

BRAIN RHYTHMS FOR COGNITION AND CONSCIOUSNESS

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What does a thought look like? In neurobiological terms, it is universally assumed to involve a neural ensemble – a subset of neurons that together represent an item of information, whether it is a computation, memory, percept, or desire. This is a bit of a truism. If neurons represent information, then a subset of them must represent a given thought. What is not so obvious is how the brain forms ensembles. Neurons, the brain’s basic processing units, do not have single functions; they do not contribute to just one thought or memory. Rather, neurons, especially at the higher areas of cortex central to cognition, are highly multivariate and dynamic. Neurons “multitask”: They process a wide range of often seemingly unrelated information that can contribute to many different functions and computations. In other words, neurons do not participate in a single ensemble. They participate in many overlapping ensembles. Further, consider that intelligent, goal-directed thought and action requires integration of a wide range of information, not only about our external environment but also our internal state, relevant stored knowledge, possible courses of action, and anticipated outcomes. It thus seems unlikely that normal, rational thought and action stems from neural activity haphazardly bouncing around the brain’s many networks. The brain must have mechanisms that coordinate interactions among its neurons in order to form the ensembles and networks of ensembles that produce clear and coherent thought and action.

Here, we discuss evidence that the brain regulates the flow of neural “traffic” via rhythmic synchrony between neurons. Neurons form ensembles, and ensembles become part of larger functional networks, when they “hum” together. Conversely, they don’t form ensembles, and don’t interact, when they don’t hum together. In other words, rhythmic synchrony can reinforce or prevent communication between neurons. Synchronizing the rhythmic activity of two sets of neurons ensures they are in the excited state at the same time

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and therefore primed to transmit information to each other. It follows that desynchronization of these rhythms would actively interfere with communication. Thus, by changing the rhythmic synchronization between neurons, their communication can be altered, changing the flow of information through the brain. Synchronized brain rhythms may also explain the most obvious and objective fact about consciousness: it is very hard, often impossible, to think about more than one or a few things at the same time.

Synchronized rhythms can regulate network interactions

It has long been known that the brain has large populations of neurons that oscillate in synchrony. These so-called “brain waves” occur across a wide range of frequencies from very low (< 1Hz) to very high (>60 Hz). They have long been known to vary with mental state. More relaxed states produce lower frequency waves and increased cognitive effort produces higher frequency waves. But, for many years, their exact role in brain function has been a mystery. This is largely because much of our understanding of brain networks has been inferred largely from indirect evidence such as anatomical connections and properties of the brain’s individual parts studied in isolation. This modular understanding stands to reason. Identifying and characterizing the brain’s components is prerequisite to any integrated understanding of the whole. And technological limitations had largely restricted us to piecemeal investigation. But technical and methodological advancements have led to increasing investigation and understanding at the network level. Beginning with the pioneering work of von der Malsburg, Singer and colleagues, there has been increasing awareness that the precise synchrony of timing of activity *between* neurons may be critical in forming functional networks.

Oscillations are useful for producing synchrony between neural impulses (“spikes”). Spikes from two neurons that arrive simultaneously at a third, downstream, neuron have a bigger impact than if the impulses arrived at different times (Aertsen *et al.* 1989; Salinas and Sejnowski 2000; Pascal Fries 2005; Engel, Fries, and Singer 2001). Thus, synchronicity between neurons can improve signal to noise ratio of neural signals while, at the same time, reducing the number of spikes (spikes cost energy) needed to represent a stimulus (Tiesinga *et al.* 2002; Siegel and König 2003; Aertsen *et al.* 1989; Azouz and Gray 2000). If true, then one might expect the activity of synchronized neurons to carry more information than non-synchronized neurons. This has been seen in the prefrontal cortex (Siegel, Warden, and Miller 2009) and, in fact, only synchronous neurons in parietal cortex predict behavior in a reach-and-saccade task (Dean, Hagan, and Pesaran 2012).

Evidence of the role of rhythmic synchrony in boosting neural signals comes from studies of visual attention. Increased attentional focus is associated with changes in oscillatory synchrony in sensory cortex. Visual cortical neurons that process a stimulus under attentional focus show increased synchronized gamma band (30–90 Hz) oscillations (P. Fries *et al.* 2001). By contrast, neurons representing an unattended stimulus showed increased low frequency (<17 Hz) synchronization. A variety of evidence suggests that low frequencies may help deselect or inhibit the corresponding ensembles (Buschman *et al.* 2012; Vijayan and Kopell 2012; Palva and Palva 2011; Ray and Cole 1985). Higher frequency (>30 Hz) synchrony may result from local interactions within a cortical area (Cardin *et al.* 2009; Börgers, Epstein, and Kopell 2008), the same interactions that underlie the computations of stimulus features within a cortical area (Wilson *et al.* 2012; Lee *et al.* 2012; Reynolds and Heeger 2009). The idea is that attention boosts the high frequency synchrony of neurons processing an attended object, thus boosting its impact on other neural processing. Supporting this hypothesis, microstimulation of the frontal eye fields induces high-frequency oscillations in parietal cortex neurons processing an attended stimulus (Premereur *et al.* 2012).

Synchrony between regions may also regulate communication across large-scale brain-wide network interactions. If two different networks in different brain areas oscillate in phase they are more likely to influence one another because, as noted above, they are both in an excited and receptive state at the same time. Conversely, if they are out of phase, they are less likely to influence each other. This has led to the suggestion that oscillatory synchrony could be used to regulate communication between brain areas (Bressler 1996; Engel, Fries, and Singer 2001; Salinas and Sejnowski 2000; Pascal Fries 2005). Support for this notion comes from observations that inter-areal oscillatory coherence within and between “cognitive” regions and sensory areas has been found to increase with attention (Buschman and Miller 2007; Saalmann, Pigarev, and Vidyasagar 2007; Siegel *et al.* 2008; Gregoriou *et al.* 2009).

Synchronized rhythms form neural ensembles

Above, we discussed how synchronized rhythms can boost neural signals and regulate which networks in the brain “talk” to one another. The same mechanisms can also play a role in forming neural ensembles. Just as humming together allows networks across the brain to communicate more effectively, individual neurons may form local networks of ensembles when their synchronized humming reinforces their mutual communication.

Some sort of mechanism for selecting specific neurons for membership in specific ensembles must exist. As mentioned above, many neurons in higher cortex are very heterogeneous and many seem to “multiplex”. They signal all sorts of seemingly unrelated information at different times. For example, at one time a given neuron may convey information about the concept “cat” whereas a few moments later, it might represent an entirely different category or precept or even seem to be issuing motor commands (Rainer, Rao, and Miller 1999; Cromer *et al.* 2011). Computational modeling suggests that this mixed selectivity allows the system to encode a large variety of memories, memories, events, rules, etc. with a biologically realistically limited number of neurons (Rigotti *et al.* 2010).

But this diversity seems to work against the demand to activate a specific ensemble that represents a specific thought. If higher cortical neurons have many connections reflecting a wide range of information, why doesn't neural activity simply run around the connections and activate many ensembles in a jumble? Synchrony between neighboring neurons can dynamically “carve” an ensemble from a greater, heterogeneous, population of neurons (Akam and Kullmann 2010) by reinforcing mutual activation between the neurons that form the ensemble (Womelsdorf *et al.* 2007). Because ensemble membership would depend on which neurons are oscillating in synchrony at a given moment, ensembles could flexibly form, break-apart, and re-form *without changing the physical structure* of the underlying neural network. In other words, this may endow ensembles with a critical feature: flexibility in their construction. Flexibility is a hallmark of higher cognition. Humans can quickly adapt and change their thoughts and behaviors in order to tailor them to the constantly changing demands of our complex world. Thus, ensembles have to be assembled, deconstructed, and reconfigured from moment to moment. Synchronized oscillations can provide the substrate.

To test this, we recently examined neural activity in the prefrontal cortex (PFC) of monkeys switching between two cognitively-demanding tasks (Buschman *et al.* 2012). The PFC is critical for cognitive flexibility. When it is damaged or dysfunctional, people are unable to suppress prepotent, reflexive reactions in favor of a more contextually-appropriate response (Owen *et al.* 1993; Bechara, Tranel, and Damasio 2000). Furthermore, patients with PFC damage often perseverate, inappropriately repeating a particular behavior or line of thought (Barceló and Knight 2002; Rossi *et al.* 2007; Milner 1963).

Monkeys were trained to switch between paying attention to either the color (either red or blue), or orientation (either horizontal or vertical) of a line. We measured fluctuations in local field potentials (LFPs) at different

points along the prefrontal cortex, from an array of electrodes spaced 1mm apart. LFPs are the summed activity of many neurons near the recording electrode, like the brain waves that can be recorded from the human scalp. When the monkeys focused their attention on the task, there was an increase in oscillations at high frequencies in so-called beta waves (19–40 Hz). Depending on which rule was in effect (i.e. whether the monkeys were paying attention to either color or orientation) different patterns of electrodes were synchronized at these beta waves. Some neuron clusters overlapped, belonging to more than one group, but each pattern of beta-wave synchrony had its own distinctive pattern. In other words, beta wave synchrony seemed to establish different, but physically overlapping ensembles across the prefrontal cortex.

We also observed oscillations in the low-frequency alpha range (6–16 Hz) among neurons that formed the orientation rule ensemble. However, this only happened when the monkey was preparing to apply the other rule, color. Alpha waves have been associated with suppression or inattention (Haegens *et al.* 2011; Gould, Rushworth, and Nobre 2011) and thus may create an inhibition of irrelevant processes (Klimesch, Sauseng, and Hanslmayr 2007; Mathewson *et al.* 2011). In our case, these alpha oscillations seemed to be acting to quiet the neurons that formed the orientation rule ensemble when the animal was preparing to do the opposite, color, rule. This alpha suppression was necessary because orientation seemed to be the dominant modality for the monkeys. Whenever they switched from paying attention to orientation to color, they cognitively “stumbled”; that is, their behavioral reactions slowed temporarily. By contrast, there was no stumbling when they switched from color to orientation. This suggests that orientation had a naturally greater hold on the animals’ attention than color. This may be due to its relative saliency, much like word-naming in the Stroop test (MacLeod 1991).

This all suggests that synchronous oscillations helped control the formation of ensembles (Kopell, Whittington, and Kramer 2011). Higher (beta) frequencies defined the two rule ensembles (pay attention to color vs orientation) while lower (alpha) frequencies were used to somehow disrupt formation of the stronger ensemble (and thus prevent an erroneous reflexive reaction) when the weaker ensemble had to be used.

If synchronized rhythms form neural ensembles, one might naturally wonder how it is that the brain can form more than one ensemble at a time. After all, would not two rhythmically defined ensembles inadvertently synchronize to each other, merging together and distorting the information each other represents? In fact, the brain does have a great deal of trouble

having more than one or (at most) a few ensembles simultaneously activated in consciousness. Humans have a very small capacity for simultaneous thoughts; it is a defining feature of consciousness (and the reason why one should not drive and use a mobile phone at the same time). As we will see next, this may be because the brain keeps ensembles from interfering with one another by having them oscillate out of phase with one another. In other words, consciousness may be a mental juggling act, and only a few balls can be juggled at once.

Synchronized rhythms, capacity limits, and consciousness

The finite resources of cognition have been well-known since the classic George Miller paper describing the capacity of working memory as the “magic number” of seven plus or minus two (Miller 1956). More recent work has lowered the magic number to four or five for the average adult human (Cowan 2001). The exact capacity of a person varies from individual to individual; some can remember only 1–2 items and others can remember up to 7 (Vogel and Machizawa 2004; Vogel, McCollough, and Machizawa 2005). An individual’s capacity is highly correlated with measures of fluid intelligence, reflecting the fact that these capacity limits are a fundamental restriction in high-level cognition (Fukuda *et al.* 2010; Conway, Kane, and Engle 2003). This makes sense: the more thoughts that can be simultaneously held “in mind” and manipulated, the more associations, connections, and relationships can be made, and the more sophisticated thought can be.

Thus, there seems to be a fundamental limitation in the number of separate items that can be represented simultaneously in neural activity, particularly in an active state that is accessible to high-level cognition. An explanation readily follows when neural ensembles are formed via synchronized rhythms. The idea is that neurons that are part of a specific ensemble tend to align their spikes to specific phases of neuronal population oscillations (O’Keefe and Recce 1993; Hopfield and Herz 1995; Laurent 2002; Mehta, Lee, and Wilson 2002; König and Engel 1995; P. Fries, Nikolic, and Singer 2007).

Multiple items are simultaneously held “in mind” by multiplexing them at different phases of population oscillations (Figure 1) (Jensen and Lisman 2005; Lisman and Idiart 1995). In other words, the mechanisms for conscious thought “juggle” separate ensembles by oscillating them out of phase of one another. Evidence for this multiplexing when information is held “in mind” was recently reported by Siegel *et al.* (Siegel, Warden, and Miller 2009). When monkeys held multiple objects in working memory, prefrontal neurons encode information about each object at different phases of an ongoing, ~32 Hz, oscillation. This phase-based coding has an inherent capacity

limitation because, presumably, only so much information can fit within an oscillatory cycle (that is, only a few “balls” can be juggled at once). Crucial tests of this hypothesis still need to be conducted, but all this suggests that making thoughts conscious may depend on generation of oscillatory rhythms and the precise temporal relationships between them and the spiking of individual neurons.

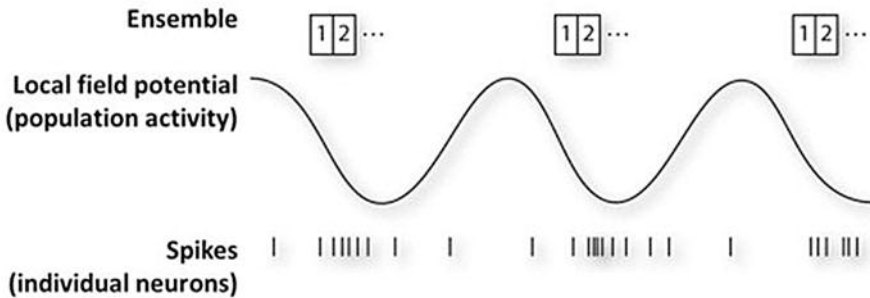


Figure 1. This figure illustrates oscillatory phase-coding. The idea is that neural ensembles of the under two simultaneous thoughts (“1” and “2”), oscillate at similar frequencies but at different phases of the oscillation. In other words, the ensembles line up on different parts of the brain wave. This may explain the severely limited capacity of consciousness. Only a few thoughts can fit in each wave.

Conclusions

We have discussed how rhythmic synchrony can provide a fundamental backbone for forming and coordinating interactions within and across disparate neural networks. The act of putting neural activity from specific neurons in precise lockstep with specific other neurons may form the ensemble representing a specific thought and regulate which ensembles and larger networks “talk” to one another. The implication is that the signals that underlie cognition do not operate continuously, but rather discretely, with pulses of activity routing packets of information. The advantage is that it constrains and shapes the flow of neural signals. In other words, the brain’s physical infrastructure (i.e., its anatomy) dictates where neural signals *can* flow; synchronized rhythms dictate where signals *do* flow. However, this comes at a cost. Any coding scheme based on repeated rhythmic activity is naturally limited in bandwidth; only so many things can be computed or carried in a single oscillatory cycle. This may explain the most fundamental property of conscious thought, its limited capacity.

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