

MULTIMODAL BRAIN NETWORKS: INTEGRATION BY SYNCHRONIZATION

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Abstract

Cognitive processes, including those important in psychophysics, arise from the coordinated activity of multiple brain regions. Such transient functional integration is especially critical in multimodal processing, for example audio-visual speech perception, or cross-modality attention orienting. We describe briefly a general theory of how such functional coupling is implemented by synchronization of the neural activity in the relevant brain areas at specific frequencies, and give examples of empirical work in audio-visual speech perception and cross-modal attention orienting to support the theory. The empirical work emphasizes phase-synchronous gamma-oscillatory networks that are transiently activated either by the perception of audiovisual speech asynchrony or by the orienting of attention in one sensory modality caused by the appearance of a cue in a different sensory modality.

In recent years Fechner's conceptualization of an inner psychophysics has been given more plausibility by the elucidation of the functional anatomy of the brain using brain imaging technologies such as fMRI and PET. The subtraction technique has been particularly illuminating, whereby a brain region that is more active than others when a specific cognitive task is accomplished, compared to its activity during a baseline task, can be identified with a specific processing stage or function. This technique identifies necessary brain regions, but unfortunately it does not identify all of the brain regions involved in a given cognitive process; those that are common to the baseline task and the studied task are subtracted out. Analysis techniques such as those tracing functional and effective connectivity can sometimes identify a brain network, but even those suffer two major limitations. First, they are based on correlational methods and thus causal interactions and their direction are only inferred. Second, the temporal resolution of such methods is insufficient to record the fast interactions which have been revealed by studies utilizing implanted electrodes in animals and in human patients, especially the reciprocal interactions that have been argued to be critical for cognitive processes such as visual awareness (e.g., Lamme & Roelfsema, 2000). EEG and MEG, conversely, excel in the role of elucidating the dynamic interactions between often distant brain regions that implement cognitive processes such as attention and consciousness because they record brain activity on a millisecond timescale. Using these and other tools, it has been discovered that synchronous oscillations, on both local and global scales, are likely to be the mechanism by which the brain is able dynamically to assign functional connectivity between neural populations in order to flexibly express the plethora of perceptions and specific cognitive acts that characterize the adaptive brain (e.g., Salinas & Sejnowski, 2001; Varela et al, 2001; Ward, 2003). Moreover, it has been argued that studying multisensory interactions is a fertile approach to understanding such functional integration in the brain (e.g., Macaluso & Driver, 2005), because in such interactions several modality-specific and multimodal brain regions must interact in complex ways to exchange and integrate sensory and cognitive information. In this paper we describe two such multisensory interaction systems and their associated neural synchrony.

General theoretical considerations for functional integration via neural synchrony

A general theory of functional integration of brain regions via neural synchrony requires that several mechanisms be specified. First, the relevant brain networks must be described. Second, their order of activation, and/or recurrent or resonant processing modes, must be determined. Third, the effects of neural synchrony on information exchange must be described. Fourth, the specific mechanism(s) by which synchrony (phase locking) is attained, and that by which it is broken (phase scattering) must be described. To accomplish all of these, or even a subset, in this paper, or probably any single paper, is impossible. We will indicate here only a sketch of how such a theory would appear.

As discussed already, fMRI among other techniques, is illuminating at least part of the functional anatomy of the brain. Although a few functional networks have been identified, there is still a paucity of information about them, including the necessary areas that are common to both baseline and experimental tasks, and especially their subcortical components, which seldom appear in published reports. Two such incomplete networks are described briefly in what follows; both involve multimodal processing.

Most networks will involve recurrent processing, as adaptive resonance is achieved between hierarchically arranged processing stages. In others a feedforward sweep will be identifiable in specific experimental situations, and neural synchrony should appear between the relevant brain regions in a specific time order. An example of this is the feedforward sweep from sensory reception, to thalamus, to primary and secondary sensory cortex, to various association areas, reported by Drewes et al. (2006). In this study significant coherence of the EEG followed exactly the time course of the feedforward sweep.

Salinas & Sejnowski (2001) have begun to describe the ways in which neural synchrony can affect the flow of neural information. In particular, they have described the way in which correlated neural input can affect downstream activity. It is not simple: input correlations can act as a switch, can enhance gain, can change overall firing rates, and can change correlations in the target population. Any of these effects could be important for the communication of information in the brain.

Finally, there are several mechanisms by which neural synchrony can be attained. Some involve reciprocal excitatory or inhibitory connections between groups of oscillating neurons, whereas others involve sending simultaneous spikes to all neurons in a population that is to be synchronized. Any of these mechanisms might be involved in particular interactions, although timing considerations might determine which is used for particular cognitive tasks. Sending simultaneous spikes is the fastest mechanism, and might be required for long distance synchronization, although it is known that local synchrony in an interconnected oscillating population can be achieved within one or a few cycles. At present measurements of long-range synchrony do not suffice to determine the mechanism.

Audio-visual integration

Doesburg et al. (in press) recorded 62-channel EEG at 500 Hz while subjects were exposed to either perceptually congruent audiovisual speech (*congruent* trials - 30 ms offset between continuous auditory and visual streams) or perceptually incongruent (*incongruent* trials - 300 ms offset). Subjects had to press one keyboard key if the presented audio and video streams were congruent and another if they were incongruent, after each randomly-chosen 2-sec segment had terminated. The scalp current densities from filtered (1-Hz intervals) EEG records from 19 distantly-spaced electrodes for correctly identified trials were analysed for synchrony by calculating the analytical signal using the Hilbert transform, which yields instantaneous amplitude and phase for each sample point. Phase locking values were then

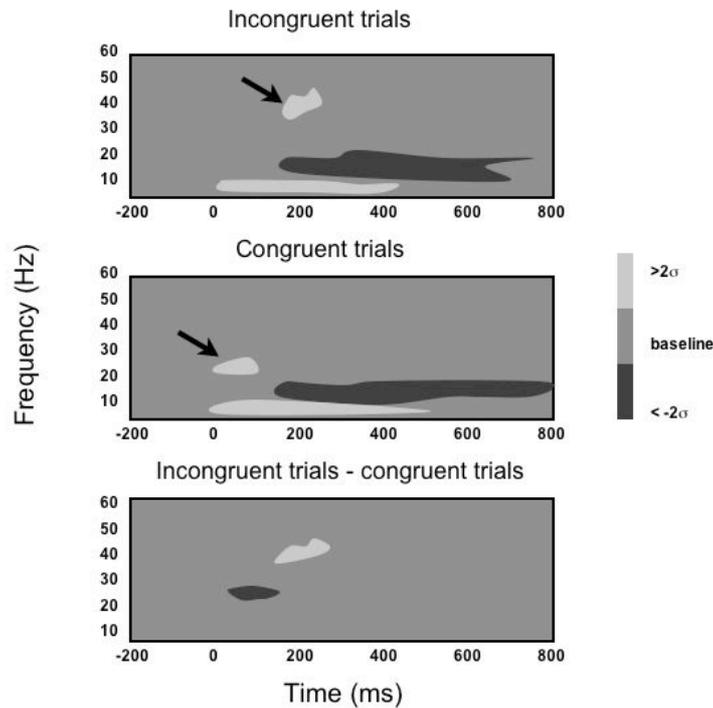


Fig. 1. Representation of average normalized phase locking value (PLV) from all pairs of 19 electrodes based on current source density from EEG in audiovisual speech synchrony experiment of Doesburg et al. (in press). $>2\sigma$ indicates significant increase in synchrony, $<-2\sigma$ indicates significant decrease in synchrony, both relative to baseline. Baseline -200 ms to 0 ms; audiovisual stimulus onset at 0 ms.

calculated by comparing phases across sensor pairs for each sample point for each frequency, aggregating across trials, and normalizing relative to a baseline period from 200 ms before stimulus onset until stimulus onset. Fig. 1 shows a simplified representation of the average of these normalized phase locking values across all 171 pairs in a time-frequency diagram. Congruent and incongruent trials gave rise to different patterns of neural synchrony, as predicted, although both showed an increase of phase locking between stimulus onset and about 400-500 ms after that in the alpha range (8 -12 Hz), and a decrease between 200 ms

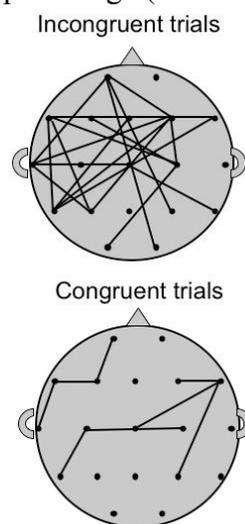


Fig. 2. Head maps of synchrony increases. Black lines indicate significant increases in phase locking at 41 Hz between electrodes indicated by black dots. Based on scalp current density, so electrodes are near superficial neural sources. Based on Doesburg et al., in press.

and 800 ms after stimulus onset in the beta range (13-25 Hz). Importantly, only the incongruent trials showed a burst of increased phase locking in the gamma range (30-50 Hz) at around 200 ms post stimulus onset, in the same time range as has previously been found to indicate the emergence of a new percept in binocular rivalry (Doesburg, Kitajo & Ward, 2005), or a coherent percept of a Mooney face (Rodriguez et al., 1999). Doesburg et al. (in press) interpreted this burst of increased gamma-band synchrony to indicate the emergence of the percept that the audio and visual streams were incongruent. Fig. 2 shows a more anatomically specific pattern of statistically significant phase-locking increases at 41 Hz between various electrodes on the incongruent trials that is largely lacking on the congruent trials. Importantly, this pattern of increased phase locking is consistent with most of the brain network that was discovered by fMRI to be specifically activated when incongruent audiovisual speech is perceived (e.g., Miller & D'Esposito, 2005). This network is crudely represented in Fig. 3. We conclude that the close correspondence between our neural synchrony data and the brain network identified by the fMRI studies implies that the various regions in the network communicate via synchronization of their activity in the gamma band.

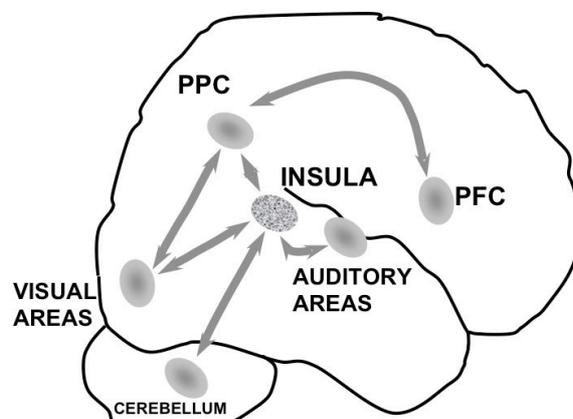


Fig. 3. Network of brain regions involved in the perception of audiovisual speech asynchrony. Bidirectional arrows between regions are hypothetical and indicate possible interactions. Note textured blob for insula indicates it is buried in a sulcus and not on cortical surface.

Cross-modal attention orienting

Another cognitive task requiring communication between widespread brain regions is that of attention orienting. Recently Corbetta and Shulman (2002) summarized a number of studies of the neurophysiology of visual attention orienting and identified two important networks of cortical regions: a ventral fronto-parietal network involved in stimulus-driven orienting, and a dorsal fronto-parietal network involved in goal-driven orienting. Both of course involve the visual areas in the occipital cortex, but the latter involves in addition the frontal eye fields (FEF) and the intraparietal sulcus (IPS), whereas the former involves the ventral frontal cortex (VFC), in particular the inferior frontal gyrus and the middle frontal gyrus, and the temporo-parietal junction (TPJ). Wright and Ward (in press), on the basis of many recent studies and consistent with recent proposals (e.g., Macaluso & Driver, 2005), argued that these attentional areas (excluding the visual cortex) are supramodal, and are engaged whenever attention is oriented within any modality or between modalities. Consistent with previous proposals (e.g., Niebur, Hsiao & Johnson, 2002), we maintain that attention control is implemented within these networks by synchronizing their neural activity in the gamma band.

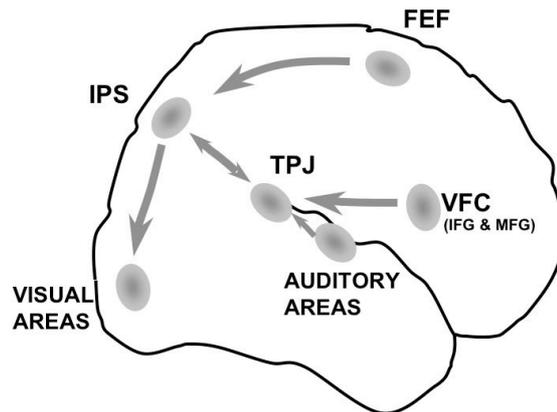


Fig. 4. Hypothetical interactions between supramodal attention control areas and auditory and visual sensory areas in a cross-modality orienting task. (Modified from a figure from Wright, R.D. and Ward, L.M. (in press) *Orienting of Attention*. Oxford University Press.)

Fig. 4 shows a representation of both attention orienting networks combined along with some of their potential interactions (note that several relevant subcortical areas, in particular the superior colliculus and the pulvinar nucleus of the thalamus, are not represented). It shows in addition one possible set of interactions through which an auditory cue stimulus could orient attention to the location of a subsequent visual target, thereby enhancing the processing of that target relative to when the same target appeared at an unattended location. In this scenario, the auditory cue activates the auditory cortex, which in turn activates the TPJ, which tells the IPS to facilitate (possibly via the thalamus) a particular location in the visual cortex where a stimulus is expected to appear. The top down influence of the FEF, and the novelty detection apparatus of the VFC, are engaged when necessary, the former in order to program the orienting apparatus and the latter when a visual target appears at an unattended location, in order to reorient attention there. All of these interactions require, or at least should result in, at least transient synchronization between the communicating areas. The contributions of the subcortical areas also involve such synchronization, although it is difficult to image those areas in intact humans at present so they are not represented.

Some evidence is available concerning such synchronizations. Doesburg et al (2007) reported a transient burst of gamma-band synchronization between visual cortex contralateral to a cued location and other, widespread cortical areas, presumably including those depicted in Fig. 4, at around 300 ms post-cue. They interpreted this synchronization as the signal that the visual cortex relevant to the cued location was being prepared for the target to come. Moreover, Doesburg, Herdman & Ward (2007) reported increased synchronization between a MEG source in the posterior parietal cortex (probably IPS) and one in visual cortex in the high alpha range (12-16 Hz) between about 400 ms after cue onset and target onset around 1000-1200 ms after cue onset. They interpreted this as an indication of the mechanism implementing the maintenance of attention at the cued location during this interval.

Finally, Kanayama, Sato & Ohira (2007) reported shorter response times and higher accuracy, accompanied by increased gamma-band synchronization 200-250 ms after stimulus onset, in a tactile discrimination task when visual and tactile stimuli were presented at congruent locations, relative to incongruent locations or unimodal conditions. The increased synchronization was highly correlated with the perception that the rubber hand that could be seen, on which the visual stimuli appeared, was coincident with the subject's own, hidden, rubber-encased hand, which actually received the tactile stimulation. Kanayama et al. (2007) interpreted the burst of increased gamma-band synchronization to indicate the onset of the illusory percept of the rubber hand being the subject's own, consistent with Rodriguez et al. (1999) and Doesburg, et al. (2005). Although not strictly concerning attention, the

synchronization observed in this study is highly similar to that observed by Doesburg et al. (2007), and would be expected from the model described in Fig. 4.

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