

# LARGE-SCALE CORTICAL NETWORK COORDINATION: A PROPOSAL FOR THE NEURAL SUBSTRATE OF EXPECTANCY

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Optimal human behavior depends on the expectancy of future events based on perceptual analysis of an individual's present situation using knowledge gained from past experience. This article explores the proposition that the neural processes underlying perceptual analysis, knowledge retrieval, and expectancy are all integrated through the coordination of large-scale networks of the cerebral cortex. It is proposed that expectancy is created when local networks expressing knowledge of the likely future events associated with an individual's present situation are coordinated as part of large-scale networks expressing the totality of knowledge relations concerning the situation.

Keywords: Cerebral cortex; expectancy; neural network.

## 1. Knowledge Relations in the Cerebral Cortex

The behavioral responses of simple organisms are bound to evoking stimuli. In humans and other mammalian species, behavior has been freed from enslavement to the immediacy of the reflex response. Although a stimulus may not lead to an immediate response in mammals, it may nonetheless have a strong effect on subsequent behavior by modifying knowledge relations that are stored in the brain. These knowledge relations may then be used to guide behavior in the future.

It is generally accepted that complex large-scale anatomical networks of the cerebral cortex, comprised of a multitude of interconnected local area networks, provide a structural framework for the perceptual analysis of events in the external and internal environments, the retrieval of knowledge about meaningful attributes of those events, and the use of perception and retrieved knowledge to form expectancies of future events.<sup>1–3</sup> Yet, the manner in which the neural processes underlying perception, knowledge retrieval, and expectancy are integrated, and in particular how expectations arise from the interaction of perception and retrieved knowledge, is not well understood. The premise for this article derives from: (1) evidence showing

that perception and knowledge retrieval are complementary operations occurring in the same cortical networks;<sup>4,5</sup> (2) the understanding that expectancy comes about as the result of perceptual and knowledge retrieval operations in cortical networks; and (3) the postulate that the coordination of local area networks, interconnected in large-scale anatomical cortical networks, offers an attractive mechanism for integrating the operations underlying expectancy with those underlying perception and knowledge retrieval. The proposal is considered that expectations occur in coordinated large-scale cortical networks as the expression of knowledge of events that are likely within the overall context of knowledge relations evoked by perceptual analysis of the individual's present situation. It is proposed that the situation, consisting of entities and events of the external and internal environments as well as cognitive and emotional states of the brain, creates a situational context, and in response the brain creates a corresponding neural context for processes within the cerebral cortex.<sup>6</sup>

Knowledge resulting from perceptual analysis is generally thought to be stored in the form of modified synaptic connections within local neuronal networks of the cortex in extended large-scale cortical networks.<sup>7–10</sup> Knowledge storage depends on the creation of preferred pathways of communication between cortical neurons by way of the modulation of synaptic transmission at, and changes in the numbers of, active synapses.<sup>11</sup> By the principle of synchronous convergence,<sup>12, 13</sup> co-activation in close temporal proximity of cortical neurons during perception causes them to form functionally associated networks, so that subsequent activity in one part of the network facilitates activity throughout the network.

Functionally associated networks are formed at different spatial scales throughout the cortex, storing knowledge of many different kinds. In occipital, parietal and temporal cortices, cortical networks are formed for the storage of perceptual knowledge, and in the frontal cortex for the storage of executive knowledge. These networks store knowledge hierarchically within the different sensory systems: concrete, elementary sensory knowledge is stored in low-level unimodal networks, and knowledge of abstract facts and concepts resides in transmodel networks that sit at the highest synaptic levels of sensory-fugal processing in anterior temporal, posterior parietal, limbic, and paralimbic cortices.<sup>14, 15</sup> A similar hierarchical structure is thought to exist for the storage of knowledge relations in the executive system of the frontal cortex.

#### 2. Large-Scale Coordination of Cortical Knowledge Networks

It has been proposed that the coordination of large-scale cortical networks is critical for normal cognitive function.<sup>3,16</sup> Cortical network coordination refers to the harmonious and effective interaction of interconnected local neuronal networks. Local cortical networks have the ability to rapidly become engaged in cooperative actions lasting fractions of a second, and then to rapidly disengage to terminate those actions.<sup>17</sup> The large-scale dynamics of coordination controlling this propensity to rapid engagement and disengagement may result from maintenance of the cerebral cortex in a state of self-organized criticality.<sup>18, 19</sup> Coordination is thought to involve both coherent activity across distributed cortical local area networks, as well as the expression of informationally coherent spatial amplitude patterns of locally generated wave activity in those local area networks.<sup>20, 21</sup>

In the case of perception, it has been proposed that sensory input is processed within the context of pre-existing knowledge networks,<sup>22</sup> with the coordination of networks occurring in hierarchical and heterarchical spatial configurations relevant for the pattern and modality of the input. In conversation, for example, a listener views the face and hears the speech of a speaker. Visual and auditory networks are coordinated, as well as transmodal networks relating to the conceptual content of the speech. The coordination of these networks expresses the knowledge used for interpreting the speech.

There is evidence that the same distributed networks that are involved in perception are also involved in knowledge retrieval.<sup>4,23</sup> For example, retrieving knowledge concerning a previous conversation involves the same networks that were involved in originally perceiving the conversation. According to the theoretical framework of Damasio and colleagues,<sup>24–26</sup> high-level transmodal networks store conceptual knowledge in a non-explicit dispositional form. A high-level network that stores knowledge of a concept, catalyzes knowledge retrieval by activating lower-level sensory and motor networks that contain specific, concrete knowledge items associated with the concept. The conceptual knowledge stored in higherlevel networks is seen as a "code" for the particular lower-level areas that must be activated to re-establish the same patterns existing in the original perception. In keeping with this framework, but with knowledge retrieval described in terms of "coordination" rather than "activation," it is proposed here that the retrieval of knowledge stored during perception involves the re-coordination of cortical local area networks in the same spatial patterns that supported the original perception.

Anatomical large-scale networks are interconnected and extended throughout the cortex. Given that the interaction of a set of local area networks will tend to spread to other connected networks, the coordination of that set may further coordinate other assemblies that are associated with the original set.<sup>16</sup> This property raises the intriguing possibility that knowledge of the future may accompany knowledge of the present. In general, knowledge retrieval occurs within the context of the present situation of the individual. Certainly, the large-scale networks that are coordinated for perception and action in that situation include local area networks representing entities existing in the environment. In addition, through extended association, coordinated large-scale networks may encompass other local area networks representing knowledge associated with, but not representing, environmental entities, including associated knowledge of likely future events associated with the present situation. The coordination of local area networks expressing knowledge of likely future events into large-scale networks reflecting the present situation expresses the expectation that such events will occur. The strength of coordination may index the degree of likelihood of expectation.<sup>21</sup>

#### 3. Expectancy and the Perception-Action Cycle

Among the transmodal areas at the highest synaptic levels of sensory-fugal processing are regions of prefrontal and posterior parietal cortex.<sup>14</sup> The prefrontal cortex in particular has been implicated in the temporal organization of cognition and the retrieval of memories required for future behavior.<sup>22, 27</sup> Prefrontal and posterior parietal cortex together have been implicated in control of the perceptionaction cycle, whereby the brain creates hypotheses about the environment based on perceptual analysis and then directs actions into the environment to test those hypotheses.<sup>27, 28</sup> The perception-action cycle emerges in the brain as the result of the integration of perceptual analysis, occurring within the context of knowledge relations stored in posterior areas including posterior parietal cortex, with the execution of action plans, transpiring within the context of knowledge relations stored in frontal areas including prefrontal cortex.<sup>29</sup>

It often occurs in the perception-action cycle that only partial sensory information is available about the individual's situation, and additional information is required before an action can be generated. In those cases, a sensory event providing additional sensory information may be anticipated, and prior experience of the individual in similar situations may produce expectations of the content of the anticipated sensory event. Although the neural events underlying this process are not well understood, some inferences about them may be made. First, we may assume that local area networks throughout the cerebral cortex are coordinated for perceptual analysis, as well as for motor preparation and execution, during the perception-action cycle. Next, from evidence that both prefrontal and posterior parietal cortical regions exert top-down modulation on sensory areas during the anticipation of a sensory event,<sup>30–33</sup> we may infer that these high-level regions serve to catalyze the retrieval of knowledge used in the perception-action cycle by the top-down coordination of distributed local area networks that express specific, concrete sensory knowledge. Thus, networks in prefrontal and posterior parietal areas may be viewed as directing the coordination of sensory cortical areas that perform perceptual analysis and retrieve associated knowledge. This scenario is similar to Freeman's proposal<sup>29</sup> that "corollary discharges [from high-level cortical control regions] prime the sensory areas by making them selectively sensitive to ... expected stimuli." Critical to the present argument is the additional proposition that sensory areas are not only primed, but also express knowledge about anticipated sensory events. Furthermore, the knowledge of expected stimuli expressed in sensory areas is made consistent with the overall context of knowledge relations underlying the perception-action cycle by coordination of these sensory areas in the large-scale cortical networks driving that cycle. A similar idea is found in Freeman's proposal:<sup>29</sup> "macroscopic self-organized

goal states ... include perceptions of present states [and] projections of future states".

#### 4. Coordination by Phase Synchronization

Phase synchronization is a particular form of coordination in which the processes in different cortical neuronal assemblies come into temporal registration. It has been postulated that this temporal registration is functionally important for allowing neurons in different assemblies to effectively interact.<sup>35–40</sup> A large body of research on olfactory,<sup>41–45</sup> visual,<sup>46–51</sup> somatosensory,<sup>45</sup> auditory,<sup>45,52</sup> and motor<sup>53–57</sup> systems suggests that the coordination of cortical neuronal assemblies occurs through phase synchronization of neuronal assembly activity. Furthermore, extensive results showing phase synchronization between systems has been found for somatosensorimotor,<sup>58–60</sup> visuomotor,<sup>61,62</sup> visuotactile,<sup>63</sup> olfactorimotor,<sup>64</sup> and limbic<sup>65,66</sup> function, as well as high-level cognitive function.<sup>67–69</sup>

Phase synchronization of distributed cortical neuronal assembly activity has also been implicated in the anticipation of sensory stimuli.<sup>70, 71</sup> Based on these results, it was postulated that the anticipatory modulation of primary sensory cortex by higher-level sensory areas is carried by oscillatory phase synchronization.<sup>21, 72</sup> Supporting evidence for this postulate was found in the visual system of highly trained macaque monkeys, that self-initiated each trial by pressing a hand lever, indicating their readiness to perform the task. Synchronized assembly activity was observed to carry top-down anticipatory influences from extrastriate areas to the primary visual cortex (V1) in the prestimulus period.<sup>73</sup>

The observation of top-down anticipatory influences was based on spectral analysis performed in a 110 ms prestimulus period during which the monkey attended a blank display screen in anticipation of an impending visual stimulus. Figure 1(a) shows the prestimulus coherence spectrum of visual Local Field Potential (LFP) recordings from extrastriate and V1 cortical areas. Phase synchronization is indicated by the peak in the beta (14–30 Hz) frequency range. Figure 1(b) shows the corresponding prestimulus Granger Causality spectra, representing top-down (from extrastriate to V1) and bottom-up (from V1 to extrastriate) influences, with beta peaks in both the top-down and bottom-up Granger Causality spectra corresponding to the beta coherence peak. The correspondence between the highly significant top-down Granger Causality peak and the coherence peak supports the idea that top-down anticipatory modulation of primary visual cortex is carried by phasesynchronized oscillations. The peak in the bottom-up Granger Causality spectrum may be indicative of feedback from V1 to the extrastriate site.

The functional role of anticipatory top-down influences was tested by examining the relation of prestimulus top-down Granger Causality to subsequent processing of the visual stimulus in V1. The amplitudes of single-trial visual event-related potentials (VERPs) in V1 were estimated with a template-matching procedure<sup>74</sup> in which the single-trial VERP waveforms were matched to the average VERP waveform



Fig. 1. Prestimulus coherence (a) and Granger Causality (b) spectra for an extrastriate-V1 site pair. The coherence spectrum shows a prominent peak in the beta (14-30 Hz) frequency range. The Granger Causality spectra also show significant beta peaks in the top-down and bottom-up directions. The p < 0.01 significance thresholds are denoted by dotted lines for both the coherence and Granger Causality spectra.



Fig. 2. A representative single-trial VERP (dashed line) from a recording site in primary visual cortex (V1) is shown superimposed on the average VERP (solid line) computed over an ensemble of trials from the same site. The average VERP was treated as the "template" for template matching. The vertical lines mark the boundaries of the period used for the template-matching procedure. The amplitude of the single-trial VERP is 32% greater than that of the average VERP, and precedes it by 3 ms. The single-trial VERP amplitude was normalized to remove possible gain differences between the recording sessions that were combined to form the ensemble. Time zero is the onset time of the visual stimulus, which lasted 100 ms.

(the "template") in a 110 ms window extending from 35 ms to 145 ms poststimulus (Fig. 2). The ensemble of trials was then ordered according to the single-trial V1 VERP amplitude and divided into subensembles of 400 trials, with 75% overlap. The top-down and bottom-up Granger Causality spectra and the mean V1 VERP amplitude were calculated for each trial subensemble. The Spearman correlation was then computed between the magnitude of top-down and bottom-up Granger Causality peaks and the average V1 VERP amplitude over all subensembles.

Figure 3 shows the relation of top-down (a) and bottom-up (b) prestimulus betarange Granger Causality with poststimulus V1 VERP amplitude. The correlation between Granger Causality and V1 VERP amplitude was found to be significant in the top-down ( $\rho = 0.49, p < 0.005$ ), but not the bottom-up ( $\rho = 0.20, p < 0.1$ ), direction. The significant correlation for the top-down influence indicates that the magnitude of prestimulus top-down beta-range Granger Causality to the V1 site predicts the early VERP amplitude at that site. Thus the magnitude of the



Fig. 3. The relation of the mean subensemble VERP amplitude with the magnitude of the subensemble top-down beta-range Granger Causality peak (a), and with that of the subensemble bottom-up beta-range Granger Causality peak (b). The Spearman correlation is significant for the top-down relation ( $\rho = 0.49, p < 0.005$ ), but not for the bottom-up relation ( $\rho = 0.20, p < 0.1$ ).

top-down influence to a V1 neuronal assembly during anticipation of the visual stimulus predicts the magnitude of that assembly's response to the stimulus.

# 5. Conclusions

The main empirical conclusion here is that top-down anticipatory modulation of sensory cortex is carried by phase-synchronized oscillatory activity of neuronal assemblies. The result was derived from the study of coordinated LFP activity in the visual cortex of monkeys that were highly trained to expect (and respond to) a small set of visual stimuli. The limited examples demonstrated here reveal this coordinated activity in the form of coherence and Granger Causality spectra between extrastriate cortex and V1. Analysis of a more extended set of cortical recordings from the same monkeys has revealed that this extrastriate-V1 coordination reflects a large-scale coordinated network that encompasses sites in widely distributed cortical areas. Because of the monkeys' extended prior exposure to this stimulus set, it can be inferred that they possessed knowledge that the stimuli in the set were likely future events once they self-initiated the task trial. These empirical findings are thus taken to support the main proposition of this report that expectancy of the likely events associated with an individual's present situation are coordinated as part of large-scale cortical networks. It has previously been proposed that largescale networks in the cortex manifest global neurocognitive states.<sup>75</sup> Although very little work has been done to examine the dynamics of such large-scale neurocognitive states in the cerebral cortex, we infer that expectation may be described dynamically as a large-scale cortical state vector entering the vicinity of a stable attractor in state space.<sup>76</sup>

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## References

- 1. P. S. Goldman-Rakic, Topography of cognition: Parallel distributed networks in primate association cortex, Annu. Rev. Neurosci. 11 (1988) 137–156.
- M. M. Mesulam, Large-scale neurocognitive networks and distributed processing for attention, language, and memory, Ann. Neurol. 28 (1990) 597–613.
- 3. S. L. Bressler, Large-scale cortical networks and cognition, *Brain Res. Rev.* **20** (1995) 288–304.
- L. L. Chao, J. V. Haxby and A. Martin, Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects, *Nat. Neurosci.* 2 (1999) 913–919.
- W. K. Simmons, V. Ramjee, M. S. Beauchamp, K. McRae, A. Martin and L. W. Barsalou, A common neural substrate for perceiving and knowing about color, *Neuropsychologia* 20 (2007) 2802–2810.
- S. L. Bressler and A. R. McIntosh, The role of neural context in large-scale neurocognitive network operations, in *Springer Handbook on Brain Connectivity*, eds. V. K. Jirsa and A. R. McIntosh (Springer, New York, 2007), pp. 403–419.

- 7. D. O. Hebb, The Organization of Behavior (John Wiley and Sons, New York, 1949).
- 8. F. A. Hayek, The Sensory Order (University of Chicago Press, Chicago, 1952).
- 9. J. M. Fuster, Network memory, Trends Neurosci. 20 (1997) 451-459.
- 10. A. Ishai, Let's face it: It's a cortical network, Neuroimage. 40 (2008) 415-419.
- 11. J. M. Fuster, Cortical memory, Scholarpedia. 2 (2007) 1644.
- G. S. Stent, A physiological mechanism for Hebb's postulate of learning, in *Proc. Natl. Acad. Sci. USA* 70 (1973) 997–1001.
- 13. J. M. Fuster, *Memory in the Cerebral Cortex* (Oxford University Press, New York, 1999).
- 14. M. M. Mesulam, From sensation to cognition, Brain. 121 (1998) 1013–1052.
- A. Martin and L. L. Chao, Semantic memory and the brain: Structure and processes, *Curr. Opin. Neurobiol.* **11** (2001) 194–201.
- S. L. Bressler and J. A. Kelso, Cortical coordination dynamics and cognition, *Trends Cogn. Sci.* 5 (2001) 26–36.
- W. J. Freeman, A cinematographic hypothesis of cortical dynamics in perception, Int. J. Psychophysiol. 60 (2006) 149–161.
- W. J. Freeman, A field-theoretic approach to understanding scale-free neocortical dynamics, *Biol. Cybern.* 92 (2005) 350–359.
- W. J. Freeman, M. D. Holmes, G. A. West and S. Vanhatalo, Fine spatiotemporal structure of phase in human intracranial EEG, *Clin. Neurophysiol.* **117** (2006) 1228– 1243.
- W. J. Freeman, The wave packet: An action potential for the 21st century, J. Integr. Neurosci. 2 (2003) 3–30.
- S. L. Bressler, Inferential constraint sets in the organization of visual expectation, Neuroinformatics. 2 (2004) 227–238.
- 22. J. M. Fuster, *Cortex and Mind: Unifying Cognition* (Oxford University Press, New York, 2003).
- L. Nyberg, R. Habib, A. R. McIntosh and E. Tulving, Reactivation of encoding-related brain activity during memory retrieval, *Proc. Natl. Acad. Sci. USA* 97 (2000) 11120– 11124.
- 24. A. R. Damasio, Time-locked multiregional retroactivation: A systems-level proposal for the neural substrates of recall and recognition, *Cognition*. **33** (1989) 25–62.
- A. R. Damasio, The brain binds entities and events by multiregional activation from convergence zones, *Neural Netw.* 1 (1989) 123–132.
- A. R. Damasio and H. Damasio, Cortical systems for retrieval of concrete knowledge: The convergence zone framework, in *Large-Scale Neuronal Theories of the Brain*, eds. C. Koch and J. L. Davis (MIT Press, Cambridge, MA, 1994), pp. 61–74.
- D. H. Ingvar, "Memory of the future": An essay on the temporal organization of conscious awareness, *Hum. Neurobiol.* 4 (1985) 127–136.
- W. J. Freeman, Neurodynamic models of brain in psychiatry, *Neuropsychopharmacology*. 28 (Suppl. 1) (2003) S54-S63.
- W. J. Freeman, Indirect biological measures of consciousness from field studies of brains as dynamical systems, *Neural Netw.* 20 (2007) 1021–1031.
- R. Desimone, Neural mechanisms for visual memory and their role in attention, in Proc. Natl. Acad. Sci. USA 93 (1996) 13494–13499.
- M. Corbetta and G. L. Shulman, Human cortical mechanisms of visual attention during orienting and search, in *Proc. Natl. Acad. Sci. USA*. 353 (1998) 1353–1362.
- M. Corbetta and G. L. Shulman, Control of goal-directed and stimulus-driven attention in the brain, *Nat. Rev. Neurosci.* 3 (2002) 201–215.

- 33. M. Corbetta, G. Patel and G. L. Shulman, The reorienting system of the human brain: From environment to theory of mind, *Neuron.* 58 (2008) 306–324.
- W. J. Freeman, The place of 'codes' in nonlinear neurodynamics, *Prog. Brain Res.* 165 (2007) 447–462.
- E. Salinas and T. J. Sejnowski, Correlated neuronal activity and the flow of neural information, Nat. Rev. Neurosci. 2 (2001) 539–550.
- A. K. Sturm and P. Konig, Mechanisms to synchronize neuronal activity, *Biol. Cybern.* 84 (2001) 153–172.
- 37. R. W. Friedrich, C. J. Habermann and G. Laurent, Multiplexing using synchrony in the zebrafish olfactory bulb, *Nat. Neurosci.* 7 (2004) 862–871.
- P. Fries, A mechanism for cognitive dynamics: Neuronal communication through neuronal coherence, *Trends Cogn. Sci.* 9 (2005) 474–480.
- J. Gross, The role of neural oscillations in attention: Perspectives for computational models, *Neural Netw.* 19 (2006) 1445–1446.
- T. Womelsdorf, J. M. Schoffelen, R. Oostenveld, W. Singer, R. Desimone, A. K. Engel and P. Fries, Modulation of neuronal interactions through neuronal synchronization, *Science.* **316** (2007) 1609–1612.
- W. J. Freeman, Spatial properties of an EEG event in the olfactory bulb and cortex, Electroencephalogr. Clin. Neurophysiol. 44 (1978) 586–605.
- 42. W. J. Freeman and W. Schneider, Changes in spatial patterns of rabbit olfactory EEG with conditioning to odors, *Psychophysiol.* **19** (1982) 44–56.
- W. J. Freeman and G. Viana Di Prisco, Relation of olfactory EEG to behavior: Time series analysis, *Behav. Neurosci.* 100 (1986) 753–763.
- 44. C. M. Gray, W. J. Freeman and J. E. Skinner, Chemical dependencies of learning in the rabbit olfactory bulb: Acquisition of the transient spatial pattern change depends on norepinephrine, *Behav. Neurosci.* 100 (1986) 585–596.
- J. M. Barrie, W. J. Freeman and M. D. Lenhart, Spatiotemporal analysis of prepyriform, visual, auditory, and somesthetic surface EEGs in trained rabbits, *J. Neurophysiol.* **76** (1996) 520–539.
- W. J. Freeman and B. W. van Dijk, Spatial patterns of visual cortical fast EEG during conditioned reflex in a rhesus monkey, *Brain Res.* 422 (1987) 267–276.
- C. M. Gray, P. Konig, A. K. Engel and W. Singer, Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties, *Nature.* 338 (1989) 334–337.
- A. K. Engel, A. K. Kreiter, P. Konig and W. Singer, Synchronization of oscillatory neuronal responses between striate and extrastriate visual cortical areas of the cat, in *Proc. Natl. Acad. Sci. USA.* 88 (1991) 6048–6052.
- 49. W. Singer and C. M. Gray, Visual feature integration and the temporal correlation hypothesis, *Annu. Rev. Neurosci.* **18** (1995) 555–586.
- S. L. Bressler, Interareal synchronization in the visual cortex, *Behav. Brain Res.* 76 (1996) 37–49.
- C. M. Gray, The temporal correlation hypothesis of visual feature integration: Still alive and well, Neuron. 24 (1999) 111–125.
- F. W. Ohl, H. Scheich and W. J. Freeman, Change in pattern of ongoing cortical activity with auditory category learning, *Nature*. 412 (2001) 733–736.
- 53. S. N. Baker, J. M. Kilner, E. M. Pinches and R. N. Lemon, *Exp. Brain Res.* 128 (1999) 109–117.
- B. Feige, A. Aertsen and R. Kristeva-Feige, Dynamic synchronization between multiple cortical motor areas and muscle activity in phasic voluntary movements, J. Neurophysiol. 84 (2000) 2622–2629.

- 55. P. Brown and J. F. Marsden, Cortical network resonance and motor activity in humans, *Neuroscientist.* 7 (2001) 518–527.
- S. Salenius and R. Hari, Synchronous cortical oscillatory activity during motor action, Curr. Opin. Neurobiol. 13 (2003) 678–684.
- 57. A. Schnitzler, L. Timmermann and J. Gross, Physiological and pathological oscillatory networks in the human motor system, *J. Physiol. Paris.* **99** (2006) 3–7.
- V. N. Murthy and E. E. Fetz, Coherent 25- to 35-Hz oscillations in the sensorimotor cortex of awake behaving monkeys, *Proc. Natl. Acad. Sci. USA*. 89 (1992) 5670–5674.
- A. Brovelli, M. Ding, A. Ledberg, Y. Chen, R. Nakamura and S. L. Bressler, Beta oscillations in a large-scale sensorimotor cortical network: Directional influences revealed by Granger causality, *Proc. Natl. Acad. Sci. USA*. **101** (2004) 9849–9854.
- S. N. Baker, M. Chiu and E. E. Fetz, Afferent encoding of central oscillations in the monkey arm, J. Neurophysiol. 95 (2006) 3904–3910.
- S. L. Bressler, R. Coppola and R. Nakamura, Episodic multiregional cortical coherence at multiple frequencies during visual task performance, *Nature*. 366 (1993) 153–156.
- J. Classen, C. Gerloff, M. Honda and M. Hallett, Integrative visuomotor behavior is associated with interregionally coherent oscillations in the human brain, J. Neurophysiol. 79 (1998) 1567–1573.
- F. Hummel, C. Gerloff, Larger interregional synchrony is associated with greater behavioral success in a complex sensory integration task in humans, *Cereb. Cortex.* 15 (2005) 670–678.
- R. Hermer-Vazquez, L. Hermer-Vazquez, S. Srinivasan and J. K. Chapin, Beta- and gamma-frequency coupling between olfactory and motor brain regions prior to skilled, olfactory-driven reaching, *Exp. Brain Res.* 180 (2007) 217–235.
- L. M. Kay and W. J. Freeman, Bidirectional processing in the olfactory-limbic axis during olfactory behavior, *Behav. Neurosci.* **112** (1998) 541–553.
- K. F. Ahrens and W. J. Freeman, Response dynamics of entorhinal cortex in awake, anesthetized, and bulbotomized rats, *Brain Res.* 911 (2001) 193–202.
- 67. T. J. Buschman and E. K. Miller, Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices, *Science*. **315** (2007) 1860–1862.
- Y. B. Saalmann, I. N. Pigarev and T. R. Vidyasagar, Neural mechanisms of visual attention: How top-down feedback highlights relevant locations, *Science*. **316** (2007) 1612–1615.
- 69. P. Sehatpour, S. Molholm, T. H. Schwartz, J. R. Mahoney, A. D. Mehta, D. C. Javitt, P. K. Stanton and J. J. Foxe, A human intracranial study of long-range oscillatory coherence across a frontal-occipital-hippocampal brain network during visual object processing, *Proc. Natl. Acad. Sci. USA*. **105** (2008) 4399–4404.
- A. K. Engel, P. Fries and W. Singer, Dynamic predictions: Oscillations and synchrony in top-down processing, *Nat. Rev. Neurosci.* 2 (2001) 704–716.
- H. Liang, S. L. Bressler, M. Ding, W. A. Truccolo and R. Nakamura, Synchronized activity in prefrontal cortex during anticipation of visuomotor processing, *Neuroreport.* 13 (2002) 2011–2015.
- A. von Stein, C. Chiang and P. Konig, Top-down processing mediated by interareal synchronization, *Proc. Natl. Acad. Sci. USA*. 97 (2000) 14748–14753.
- S. L. Bressler, C. G. Richter, Y. Chen and M. Ding, Cortical functional network organization from autoregressive modeling of local field potential oscillations, *Stat. Med.* 26 (2007) 3875–3885.
- C. D. Woody, Characterization of an adaptive filter for the analysis of variable latency neuroelectric signals, *Med. Biol. Eng.* 5 (1967) 539–553.

- S. L. Bressler, The formation of global neurocognitive state, in *Neurodynamics of Cognition and Consciousness*, eds. L. I. Perlovsky and R. Kozma (Springer, New York, 2007), pp. 61–72.
- W. J. Freeman, Simulation of chaotic EEG patterns with a dynamic model of the olfactory system, *Biol. Cybern.* 56 (1987) 139–150.