

The Role of Gamma Oscillations in Object Representation

The perceptual binding problem was first formulated by von der Malsburg (1981), who asked how different features of an external object are “bound” together to form a coherent representation of that object. Take, for example, a police car fast approaching from behind. The location of the police car, the sound of the siren, and eventually all the visual features of the car, are all dynamically changing with respect to the rest of the scene and must be grouped together to form a dynamic, yet coherent, percept in order for that information to be translated into a meaningful action (moving to the side of the road). The above example actually illustrates several types of binding, one for the auditory features, one for the visual features, one to bring the auditory and visual features together, and finally the binding of the object to a behavioral response. I will discuss mainly the first three types of binding. From a neuronal point of view, the binding problem is extended with the generally accepted notion that different features of an object are represented with different spatiotemporal patterns of neuronal activity. How each feature’s respective neural patterns are bound together still generates much discussion and is thought to be a major unsolved problem in neuroscience (Roskies, 1999; Buzsaki, 2006).

The first neurophysiological theory attempting to solve the binding problem was provided by Hubel and Wiesel, who postulated a hierarchy of anatomically connected neural assemblies processing more and more complex features of a visual object. The theory, in its most extreme form, culminates in either a single neuron or a single population of neurons which invariantly encode a single object. There is some support for the theory, mainly in the visual system probably because more scientists study it than

other sensory systems (Ungerleider and Mishkin, 1982). The hierarchy theory, as some point out, also has at least one major hole in it: (1) The possible number of objects that must be independently represented gets large quickly with increasing the possible number of features and (2) it does not attribute a role to descending projections, which make up a large portion of neural anatomy.

Gamma oscillations, that is, electric field oscillations in the 30 – 80 Hz range, were first reported in early 30s soon after the discovery and measurement of the electroencephalogram (EEG). These small variations in the EEG were originally considered noise, especially when compared with the larger, slower rhythms and evoked responses. Indeed, EEGs were typically labeled as desynchronized or noisy when high-frequency oscillations were present. More recently, however, the general view of gamma oscillations has shifted from epiphenomena to perhaps a fundamental role in perception and cognition. Wolf Singer of the Max Planck Institute was the first to hypothesize critical importance for gamma oscillations by proposing that they could be the mechanism which would account for perceptual binding (for review, see Singer, 2001). By synchronizing assemblies of neurons which process various features of an object within integrating time windows (note that $1/40\text{Hz} = 25\text{ms}$), gamma oscillations might allow ordinarily de-synchronous neurons to synchronize and therefore multiple their output on subsequent neurons. Moreover, the gamma-binding hypothesis has been extended to include not just feature binding in one sensory modality, but also binding across sensory modalities (e.g. audio-visual integration) and even binding in a top-down sense, allowing for a more general object representation from memory rather than just bottom-up grouping. (Tallon-Baudry and Bertrand, 1999).

When discussing gamma oscillations and their potential implications for theories of neuroscience and mind, it is important to distinguish between at least four different types which are engendered and analyzed in different ways (Tallon-Caudry and Bertrand, 1999). First, steady-state oscillations can be observed in response to a stimulus containing amplitude modulations in the gamma band. These are interesting because the steady-state response seen in the brain has a maximum amplitude which lies in the gamma band, suggesting neural resonances and their importance. Second, evoked oscillations around 40 Hz are seen in response to transient stimuli. The difference between evoked responses and the third type of gamma oscillations, induced oscillations, is that the evoked responses are phase-locked to the stimulus whereas induced responses are not. Thus, traditional signal averaging of phase-locked neural signals cannot reveal induced gamma responses, which is perhaps why they were reported later than evoked gamma responses with the use of time-frequency averaging of single trials. The fourth type of gamma activity is purely spontaneous, although could be in response to some internal event, such as recall of an object. Of the four types, induced responses and spontaneous activity seem to have the most relevance with the binding problem. Figure 1 shows the issues associated with detection of evoked gamma responses and induced gamma responses.

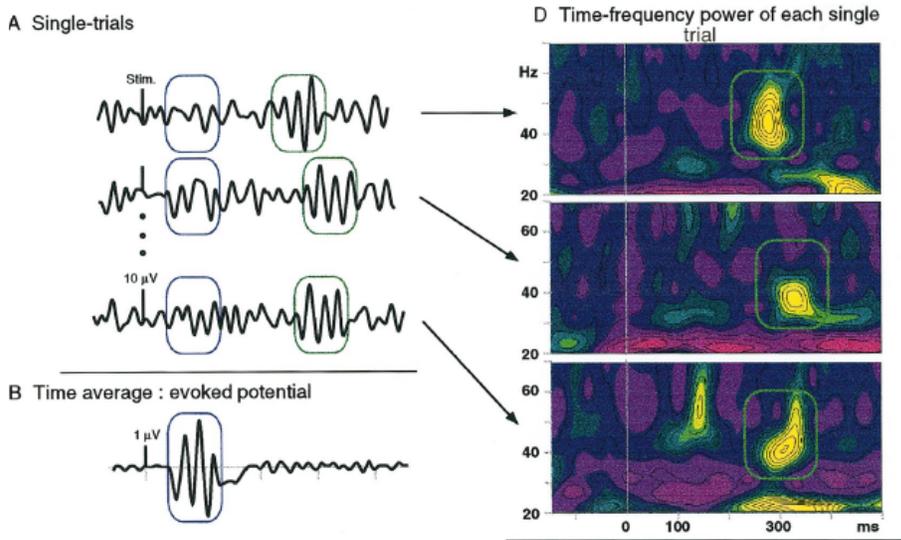


Figure 1. Evoked vs. induced gamma responses and how they are detected.

Evidence for the role of oscillatory synchrony in bottom-up feature binding is most abundant in the visual system. Stimulus-related gamma responses have been observed in anesthetized cats (Gray et al., 1989) as well as awake monkeys (Frien et al., 1994)). In particular, larger power in the gamma band was seen for more coherent moving bars. That some of these responses were seen under anesthesia calls their relation to binding into question, however, as no object could have been perceived for binding to be necessary. In humans, increased gamma activity over the frontal lobe was present when a bi-stably perceived box switched between foreground/background. Similar patterns might be seen for bi-stably perceived auditory stimuli, such as alternating sequence of tones (Bregman, 1990). Another oft-cited result is that of increased gamma power when the presence of an ambiguous dalmation was detected vs. when it wasn't (Tallon-Baudry et al., 1997). See figure 2 below. Similar experiments in the auditory system have yet to be carried out. A possible analogy might be increasing iterations in iterated ripple noise, engendering a percept of pitch. Perhaps the most

interesting result suggestive of the binding-by-synchrony hypothesis is that learned associations between a visual and a tactile stimulus evoked a coherent gamma oscillation in both the visual and sensory cortices after the visual stimulus alone. This promises to be a fruitful path of research for audiovisual integration.

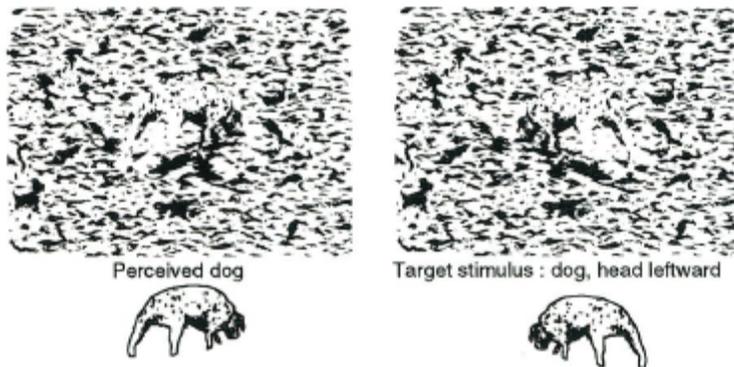


Figure 2. Ambiguous percepts. Higher gamma activity is seen when the dalmation is perceived.

A landmark study of gamma oscillations in the auditory system came from Joliot et al. (1994). They showed that the 40Hz oscillations they observed with MEG tracked the perception of 1 or 2 auditory objects (clicks). This study was important mainly because it was the first showing the binding, or lack thereof, of objects in time and neural correlate which tracked it. Two more recent studies, while they are discussing different types of gamma activity (steady-state vs. spontaneous), also relate to object representation. Ross et al. (2005) showed disruption of the 40-Hz steady-state response seen in MEG (to an amplitude-modulated 500Hz tone) through a contra-lateral broadband noise followed a subsequent buildup of that response. The authors interpret the results as a reset of the representation of the environmental scene. And finally, Lakatos et al. (2005), using a linear array of electrodes inserted into a cortical column of the primary auditory cortex of awake monkeys, report an oscillatory hierarchy such that slower

oscillations modulate faster ones, and suggest that the auditory cortex might be optimized to process rhythmic inputs.

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