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Neural correlations, decisions, and actions

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Multielectrode recording experiments let us measure correlations between the activity of individual neurons and the neural circuits in which they are embedded. Recently, multielectrode studies have been emphasizing how correlated neuronal activity is linked with behavior. Decisions are fundamental to voluntary behavior. Here, we discuss computations necessary to turn a decision into an action and review progress in studying correlated neural activity in areas of the brain which link sensory and motor representations. The themes that emerge are that correlated patterns of activity in populations of neurons can be revealed by measurements of field potential fluctuations and that these measurements can relate the activity of individual neurons to the activity of populations of neurons distributed across different regions of the brain. Investigations into patterns of neuronal correlation are helping us to understand how decisions and other cognitive processes result from the interactions between different brain systems that are responsible for controlling and regulating our behavior.

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Introduction

Decisions have an almost universal appeal. We experience our own decisions and the sense we have of choosing. We speak of cells choosing to divide or to die, of algorithms that divide inputs into different outputs, and of rational markets. Even the neurophysiological study of decision, with its emphasis on animal models and the simplifications that implies, brings many different influences such as sensation, reward, emotion, learning, and memory to our understanding of making a decision.

Here, the focus is on how analyzing neuronal correlations can inform sensory–motor decisions: decisions that involve a voluntary, flexible association between a set of sensory inputs and a motor output that is modifiable by experience. We will start by reviewing recent evidence that sensory–motor decisions can be viewed as the combination of two processes. One process assigns values to sensory stimuli and another process leads to the movement expressing the choice. Valuations involve making predictions about the outcomes of different choices, the potential rewards, and costs of choices. Choice, in turn, involves weighing the valuations for different alternatives and selecting one to act on.

We then highlight how analyzing neuronal correlations may reveal how neural circuits perform distributed processes like valuation and choice. Understanding the distributed neural computations that underlie decision making and other cognitive processes represents a major challenge for systems neuroscience. A rapidly growing body of work is developing a new approach that uses the dynamics of neural activity to link the spiking activity of neurons to the neural circuits within which they are embedded. A notable direction in current research is the emerging spike-field approach which has the potential to resolve how information is transformed between different regions of the brain.

Sensory–motor decisions activate distributed brain networks

To allow voluntary, flexible associations, sensory–motor decisions must integrate incoming sensory information with prior experiences involving costs and rewards. An important issue in understanding voluntary behavior is understanding the neural circuit mechanisms by which information about decisions, such as costs and rewards, ultimately drives movements.

The frontal and parietal cortices comprise the classical sensory–motor association cortex and contain areas responsible for integrating sensory information to guide ongoing motor behavior. The functional roles of the frontal–parietal cortices involve sensory, motor, and cognitive aspects and individual areas are specialized for representing different parts of the body such as the eye, arm, and hand [1–3]. In the context of decision making and preparation for choice, there is strong evidence that the valuation of an alternative modulates the firing of parietal neurons that have been implicated in planning eye and arm movements (for a review see [4]). The activity of these neurons is, in turn thought to bias processing in frontal regions and, ultimately, which movements are made. When movements are being selected there is increasing evidence that the process of selecting an alternative for action and preparing action do not occur

sequentially in time. Instead, movement planning occurs concurrently across frontal and parietal areas for different currently available alternatives before one alternative is used to generate a movement [5]. Choice information does not always emerge across frontal and parietal cortex at the same time. In top-down, experience-based tasks, frontal areas precede parietal areas in signaling selection [6•,7••,8]. A useful conceptual framework for these results is that choices are made in the frontal–parietal networks through competition between different action representations.

Action representations in the frontal–parietal cortices may incorporate value signals by taking in inputs from other areas. Areas of the limbic cortex, prefrontal cortex, and related subcortical structures could provide these inputs. These areas are believed to serve a modulatory role and provide information necessary to regulate ongoing behavior, for example by monitoring performance and signaling rewards. Such areas are well-positioned to bias frontal–parietal action representations. An established line of work has studied how rewards are processed by the dopaminergic system. Current theories posit that reward processing involves the signaling of reward prediction errors by dopaminergic neurons which project to the ventral striatum.

Unlike rewards which can be objectively determined, costs and other biases are subjective in nature. How subjective choices are processed in the brain has historically received relatively little attention but costs are likely to play an important role in shaping many behaviors. In one recent study, costs were seen to drive choice behavior. Monkeys were presented with three alternatives and rewards were randomly assigned to each alternative with equal probability. Even though the reward distribution could not be learned, each animal adopted a specific strategy for performing the task which reflected the effort associated with moving to select each choice [8]. Several studies have examined subjective choice using an intertemporal choice paradigm in which subjects discount delayed rewards [9–11]. Temporal discounting is inherently subjective and the tendency to discount larger, delayed rewards and prefer smaller, immediate rewards, differs between subjects and correlates with other personality traits. Brain imaging during intertemporal choice reveals that activity in the ventral striatum, medial prefrontal cortex, and posterior cingulate cortex track subjective valuations expressed by choices for the timing of primary and monetary rewards [12,10,11]. In monkeys, electrical recordings of neurons in the striatum and anterior cingulate cortex support this picture and identify a network of areas specifically involved in representing the costs and rewards of actions [13–15]. In addition to temporal delays, costs can depend on the effort required to obtain a reward. In rats, lesions to orbitofrontal cortex cause impulsive choices but not effort-based decisions while anterior cingulate cortex lesions lead to apathy but not impulsiveness [16]. Evaluating the costs of time and effort may depend on distinct brain regions within frontal cortex and depend on different decision circuits.

These considerations can be conceptually summarized into two different systems, a sensory–motor choice system and decision theoretic valuation system [17•]. These systems are distributed across different regions of the brain. A major challenge facing the neurobiological understanding of decision making is understanding how valuation drives choice to transform decisions into actions. Addressing this challenge requires the development of new techniques and concepts for studying neural circuits. These neural circuit tools will be broadly relevant to understanding many cognitive processes such as those involved in perception, action, attention, learning, and memory.

Using correlated neural activity to understand neural circuits

Understanding the computational function of interactions across neural circuits, why brain regions communicate, involves eavesdropping on the activity of groups of neurons while computations are being performed. Neural ensemble recordings are increasingly focusing on characterizing the correlations in neural activity between brain regions. The premise is that the presence or absence of correlations in neural activity across a circuit reflects the underlying computational demands being placed on the circuit. Pair-wise correlations, higher dimensional subspaces and manifolds, information metrics, and model-based analyses of neural signals have all come to the fore in recent years with the goal of resolving correlations in neural circuits [18–26].

The massive divergence and convergence of synaptic connectivity within the neuropil mean that individual neurons have measurable correlations mainly with neurons in local microcircuits [27]. A recent study reexamining V1 neuron correlations within local circuits finds pairs of individual neurons can be strikingly uncorrelated in their activity, although the role of stimulus size is likely to be important and remains to be accounted for [28]. The relative lack of correlation between spike trains from pairs of neurons makes sense when you consider that even the activity of a neuron firing at 50 Hz is relatively sparse point process. A barrage of synaptic events driven by correlated inputs may still fail to raise the membrane potential to the threshold for action potential initiation [29].

The relative lack of correlation in the activity of pairs of neurons should not, however, be taken to imply that the activity of groups of neurons does not show strong correlations. In fact, there is strong evidence that populations of neurons which have only weak correlations between

pairs of neurons can form correlated states with strong collective dynamics. Collective dynamics in the spiking activity of groups of neurons have been characterized in the retina and in neuronal cell cultures [18]. *In vivo* evidence for collective dynamics is also available using neural ensemble recordings made in rats, monkeys, and humans [30,19]. The available evidence points to strongly collective states that extend across long-range circuits. Truccolo *et al.* used model-based analyses of recordings of neural ensembles in frontal–parietal cortex to show that activity of neurons in frontal motor cortex was as strongly correlated with other motor cortical neurons as it was with another group of neurons in parietal cortex [19]. These reports do not tie correlated states to specific behavioral processes, like making decisions, but the signs point in the right direction.

Measuring neural correlations with local field potentials

Local field potentials (LFPs) offer another approach to study neural circuits through correlated neural activity. LFPs are measured by placing an electrode within or directly on the surface of the brain. Unlike action potentials which are generated by individual neurons, LFPs predominantly measure synaptic potentials pooled across groups of neurons near the recording electrode and are closely linked to trans-membrane currents [31]. As a result, LFP signals reflect the presence of correlations in the activity of many neurons. While recording from individual neurons is challenging, measuring LFPs is easier. Crucially, while LFP signals are related to EEG signals measured at the scalp because both measure voltages from pooled synaptic potentials, LFP signals can reveal quite different activity patterns than EEG signals. For example, unlike EEG, response fields calculated from LFP signals can be as informative as response fields measured from the activity of individual neurons [32,33]. The relationship between LFP signals and action potentials is hard to disentangle as correlated firing in groups of neurons can be measured in both action potentials and LFPs. Therefore, there are reasons to be concerned that LFP signals are biased by action potential recordings [34]. Increased confidence that LFP signals are not significantly biased by action potentials comes from observations that the coupling between action potentials and LFP signals varies in a task-dependent manner [33] and that informative LFP signals can be measured on electrodes even when the spiking activity of neurons cannot [35].

Since LFPs are sensitive to correlations in neural activity and are relatively easy to record, LFPs may play an important role in understanding how information is processed between different regions of the brain. The study of LFPs has a long history in, for example, the olfactory bulb and the hippocampus and has played a fundamental role in our understanding of sleep and clinical states like epilepsy. In contrast, the use of LFPs to study how information is processed in other neural circuits remains at a relatively early stage. That said, more and more work shows that LFPs measured in cortex and in subcortical structures like the basal ganglia, amygdala, and thalamus have rich dynamics reflecting strongly correlated states [36,37,38••,39]. In the sensory–motor areas of the frontal and parietal cortex, studies have implicated LFPs in plans to make saccadic movements of the eyes [33], reaching movements of the arm [40], grasping movements of the hand [41], ongoing motor control and processing of visual-motor information [42,43], the orientation of spatial attention [7••], working memory [33,44], and decision making [8]. Recent work using MEG extends some of these results to human parietal cortex [45].

The mechanism of LFP measurements involves a complex dependence between the electrode and the current sources in the brain [46]. At root, measuring the LFP voltage involves summing across many neural elements with particular spatial and temporal correlations. If the currents generated by neural activity flow in different directions and are uncorrelated across the spatial extent of tissue, LFP signals will be small. LFPs also selectively represent neural signals that share temporal correlations such as those found when many neurons fire together in synchrony. Consequently, LFPs are intrinsically measures of neural correlation. Getting to the heart of LFP measurements involves understanding how correlated neural activity is reflected in the LFP.

Progress on understanding how current sources generate different features of LFP activity is most advanced in the hippocampal formation where the mechanisms and properties of different rhythms in the theta and gamma frequency bands are being elucidated, most recently through studies of travelling waves and coherence between CA1, CA3, and entorhinal cortical regions [47,48]. In the neocortex, studies of the mechanism of LFP measurements have focused on understanding how LFP signals propagate passively within tissue and place limitations on how LFPs are passively filtered by the cortex. Two recent studies examine how far LFP signals passively spread in cortex using very different approaches [49,50•]. The results are remarkably similar. Katzner *et al.* optically image orientation selectivity columns and fit LFP responses to visual stimuli by blurring the orientation maps [49]. They find a best fit between LFP tuning and orientation selectivity when blurring with a Gaussian with radius of $\sim$250 μm. Xing *et al.* use the retinotopy of V1 to infer the spread of LFP signals driven by visual input [50•]. They analyze the difference between the sizes of response fields measured using multiunit and LFP activity and reason that if the increased size of LFP response fields compared with multiunit response fields can be purely attributed to passive current spread, the

LFP spreads by no more than ~250 μm. This is an upper bound on the degree of spread because of passive mechanisms because the difference in response field size likely includes a contribution from active neural correlations. How much LFP signals at different frequencies can be distorted by capacitive components in cortical tissue has also been measured. Measuring the impedance of cortical tissue reveals that, at the frequencies of interest, <300 Hz, cortical tissue behaves like an anisotropic ohmic resistor [51]. As a result, the passive propagation of LFP signals is influenced by cortical layers but is relatively undistorted by capacitive neural elements.

While these studies do not directly speak to how LFP signals reflect correlated neural activity, they provide important bounds beyond which active neural processes must shape LFP signals. The message is that correlations in LFP signals that extend beyond several hundred microns are because of active neural mechanisms and the fact that LFP power is present at lower temporal frequencies (<100 Hz) and reduced at higher temporal frequencies (>100 Hz) is not because of capacitive cortical filtering.

Measuring neural interactions between distant neural populations

Understanding how neural correlations can inform us about interactions between neural populations in different brain regions is likely to be essential for understanding distributed computations like the transformation of value into choice. One promising approach to understanding long-range interactions is the spike-field approach that depends on the combined analysis of spiking and LFP activity.

There are several reasons why analyzing both spiking and LFP activity could offer advantages over studying either signal alone. The distinction between action potentials and synaptic potentials means spiking and LFP activity represent different yet complementary aspects of neural processing. In the context of a distributed network, spiking of a population of neurons will form the output of an area while LFP activity may be more sensitive to the local processes within the area and inputs to the area from other areas. Dissociations between the content of spiking and LFP signals within an area could be informative about how an area transforms inputs into outputs [52]. In FEF, this line of argument has been used to implicate FEF as the site where selection for eye movements first emerges [7••]. Supporting evidence comes from the properties spike and LFP responses in MT and MST to visual motion. LFPs in MST were found to encode motion with properties similar to spiking in MT while LFPs in MT had properties more similar to neurons in V1 [38••]. The implication of this work is that LFPs encode the feed-forward sensory afferents into each area.

Reasoning about how spiking and LFP activity differentially encode decision signals may be effective in understanding how areas transform values into choices. There are many studies of how single unit activity encodes value-based signals in a variety of frontal and parietal regions. Studies of LFP activity in monkeys performing decision tasks that parametrically manipulate value-based signals have not yet been reported. Establishing whether the spike-field approach can track transformations between the interlinked brain regions that form decision circuits is an exciting new direction.

Another advantage of the spike-field approach involves the analysis of correlations in simultaneous recordings between brain regions. When faced with the task of understanding multiple brain areas, LFP signals may provide a measure of correlated local activity that can be linked to the activity of nearby neurons in the local circuit as well as to the activity of neurons in other regions. Unlike correlations between individual neurons, LFP signals in different brain regions display rich patterns of correlation. Such correlations likely reflect the underlying computational demands being placed on the circuit. The role of gamma band synchronization has received particular emphasis [53] and correlations at other frequencies may also play an important role.

A growing number of spike-field studies report task-dependent long-range correlations, indicating that synchronization at specific frequencies may reflect inter-area communication [6•,8,54••,55]. Buschman and Miller examine prefrontal interactions with parietal cortex during attentional processing and link bottom-up attention with synchronization at 22–35 Hz while synchronization at 35–55 Hz is linked to top-down attention [6•]. Gregoriou *et al.* examine gamma frequency band interactions between FEF and V4 during attention and find evidence for a driving influence of activity in FEF on activity in V4 [54••]. Saalman *et al.*, find that correlations between parietal area LIP and visual area MT are consistent with parietal neurons selectively increasing activity in the sensory area during attention [55]. During a decision making task, we found that activity at a lower 15 Hz frequency band was correlated between the dorsal premotor cortex and the parietal reach region, two interconnected reach-related areas of the frontal and parietal cortex, when monkeys were freely choosing reach targets more than when they followed externally imposed instructions [8]. Interestingly, in this last study, the neurons that exhibited long-range correlation predicted the outcome of the decision earlier than neurons that did not suggest that a decision circuit was activated between frontal and parietal cortex. Since freely choosing targets required costs and not rewards to drive choices, frontal–parietal correlations may be modulated by inputs from valuation system.

Overall, these and other similar studies open the door to using neural correlations to understand how brain areas communicate with each other to guide behavior. At this point, processing in particular frequency bands seems to be linked to specific brain circuits and, perhaps, cognitive processes. How patterns of correlated activity reflect the communication of information between brain regions and how communication drives behavioral processes remain important, challenging goals for the future.

Conclusions

Analyzing neural correlations between spiking activity and LFP signals to identify interactions between distant areas is a new approach that is already starting to bear fruit. Simultaneous neural ensemble recordings from different brain regions, while technically more demanding than spike-field measurements, also have the potential to reveal how correlated states reflect neural computations that are distributed across brain regions. In this review, integration of value and choice activity when making a decision has been highlighted and used to illustrate a potentially general approach to tackling the challenge of understanding how interactions between different brain regions can drive behavior.

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