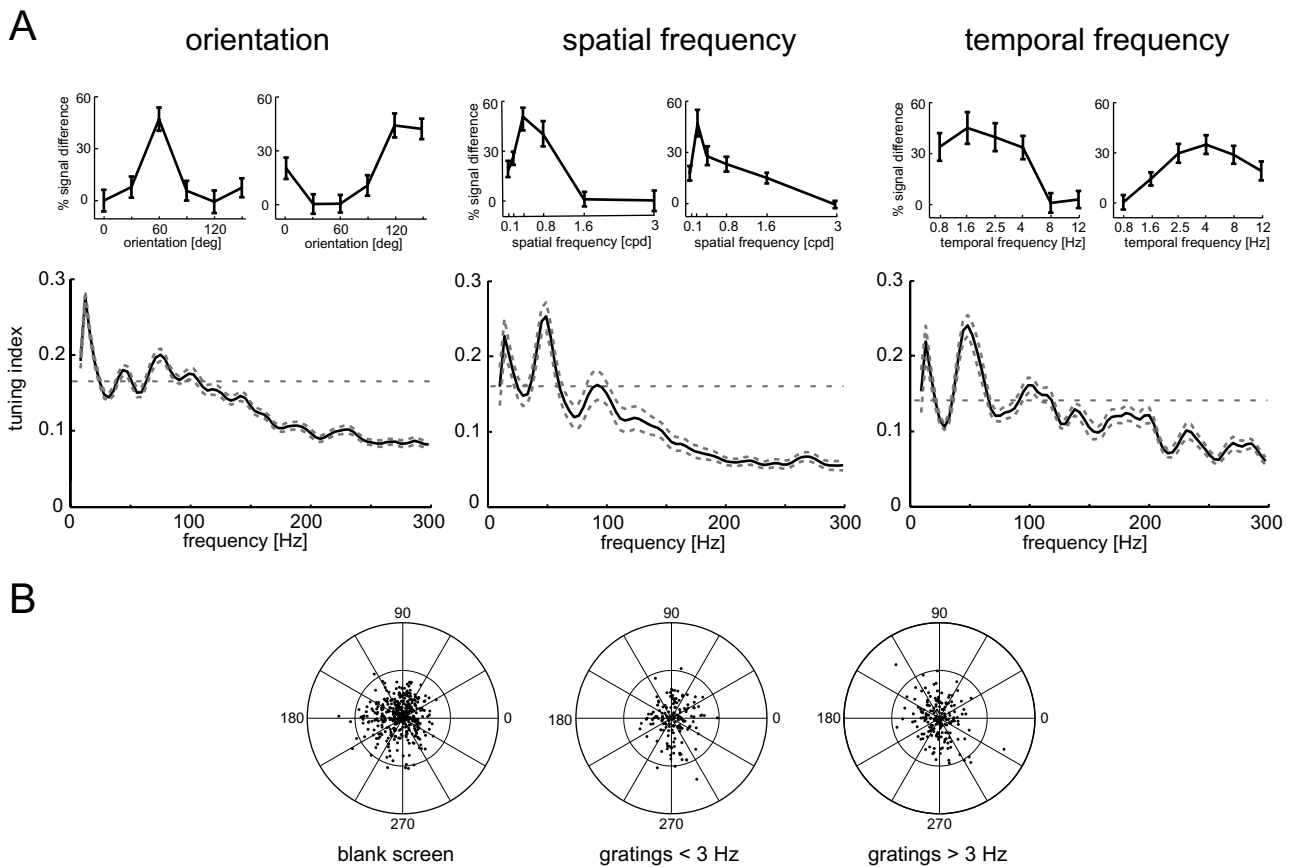


FIG. 1. Feature tuning in the LFP. (A) Upper row shows examples of tuning curves obtained from the average power between 30 and 100 Hz based on 20 repeats of the stimulus. Error bars denote SEM. The magnitude of the response at each feature value is expressed in units of percentage difference compared with the response at the feature value yielding the lowest response. The response at this null feature was normalized to zero. Lower row shows the frequency dependence of the tuning-index averaged across recording sites ($n = 37, 45, 41$ from eight animals (for orientation, spatial and temporal frequency, respectively)). The solid lines denote the mean, the dashed line the SEM. The dashed horizontal lines indicate the 95% confidence level. (B) Distribution of saccadic eye movements during the presentation of the blank screen (left, 380 saccades), gratings drifting below 3 Hz (middle, 154 saccades) and gratings drifting faster than 3 Hz (right, 184 saccades). The stimulus was drifting in the direction of 0° . The inner circle denotes two standard deviations of the entire region covered by all eye movements (corresponding roughly to 15°) the outer circle denotes four standard deviations (corresponding roughly to 30°).

Tuning to spatial frequency is most prominent between 8 and 20 Hz and between 39 and 59 Hz. Temporal frequency tuning is most prominent between 39 and 63 Hz. We concluded therefore that the LFP power is tuned to all three features to a similar degree and within strongly overlapping frequency bands.

These results were obtained by averaging across all different directions of gaze of the animal. To determine whether eye movements could confound these results, we measured the animals' eye movements in a number of recording sessions during presentation of the stimuli used to assess temporal frequency tuning. From these data saccadic eye movements were extracted and grouped according to three different conditions: blank screen; slowly drifting gratings (below 3 Hz); and fast drifting gratings (above 3 Hz). In each case the saccadic eye movements scatter in all directions of the visual field (Fig. 1B). However, the median of the horizontal component is only shifted from zero by a small fraction of the average amplitude of the eye movements (8.1%, 5.7% and 6.5% for blank screen, slowly and fast drifting gratings). In all three cases this shift is not significantly different from zero ($P > 0.7$ in all three cases, Wilcoxon rank test). This indicates that the animals did not systematically follow the drifting stimuli.

Figure 2A shows an example of the curve describing the velocity in a natural movie clip together with the power in the LFP at 200 Hz. These

curves form the basis of the cross-correlation between stimulus velocity and LFP power. An example of such cross-correlation is shown in Fig. 2B. Strong correlations occur in two frequency bands of the LFP: around 25 Hz and well above 100 Hz. The time lag between neuronal response and stimulus velocity that leads to the strongest correlation is different for these two frequency regimes. For the first range the stimulus leads the response by roughly 100 ms; for the second by 50 ms. This latency difference is in agreement with known temporal lags between beta and gamma activity (Bekisz & Wrobel, 1999). On average we found significant locking in two frequency ranges: between 20 and 35 Hz and above 102 Hz (Fig. 2C, black curve). To control whether these frequency bands depend on the spatial structure of the stimulus, we computed the same cross-correlation using randomly jittering gratings (Fig. 2C, grey curve). The frequency ranges with significant locking were similar to those obtained using natural movies, except that now locking occurred also between 35 and 43 Hz. This locking led to significant correlations of LFP power across trials (Fig. 2D). For natural movies the average intertrial correlations are significant between 16 and 43 Hz and above 133 Hz, in rough agreement with the above. For the pink pixel noise significant correlations occur in a similar way. The fact that locking occurs also for broadband stimuli within a limited range of LFP frequencies indicates that it is indeed a property of the brain. Furthermore, this locking

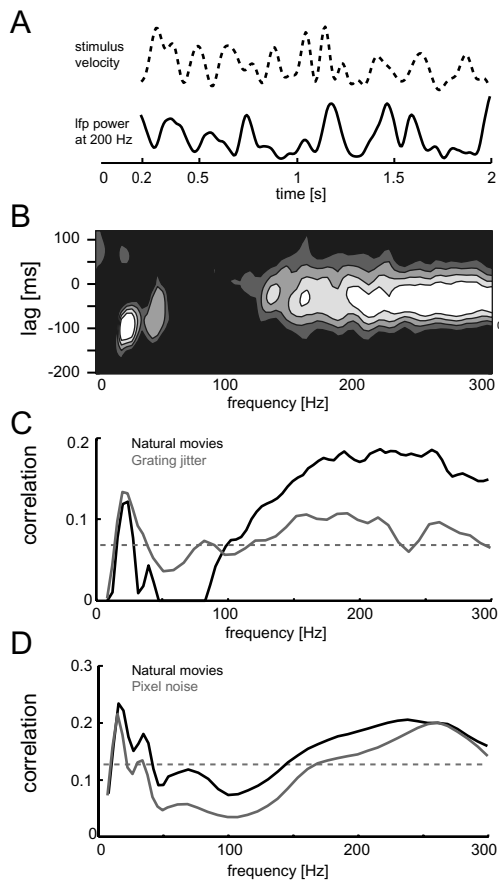


Fig. 2. Locking of the LFP activity to the stimulus motion. (A) Examples of stimulus velocity and the power in the LFP at 200 Hz during the presentation of a natural movie. The power was averaged over 50 repeats of the stimulus. (B) Example of the cross-correlation between LFP power and stimulus velocity for one natural movie and one recording site. At negative time lags the stimulus leads the LFP activity. (C) Grand average of the cross correlation of LFP power and stimulus velocity at the optimal lag for each LFP frequency for natural movies (five animals, 152 recording sessions, three natural movies) and jittering gratings (three animals, 21 sessions). The dashed horizontal line indicates the 95% confidence interval of a bootstrap estimate. (D) Cross-correlation of LFP power across trials for natural movies and pink pixel noise stimuli (five animals, 152 recording sessions). The dashed horizontal line indicates the 95% confidence interval of a bootstrap estimate.

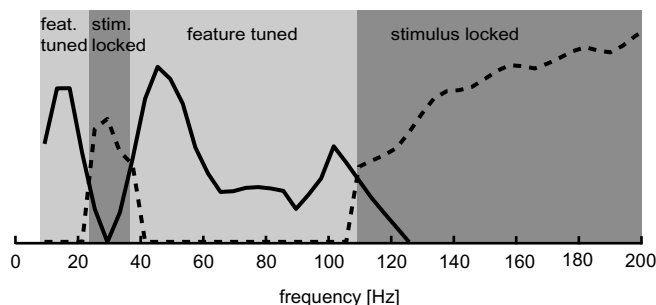


Fig. 3. Feature tuning and stimulus locking prevail in complementary frequency ranges. Solid line: the three curves describing the tuning indices from Fig. 1A have each been cut off at their respective significance threshold and averaged. Dashed line: the two curves describing the correlation between LFP power and stimulus velocity from Fig. 2B have each been cut off at the corresponding significance threshold and averaged as well. For visualization, the dashed and solid lines have been scaled to the same maximum.

phenomenon is not restricted to natural stimuli or stimuli with highly irregular motion, but occurs in the same frequency ranges also for stimuli with smoothly varying structure.

Discussion

The results of this study show that the frequency axis of the LFP can be divided into four regimes (Fig. 3). In two of these, modulations of the power are locked tightly to the temporal structure of the stimulus, roughly between 23 and 36 Hz and above 109 Hz. In the other two, the LFP power is tuned to structural features of the stimulus, roughly between 8 and 23 Hz and between 36 and 109 Hz. These four frequency ranges are complementary and together cover the range of frequencies investigated.

Stimulus locking occurs in different forms. In a previous study locking of the phase of the LFP to the temporal structure of the visual stimulus was studied (Rager & Singer, 1998). This relates directly to the well-known evoked potential. In contrast, here we investigate modulation of the power in different frequency bands of the LFP. The modulation of the power of a given LFP frequency can take place on much slower time scales than the oscillation of this LFP frequency. In the present case, the modulations of the LFP are driven by the motion in the stimulus. For the natural movies used here, the typical time scale of the auto-correlation of the stimulus velocity is around 100 ms (Moeller *et al.*, 2003). Consequently, the signal driving the locking of the LFP power changes with a typical frequency of approximately 10 Hz. Thus, the power of the 130-Hz frequency component of the LFP can be modulated by a 10-Hz signal in the visual stimulus. As a consequence, the details of visual stimulation, such as the monitor refresh rate and the flicker fusion frequency limit only the signal in the stimulus that could cause the locking, i.e. the 10 Hz signal. The LFP frequency at which locking is observed, i.e. 130 Hz in this example, is only limited by the Nyquist frequency of the sampling of the electrode signals.

Working with awake animals introduces a number of complications. First, the level of alertness of the subject is difficult to define even when continuously monitoring the animals. The little power in the low frequency bands of our data supports the view that epochs of drowsiness or sleep are a small contamination at most and quantitatively not relevant. Second, the animals can, and do, freely move their eyes. This introduces a difference between the visual projection of the stimulus, and the retinal image. Stimuli similar to those used for the tuning experiments here are often used to induce an optokinetic nystagmus. This results in a regular alternation of pursuit and saccadic eye movements (Goldberg, 2000). Under the conditions of the present study, however, we found no evidence for a systematic relation of fast eye movements and drift direction. In agreement with this, a previous study found that the gain of pursuit movements in cats is low (Moeller *et al.*, 2002). Furthermore, the gain drops with increasing stimulus velocity, suggesting that cats do not frequently follow drifting gratings with their eyes. We conclude that there is no indication that eye movements confound the results presented here.

The tuning curves of the LFP in the awake cat reported here are compatible with previous results (Bonds, 1982; Gray & Singer, 1989) and similar to those obtained from the firing rates of single cells (e.g. DeAngelis *et al.*, 1993). Thus, the LFP exhibits qualitatively similar selectivity as individual neurons, although the difference between activity induced by optimal and nonoptimal stimuli is smaller. Furthermore, the frequency bands for orientation tuning reported here are largely overlapping with those of optimal orientation tuning reported earlier in monkey (Frien *et al.*, 2000) and cat (Siegel & König, 2003).

The present results indicate that the frequency axis of the LFP can be split into complementary regimes exhibiting correlates of different aspects of visual processing. These frequency bands have little overlap and together cover the whole frequency axis. We do not want to create the impression that the stated frequency bands serve a single purpose. From numerous studies, either recording LFP or electroencephalograms (EEG), it is well known that state changes of the subject modulate low frequency activity in very narrow bands (McCormick & Bal, 1997; Destexhe *et al.*, 1999). Similarly, attention and memory have profound effects on the activity recorded in EEG studies (Tallon-Baudry *et al.*, 1998; Herrmann & Knight, 2001; Jensen *et al.*, 2002). Although our results indicate a division of the frequency scale in feature-tuned and stimulus-locked parts, phenomena like attention and memory can modulate similar frequency ranges as well. The mechanisms, however, that generate and modulate oscillatory activity patterns are only understood partially. Although many properties of single cell types, intracortical and thalamocortical connectivity have been shown to be involved, it is not clear how cognitive functions or stimulus properties can selectively modulate certain frequency bands (for recent reviews see Ritz & Sejnowski, 1997; Salinas & Sejnowski, 2001; Destexhe & Sejnowski, 2003).

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Abbreviations

EEG, electroencephalogram; LFP, local field potential; SF, spatial frequency; TF, temporal frequency.

References

- Barth, D.S. (2003) Submillisecond synchronization of fast electrical oscillations in neocortex. *J. Neurosci.*, **23**, 2502–2510.
- Bekisz, M. & Wrobel, A. (1999) Coupling of beta and gamma activity in corticothalamic system of cats attending to visual stimuli. *Neuroreport*, **10**, 3589–3594.
- Bonds, A.B. (1982) An 'oblique effect' in the visual evoked potential of the cat. *Exp. Brain Res.*, **46**, 151–154.
- Brosch, M., Budinger, E. & Scheich, H. (2002) Stimulus-related gamma oscillations in primate auditory cortex. *J. Neurophysiol.*, **87**, 2715–2725.
- DeAngelis, G.C., Ohzawa, I. & Freeman, R.D. (1993) Spatiotemporal organization of simple-cell receptive fields in the cat's striate cortex. I. General characteristics and postnatal development. *J. Neurophysiol.*, **69**, 1091–1117.
- Destexhe, A., Contreras, D. & Steriade, M. (1999) Spatiotemporal analysis of local field potentials and unit discharges in cat cerebral cortex during natural wake and sleep states. *J. Neurosci.*, **19**, 4595–4608.
- Destexhe, A. & Sejnowski, T.J. (2003) Interactions between membrane conductances underlying thalamocortical slow wave oscillations. *Physiol. Rev.*, **83**, 1401–1453.
- Eckhorn, R., Frien, A., Bauer, R., Woelbern, T. & Kehr, H. (1993) High frequency (60–90 Hz) oscillations in primary visual cortex of awake monkey. *Neuroreport*, **4**, 243–246.
- Freeman, W. (1975) *Mass Action in the Nervous System*. Academic Press, New York.
- Frien, A. & Eckhorn, R. (2000) Functional coupling shows stronger stimulus dependency for fast oscillations than for low-frequency components in striate cortex of awake monkey. *Eur. J. Neurosci.*, **12**, 1466–1478.
- Fries, P., Schröder, J.H., Roelfsema, P.R., Singer, W. & Engel, A.K. (2002) Oscillatory neuronal synchronization in primary visual cortex as a correlate of stimulus selection. *J. Neurosci.*, **22**, 3739–3754.
- Goldberg, M.E. (2000) The control of gaze. In Kandel, E.R., Schwartz, J.H., & Jessel, T.M. (eds) *Principles of Neural Science*. McGraw Hill, New York, pp. 782–798.
- Gray, C.M., König, P., Engel, A.K. & Singer, W. (1989) Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature*, **338**, 334–337.
- Gray, C.M. & Singer, W. (1989) Stimulus-specific neuronal oscillations in orientation columns of cat visual cortex. *Proc. Natl. Acad. Sci. USA*, **86**, 1698–1702.
- Herrmann, C.S. & Knight, R.T. (2001) Mechanisms of human attention: event-related potentials and oscillations. *Neurosci. Biobehav. Rev.*, **25**, 465–476.
- Hubel, D. & Wiesel, T.N. (1962) Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.*, **160**, 106–154.
- Jensen, O., Gelfand, J., Kounios, J. & Lisman, J.E. (2002) Oscillations in the alpha band (9–12 Hz) increase with memory load during retention in a short-term memory task. *Cereb. Cortex*, **12**, 877–882.
- Kayser, C., Salazar, R.F. & König, P. (2003) Responses to natural scenes in cat V1. *J. Neurophysiol.*, **99**, 1910–1920.
- König, P. & Engel, A.K. (1995) Correlated firing in sensory-motor systems. *Curr. Opin. Neurobiol.*, **5**, 511–519.
- König, P., Engel, A.K. & Singer, W. (1995) Relation between oscillatory activity and long-range synchronization in cat visual cortex. *Proc. Natl. Acad. Sci. USA*, **92**, 290–294.
- Körding, K., Kayser, C., Betsch, B. & König, P. (2001) Non contact eye-tracking on cats. *J. Neurosci. Methods*, **110**, 103–111.
- Kruse, W. & Eckhorn, R. (1996) Inhibition of sustained gamma oscillations (35–80 Hz) by fast transient responses in cat visual cortex. *Proc. Natl. Acad. Sci. USA*, **93**, 6112–6117.
- Logothetis, N.K. (2003) The underpinnings of the BOLD functional magnetic resonance imaging signal. *J. Neurosci.*, **23**, 3963–3971.
- McCormick, D.A. & Bal, T. (1997) Sleep and arousal: thalamocortical mechanisms. *Annu. Rev. Neurosci.*, **20**, 185–215.
- Mitzdorf, U. (1985) Current source-density method and application in cat cerebral cortex: investigation of evoked potentials and EEG phenomena. *Physiol. Rev.*, **65**, 37–100.
- Mitzdorf, U. (1987) Properties of the evoked potential generators: current source-density analysis of visually evoked potentials in the cat cortex. *Int. J. Neurosci.*, **33**, 33–59.
- Moeller, G., Einhäuser, W., Conrath, J. & König, P. (2003) Exploring the stability of the retinal image in the freely behaving cat. *Soc. Neurosci. Abstr.*, **38**, 5.
- Moeller, G., Kayser, C., Knecht, F. & König, P. (2002) Interactions of different types of eye movements in humans and cats. In *Annual Meeting of the German Physiological Society 2002*. Tuebingen, Germany, s310.
- Press, W., Teukolsky, S., Vetterling, W. & Flannery, B. (1992) *Numerical Recipes in C*, 2nd edn. Cambridge University Press, New York.
- Rager, G. & Singer, W. (1998) The response of cat visual cortex to flicker stimuli of variable frequency. *Eur. J. Neurosci.*, **10**, 1856–1877.
- Ritz, R. & Sejnowski, T.J. (1997) Synchronous oscillatory activity in sensory systems: new vistas on mechanisms. *Curr. Opin. Neurobiol.*, **7**, 536–546.
- Rols, G., Tallon-Baudry, C., Girard, P., Bertrand, O. & Bullier, J. (2001) Cortical mapping of gamma oscillations in areas V1 and V4 of the macaque monkey. *Vis. Neurosci.*, **18**, 527–540.
- Salinas, E. & Sejnowski, T.J. (2001) Correlated neuronal activity and the flow of neural information. *Nat. Rev. Neurosci.*, **2**, 539–550.
- Siegel, M. & König, P. (2003) A functional gamma-band defined by stimulus-dependent synchronization in area 18 of awake behaving cats. *J. Neurosci.*, **23**, 4251–4260.
- Tallon-Baudry, C., Bertrand, O., Peronnet, F. & Pernier, J. (1998) Induced gamma-band activity during the delay of a visual short-term memory task in humans. *J. Neurosci.*, **18**, 4244–4254.
- Woelbern, T., Eckhorn, R., Frien, A. & Bauer, R. (2002) Perceptual grouping correlates with short synchronization in monkey prestriate cortex. *Neuroreport*, **13**, 1881–1886.