

## CONCLUDING COMMENTARY

### Does Time Help to Understand Consciousness?

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#### INTRODUCTION

In response to our target paper on the possible role of temporal binding for consciousness (Engel et al., 1999), a number of arguments have been raised that, to varying degrees and on varying grounds, doubt the validity of our approach. To facilitate understanding of the key points in the debate, we will first summarize the essential statements of our paper. Subsequently, we will respond to the objections formulated in various contributions to this special issue (Gold, 1999; Hardcastle, 1999; Kurthen, 1999; Revonsuo, 1999; Vanni, 1999). A separate section of our commentary is devoted to the paper authored by Zeki & Bartels (1999), which describes an alternative view on the relation between binding and consciousness.

The hypothesis discussed in our target paper can be summarized as follows. The key idea is that synchronization on a millisecond time scale may serve to express specific relations in distributed activity patterns and, thus, accomplishes dynamic binding of information carried by different network elements. Such a mechanism has the advantage that it raises jointly and with high temporal resolution the saliency of coherent subsets of signals, because downstream neuronal populations respond better to synchronized than to temporally dispersed spikes. For this reason, it is ideally suited to mediate selective transmission of coherent responses and, thus, for gating the access of relevant signals to phenomenal consciousness. As described in our paper, a large body of evidence has accumulated which supports the notion that response synchronization is involved in selection and binding of distributed responses. In particular, our study of binocular rivalry in awake cats (Fries et al., 1997) suggests that synchronization is involved in gating access of signals to awareness. In primary visual cortex synchronization of neuronal responses, rather than average activity levels, was found to correlate with the perceptual selection of signals. Together with recent evidence obtained in humans (Herrmann et al., 1999; Müller et al., 1997; Revonsuo et al., 1997; Rodriguez et al., 1999; Tallon et al., 1995), these data suggest that only well-synchronized neuronal responses can contribute to perception

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and that synchrony may be one of the necessary conditions for the occurrence of awareness.

Interestingly, almost all authors contributing to this special issue seem to agree that (i) there are binding problems at both the phenomenal and the physiological level (Gold, 1999; Newman & Grace, 1999; Revonsuo, 1999; Sauvé, 1999; Smythies, 1999; Zeki & Bartels, 1999), (ii) that timing of neural signals may be a plausible solution to at least some binding problems (Gold, 1999; Newman & Grace, 1999; Revonsuo, 1999; Sauvé, 1999), and (iii) that solving the issue of binding and response selection may be critical for understanding the neural correlate(s) of consciousness (Newman & Grace, 1999; Revonsuo, 1999; Sauvé, 1999; Zeki & Bartels, 1999). However, the present collection of papers illustrates that there are quite divergent views on what precisely the nature of the binding problem is (Revonsuo, 1999; Smythies, 1999) and on how to understand exactly the possible relation between synchronization phenomena and phenomenal consciousness (Gold, 1999; Hardcastle, 1999; Kurthen, 1999; Revonsuo, 1999).

### REPLY TO OBJECTIONS

In the following, we consider the objections directly addressing the validity of our approach and the conclusions drawn from our rivalry experiment (Fries et al., 1997).

*Objection 1 (Kurthen): Data of the kind obtained in the rivalry experiment can, at best, contribute to explaining conscious behavior, but not consciousness itself. Physiological measurements cannot account for the phenomenal properties of subjective experience.*

In his commentary, Kurthen (1999) emphasizes the distinction between “conscious behavior” and phenomenal consciousness “itself.” Whereas the former constitutes the third-person aspect, i.e., behavioral patterns (including verbal reports) that usually justify the assignment of conscious mental states to a subject, the latter refers to the first-person perspective on phenomenal states that are entirely in the subject’s privacy. He argues that, by necessity, neuroscientific approaches make reference to conscious states only via behavioral data and, thus, they can only account for variables captured by the third-person perspective. Essentially, this is a version of the well-known “explanatory gap” argument (Levine, 1983), and we cannot but agree with Kurthen’s demand for caution with respect to the explanatory power of current neurobiological approaches. Possibly, one should indeed replace, in the current debate, the term “neural correlates of consciousness (NCC)” by the notion “neural correlates of conscious behavior (NCCB).”

At this point, we wish to add three remarks. First, being aware of the “hard problem” of potential explanatory gaps, we have been careful enough to emphasize that models of temporal binding can, at best, reveal *necessary* components of NCCB. This, by no means, excludes that additional factors are relevant to a theory of NCCB (as with, e.g., rate changes of neurons in inferotemporal visual cortex). Second, on philosophical grounds (e.g., Wittgenstein’s famous private-language argument; see Kripke, 1982), it has been doubted that there really are “private facts” about a subject’s mental life that, in principle, are bound to escape a third-person account. Possibly, the hard problem softens if one decides to dismiss the notion of *strictly private*

phenomenal properties in favor of the assumption that phenomenal states may be amenable to a relational or functional analysis (e.g., Dennett, 1990). If so, a theory about NCCB might finally be coextensive with a theory about NCC. Third, as Kurthen and colleagues have argued elsewhere (Kurthen et al., 1998), neurobiological research may itself contribute to changing the explananda for a NCC theory, i.e., to modifications in our understanding of the essential features of “consciousness itself.” As Kurthen et al. emphasize, all versions of the explanatory gap argument ultimately rest on *intuitions* about subjective phenomenal features that possibly might be missed by scientific approaches. However, such intuitions, which are largely imported from a prescientific discourse into the philosophical debate, may well change over time under the influence of scientific developments. This, in turn, might finally make the “gap” less conspicuous than currently assumed.

*Objection 2 (Gold): The rivalry experiment does not disentangle binding and consciousness. Thus, we cannot decide whether synchronized oscillations are just required for binding or whether they are indeed necessary for consciousness.*

Gold argues that our conclusions are “confounded by the fact that a conscious percept is always also a percept that is bound” (1999). Thus, he suggests, we cannot take the data as evidence that synchrony is a prerequisite for the selection of information during the buildup of phenomenal states. Indeed, it seems difficult to imagine cases of conscious perception which do not entail binding in the sense described in our target paper. The reason is simply that consciously perceiving always also implies being aware of phenomenal *structure*, i.e., of *relations* of some sort between phenomenal items. However, the inverse does not necessarily hold true—there seem to be cases of binding without consciousness as suggested, e.g., by priming and pattern completion effects in blindsight or spatial hemineglect (for review, see Farah, 1997). Thus, Gold is possibly wrong in assuming that “it is not clear whether the relation between binding and consciousness can in fact be disentangled. . . .” Apart from that, Gold’s objection seems to imply a misunderstanding of the core of our argument. We are suggesting, in fact, that there *is* a close relation between binding and consciousness, precisely because temporal binding is a way to accomplish selection, and selection (at least in our view) is necessary for awareness. A second, but less important misreading is that—contrary to what Gold surmises—we are *not* proposing a “40-Hz thesis.” As we have made explicit in our target paper, synchrony is the essential feature at stake, and there is no a priori restriction to oscillations, because nonoscillatory signals can also be synchronized and used for response selection. Yet, it is true that de facto there is a clear association between perceptual selection and gamma-oscillations (Fries et al., 1997; Rodriguez et al., 1999; Tallon et al., 1995). As we have argued elsewhere (König et al., 1995), oscillations in this frequency range may be particularly suitable for setting up long-range synchronization. Thus, they may indeed be important for establishing representational patterns that are coherent across areas and even different neural systems, which, in turn, is very likely among the requirements for consciousness.

*Objection 3 (Hardcastle): The rivalry experiment does not show that synchrony is causally relevant for consciousness; it just demonstrates that synchrony indexes consciousness. Rather than being directly involved in establishment of conscious states, synchrony could be a mere*

*distal cause, or it could just reflect the activity of some other mechanism creating perceptual awareness.*

Hardcastle's (1999) objection is twofold: first, she argues that the correspondence between synchrony and perceptual selection observed in our rivalry experiment does not justify the conclusion that synchrony is part of the NCC (or NCCB, respectively). Synchrony might just be a "distal" causal factor involved in consciousness—just as, say, glucose uptake and oxygen supply, which are both unavoidably necessary but presumably not *directly* relevant for the buildup of phenomenal states. Second, while agreeing with our assumption that attention, working memory, and structured representations are important prerequisites for awareness (cf. Introduction of Engel et al., 1999), she claims that our experimental paradigm does not involve any of these phenomena and, thus, our approach cannot help in elucidating the possible role of synchrony for consciousness. Both objections are worth consideration.

Certainly, the rivalry experiment does not prove the causal relevance of synchrony for perceptual selection. To achieve this, a manipulative approach would be needed where synchrony could be selectively abolished without perturbation of any other computationally relevant features of neural activity. Unfortunately, it is very unlikely that such an experiment can be performed in vertebrates in the near future. However, recent studies in insects have shown that selective blocking of synchrony (achieved by pharmacological measures) without accompanying changes of average neuronal firing rates impairs the animal's capacity for sensory discrimination (MacLeod & Laurent, 1996). Similarly, both our studies on binocular rivalry (Fries et al., 1997) and on cats with strabismic amblyopia (Roelfsema et al., 1994) show a selective correspondence between synchrony and perceptual states, while other parameters such as strength of neural responses or neural tuning properties do not bear such a relation. It is obviously true that most of the available evidence (Engel et al., 1999; see also Sauv e, 1999) comes from correlative approaches. Still, these data suggest that synchrony is among the good candidates for the NCCB.

We also agree only partly with Hardcastle's second argument. She correctly points out that attention and working memory were not explicitly controlled as variables in our experiment. It should be emphasized, however, that this does not necessarily imply that these capacities are not involved in the rivalry situation. Moreover, there is evidence from other studies that synchrony is enhanced during attentive processing of stimuli (Rougeul et al., 1979; Roelfsema et al., 1997; Steinmetz et al., 1998) and during tasks involving working memory (Nakamura et al., 1992; Sarnthein et al., 1998). Contrary to what Hardcastle claims, the third item on the list of prerequisites for awareness, i.e., structured representations, does very likely play a role in the rivalry paradigm, because tracking the patterns used in our study requires binding of local features into a pattern of coherently moving contours. Indeed, the occurrence of binding is precisely what our physiological results suggest, because synchrony is observed only for the pattern which is tracked by the animal. Taken together, we do not share Hardcastle's pessimistic belief that the conceptual "framework [we] use does not cohere with the data."

*Objection 4 (Revonsuo): The rivalry experiment may reflect stimulus-related binding rather than consciousness-related binding. Synchrony may help to organize perceptual information,*

*but it is not clear whether synchronization is necessary to maintain stable states of perceptual awareness.*

The most challenging part of Revonsuo's contribution (1999) is based on an experiment his group has recently performed, suggesting that gamma-synchronization may be particularly strong during transfer of perceptual information into consciousness, but not during maintenance of awareness. In this study (Revonsuo et al., 1997) gamma-band responses were recorded from subjects during fusion of random-dot stereograms. Revonsuo concludes that "40-Hz synchronization . . . seems to participate in the construction of a unified percept, but not in the continuous viewing of the same stimulus once it has been constructed. . . ." These results seem to tie in very nicely with our suggestion that synchrony is of particular importance during the selection process and in instances which require disambiguation of sensory information. However, the observation that gamma-synchronization did not differ, during continuous viewing, between coherent and incoherent stimulus arrangements is—at first glance—somewhat surprising and seems to be in conflict with other recent EEG studies that have used conceptually similar approaches (Tallon et al., 1995). Possibly, several factors account for this: First, subjects were presumably highly trained and, due to knowing in advance the percept that they had to establish, the task actually involved relatively little need for disambiguation. Since the constant viewing condition itself did not involve establishment of new relations in phenomenal space, it is conceivable that other coding strategies may have been dominating. Second, the contents of the percept were of no relevance to the task. Possibly, enhanced synchrony would be observed if the subjects were forced to attentively discriminate objects during the viewing condition, rather than always seeing the same object after fusion of the random-dot stereograms has occurred. It would be interesting to repeat the experiment with such a modification of the task. Third, the authors evaluated only relative changes in gamma-power at their electrodes. However, in addition to local spectral changes it would presumably be highly relevant to consider coherence across electrodes in different frequency bands (cf. Sarnthein et al., 1998; Rodriguez et al., 1999). At least from the animal studies available one would predict that strong coherence changes are possible without major changes in local power distribution.

*Objection 5 (Vanni): Based on physiological and psychophysical evidence, it can be doubted that synchrony subserves a binding function. Presumably, synchrony just reflects anatomical connections between cells. Furthermore, it can be doubted that there is a binding problem at all, so synchrony would not even be needed.*

Clearly, Vanni (1999) presents the most skeptical of all objections raised in this issue, since he questions not only the relevance of temporal selection for consciousness, but also a role of synchrony for binding and, even more radically, a need for binding altogether. At this point, it would be inappropriate to replicate the whole series of arguments in favor of the two latter notions, as presented in our target article (Engel et al., 1999) and complemented by the review of supportive evidence in the contributions by Sauv e (1999), Gold (1999), and Newman & Grace (1999). Thus, we restrict ourselves to some brief comments: First, the recent study by Lamme & Spekreijse (1998) does indeed not provide convincing evidence in favor of binding by synchrony in monkey striate cortex. However, it also does not disprove the notion

because, on the one hand, there is a change in induced synchrony with large orientation differences between figure and ground and, on the other hand, the study is not free of methodological problems (such as, e.g., including only broadly tuned units which must respond to a wide variety of different orientations while using orientation as the discrimination cue). Moreover, even if methodologically flawless, their results would invalidate the notion of temporal binding only under the assumption that V1 (where the recordings were exclusively taken from) *alone* should be capable of solving the binding problem. In this context, it should be emphasized that other groups have, in fact, provided very clear evidence for stimulus-specific synchronization in monkey V1 (Livingstone, 1996; Friedman-Hill et al., 1999; Maldonado et al., 1999). Second, Vanni cites one of the recent studies by Murthy & Fetz (1996a) as counterevidence. What he does not cite is the companion paper (Murthy & Fetz, 1996b) which describes the relation of oscillations and synchrony to behavior. The study clearly demonstrates an enhancement of both local and long-range coherence during exploratory movements, particularly those requiring somatosensory feedback. Third, Vanni suggests that synchrony merely reflects anatomical connections between cells, thus expressing the viewpoint of classical cross-correlation analysis. Obviously, synchrony is mediated by the underlying anatomy, but as discussed at length elsewhere (e.g., Singer & Gray, 1995; Singer et al., 1997; Engel et al., 1997), the dynamics are far too complicated to be compatible with such a simplified hypothesis. Overwhelming evidence shows that the temporal dynamics is not stereotyped, but critically influenced by stimulus coherence, modulatory systems, and behavioral states. Fourth, Vanni argues that a binding problem does not arise because there is functional specialization in the cortex and, thus, “we probably need distinct brain areas to represent the attended visual object and its background.” We do not share this intuition because the high degree of functional specialization is, in our view, actually one of the major sources of binding problems, and there are good reasons to believe that attention does not provide a solution to the binding problem but, conversely, binding and segmentation are prerequisites for attentional selection processes (Singer & Gray, 1995; Singer et al., 1997; Engel et al., 1997).

### COMMENTS ON ZEKI & BARTELS

The paper on a “theory of visual consciousness” by Zeki & Bartels (1999) describes an alternative view on integrative processes in the visual system and on the relation between binding and consciousness. Given the richness of their proposal, the paper deserves a more extensive discussion than we can accomplish here, and we regretfully confine our commentary to a few key aspects of the paper that contrast with our view: (i) In the first part of their paper, Zeki & Bartels discuss the modular organization of the visual system and the role of different types of connections in such a hierarchical–parallel architecture. While we agree with most of their statements regarding this point, we find their conclusion surprising that “lateral connections . . . do not appear to bring about the integration of different submodalities” (Proposition 3). There is substantial evidence that these lateral connections mediate synchrony within and between areas (for review, see Singer & Gray, 1995; Engel et al., 1997) and, thus, it seems not unreasonable to hypothesize that they are well suit-

able for integration of different modules operating in parallel. (ii) The authors propose that each specialized node in the system can create a conscious percept on its own in the respective feature domain. To denote this, they introduce the term “microconsciousness” (Propositions 9 and 11). Binding between modules, then, is “postconscious” (as they phrase it) because it just brings together the contents of the respective microconsciousnesses, but does not per se help to establish awareness. We are skeptical as to the usefulness of this notion of microconsciousness for at least two reasons. First, there seems to be broad consensus in the philosophical debate that consciousness (or, if one prefers, conscious behavior—cf. above) can meaningfully only be ascribed at the personal level, i.e., at a level where the actions of the cognitive system as a whole become manifest. Ascribing multiple consciousnesses at the subpersonal level means running into the “homuncular fallacy” that has been diagnosed on similar occasions by Kenny (1984). Second, conscious behavior very likely must be understood as a result of a large-scale integrative process operating on many subsystems which include not only sensory systems, but also premotor and motor areas, prefrontal cortex, limbic structures, and basal ganglia (for review, see Newman & Grace, 1999). Therefore, introducing the notion of multiple small-scale consciousnesses may obscure, rather than elucidate, the phenomena in question. Nonetheless, we agree with one of the intuitions that motivate the author’s proposal: it is certainly true that “large-scale consciousness” is not a homogeneous all-or-nothing phenomenon since it can, under both natural and pathological conditions, be graded and fragmented. Thus, presumably, Zeki & Bartels are correct in pointing out that the philosophical notion of “homogeneity” or “unity” of phenomenal consciousness itself requires more elaboration (see also Metzinger, 1995). (iii) In part, the notion of modularity of consciousness as described by the authors is motivated by recent psychophysical experiments in which they demonstrate that information in different visual submodalities such as color or motion can be perceived with temporal offsets (Moutoussis & Zeki, 1997). From this they conclude that the subsystems participating in the generation of consciousness are “fairly autonomous of one another” (Proposition 15). Yet, there can be little doubt that, as the final result of integration across subsystems, we do correctly bind the different features that have been processed in parallel. At this point, the authors do not offer a clear solution but admit that their theory “. . . leaves us with the grand problem of how, in physiological terms, the microconsciousnesses are bound together.” Indeed, as we have suggested, this is precisely the point where temporal binding may enter the stage.

## CONCLUSION

In our view, the papers collected in this issue display a surprising degree of agreement with respect to basic premises. Thus, most authors subscribe to the view that binding may be among the prerequisites for awareness and that synchrony could be a way of accomplishing binding and enabling perceptual selection. As we have tried to show, there is substantial experimental support for this notion, and the studies reviewed by Sauvé (1999) and Newman & Grace (1999) further add to this evidence. Not unexpectedly, there is substantial disagreement with respect to the assessment of our rivalry experiment and of the conclusions that potentially can be drawn from

this approach. However, what the present data seem to demonstrate at least is—as Hardcastle (1999) puts it—that synchrony “indexes” perceptual awareness. Whether it can actually do more than that remains a challenging question for future experiments.

## REFERENCES

- Dennett, D. C. (1990). Quining qualia. In W. G. Lycan (Ed.) *Mind and Cognition*, pp. 519–547. Oxford: Blackwell.
- Engel, A. K., Roelfsema, P. R., Fries, P., Brecht, M., & Singer, W. (1997). Role of the temporal domain for response selection and perceptual binding. *Cerebral Cortex*, **7**, 571–582.
- Engel, A. K., Fries, P., König, P., Brecht, M., & Singer, W. (1999). Temporal binding, binocular rivalry, and consciousness. *Consciousness and Cognition*, **8**.
- Farah, M. J. (1997). Visual perception and visual awareness after brain damage: A tutorial overview. In N. Block, O. Flanagan, & G. Güzelidere (Eds.) *The Nature of Consciousness*, pp. 203–236. Cambridge, MA: MIT Press.
- Friedman-Hill, S., Maldonado, P. E., & Gray, C. M. (1999). Temporal dynamics of neuronal activity in the striate cortex of alert macaque: I. Incidence and stimulus-dependence of oscillations. *Journal of Neuroscience*, in press.
- Fries, P., Roelfsema, P. R., Engel, A. K., König, P., & Singer, W. (1997). Synchronization of oscillatory responses in visual cortex correlates with perception in interocular rivalry. *Proceedings of the National Academy of Sciences USA*, **94**, 12699–12704.
- Gold, I. (1999). Does 40-Hz oscillation play a role in visual consciousness? *Consciousness and Cognition*, **8**.
- Hardcastle, V. G. (1999). On being importantly necessary for consciousness. *Consciousness and Cognition*, **8**.
- Herrmann, C. S., Mecklinger, A., & Pfeifer, E. (1999). Gamma responses and ERPs in a visual classification task. *Electroencephalography and Clinical Neurophysiology*, in press.
- Kenny, A. (1984). *The Legacy of Wittgenstein*. Oxford: Blackwell.
- König, P., Engel, A. K., & Singer, W. (1995). The relation between oscillatory activity and long-range synchronization in cat visual cortex. *Proceedings of the National Academy of Sciences USA*, **92**, 290–294.
- Kurthen, M., Grunwald, T., & Elger, C. E. (1998). Will there be a neuroscientific theory of consciousness? *Trends in Cognitive Sciences*, **2**, 229–234.
- Kurthen, M. (1999). Conscious behaviour explained. *Consciousness and Cognition*, **8**.
- Kripke, S. A. (1982). *Wittgenstein on Rules and Private Language. An Elementary Exposition*. Oxford: Blackwell.
- Lamme, V. A. F., & Spekreijse, H. (1998). Neuronal synchrony does not represent texture segregation. *Nature*, **396**, 362–366.
- Levine, J. (1983). Materialism and qualia: The explanatory gap. *Pacific Philosophical Quarterly*, **64**, 354–361.
- Livingstone, M. S. (1996). Oscillatory firing and interneuronal correlations in squirrel monkey striate cortex. *Journal of Neurophysiology*, **75**, 2467–2485.
- MacLeod, K., & Laurent, G. (1996). Distinct mechanisms for synchronization and temporal patterning of odor-encoding neural assemblies. *Science*, **274**, 976–979.
- Maldonado, P. E., Friedman-Hill, S., & Gray, C. M. (1999). Temporal dynamics of neuronal activity in the striate cortex of alert macaque: II. Short- and long-range temporally-correlated activity. *Journal of Neuroscience*, in press.
- Metzinger, T. (1995). Faster than thought. Holism, homogeneity and temporal coding. In T. Metzinger (Ed.), *Conscious Experience*, pp. 425–461. Paderborn: Schöningh.

- Moutoussis, K., & Zeki, S. (1997). Functional segregation and temporal hierarchy of the visual perceptive systems. *Proceedings of the Royal Society London B*, **264**, 1407–1414.
- Müller, M. M., Junghöfer, M., Elbert, T., & Rockstroh, B. (1997). Visually induced gamma-band responses to coherent and incoherent motion: A replication study. *Neuroreport*, **8**, 2575–2579.
- Murthy, V. N., & Fetz, E. E. (1996a). Oscillatory activity in sensorimotor cortex of awake monkeys: Synchronization of local field potentials and relation to behavior. *Journal of Neurophysiology*, **76**, 3949–3967.
- Murthy, V. N., & Fetz, E. E. (1996b). Synchronization of neurons during local field potential oscillations in sensorimotor cortex of awake monkeys. *Journal of Neurophysiology*, **76**, 3968–3982.
- Nakamura, K., Mikami, A., & Kubota, K. (1992). Oscillatory neuronal activity related to short-term memory in monkey temporal pole. *Neuroreport*, **3**, 117–120.
- Newman, J., & Grace, A. A. (1999). Binding across time: The selective gating of frontal and hippocampal systems modulating working memory and attentional states. *Consciousness and Cognition*, **8**.
- Revonsuo, A., Wilenius-Emet, M., Kuusela, J., & Lehto, M. (1997). The neural generation of a unified illusion in human vision. *Neuroreport*, **8**, 3867–3870.
- Revonsuo, A. (1999). Binding and the phenomenal unity of consciousness. *Consciousness and Cognition*, **8**.
- Rodriguez, E., George, N., Lachaux, J.-P., Martinerie, J., Renault, B., & Varela, F. J. (1999). Perception's shadow: Long-distance synchronization of human brain activity. *Nature*, **397**, 430–433.
- Roelfsema, P. R., Engel, A. K., König, P., & Singer, W. (1997). Visuomotor integration is associated with zero time-lag synchronization among cortical areas. *Nature*, **385**, 157–161.
- Rougeul, A., Bouyer, J. J., Dedet, L., & Debray, O. (1979). Fast somato-parietal rhythms during combined focal attention and immobility in baboon and squirrel monkey. *Electroencephalography and Clinical Neurophysiology*, **46**, 310–319.
- Sarnthein, J., Petsche, H., Rappelsberger, P., Shaw, G. L., & von Stein, A. (1998). Synchronization between prefrontal and posterior association cortex during human working memory. *Proceedings of the National Academy of Sciences USA*, **95**, 7092–7096.
- Sauvé, K. (1999). Gamma-band synchronous oscillations: Recent evidence regarding their functional significance. *Consciousness and Cognition*, **8**.
- Singer, W., & Gray, C. M. (1995). Visual feature integration and the temporal correlation hypothesis. *Annual Review of Neuroscience*, **18**, 555–586.
- Singer, W., Engel, A. K., Kreiter, A. K., Munk, M. H. J., Neuenschwander, S., & Roelfsema, P. R. (1997). Neuronal assemblies: Necessity, significance, and detectability. *Trends in Cognitive Sciences*, **1**, 252–261.
- Smythies, J. (1999). Consciousness: Some basic issues—A neurophilosophical perspective. *Consciousness and Cognition*, **8**.
- Steinmetz, P. N., Roy, A., Fitzgerald, P., Hsiao, S. S., Niebur, E., & Johnson, K. O. (1998). Synchronous firing in the second somatosensory cortex (SII) covaries with the attentional state of alert monkey. *Society for Neuroscience Abstracts*, **24**, 1513.
- Tallon, C., Bertrand, O., Bouchet, P., & Pernier, J. (1995). Gamma-range activity evoked by coherent visual stimuli in humans. *European Journal of Neuroscience*, **7**, 1285–1291.
- Vanni, S. (1999). Neural synchrony and dynamic connectivity. *Consciousness and Cognition*, **8**.
- Zeki, S., & Bartels, A. (1999). Towards a theory of visual consciousness. *Consciousness and Cognition*, **8**.

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