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Neural mechanisms of sensorimotor transformation and action selection

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Abstract

Ray Guillery made major contributions to our understanding of the development and function of the brain. One of his principal conceptual insights, developed together with Murray Sherman (Sherman & Guillery, 2001; Sherman & Guillery, 2006; Sherman & Guillery, 2013) and then in his last book (Guillery, 2017), was that the brain is a ‘tool’ to understand the world. In this view, the brain does not passively process sensory information and use the result to inform motor outputs. Rather, sensory and motor signals are widely broadcast and inextricably linked, with ongoing sensorimotor transformations serving as the basis for interaction with the outside world. Here, we describe recent studies from our laboratory and others which demonstrate this astute framing of the link between sensation, perception and action postulated by Guillery and others (Deco & Rolls, 2005; Cisek & Kalaska, 2010). Guillery situated his understanding in the deeply intertwined relationship between the thalamus and cortex, and importantly in the feedback from cortex to thalamus which in turn influences feedforward drive to cortex (Sherman & Guillery, 2001; Sherman & Guillery, 2006). We extend these observations to argue that brain mechanisms for sensorimotor transformations involve cortical and subcortical circuits that create internal models as a substrate for action, that a key role of sensory inputs is to update such models, and that a major function of sensorimotor processing underlying cognition is to enable action selection and execution.

Keywords

Attention; evidence accumulation; decision-making

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Sensorimotor transformations and action selection

Imagine you are driving a car on a rainy day, which creates a noisy visual environment. As you approach the intersection, you drown out the music and divert attention to the upper portion of the visual field. As you catch glimpses of the stoplight through the rapidly moving windshield wipers and the pouring rain, you detect that the green light has turned to yellow and you decide to stop the car. You wait until the right moment, carefully withdraw your foot from the accelerator, prepare your foot for moving and apply the brakes. This example highlights that even simple sensorimotor behaviors involve several processes. Our senses are constantly overloaded with a myriad of sensory inputs from the environment, requiring attention to guide neural resources to prioritize processing of behaviorally relevant stimuli. Moreover, responding to environmental cues with appropriate actions requires integration of noisy sensory evidence that must be accumulated over time. Once sufficient evidence in favor of a prospective choice is gathered, the correct action must be selected from a large behavioral repertoire. Of course, many of these processes are largely interdependent and occur concurrently in naturalistic settings. In the example above, attention must be deployed to the appropriate location in visual space (i.e., on the traffic light) to accumulate evidence, generate a percept/decision, and select and execute an action. Indeed, the example illustrates that action goals determine which sensory inputs deserve attention, how sensory evidence is gathered, and what action is ultimately selected.

Intense efforts over the past decades have focused on deconstructing the neural mechanisms underlying these aspects of perceptual decision-making using controlled behavioral task designs in experimental animals (Gold & Shadlen, 2007). Recent technological advances in virus-mediated anatomical tracing, tools for manipulating neural activity with high spatiotemporal precision (such as optogenetics), and simultaneous monitoring of a large number of neurons with multiphoton imaging or extracellular electrophysiological recording presents a unique opportunity to gain mechanistic understanding of these questions. Although the neural basis of sensorimotor behaviors has traditionally been studied primarily in non-human primates, the ease with which these techniques can be used in rats and mice has led to parallel advancements in training paradigms for these model organisms on sensorimotor tasks. Such complementary studies in rodents have uncovered important mechanisms underlying task-specific sensorimotor transformations and choice, defined generically here as action selection.

Brain areas causally involved in the accumulation of sensory evidence

Recent studies of evidence accumulation during perceptual decision tasks are a particularly striking example of the way sensory inputs are used to build and update internal models of a latent decision variable that guides action selection. In such tasks, animals are presented with noisy sensory evidence that is mentally accumulated over time to reach a categorical decision about its attributes. Importantly, the amount of sensory evidence is varied across trials. As expected, animals reach a decision quickly on ‘easy’ trials (i.e., with high evidence for one alternative), and respond slowly on ‘hard’ trials with more ambiguous sensory evidence. Seminal neurophysiological work in non-human primates identified neural correlates of evidence accumulation in the lateral intraparietal area (LIP) of the posterior parietal cortex (PPC) and the frontal eye field (FEF) division of the prefrontal cortex (PFC), amongst other areas. For instance, average firing rate activity of single FEF and LIP neurons show ramp-like increases in activity during stimulus presentation, a temporal epoch during which decision formation is underway. Importantly, this activity develops faster on ‘easy’ trials when animals respond quickly, but rises sluggishly on ‘hard’ trials in which responses are slower (Kim & Shadlen, 1999; Shadlen & Newsome, 2001). Together, these studies suggest that the PFC and PPC are crucial nodes in a distributed network necessary for evidence accumulation. However, their causal involvement remained largely unclear from these studies alone.

Several groups have now successfully devised paradigms for studying evidence accumulation in rats and mice (Brunton et al., 2013; Raposo et al., 2014; Morcos & Harvey, 2016; Marques et al., 2018; Pinto et al., 2018). Specifically, Hanks et. al. (2015) used a previously established auditory evidence accumulation task in which freely moving rats fixated in a central port while speakers on either side presented randomly timed pulses of evidence in the form of auditory clicks (Brunton et al., 2013). At the end of the stimulus presentation period, rats were required to make an orienting movement towards the side with the greater number of clicks. Temporally-specific optogenetic inactivation of the frontal orienting fields (FOF), a subdivision of the rodent PFC, affected choice behavior when inactivated during the end of the evidence accumulation period. However, choices were not affected by inactivating the FOF during the early stimulus presentation period (Hanks et al., 2015). This finding suggests that this area is not necessary for accumulating auditory evidence per se, but rather plays a role in selecting the action associated with the accumulated evidence.

If the rat FOF is not necessary, then where is auditory evidence accumulated? Intriguingly, a recent study suggests that neurons in anterior dorsal striatum (ADS), a large subcortical area crucially involved in perceptual and value guided action selection (Redgrave et al., 1999; Ding & Gold, 2013), encode accumulated auditory evidence in a graded manner. Importantly, optogenetic inactivation experiments showed that their activity is necessary for choice behavior throughout the evidence accumulation period (Yartsev et al., 2018). Together, these experiments suggest that the ADS accumulates auditory evidence necessary for guiding action selection. These findings open up intriguing new questions for future studies that will not only shed more light on the neural underpinnings of auditory evidence accumulation, but also influence theories of striatal function. Spiny projection neurons, the major output neurons of the striatum, are largely divided into two distinct cell types, distinguished by their expression of D1/D2 receptors, and give rise to the direct and indirect striatal output pathways, respectively (Surmeier et al., 2007). Moreover, the striatum is composed of distinct compartments, striosome and matrix, that have long been proposed to fulfill distinct functional roles (Graybiel, 1990; Friedman et al., 2015; Bloem et al., 2017). The inactivation strategy employed by Yartsev et al. (2018) non-specifically inactivated the striatum and whether the accumulator function localizes to specific striatal subpopulation population remains an open question. Future experiments using projection-specific optogenetic manipulations could identify if distinct inputs to the striatum preferentially contribute to the accumulator function or whether it is dependent on integration of inputs from multiple areas.

Another important question is whether the striatum causally contributes to sensory accumulation in a modality-invariant way, or if its role is specific to audition. A recent study probing the role of striatum in visually-guided action selection in mice showed that activating direct/indirect pathway output neurons did not change perceptual sensitivity (Wang et al., 2018). Instead, there was a change in the response criterion (i.e., the decision boundary used to select an action based on the accumulated evidence). Similarly, a modest change in response criterion was also detected in the auditory evidence accumulation study (Yartsev et al., 2018). Hence, to what extent the striatum plays a general role in evidence accumulation or determining the response criterion (or both) remains to be resolved.

These studies highlight that brain areas traditionally associated with action selection are intricately involved when decisions require perceptual evidence. Taken together, these findings indicate that evidence accumulation should not be viewed as a purely sensory process, but rather as inextricably linked to sensorimotor transformation and action selection.

Brain regions for attentional processing of behaviorally-relevant stimuli

A significant and growing body of work indicates that fundamental substrates of cognition, such as attention, deeply engage and might even arise from mechanisms of action selection (Squire et al., 2013). When action selection is perceptually-guided, top-down attention must first be deployed to select sensory stimuli carrying information relevant for current behavioral goals while ignoring irrelevant distractors. During naturalistic visual behavior, attention is often overtly oriented to bring objects of interest into view with eye and head movements. However, attention can also be deployed covertly in the absence of such movements. The neural basis and implementation of attention has been studied most extensively in monkeys using paradigms that probe covert spatial visual attention, although many authors have also studied attention guided by non-spatial stimulus features such as color or specific orientations (Treue & Martinez Trujillo, 1999; Martinez-Trujillo & Treue, 2004; Maunsell & Treue, 2006; Buschman & Miller, 2007). When perceptual decisions are guided by attention, they are more accurate and faster (Carrasco, 2011). A general conclusion from many neurophysiological studies is that attention strongly modulates the activity of neurons that represent the attended stimulus widely across the brain, including in visual, parietal, and prefrontal cortical regions, and in subcortical areas like the superior colliculus (Desimone & Duncan, 1995; Treue, 2001; Maunsell & Cook, 2002; Reynolds & Chelazzi, 2004; Moore & Zirnsak, 2017; Paneri & Gregoriou, 2017). Causal activity manipulation studies have also established that both cortical and subcortical structures are involved in mediating the effect of attention on perceptual behavior (Noudoost et al., 2010; Zénon & Krauzlis, 2012; Krauzlis et al., 2013; Paneri & Gregoriou, 2017).

The benefits of attention on perceptual decisions can be mediated by two mechanisms: attention could increase the perceptual sensitivity of stimuli or decrease the criterion used for classifying perceptual evidence into categorical decisions at attended locations (Carrasco, 2011; White et al., 2012; Luo & Maunsell, 2015; Banerjee et al., 2017). Recent studies suggest that different brain structures contribute specifically to each of these aspects of attention (Sridharan et al., 2017; Luo & Maunsell, 2018). In a task designed to separately assay perceptual sensitivity or response criterion by manipulating reward contingencies at specific spatial locations, the activity of visual cortex neurons was modulated only when attention was implemented through enhanced perceptual sensitivity (Luo & Maunsell, 2015). In contrast, the activity of superior colliculus neurons recorded in a similar task was strongly associated with response criterion (Crapse et al., 2018). A model-based analysis of studies in which the SC was inactivated (Cavanaugh & Wurtz, 2004; Müller et al., 2005; Lovejoy & Krauzlis, 2009; Zénon & Krauzlis, 2012) showed that it facilitates spatial attention predominantly by lowering the response criterion at the attended location (Sridharan et al., 2017). Hence, the sensitivity and criterion components of visual selective attention are dissociable behaviorally and may be subserved specifically by circuits in the visual cortex and the superior colliculus, respectively (Crapse et al., 2018; Luo & Maunsell, 2018).

The prefrontal cortex (PFC) has long been thought to be a nexus for linking perception and action selection through attention (Moore & Fallah, 2001; Wardak et al., 2006; Zikopoulos & Barbas, 2006; Barbas & Zikopoulos, 2007; Monosov & Thompson, 2009; Noudoost et al., 2010; Squire et al., 2013; Gregoriou et al., 2014; Paneri & Gregoriou, 2017). Consistent with its general role in guiding attention, PFC activity is differentially modulated depending on whether spatial visual attention operates through changes in perceptual sensitivity or response criterion (Luo & Maunsell, 2018). Differential modulation of PFC activity may in turn generate different behavioral strategies suited to task demands and contingencies (Baruni et al., 2015; Luo & Maunsell, 2015; Banerjee et al., 2017; Crapse et al., 2018). An important question is how the optimal strategy is selected to produce goal-oriented deployment of spatial visual attention. The PFC has been widely implicated in dynamically coordinating behavior by biasing the flow of activity in downstream cortical and subcortical structures (Miller & Cohen, 2001). Given that distinct neuronal populations in the prefrontal cortex send direct projections to either the visual cortex or the superior colliculus (Pouget et al., 2009), an enticing possibility is that the PFC arbitrates between the expression of these strategies in a context-dependent manner by using anatomically-specific pathways. For example, during task-conditions in which decreasing the response criterion is maladaptive but increasing perceptual sensitivity is advantageous (Baruni et al., 2015; Luo & Maunsell, 2015; Luo & Maunsell, 2018), PFC outputs to the visual cortex may enhance the perceptual sensitivity of visual cortex responses while outputs to the superior colliculus prevent shifts in response criterion. Consistent with this hypothesis, there is considerable evidence that the PFC provides top-down signals necessary for the observed attentional modulation of visual cortex neurons in monkeys (Moore & Armstrong, 2003; Gregoriou et al., 2009; Squire et al., 2013; Gregoriou et al., 2014; Paneri & Gregoriou, 2017). The contribution of the PFC to attentional modulation by the superior colliculus is presently unclear and awaits future studies.

Once again, attentional processing (like evidence accumulation), is not just a passive sensory process, but rather appears to be intimately linked to action selection.

Cortical and subcortical roles of frontal cortex in visuomotor behavior

Although much progress has been made in identifying the mesoscale brain regions that contribute to spatial attention, the contribution of distinct cell types remains largely unknown. Given the arsenal of tools available in mice for cell-specific dissection of neural circuits, complementary studies probing perceptual decisions in the rodent model offer great promise for complementing non-human primate research. Optogenetic actuators can be spatially targeted to specific brain areas using viruses and expressed in cell bodies as well as axons, allowing for local activation or inactivation of specific outputs to target structures (Tye & Deisseroth, 2012). Such a strategy has been successfully employed by many groups in mice, making them a valuable model system to address the role of specific prefrontal circuits in perceptual decisions. Recent work has identified an area in the mouse medial frontal cortex with anatomical and functional characteristics suggesting that it exerts top-down control over perceptual behavior, similar to the prefrontal cortex in monkeys. This area has been variously called anterior cingulate cortex (ACC), M2, and A24b by different groups (Koike et al., 2016; Zhang et al., 2016; Leinweber et al., 2017); we refer to it here with the generic term ACC in keeping with the nomenclature used by common mouse brain atlases (Paxinos & Franklin, 2004). Importantly, the ACC receives inputs from both primary and higher visual cortex (Huda et al., 2015; Fillinger et al., 2017; Huda et al., 2018), exhibits visual responses at network and single-neuron levels (Huda et al., 2015; Murakami et al., 2015), and sends top-down projections to the visual cortex and the superior colliculus (Zhang et al., 2014; Zhang et al., 2016; Leinweber et al., 2017; Fillinger et al., 2018; Huda et al., 2018). Studies employing causal manipulations using chemogenetics and optogenetics show that ACC activity guides optimal performance on visual detection tasks that require sustained attention in freely moving mice (Koike et al., 2016; White et al., 2018). Interestingly, ChR2-mediated activation of direct ACC outputs to the visual cortex enhances the gain of its sensory responses in a spatially-specific manner and enhances performance on a visual discrimination task, suggesting a role in visual spatial attention (Zhang et al., 2014). Together, these studies suggest that the ACC is crucially involved in visual perceptual behavior in mice.

Recent studies have also identified the contribution of specific ACC outputs to visual behavior. Distinct subpopulations of ACC projection neurons target either the visual cortex or the superior colliculus (Huda et al., 2018). Anatomical analysis using virus-mediated disynaptic tracing revealed that these two subpopulations receive inputs from overlapping but distinct set of presynaptic areas, suggesting anatomical and functional specialization of these two output circuits (Zhang et al., 2016). In agreement, we recently showed that these outputs exert context-dependent modulation over visually-guided action selection. We trained head-fixed mice on a two-choice visual detection task and used projection-specific optogenetics to probe the contribution of ACC outputs to visual cortex and superior colliculus to behavior (Huda et al., 2018). We found that top-down outputs from the ACC to the visual cortex are necessary for selection of correct actions. Surprisingly, outputs to the superior colliculus are crucially involved in preventing erroneous responses (Huda et al., 2018). Whether circuits centered around ACC outputs to the visual cortex and superior colliculus differentially contribute to visual attention is not yet clear, but our findings provide the first evidence that these outputs coordinate distinct aspects of visuomotor behavior. Given the recent advancements in training mice on perceptual decision-making tasks in which selective visual attention can be probed (Wang & Krauzlis, 2018), it should soon be possible to gain a cell-specific understanding of how distinct output pathways from the frontal cortex coordinate specific aspects of attention to guide perceptual decisions.

A distributed network of brain areas contributes to rapid sensorimotor transformations

As our discussion above suggests, perceptual decision-making involves multiple processes that are instantiated via coordinated activity and information flow between many different brain areas. Enabled by temporally-specific causal manipulations made possible by optogenetics, recent studies have highlighted how information flow across brain areas contributes to perceptual behaviors driven by somatosensory, auditory, and visual stimuli in mice (Chen et al., 2013; Znamenskiy & Zador, 2013; Guo et al., 2014; Li et al., 2015; Goard et al., 2016). For example, we recently examined the contribution of a circuit spanning the visual cortex, posterior parietal cortex (PPC), and frontal motor cortex (fMC) to memory-guided visual decisions (Goard et al., 2016). Mice were trained on a go/no-go visual orientation discrimination task in which the sensory stimulus epoch was temporally separated from the motor response period with an intervening delay, requiring them to hold the correct motor response in short-term memory. Two-photon calcium imaging of task responses showed that a majority of neurons in the visual cortex responded during the stimulus epoch. As expected, optogenetic inactivation experiments showed that the visual cortex was necessary for task performance only during the stimulus epoch. Most neurons in the fMC were active during the delay and response epochs; surprisingly, a substantial minority were also active during the sensory period. Consistent with this pattern of responses, fMC was necessary during all task epochs, including the delay. These results, together with other recent studies (Erlich et al., 2011; Li et al., 2015; Kamigaki & Dan, 2017), suggest that frontal motor cortical areas such as M2, FOF, and ALM, all of which overlap in anatomical space (Svoboda & Li, 2018), are a crucial node in the brain circuitry responsible for action selection, including maintaining the motor plan in short-term memory for later execution.

Previous studies examining the causal role of the PPC in perceptual decisions suggested that it plays a minimal role in guiding choices driven by auditory stimuli in rodents (Raposo et al., 2014; Erlich et al., 2015). However, we and others have found that its activity is necessary for visually-guided behavior (Harvey et al., 2012; Raposo et al., 2014; Goard et al., 2016; Driscoll et al., 2017; Licata et al., 2017; Pho et al., 2017). Importantly, activity of PPC neurons reflected both stimulus parameters and the animal’s choice, suggesting that it plays a key role in visuomotor transformation (Pho et al., 2017). Together, these results begin to sketch out a candidate interareal circuit in which stimulus identity is rapidly transformed into a choice (possibly within PPC), and then the behavioral choice is maintained in higher motor regions (e.g., fMC) until the relevant motor action is performed. Future studies employing projection-specific activity manipulations and recordings will be instrumental in testing this hypothesis.

Concluding remarks

These findings from a number of laboratories, including ours, lend support to Ray Guillery's hypothesis that sensory and motor processing should not be seen as the domain of separate and distinct neural circuits, but as extensively and intimately intermingled networks spanning the cerebral cortex and subcortical structures. Sensory (input) information is modulated at subcortical and cortical sites, at almost every stage of processing, by motor (output) signals. Furthermore, sensory signals are transformed as early as possible into explicit motor signals. Together, these findings suggest that perception and action are co-determined, and sensory inputs that lead to perception derive meaning in light of task-dependent goals and the actions that are selected to achieve them.

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Mriganka Sur: My co-authors and I dedicate this review to Ray Guillery. I regard Ray as my intellectual grandfather: I trained with Jon Kaas for my doctoral studies and Murray Sherman for my postdoctoral research, both of whom worked with Ray. In hindsight, Ray's work influenced me to a remarkable extent. His early studies on EM analysis of retinogeniculate synapses and of retinal axon development inspired our studies of the developmental segregation of X and Y, and on-center and off-center, retinogeniculate axons (Sur et al., 1984; Hahm et al., 1991). His studies of the critical period had echoes in later work from our lab on mechanisms of ocular dominance plasticity in visual cortex (Tropea et al., 2009; McCurry et al., 2010). His use of ferrets as a model system for early visual development led the way for the use of ferrets in our laboratory as a model to understand cortical plasticity induced by 'rewiring' retinal projections to the auditory pathway (Sur et al., 1988; Sharma et al., 2000). Ray's work with Murray Sherman on corticocortical communication via the thalamus, and their ideas of sensorimotor interactions underlying perception, has deeply influenced our analysis of information flow between cortical areas and cortical-subcortical structures for perception, decisions and action selection.

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