

# Localizing Cortical Computations during Visual Selection

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Local field potentials (LFPs) and spikes are two signals that can be recorded from the brain using extracellular microelectrodes. A study by Monosov et al. in this issue of *Neuron* using timing relations between these signals suggests that selection of a target from an array of distractors is a computational operation performed specifically and locally in the frontal eye field (FEF).

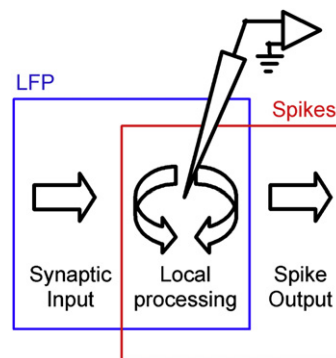
Much of what we know about the functional organization of the brain comes from single-unit activity recording studies, which have examined how spiking activity in given brain regions correlates with sensory, motor, or cognitive aspects of behavioral tasks. Spiking activity recorded using extracellular microelectrodes measures the output of neurons near the tip of the electrode. It is estimated that for cortical pyramidal cells well over 60% of connections remain local and generate synaptic activity in the same cortical region (Braitenberg and Schüz, 1998). The remaining connections are with remote cortical areas, to which the results of the cortical computations are transmitted (see Figure 1). The demonstration that a given task attribute is represented in spiking activity in a given brain region, however, does not mean that this task attribute is actually computed there. It could have been present already in the synaptic inputs, and therefore the computational work might have been performed elsewhere, and is merely being transmitted to further stages of processing. In principle, one might rule this out by simultaneously recording not only from the brain region of interest, but also from the major regions which provide its synaptic input. This is feasible for early sensory cortices, as demonstrated for example by joint recordings from the LGN and V1. For higher cortical areas, it cannot be done, mainly due to the large number of connections among cortical areas (Felleman and Van Essen, 1991). It is simply not feasible to record simultaneously from the required number of brain regions. It turns out, however, that considering the local field potential (LFP) together with spiking activity is an approach that can be used to resolve this question. Because LFPs reflect syn-

aptic processing in a volume around the electrode tip, they are influenced by synaptic inputs arriving from other brain regions as well as by local processing (see Figure 1). In this scheme, spikes are related to local processing and output, whereas LFPs are related to local processing and input. Simultaneous measurement of spikes and LFPs in appropriate behavioral tasks could thus be used to compare these two measurements of neural activity, and thus provide estimates of which signals are already present in the inputs to the brain region under study and which signals are computed there de novo.

In this issue of *Neuron*, Monosov et al. (2008) report on joint LFP and spike recordings during spatial selection in the frontal eye fields (FEFs). During their spatial selection task, monkeys had to report the orientation or location of a target stimulus embedded in a visual array of distractors. They compared timing of LFP and

spike responses in relation to two important events during each trial: array onset and selection time. In relation to the onset of the array, LFP latencies were shorter than spike latencies, as one expects since the visual inputs arriving from the sensory periphery first cause synaptic activity in the FEF before this synaptic activity is converted to spike output. In relation to selection time, i.e., the time the neural response first distinguishes the target from the distractors, they observed the opposite pattern: selection times occurred earlier in spikes than in LFPs. This suggests that information related to the target is not received from distant brain regions, but rather computed locally in the FEF. The results of the local computations are first visible in FEF spiking activity, and subsequently amplified in recurrent circuits such that they are later measurable also at the level of the LFP in the same brain area. This is a particularly exciting finding, because it allows us to consider a brain area as a computational unit that transforms incoming input signals to outputs, and to actually estimate both inputs and outputs directly from extracellular recordings. The implication is that timing differences between LFP and spike-related task-relevant neural signals can be used to distinguish whether the brain region under study is performing computational operations on incoming neural signals or simply acting to relay this activity to other brain regions.

The LFP is a mass signal that is related to synaptic activity in large populations of many thousands of neurons near the electrode tip. By contrast, spiking activity represents the output of a single neuron. This raises methodological concerns; for example, LFPs might be poorly selective to target location, and therefore selection



**Figure 1. Simple Scheme Describing Relation of LFP and Spike Signals to Information Flow**

LFPs are related primarily to local processing in synaptic inputs from other brain areas, whereas spikes are related to local processing and spike outputs.

times estimated from LFP signals might be delayed compared with single-unit values. This was not the case in the study from Monosov and colleagues: although LFP tuning width for target location tended to be somewhat larger than those estimated from spiking activity, there was highly robust directional tuning present in both signals. In addition, directional preference was highly correlated across the two signal types, suggesting that the LFP measurements were not spatially broadly distributed and unselective, but rather precisely related to the properties of single neurons encountered at the same site. Related findings have been reported in area MT for speed and directional tuning (Liu and Newsome, 2006), and in the posterior parietal cortex for movement direction (Scherberger et al., 2005). In these cases authors examined oscillatory LFP activity and not evoked responses as in the present study, but found robust tuning for task parameters in the LFPs as well as correlations to unit activity. How does the FEF take nonselective inputs and convert them to directional signals for eye movement control? If the interpretation of the authors is correct, the neural signals entering the FEF upon array onset already contain information about the distractors and the target in their respective locations, as well as the current behavioral goals of the animal. Presumably, the job of the FEF in this context is to extract target information and convert it to an explicit representation suitable for control of action. How this conversion is achieved by FEF neural networks still needs to be worked out, but the general approach now provides a method that can be used to address this question.

In the context of understanding cortical information processing, it is of great interest whether particular influences on a given brain region have a bottom-up or top-down origin, because this would allow a dissociation between effects of sensory origin and those derived from internal representations of task demands.

A recent study has presented evidence that top-down and bottom-up communication in the brain might be supported by different frequency bands of the LFP (Buschman and Miller, 2007). During an easy visual search task, the target was reflected first in the lateral intraparietal (LIP) cortex and subsequently in a frontal cortical region that included the FEF, whereas the opposite was true during difficult visual search. At the same time, the authors found task-dependent differences in LIP-frontal LFP coherence, such that a 22–34 Hz LFP band showed greater activity during the difficult search task, whereas a 35–55 Hz band showed less activity. The authors suggest that LIP identifies the target first in the easy task and communicates this information to the frontal cortex in a bottom-up fashion, whereas during the hard task, the target is first reflected in frontal activity and then sent to LIP in a top-down manner. Joint LFP-spiking analyses of the kind employed by Monosov and colleagues could be used to directly test this idea; during the easy task, frontal target-related signals should appear first in the LFP, and later, in spiking activity. More generally, it is known that top-down and bottom-up projections tend to have different projection patterns, forming synapses preferentially in apical and proximal parts of dendrites, respectively. This makes it particularly appealing to extend electrical recordings of neural activity with imaging methods such as  $\text{Ca}^{+2}$  imaging (Stosiek et al., 2003), particularly if these can be further developed to examine layer-specific synaptic activity in populations of neurons. Such an approach would yet further refine our picture of information processing by including the measurement of top-down and bottom-up inputs into the brain region under study, in addition to electrical neuronal activity measurements.

The approach used by Monosov and colleagues is related to one used in a recent study of inferior temporal (IT) cortex (Nielsen et al., 2006). That study de-

scribed a dissociation between spiking and LFP activity as a function of recording location in IT cortex. For posterior sites, learning-dependent object selectivity was seen in spiking activity, but not LFP activity, whereas at anterior sites this selectivity was present in both LFP and spiking activity. The interpretation of this result was that the learning-dependent signals were first generated in posterior IT and thus present in the output of that brain area and not in the input. Anterior IT sites already showed these signals in their inputs, consistent with receiving signals from posterior IT regions. This represents in a sense an orthogonal approach to one used in the study by Monosov and colleagues. The two studies have applied a similar logic to describe differences between LFP and spiking activity as a function of brain topography and temporal response dynamics. Both of these approaches can in principle also be applied together, and this combination promises substantial further advances in our understanding of computational and informational flow in cortex.

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