# Beta and Gamma Rhythms Go with the Flow

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**Information flows through visual areas in opposite directions during "bottom-up" intake of current stimuli and "top-down" processes such as attention or memory. In this issue of *Neuron*, Bastos et al. (2015) report that rhythms of different frequencies coordinate bottom-up and top-down information streams.**

Brain rhythms reflect synchronized activity across distributed groups of neurons. Accordingly, brain rhythms are believed to provide a mechanism for coordinating activity within and across brain regions. There are several different classes of brain rhythms, and these different brain rhythms exhibit characteristic frequencies and behavioral correlates. Three major rhythms seen in the cortex during active behaviors are theta ($\sim$4–8 Hz), beta ($\sim$14–18 Hz), and gamma ($\sim$40–100 Hz). Theta rhythms are associated with active intake of sensory stimuli and are linked with movements involved in stimuli sampling (e.g., whisking, sniffing, and eye movements) (Colgin, 2013). Gamma rhythms have been proposed to bind the activity of distributed neurons, processing different features of visual stimuli, to transform these different features into coherent percepts (Gray, 1994). Gamma rhythms are also thought to be involved in interregional communication and selection of salient stimuli (Fries, 2009). Compared to gamma rhythms, beta rhythms have been studied less in visual areas. In sensorimotor cortex, beta rhythms have been linked to anticipation of visual stimuli that cue a subsequent motor response (Kilavik et al., 2013). Beta oscillations in sensorimotor cortex have also been shown to decrease during the presentation of such cues. Yet, many questions remain regarding the functional significance of beta rhythms in visual cortex.

In this issue of *Neuron*, Bastos and colleagues (2015) tested a novel hypothesis regarding the functions of beta rhythms in visual cortex. They recorded local field potentials from grids of electrodes covering multiple areas of visual cortex in monkeys performing a task that incorporated both bottom-up and top-down processing. Specifically, the monkeys were cued to pay attention to one of two visual stimuli and were rewarded for responding when the stimulus changed. The authors employed a method known as Granger causality to test the directionality of activity flow in the visual networks. This method assesses directionality by determining the extent to which signals in one area are related to signals from the recent past in another area. The authors used this method to examine signals in various frequency ranges and found that the directionality of activity flow differed for cortical rhythms of different frequencies. Specifically, theta and gamma rhythms in areas that were lower in the visual cortex hierarchy (i.e., closer to the lateral geniculate nucleus) influenced theta and gamma activity in higher areas. These results suggest that theta and gamma rhythms promote information flow in the feedforward direction during bottom-up processing (Figure 1). In contrast, beta rhythms in areas that were higher in the hierarchy influenced beta rhythms in lower areas. These results imply that beta rhythms promote feedback interactions across visual areas during top-down processing (Figure 1). Interestingly, the effects were related to attentional processing because beta influences in the top-down direction were significantly diminished when attention was directed toward stimuli in the ipsilateral visual field. Gamma influences in the bottom-up direction were also significantly lower when the salient stimulus was in the ipsilateral visual field, which the authors explained as top-down enhancement of bottom-up signals.

The new findings from Bastos and colleagues (2015) significantly impact our understanding of network operations beyond the visual cortex. Mounting evidence supports the view that rhythms of different frequencies act as distinct channels that differentially route top-down and bottom-up signals. A key study employing simultaneous recordings from frontal and parietal cortices showed that the regions were coupled by $\sim$25–30 Hz beta rhythms during top-down processes and by $\sim$40–55 Hz gamma rhythms during bottom-up processes (Buschman and Miller 2007). Also, distinct low- and high-frequency gamma rhythms have been reported to channel different information streams in the rodent hippocampal network (Colgin et al., 2009). Recent studies suggest that these different information streams are related to bottom-up and top-down processing. Higher-frequency ($\sim$55–95 Hz) gamma rhythms were enhanced relative to lower-frequency ($\sim$23–40 Hz) rhythms when mice used current sensory cues to navigate through a maze, rather than relying on their memory of previous maze traversals (Cabral et al., 2014). Additionally, hippocampal place cells, neurons with receptive fields for particular locations in space (O'Keefe and Dostrovsky, 1971), represented recent locations during $\sim$80 Hz rhythms and predicted upcoming locations during $\sim$40 Hz rhythms (Bieri et al., 2014). Representing current or recent locations likely requires bottom-up processing of sensory signals, whereas predicting upcoming locations involves previously stored memories and thus likely requires top-down processing. Although the frequency associated with top-down processes in the rodent hippocampus is higher than the beta rhythm frequency in the Bastos et al. (2015) study, it is possible that slower rhythms are necessary in the larger primate brain to tolerate longer conduction delays (Kopell et al., 2000).

Why would bottom-up processing employ a higher-frequency rhythm than

top-down processing? One possibility is that bottom-up signals carry information about ongoing experiences, information that may need to be encoded into long-term memory. Encoding of long-term memories is thought to involve long-lasting increases in the strength of synaptic connections. The optimal activation pattern for inducing such changes in synaptic strength resembles fast gamma (~100 Hz) rhythms occurring across successive theta cycles (Larson et al., 1986). Fittingly, then, the bottom-up influences observed by Bastos and colleagues (2015) involved not only fast gamma (~60–80 Hz) but also theta (~4 Hz) rhythms. The lower frequency associated with beta rhythms would not be expected to induce changes in synaptic strength, which fits well with top-down functions. Top-down signals would then influence the activation of relevant cell assemblies without producing changes in the neuronal circuitry underlying the assemblies.

What about the role of another rhythm that occurs prominently in visual cortex, the ~10 Hz alpha rhythm? Alpha rhythms have been suggested to exert inhibitory top-down influences on incoming visual signals carried by gamma (Spaak et al., 2012). Consistent with this idea, a recent study of monkey visual cortex reported feedforward influences (from V1 to V4) during ~40–90 Hz gamma rhythms and feedback influences during ~10 Hz alpha rhythms (van Kerkoerle et al., 2014). It is possible that alpha and beta constitute distinct rhythm classes and that both are involved in top-down processing. On the other hand, the high end of the alpha frequency range (~13–14 Hz) overlaps with the low end of the beta frequency range. Thus, it is also possible that the same physiological activity pattern has been called alpha or beta in different studies (Bressler and Richter, 2014) and that its frequency varies due to still
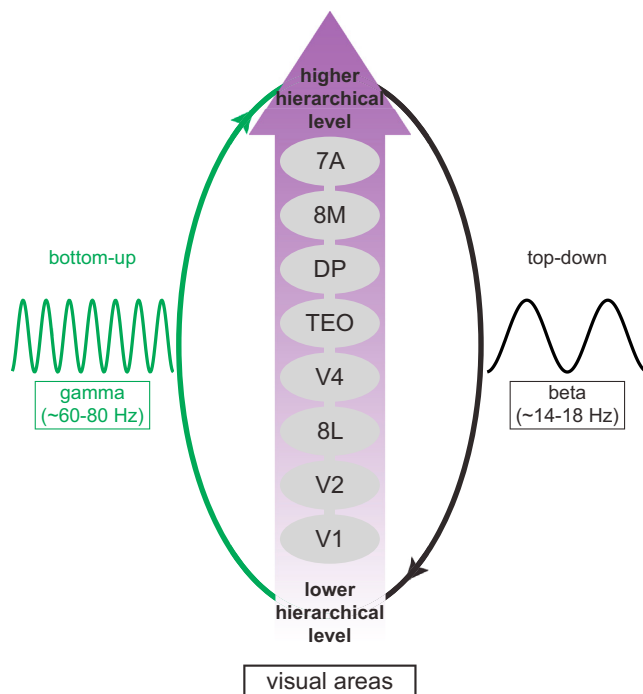


**Figure 1. Differences in the Direction of Information Flow through Visual Networks during Different Cortical Rhythms**
Gamma rhythms (and theta, not shown) promote the feedforward (bottom-up, green) flow of information from lower visual areas to higher visual areas. Beta rhythms promote feedback influences (top-down, black) from higher visual areas to lower visual areas.

unknown factors. Future studies may be able to resolve this question by determining whether beta and alpha rhythms have different mechanisms of generation, or whether they exert different influences on neuronal spiking rates.

In summary, the findings from Bastos and colleagues (2015) improve our understanding of how the brain processes visual information. These new results have exciting implications for the fields of artificial intelligence and brain-computer interfaces. The human brain is highly skilled at accurately and quickly recognizing objects in visual scenes, more skilled than computer networks designed for the same purpose. It is possible that the use of different frequency channels for top-down and bottom-up signals may be a key mechanism that can be implemented in future approaches to computer vision. Brain-computer interfaces should also benefit from the new insights. Brain-computer interfaces record neuronal signals and feed these signals through a

translation algorithm that decodes neuronal activity. Algorithms for decoding neuronal activity may be improved by incorporating information about the rhythmic state of the network, with beta rhythms signifying feedback signals and theta-gamma rhythms indicating feedforward flow of current sensory information. The new findings provide a solid foundation for future testing of these ideas in the visual system, and perhaps throughout the rest of the brain as well.

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