Neural Mechanisms for Interacting with a World Full of Action Choices

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Abstract

The neural bases of behavior are often discussed in terms of perceptual, cognitive, and motor stages, defined within an information processing framework that was originally inspired by models of human abstract problem solving. Here, we review a growing body of neurophysiological data that is difficult to reconcile with this influential theoretical perspective. As an alternative foundation for interpreting neural data, we consider frameworks borrowed from ethology, which emphasize the kinds of real-time interactive behaviors that animals have engaged in for millions of years. In particular, we discuss an ethologically-inspired view of interactive behavior as simultaneous processes that specify potential motor actions and select between them. We review how recent neurophysiological data from diverse cortical and subcortical regions appear more compatible with this parallel view than with the classical view of serial information processing stages.

Contents

INTRODUCTION

In this review, we discuss some potential implications of recent neurophysiological results to large-scale theories of behavior. We focus primarily on data from the cerebral cortex of non-human primates, data that are often interpreted in terms of a theoretical framework influenced by studies of human cognition. In that framework, the brain is seen as an information processing system that first transforms sensory information into perceptual representations, then uses these to construct knowledge about the world and make decisions, and finally implements decisions through action.

However, neurophysiological data we review below appear to be at odds with many of the assumptions of this influential view. For example, studies on the neural mechanisms of decision making have repeatedly shown that correlates of decision processes are distributed throughout the brain, notably including cortical and subcortical regions that are strongly implicated in the sensorimotor control of

movement. Neural correlates of putative decision variables (such as payoff) appear to be expressed by the same neurons that encode the attributes (such as direction) of the potential motor responses used to report the decision, which reside within sensorimotor circuits that guide the on-line execution of movements. These data and their implications for the computational mechanisms of decision making have been the subject of several recent reviews (Glimcher 2003, Gold & Shadlen 2007, Schall 2004). Here, we consider more general questions of what these and other recent data imply for large-scale theories of the neural organization of behavior. Why should supposedly cognitive processes take place within sensorimotor circuits? Why should individual neurons appear to change in time from encoding sensory qualities to encoding motor parameters? What should be the time course of neural processing? Many recent results do not appear to be compatible with the classical distinctions between perceptual, cognitive, and motor systems (Lebedev & Wise 2002); and we consider whether an alternative framework can more readily account for these observations.

As an alternative perspective, we consider frameworks inspired by many decades of ethological research focused on natural animal behavior in the wild. Such behavior involves continuous sensorimotor interaction between an organism and its environment, in contrast with conditions often used in the laboratory in which time is divided into a series of individual trials. Because the brain's functional architecture originally evolved to serve the needs of interactive behavior, and was strongly conserved during phylogeny, we believe an ethological foundation may be more appropriate for understanding neurophysiological data about voluntary sensorimotor behavior compared to frameworks inspired by studies of advanced human abilities. Indeed, we believe that a wide variety of neurophysiological results are more readily interpreted within the perspective of ethologically-based theories.

COGNITIVE NEUROSCIENCE AND THE INFORMATION PROCESSING FRAMEWORK

Imagine yourself sitting at a computer, replying to a friend's email message. From the outside, the act looks simple: A person is seated, hardly moving their body, looking at a computer screen. After some time, fingers begin to tap some keys on the keyboard. Of course, on the inside, this behavior involves a large set of incredibly complex processes. These include visual recognition of the letters displayed on the screen, parsing of the words and sentences, analysis of their meaning, emotional reactions to it, consideration of the many factors that influence the nature of the answer and how to phrase the reply, and finally, the production of precise finger movements to produce a new set of letters. We can classify these processes into three general categories: perception—the processes that take information from the outside world to build knowledge about it; cognition—the internal processes of knowledge manipulation, including semantic analysis, decision making, etc.; and action—the control of the muscular contractions that produce our response. In tasks such as replying to an email, these processes are likely performed in a largely serial manner. We sense the world, think about it, and then act upon it.

This informal description of behavior is often reflected in how we study it in the lab. Perceptual scientists study how the brain processes information to produce internal representations of external phenomena. Cognitive scientists study, among other things, how knowledge is acquired, how memories are stored and retrieved, and how abstract decisions are made between distinct choices such as whether to try gamble A or B. Motor scientists like us study how a voluntary plan of action is transformed into patterns of muscular contraction that move our limbs or eyes or produce utterances. This division of labor among neuroscientists reflects how we think about behavior and influences how we teach brain science. Indeed, the view of the brain as an information processing system is formalized in a theoretical framework that has dominated psychological thinking and teaching for more than 50 years.

Information processing was established as the theoretical foundation of cognitive psychology during the mid-twentieth century, when it replaced the then-dominant paradigm of behaviorism. From the information processing perspective, perception involves the construction of increasingly sophisticated and abstract internal representations of the world (Marr 1982) that are used as the input to cognitive systems. These cognitive systems bring salient context-dependent information together in a temporary working memory buffer (Miller 1956), manipulate representations to build complex knowledge (Johnson-Laird 1988, Pylyshyn 1984), store and retrieve information from long-term memory (Newell & Simon 1972), perform deductive reasoning (Smith & Osherson 1995), and make decisions (Shafir & Tversky 1995, Tversky & Kahneman 1981). Finally, the motor systems are seen simply as tools that implement action plans chosen by cognitive processes. They are often conceived according to formalisms borrowed from engineering control theory, in which a predetermined motor program or desired trajectory (Keele 1968, Miller et al. 1960) is passed to a controller that executes it via feedforward and feedback control mechanisms.

This classical framework was originally proposed as an explanation of complex human abilities of abstract problem solving, such as chess playing (Newell & Simon 1972, Pylyshyn 1984)—the kinds of problems that require the subject to obtain information about the world and perform a great deal of computation before taking any external actions. It was not originally meant to be a general theory of all behavior. Eventually, however, the architecture of an information processing system was seen as so powerful that its basic concepts have come to influence nearly every domain of brain theory. For example, the concept of the bandwidth of transmission in information processing channels has provided a foundation for theories

Motor program: a theoretical representation of planned movements

of attention (Broadbent 1958) and working memory (Miller 1956), as well as studies of motor control (Fitts 1954). The project of explaining complex behavior in terms of neural mechanisms is often called cognitive neuroscience (Albright et al. 2000, Gazzaniga 2000). It is an approach that inherits specific concepts from cognitive psychology and maps them onto particular regions of the brain. Today, even those of us who study sensorimotor control have a tendency to phrase the problem as one of transforming input representations to output representations through a series of intermediate processing stages.

However, attempts to interpret neural data from this perspective encounter several challenges. For example, functions that should be unified appear distributed throughout the brain, whereas those that should be distinct appear to involve the same regions, or even the same cells. Below, we discuss several examples of such challenges, which lead us to question whether the basic structure of sensing, thinking, and acting is indeed the optimal blueprint for understanding how the brain implements much of the real-time interactive behavior whose demands drove neural evolution.

Perceptual Processing

Psychological and computational theories often propose that our perception of the world is the result of a reconstruction process that uses sensory information to build and update an internal representation of the external world (Marr 1982, Riesenhuber & Poggio 1999, Riesenhuber & Poggio 2002). We usually assume that this internal representation must be unified (linking diverse information into a common form available to diverse systems) and stable (reflecting the stable nature of the physical world) to be useful for building knowledge and making decisions. To date, however, neural data does not support the existence of such an internal representation. Indeed, the representation of the external world generated by the most studied sensory modality, the visual system, appears to be neither unified nor

stable at the level of single neurons or neural populations.

For example, Ungerleider & Mishkin (1982) reviewed data indicating that visual information in the cerebral cortex diverges into two partially distinct streams of processing: (*a*) an occipitotemporal ventral stream in which cells are sensitive to information that pertains to the identity of objects and (*b*) an occipitoparietal dorsal stream in which cells are sensitive to spatial information. Within each of these, information diverges further. There are separate visual streams for processing color, shape, and motion (Felleman & Van Essen 1991); and there are multiple representations of space within the posterior parietal cortex (Colby & Goldberg 1999, Stein 1992). From the traditional cognitive perspective, the ventral stream builds a representation of what is in the environment, whereas the dorsal stream builds a representation of where things are. Presumably, all of these visual substreams must be bound together to form a unified representation of the world; but whether and how this binding occurs remain unresolved, despite vibrant research efforts (Engel et al. 2001, Shadlen & Movshon 1999, Singer 2001).

Furthermore, activity in much of the visual system appears to be strongly influenced by attentional modulation (Boynton 2005, Colby & Goldberg 1999, Moran & Desimone 1985, Treue 2001), even when a quiescent monkey spontaneously scans a familiar stable environment (Bushnell et al. 1981, Gottlieb et al. 1998, Mountcastle et al. 1981). This is usually exhibited as an enhancement of neural activity from the regions of space to which attention is directed and a suppression of activity from unattended regions. Such attentional modulation is found in both the ventral and dorsal streams and increases as one ascends the visual hierarchy (Treue 2001). Consequently, the neural representation of the visual world, at least in higher visual areas, appears "dominated by the behavioral relevance of the information, rather than designed to provide an accurate and complete description of it" (Treue 2001, p. 295). Furthermore, because the direction of

attention is frequently shifting from one place to another, the activity in visual regions is anything but stable. It is constantly changing, even if one is fixating a completely motionless scene.

To summarize, the classical assumption of a unified and stable internal representation (an internal replica of the external world) does not appear to be well supported by the divergence of the visual system and the widespread influence of attentional and contextual modulation. If something that resembles a perception module exists, it overlaps so strongly with cognitive processes that the distinction between them becomes blurred.

Motor Control

According to the information processing view of voluntary behavior, the role of the motor system is to implement the course of action commanded by the cognitive system. This has led to the common assumption that by the time motor processing begins, cognitive processes have decided what to do, and only a single motor program is prepared before movement initiation (Keele 1968, Miller et al. 1960). However, neural data do not appear to support this assumption. First, many of the same regions that appear to be involved in movement planning are also active during movement execution (Alexander & Crutcher 1990b, Crammond & Kalaska 2000, Hoshi & Tanji 2007, Kalaska et al. 1998, Wise et al. 1997). Neural correlates of both planning and execution processes can be found even in the activity of individual cells, whose association with motor output changes in time from abstract aspects of the task to limb movement-related parameters (Cisek et al. 2003, Crammond & Kalaska 2000, Shen & Alexander 1997). Furthermore, whenever planning activity has been studied in tasks that present animals with choices, that same activity also appears related to decision making processes that should have been completed by the cognitive system (Cisek & Kalaska 2005, Gold & Shadlen 2007, Hoshi & Tanji 2007, Platt & Glimcher 1999, Romo et al. 2004, Wallis & Miller 2003). Such functional

heterogeneity at the level of single neurons is difficult to reconcile with the breakdown of behavior into perception, cognition, and action.

Instead of encoding the unique and detailed motor program predicted by classical models (Keele 1968, Miller et al. 1960), neural activity in motor regions appears to initially encode information about relevant stimuli and then changes to represent motor variables, such as the direction of movement. For example, during visual search tasks, cells in frontal eye fields (FEF) initially respond to all salient stimuli, including multiple distracters, but later reflect only the final selected target (Schall & Bichot 1998). During reach/antireach tasks, neural activities in the dorsal premotor cortex (PMd) first appear to encode the location of a stimulus and later reflect the movement direction instructed by that stimulus (Crammond & Kalaska 1994, Gail et al. 2009). Such findings have often been interpreted as early visual responses, which are followed by motor activity, but it is unclear how a traditional model could account for both of these being encoded in the same region, sometimes by the same neurons. Additionally, neural activity in motor regions appears to be modulated by a variety of putatively cognitive variables, as described below. In summary, if an action module exists, then it appears to be closely entwined with both perceptual and cognitive processes (Lebedev & Wise 2002).

Cognitive Functions

The search for the modules that lie between perception and action has been even more problematic. According to classical views (Fodor 1983, Pylyshyn 1984), cognition is separate from sensorimotor control. However, a hallmark executive function, decision making (Tversky & Kahneman 1981), does not appear to be localized within particular higher cognitive centers such as the primate prefrontal cortex. Instead, there is growing evidence that decisions, at least those reported through action, are made within the same sensorimotor circuits that are responsible for planning and executing the associated actions (Cisek & Kalaska 2005, Gold

Motor program: a theoretical representation of planned movements

FEF: frontal eye fields

PMd: dorsal premotor cortex

& Shadlen 2007, Pesaran et al. 2008, Romo et al. 2002, Romo et al. 2004, Scherberger & Andersen 2007). For example, Romo and colleagues (Hernandez et al. 2002, Romo et al. 2002, Romo et al. 2004) found that during tasks in which a nominally tactile perceptual decision is reported by an arm movement, correlates of all of the putative sensory encoding, memory, discrimination, and decision-making processes were much stronger within premotor regions than in classical somatic sensory areas. Similarly, when monkeys were required to decide whether to hold or release a lever in response to a sequence of visual stimuli, neural correlates of the behavioral rule (match/nonmatch) and the action decision (release/hold) were stronger and appeared earlier in the premotor regions related to hand movements than in the prefrontal cortex (Wallis & Miller 2003). Likewise, decisions about eye movements appear to involve the same circuits that execute eye movements, which include the lateral intraparietal area (LIP) (Dorris & Glimcher 2004, Gold & Shadlen 2007, Platt & Glimcher 1999, Sugrue et al. 2004, Yang & Shadlen 2007), the FEF (Coe et al. 2002, Schall & Bichot 1998), and the superior colliculus (Basso & Wurtz 1998, Carello & Krauzlis 2004, Horwitz et al. 2004, Thevarajah et al. 2009), which is a brainstem structure that is just two synapses away from the motor neurons that move the eye. In all of these cases, the same neurons appear to first reflect decision-related variables such as the quality of evidence in favor of a given choice and then later encode the metrics of the action used to report the decision (Cisek & Kalaska 2005, Kim & Basso 2008, Roitman & Shadlen 2002, Schall & Bichot 1998, Yang & Shadlen 2007).

Consequently, it has proven to be notoriously difficult to assign a specific perceptual, cognitive, or motor function to cortical associative regions such as the posterior parietal cortex (PPC), where cells appear to be related to all of these functions (Andersen & Buneo 2003, Colby & Duhamel 1996, Colby & Goldberg 1999, Culham & Kanwisher 2001, Kalaska & Crammond 1995). The PPC represents spatial sensory information on the location of behaviorally salient objects in the environment (Colby & Duhamel 1996, Colby & Goldberg 1999, Stein 1992), strongly modulated by attention and behavioral context (Colby & Duhamel 1996, Colby & Goldberg 1999, Kalaska 1996, Mountcastle et al. 1975). This has led to the hypothesis that the parietal cortex is involved in directing attention to different parts of space and in constructing a salience map of the environment (Constantinidis & Steinmetz 2001, Kusunoki et al. 2000). Presumably, this forms part of the perceptual representation that serves as input to the cognitive system. However, there is also strong evidence that parietal cortical activity contains representations of action intentions (Andersen & Buneo 2003, Colby & Duhamel 1996, Kalaska et al. 1997, Mazzoni et al. 1996, Platt & Glimcher 1997, Snyder et al. 2000), which include activity that specifies the direction of intended saccades (Snyder et al. 2000) and arm reaching movements (Andersen & Buneo 2003, Buneo et al. 2002, Kalaska & Crammond 1995), and different subregions of the PPC are specialized for different effectors (Calton et al. 2002, Cui & Andersen 2007). Because action representations are supposedly activated by the output of the cognitive system, it is difficult to reconcile these findings with the sensory properties of the PPC, which leads to persistent debates about its role. Furthermore, neural activity in the PPC is also modulated by a range of variables associated with decision making, such as expected utility (Platt & Glimcher 1999), local income (Sugrue et al. 2004), relative subjective desirability (Dorris & Glimcher 2004), and log-likelihood estimates (Yang & Shadlen 2007). In short, the PPC does not appear to fit neatly into any of the categories of perception, cognition, or action; or alternatively, the PPC reflects all categories at once without respecting those theoretical distinctions. Indeed, it is difficult to see how neural activity in the PPC can be interpreted using any of the concepts of classical cognitive psychology (Culham & Kanwisher 2001).

The data and resulting disagreements reviewed above have motivated us to reflect on some of our assumptions for interpreting neural

activity. Perhaps specific functions such as perception are not implemented by particular cortical regions. Instead, they may be implemented by different layers or subnetworks of cells distributed within many parts of the nervous system. Perhaps distinct roles such as perceptual or motor representations can be performed by the same neurons at different times. These possibilities are worth considering and studying experimentally. Here, however, we explore a different possibility. We consider whether the distinctions among perceptual, cognitive, and motor systems may not reflect the natural categories of neural computations that underlie sensory-guided behavior (Hendriks-Jansen 1996, Lebedev & Wise 2002). The framework of serial information processing may not be the optimal blueprint for the global functional architecture of the brain. Instead, we consider whether alternative theoretical frameworks for the large-scale organization of behavior may facilitate interpretations of neural activity.

AN ECOLOGICAL PERSPECTIVE

One of the most important facts we know about the brain is that it evolved. This not only motivates our theories to describe mechanisms that confer selective advantage, but more importantly, it constrains theories to respect the brain's phylogenetic history. Contrary to popular belief, brain evolution has been remarkably conservative. Since the development of the telencephalon, the basic outline of the vertebrate nervous system has been strongly conserved (Butler & Hodos 2005, Holland & Holland 1999, Katz & Harris-Warrick 1999). Even recently elaborated structures such as the mammalian neocortex have homologs among nonmammals (Medina & Reiner 2000), and the topology of neural circuitry is analogous across diverse species (Karten 1969).

The conservative nature of brain evolution motivates us to think about large-scale theories of neural organization from the perspective of the kinds of behaviors that animals engaged in many millions of years ago, when that neural organization was being laid down. Throughout evolutionary history, organisms and their nervous systems have been preoccupied by almost constant interaction with a complex and ever changing environment, which continuously offers a potentially bewildering variety of opportunities and demands for action. Interaction with such an environment cannot be broken down into a sequence of distinct and self-contained events that each start with a discrete stimulus and end with a specific response, similar to the isolated trials we typically use in many psychological or neurophysiological experiments. Instead, it involves the continuous modification of ongoing actions through feedback control, the continuous evaluation of alternative activities that may become available, and continuous tradeoffs between choosing to persist in a given activity and switching to a different one. The internal processes that are most useful for such behavior may not be those that first construct an accurate internal description of objective and abstract knowledge about the world and then reflect upon it with some introspective, intelligent circuits. Instead, pragmatic processes that mediate sensorimotor interaction in the here and now, on the basis of continuous streams of sensory inputs as well as prior knowledge and experiences, are much more useful for guiding interactive behavior (Gibson 1979).

An emphasis on real-time, natural behavior has been the foundation of ethological research for a long time (Hinde 1966). In the early twentieth century, researchers such as Von Uexküll, Tinbergen, and Lorenz focused their studies on the observation of animals in the wild rather than in the laboratory. Consequently, instead of focusing on how knowledge is represented or what variables are included in the motor program, they focused on how competition between potential actions is resolved, how ongoing behavior is fine tuned by feedback mechanisms that operate at multiple hierarchical levels, and how animals trade off activity against metabolic costs.

Some of the original founders of psychological science also emphasized the importance of interactions with the environment. For

example, John Dewey (1896) criticized the view of behavior as a process of receiving a stimulus and producing a response, and wrote that "[w]hat we have is a circuit...the motor response determines the stimulus, just as truly as sensory stimulus determines movement." (p. 363). Similar emphases on sensorimotor control were made by Hughlings Jackson (1884) and Merleau-Ponty (1945), among many others. Perhaps the best known example is the work of the eminent psychologist Jean Piaget (1954), who suggested that the abstract cognitive abilities of adult humans are constructed upon the basis of the sensorimotor interactions experienced as a child. This is supported by a variety of neural studies, which include the classic experiments of Held & Hein (1963), who found that the visual behavior of newborn kittens did not develop properly unless they were allowed to exert their own active control upon their visual input.

The perceptual psychologist James Gibson was another well-known proponent of an ecological view of behavior. Similar to ethologists, Gibson viewed the constrained environment of a typical psychological experiment as concealing the true interactive nature of behavior. He argued that perception is not about passively constructing an internal representation of the world, but rather it is about actively picking up information of interest to one's behavior. Inspired by earlier work of Gestalt psychologists such as Koffka, he emphasized that the environment contains information relevant for an animal's activity and that a large part of perception is the accumulation of that information. He defined the concept of affordances (Gibson 1979) as the opportunities for action that the environment presents to an animal.

Ethological concepts have been very useful in research on autonomous robotics, which is increasingly abandoning classical serial architectures based on explicit representations of the environment in favor of hierarchical control systems in which the basic elements are sensorimotor feedback loops (Ashby 1965, Brooks 1991, Hendriks-Jansen 1996, Meyer 1995, Sahin et al. 2007). For a robot that

interacts in the real world, such architectures have simply proven to be more effective than serial information processing through distinct perception, cognition, and action modules. These concepts are also becoming increasingly influential in a branch of cognitive science that is sometimes called embodied cognition (Clark 1997, Klatzky et al. 2008, Núñez & Freeman 2000, Thelen et al. 2001).

Such concepts may also be useful for interpreting neurophysiological data. For example, Graziano & Aflalo (2007) proposed that the multiple motor areas in the precentral gyrus may not be organized on the basis of a sequential planning and execution architecture, as commonly assumed. Instead, the precentral gyrus may reflect the animal's natural behavioral repertoire, with different regions that are specialized for different actions such as bringing objects to the mouth, manipulating objects in central vision, climbing, or defensive behavior. Although controversial, this conjecture has intriguing similarities to theoretical proposals that evolution constructs complex behaviors by using simpler ones as building blocks (Brooks 1991, Hendriks-Jansen 1996). This has clear ecological advantages because it reflects the need for animals to partially plan many different classes of potential actions, such as grasping a piece of fruit while also being ready to scamper away in case of danger.

One particularly important and influential example of how a perspective of interactive behavior may shed light on neurophysiology is the work of Melvyn Goodale and David Milner (1992, Milner & Goodale 1995). As discussed above, visual processing diverges in the cerebral cortex into a ventral stream, where cells are sensitive to stimulus features, and a dorsal stream, where cells are sensitive to spatial relationships (Ungerleider & Mishkin 1982). Instead of describing these, respectively, as the what and where systems, Goodale & Milner suggested that the predominant role of the dorsal stream is to mediate visually guided behavior. They proposed that the dorsal stream (now often called the how system) is sensitive to spatial information, not to build a representation of the

environment for central knowledge acquisition, but because spatial information is critical for specifying the parameters of potential and on-going actions. This view explains many other properties of dorsal pathway processing, such as its emphasis on concrete and current information (Milner & Goodale 1995) and its intimate interconnection with frontal regions involved in movement control (Johnson et al. 1996, Wise et al. 1997). From this perspective, processing in the parietal cortex and reciprocally connected premotor regions is not exclusively concerned with descriptive representations of objects in the external world but primarily with pragmatic representations of the opportunities for action that those objects afford (Cisek 2007, Colby & Duhamel 1996, Fadiga et al. 2000, Kalaska et al. 1998, Rizzolatti & Luppino 2001). Indeed, parietal activity in both monkeys (Iriki et al. 1996) and humans (Gallivan et al. 2009) is stronger when objects are within reach.

Several groups have developed these ideas further. For example, Fagg & Arbib (1998) have suggested that the PPC represents a set of currently available potential actions, one of which is ultimately selected for overt execution. Similarly, we and others have suggested that the dorsal stream is involved in specifying the parameters of potential actions, whereas the ventral stream provides further information for their selection (Andersen & Buneo 2003, Cisek 2007, Kalaska et al. 1998, Passingham & Toni 2001, Sakagami & Pan 2007). This has much in common with a long history of proposals, made on the basis of EEG studies (Coles et al. 1985) and stimulus-response compatibility effects (Kornblum et al. 1990), that neural processing is continuous and not organized in distinct serial stages. It is also similar to the proposal that the brain begins to prepare several actions in parallel while collecting evidence for selecting between them (Shadlen et al. 2008), a view that is strongly supported by neurophysiological studies of decision making (Gold & Shadlen 2007, Kim & Basso 2008, Ratcliff et al. 2007).

Some of these ideas are summarized in **Figure 1**, which shows what we call the affordance competition hypothesis (Cisek 2007). This general hypothesis is directly inspired by the work of Gibson, Ashby, Goodale & Milner, Arbib, and many others mentioned above. It begins with a distinction between two types of problems that animals behaving in the natural environment continuously face: deciding what to do and how to do it. We can call these the problems of action selection and action specification. However, although traditional psychological theories assume that selection (decision making) occurs before specification (movement planning), we consider the possibility that, at least during natural interactive behavior, these processes operate simultaneously and in an integrated manner (Cisek 2007).

For the particular case of visually-guided movement, action specification (**Figure 1**, dark blue lines) may involve the dorsal visual stream and a distributed and reciprocally interconnected network of areas in the posterior parietal and caudal frontal cortex (Andersen & Buneo 2003; Andersen et al. 1997; Goodale & Milner 1992; Johnson et al. 1996; Kalaska 1996; Kalaska & Crammond 1995; Milner & Goodale 1995; Rizzolatti & Luppino 2001; Wise et al. 1996, 1997). These circuits perform transformations that convert information about objects in sensory coordinates into the parameters of actions (Andersen & Buneo 2003, Andersen et al. 1997, Wise et al. 1997). Along the way, each area can represent information that is pertinent to several potential actions simultaneously as patterns of tuned activity within distributed populations of cells. This forms a representation of possible movements that is conceptually similar to a probability density function (Sanger 2003). Importantly, these same brain regions ultimately guide the execution of those actions. Because multiple actions usually cannot be performed at the same time, there is competition between options, perhaps through mutual inhibition among cells with different tuning properties (Cisek 2006) and/or through differential selection in corticostriatal circuits (Leblois et al. 2006).

Action selection: the process of choosing an action from among many possible alternatives

Action specification: the process of specifying the spatiotemporal aspects of possible actions
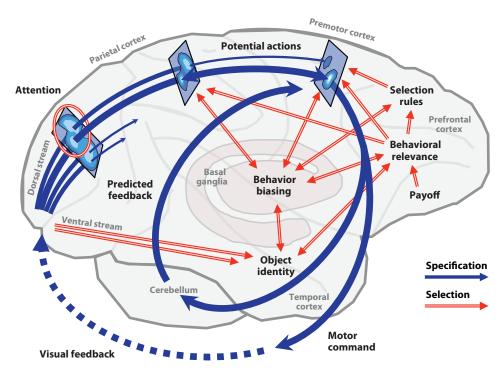
Figure 1

Sketch of the affordance competition hypothesis in the context of visually-guided movement. The primate brain is shown, emphasizing the cerebral cortex, cerebellum, and basal ganglia. Dark blue arrows represent processes of action specification, which begin in the visual cortex and proceed rightward across the parietal lobe, and which transform visual information into representations of potential actions. Polygons represent three neural populations along this route. Each population is depicted as a map where the lightest regions correspond to peaks of tuned activity, which compete for further processing. This competition is biased by input from the basal ganglia and prefrontal cortical regions that collect information for action selection (*red double-line arrows*). These biases modulate the competition in several loci, and because of reciprocal connectivity, their influences are reflected over a large portion of the cerebral cortex. The final selected action is released into execution and causes overt feedback through the environment (*dotted blue arrow*) as well as internal predictive feedback through the cerebellum. Modified with permission from Cisek (2007).

If a competition between representations of potential actions exists in frontoparietal circuits, then intelligent behavior requires a way to influence that competition by factors related to rewards, costs, risks, or any variable pertinent to making good choices. A variety of brain systems can contribute their votes into this selection process simply by biasing activity within the ongoing frontoparietal competition (**Figure 1**, red double-line arrows). This includes influences from subcortical structures such as the basal ganglia (Mink 1996, Redgrave et al. 1999, Schultz 2004) and cortical regions such as the prefrontal cortex (Miller 2000, Sak-

agami & Pan 2007, Tanji & Hoshi 2001, Wise 2008). In turn, the prefrontal areas receive information pertinent to action selection that include object identity from the temporal lobe (Pasupathy & Connor 2002, Tanaka et al. 1991) and subjective value from the orbitofrontal cortex (Padoa-Schioppa & Assad 2008, Schultz et al. 2000, Wallis 2007). In summary, the hypothesis is that interaction with the environment involves continuous and simultaneous processes of sensorimotor control and action selection from among the distributed representations of a limited number of response options. This perspective is consistent with a

large family of computational models of decisions, which suggest that neural activity related to different response choices builds up in separate accumulators as a function of the evidence for or against those choices until a threshold is reached that favors one over the others (Gold & Shadlen 2007, Ratcliff et al. 2007). Whereas classic decision models have treated the accumulators as separate modules that correspond to distinct choices, our hypothesis suggests that they emerge from a continuous population that represents parameters of potential actions (Cisek 2006, Erlhagen & Schöner 2002, Furman & Wang 2008, Tipper et al. 2000), at least in cases when decisions are reported through specific actions. Indeed, the neurons that have been implicated in the evidence accumulation process are always found within populations tuned for motor output parameters such as direction (Glimcher 2003, Gold & Shadlen 2007, Kim & Basso 2008, Ratcliff et al. 2007).

We propose that the kind of general theoretical architecture shown in **Figure 1**, although highly simplified, can nevertheless help us interpret much of the neural data briefly reviewed above, data that have proven difficult to interpret within the traditional view of serial information processing stages. The rest of this review is devoted to discussing data relevant to that claim.

REVISITING NEURAL DATA

In revisiting some of the neural data discussed at the beginning of this review, we emphasize two main conjectures: (*a*) The control of interactive behavior involves competition between parallel sensorimotor control loops, and (*b*) neural representations involved in this control are pragmatic—that is, they are adapted to produce good control as opposed to producing accurate descriptions of the sensory environment or a motor plan. Both of these proposals have been made repeatedly for over a hundred years of research from Dewey to Gibson to Goodale & Milner and others, but they have not often been used as the theoretical framework for interpreting neurophysiological data.

Frontoparietal Specification of Potential Actions

Following Goodale & Milner (1992, Milner & Goodale 1995), one can interpret the dorsal visual stream as part of the system for specifying the parameters of potential actions using visual information, a process that continues during movement execution (Resulaj et al. 2009). As mentioned above, the dorsal stream is not unified but progressively diverges into parallel subsystems, each specialized toward the demands of different sensorimotor functions and effectors (Andersen et al. 1997, Colby & Duhamel 1996, Colby & Goldberg 1999, Rizzolatti & Luppino 2001, Stein 1992, Wise et al. 1997). Area LIP represents space in an ego-centered reference frame (Colby & Duhamel 1996, Snyder et al. 1998), is involved in control of gaze (Snyder et al. 2000), and is interconnected with other parts of the gaze control system that includes the FEF and the superior colliculus (Paré & Wurtz 2001). The medial intraparietal area (MIP) is involved in the control of arm reaching movements (Cui & Andersen 2007, Kalaska & Crammond 1995, Pesaran et al. 2008, Scherberger & Andersen 2007, Snyder et al. 2000), represents target locations with respect to the direction of gaze and the position of the arm (Buneo et al. 2002), and is interconnected with frontal regions that are involved in reaching, such as PMd (Johnson et al. 1996, Wise et al. 1997). Neurons in the anterior intraparietal area (AIP) are involved in grasping (Baumann et al. 2009), their activity is sensitive to object size and orientation, and they are interconnected with the grasp-related ventral premotor cortex (PMv) (Nakamura et al. 2001, Rizzolatti & Luppino 2001). To summarize, the dorsal stream diverges into parallel subsystems, each of which specifies the spatial parameters of different kinds of potential actions and plays a direct role in guiding their execution during movement.

In such a distributed system, several actions can be specified simultaneously. For example, if a monkey is presented with a spatial target but not instructed about whether an arm or

MIP: medial intraparietal area

AIP: anterior intraparietal area

PMv: ventral premotor cortex

eye movement is required, neurons begin to discharge in both LIP and MIP (Calton et al. 2002, Cui & Andersen 2007). Later, if an arm movement is instructed (Calton et al. 2002) or autonomously chosen (Cui & Andersen 2007), the activity becomes stronger in MIP than LIP. Conversely, if a saccade is instructed or chosen, activity becomes stronger in LIP than MIP. This is consistent with the proposal that before the effector is selected, reach and saccade plans begin to be specified simultaneously by different parts of the PPC. Indeed, during natural activity, eye and hand movements are usually executed in unison. Similar findings have been reported for decisions regarding hand choice. For example, Hoshi & Tanji (2007) showed that when monkeys are first presented with a reach target location in a bimanual response-choice task without specifying which arm to use, neural activity in the premotor cortex reflects the potential movements of both hands until the monkey is instructed about which hand to use.

Simultaneous specification of multiple potential actions can occur even within the same effector system (Basso & Wurtz 1998, Bastian et al. 1998, Baumann et al. 2009, Cisek & Kalaska 2005, McPeek & Keller 2002, Platt & Glimcher 1997, Powell & Goldberg 2000, Schall & Bichot 1998, Scherberger & Andersen 2007). For example, behavioral data (McPeek et al. 2000) and neurophysiological data (McPeek & Keller 2002) suggest that the preparation of multiple sequential saccades can overlap in time. When two or more potential saccade targets are presented simultaneously, neural correlates for each are observed in area LIP (Platt & Glimcher 1997, Powell & Goldberg 2000) and even in the superior colliculus, where they are modulated by selection probability (Basso & Wurtz 1998, Kim & Basso 2008).

Likewise, behavioral studies of reaching have suggested that the brain simultaneously processes information about multiple potential actions. For example, the trajectory of a reaching movement to a target is influenced by the presence of distracters (Song & Nakayama 2008, Tipper et al. 2000, Welsh et al. 1999)

and veers away from regions of risk (Trommershauser et al. 2006). Patients with frontal lobe damage often cannot suppress actions associated with distracters even while they are planning actions directed elsewhere (Humphreys & Riddoch 2000), and such effects may be the result of competition among parallel simultaneous representations of potential actions, with a bias toward the actions with the highest stimulus-response compatibility (Castiello 1999).

Neurophysiological studies support this interpretation. For example, partial information on possible upcoming movements engages the activity of cells in reach-related regions before the animal selects the movement that will be made (Bastian et al. 1998, Kurata 1993, Riehle & Requin 1989). In particular, when a reach direction is initially specified ambiguously by sensory information, neural activity arises in the motor and premotor cortex that spans the entire angular range of potential directions. Later, when the direction is specified more precisely, the directional spread of population activity narrows to reflect this choice (Bastian et al. 1998). Neural correlates of multiple potential reaching actions have been reported in the dorsal premotor cortex (PMd) even when the choices are distinct and mutually exclusive (Cisek & Kalaska 2005). As shown in **Figure 2**, when a monkey was presented with two opposite potential reaching actions, only one of which would later be indicated as the correct choice by a nonspatial cue, neural activity in the premotor cortex specified both directions simultaneously. When information for selecting one action over the other became available, the representation of the chosen direction was strengthened while that of the unwanted direction was suppressed. The monkey used a strategy of preparing both movements simultaneously during the initial period of uncertainty despite the fact that the task design permitted the use of an alternative strategy (more consistent with traditional models of processing) in which target locations are stored in a general-purpose working memory buffer that is distinct from motor representations and only
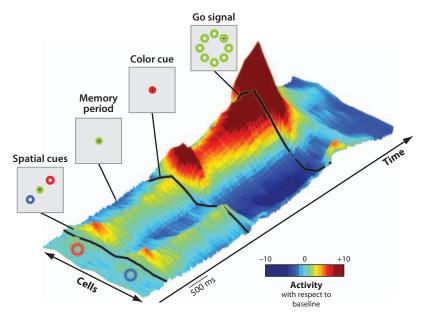
Figure 2

Population activity in the dorsal premotor cortex during a reach-selection task. The 3D colored surface depicts neural activity with respect to baseline, with cells sorted by their preferred direction along the bottom edge. Diagrams on the left show the stimuli presented to the monkey at different points during the trial (cross indicates the cursor). Note that during the period of ambiguity, even after stimuli vanished, the population encodes two potential directions. Data from Cisek & Kalaska (2005).

converted to a motor plan after the decision is made. In contrast, we propose that multiple movement options are specified within the same system that is used to prepare and guide the execution of the movement that is ultimately selected. The simultaneous specification of multiple actions can even occur when only a single object is viewed. For example, the multiple affordances offered by a single object can evoke neural activity in the grasp-related area AIP that can represent several potential grasps until one is instructed (Baumann et al. 2009), in agreement with the predictions of theoretical models (Fagg & Arbib 1998).

Evidence that the nervous system can simultaneously represent multiple potential actions suggests a straightforward interpretation of the finding, described above, that early responses in many premotor and parietal regions first appear to encode information about relevant stimuli and later change to encode motor variables. Perhaps the early activity,

time-locked to stimulus appearance, does not encode the stimuli themselves but rather the set of potential actions that are most strongly associated with those stimuli (Wise et al. 1996), such as actions with high stimulus-response compatibility (Crammond & Kalaska 1994). This would imply that the functional role of this activity does not change in time from sensory to motor encoding but simply reflects the arrival of selection influences from slower but more sophisticated mechanisms for deciding which action is most appropriate.

Recent computational models have proposed that whenever multiple potential targets are available, representations of potential actions emerge within several frontoparietal neural populations, each composed of a continuum of cells with different preferences for the potential parameters of movement (Cisek 2006, Erlhagen & Schöner 2002, Tipper et al. 2000). In each population, cells with similar preferences mutually excite each other (even if they

are not physically adjacent), which leads to the activation of groups of cells with similar tuning. At the same time, cells with different preferences inhibit each other, thus implementing a competition between representations of actions that are mutually exclusive. Unlike classical models of decisions, in which the different choices are abstract and clearly distinct (e.g., choosing between gamble A or B), models in which decisions emerge within tuned populations suggest that the same mechanism—lateral inhibition—is responsible for defining the choices as well as for implementing the competition between them. Importantly, they suggest that decisions about actions emerge within the same populations of cells that define the physical properties of those actions and guide their execution.

This proposal can account for phenomena that cannot be explained using models in which the decision process occurs in an abstract space that is separate from a representation of the metrics of motor options. For example, although it is well-known that reaction time (RT) generally increases with the number of choices presented to a subject, it is less widely recognized that RT is also dependent upon the spatial separation of the response options (Bock & Eversheim 2000). As another example, Ghez et al. (1997) showed that rapid choices between precued options are dependent on target separation. If cues are close together, subjects initially move in between them (continuous mode) before deviating toward one or the other in mid-reach. If the cues are far apart, they choose one at random and move to it directly (discrete mode). To explain such results, models of decisions must capture how the choices themselves are defined in physical space and how the similarity of potential actions influences their interactions (Cisek 2006, Erlhagen & Schöner 2002). This is straightforward if the representations of choices exist within neural populations that encode the physical parameters of the movements used to report the choice.

From this perspective, it is not surprising that neural activity in the frontal and parietal cortex encodes information that appears to be sensory, motor, and cognitive in nature (Wise et al. 1996). The case of area LIP is particularly instructive. If LIP is involved in the specification of potential saccades, then its activity must correlate with the location of possible saccade targets (Mazzoni et al. 1996, Snyder et al. 2000), even when multiple potential saccades are processed simultaneously (Platt & Glimcher 1997, Powell & Goldberg 2000). At the same time, however, the ongoing selection of potential actions will modulate the strength of activities in LIP. Such modulation is influenced by target salience (Colby & Goldberg 1999, Kusunoki et al. 2000), reward size and selection probability (Platt & Glimcher 1999, Yang & Shadlen 2007), and other decision variables (Dorris & Glimcher 2004, Sugrue et al. 2004), as well as prior information on the type of action to be performed (Calton et al. 2002, Cui & Andersen 2007). The progressive elimination of potential saccade targets along the dorsal stream also explains why the representation of visual space in LIP is so sparse (Gottlieb et al. 1998): Only the most promising and salient targets make it to LIP.

If the presence of salient targets can engage the simultaneous specification of several potential actions in a variety of frontoparietal systems, then this process is closely related to the concept of a salience map (Kusunoki et al. 2000, Powell & Goldberg 2000). In particular, the front end of a system for action selection should enhance the most behaviorally salient information in the environment to bias sensorimotor systems toward the most behaviorally relevant potential actions. Thus, it will be action dependent (Snyder et al. 2000) but still influenced by the salience of stimuli, even while actions are instructed elsewhere (Kusunoki et al. 2000). In short, attention and intention may be different aspects of a common process that progressively narrows the set of potential actions that will be processed further downstream. This agrees with the proposal (Allport 1987, Neumann 1990) that attention is a mechanism for early action selection and not a solution to the purely internal problem of a computational bottleneck for processing sensory information

(Broadbent 1958), as is often assumed. Indeed, models of action selection compatible with the kind of framework shown on **Figure 1** (Cisek 2006, Erlhagen & Schöner 2002) are functionally equivalent to the biased competition model used to explain data on visual attention (Boynton 2005, Desimone & Duncan 1995, Treue 2001). In both cases, parallel representations of targets/actions compete through lateral inhibition; and in both cases, they are biased by top-down and or bottom-up influences.

The idea that decisions emerge within a continuum of tuned cells can even go beyond strictly action-related decisions (Song & Nakayama 2009) and may provide insights into mechanisms that have traditionally been studied using tasks in which subjects report choices by pressing distinct keys on a keyboard. For example, when subjects are asked to report on seemingly binary yes/no questions (such as, is the sky ever green?) by moving a cursor instead of just pressing one key or another, their movement trajectories reveal a wealth of phenomena that suggest the decision is represented in a continuous space that spills into overt movement (McKinstry et al. 2008). For example, features of the trajectory such as its endpoint and peak velocity correlate with the subject's confidence about their choice. Even linguistic decisions, such as those made while parsing an ambiguous sentence, appear to occur in a continuous parameter space that can influence movement trajectories (Farmer et al. 2007). These findings are difficult to reconcile with the idea that cognition is separate from sensorimotor control (Fodor 1983) but make good sense if the continuous nature of the representations that underlie the selection of actions has been retained as selection systems evolved to implement increasingly abstract decisions.

Action Selection Signals from Prefrontal and Subcortical Sources

From the perspective of the parallel architecture reviewed here, there may be no single central executive module that guides decisions. As shown by many of the studies reviewed above,

neural correlates of cognitive processes can be seen throughout the brain during sensorimotor and decision tasks. When we look for the neural correlates of cognition, it does not appear as an independent module (Fodor 1983) that receives input from perceptual modules and sends goal signals to motor centers. Instead, it appears as a process that is closely integrated with action selection, evaluation, and motor execution (Cisek 2007, Glimcher 2003, Gold & Shadlen 2007, Heekeren et al. 2008, Hoshi & Tanji 2007, Pesaran et al. 2008, Rizzolatti & Luppino 2001, Shadlen et al. 2008).

The recent evolution of primates is distinguished by advances in the ability to select actions based on increasingly abstract and arbitrary criteria. This kind of selection may have been made possible by the dramatic elaboration of the prefrontal cortex (Hauser 1999), especially the granular frontal cortex, which does not appear to have a homolog in rodents (Wise 2008). These frontal regions are strongly implicated in decision making and action selection (Fuster et al. 2000, Kim & Shadlen 1999, Miller 2000, Romo et al. 2004, Rowe et al. 2000, Tanji & Hoshi 2001). For example, neurons in the dorsolateral prefrontal cortex (DLPFC) are sensitive to various combinations of stimulus features, and this sensitivity is always related to the particular demands of the task at hand (Barraclough et al. 2004, Hoshi et al. 1998, Kim & Shadlen 1999, Quintana & Fuster 1999, Rainer et al. 1998). For example, an experiment on reach target selection (Hoshi et al. 2000) found that when arbitrary iconic stimuli were presented, activity in the DLPFC was sensitive to potentially relevant stimulus features, such as shape and location. After the presentation of a signal that indicated the correct selection rule (shape-match or location-match), rule-sensitive neurons briefly became active, selecting out the relevant memorized stimulus features needed to make the response choice. After this process was complete, the remaining activity reflected the intended movement choice. Prefrontal decisions appear to evolve through the collection of votes for categorically selecting one choice over others. For example, when monkeys were

trained to report perceptual discriminations using saccades (Kim & Shadlen 1999), DLPFC activity initially reflected the quality of evidence in favor of a given target and later simply reflected the monkey's choice. Similar effects have been reported in PMv and prefrontal cortex during tactile vibration frequency discrimination tasks (Romo et al. 2004).

The information for visually-based action selection can also come from the ventral visual stream (Cisek 2007, Kalaska et al. 1998, Passingham & Toni 2001, Sakagami & Pan 2007), where cells are sensitive to object identity (Pasupathy & Connor 2002, Sugase et al. 1999, Tanaka et al. 1991) and modulated by attention (Treue 2001). The detection of stimulus features relevant for action selection is reminiscent of what ethologists referred to as the detection of a key stimulus that releases specific behaviors (Ewert 1997, Tinbergen 1950). The detection of key stimuli need not require full-fledged object recognition (and indeed may be its precursor) because often a fragment or specific feature that has consistent meaning within an animal's niche is all that is necessary to elicit behavior. Therefore, the properties of ventral stream processing may not have originally evolved for its role in pure perception, but may instead reveal its earlier and more fundamental role in collecting information useful for action selection. Indeed, the distinction between pure vision-for-perception versus vision-for-action systems is difficult to make at the neuroanatomical level (Lebedev & Wise 2002).

Wallis (2007) reviews evidence that the motivational value of potential actions is computed by the orbitofrontal cortex (OFC), which integrates sensory and affective information to estimate the value of a reward outcome. Single-neuron studies have shown that the OFC represents the value of goods in a manner that is not dependent on their relative value with respect to other available choices (Padoa-Schioppa & Assad 2008) but scales with the range of values in a given context (Padoa-Schioppa 2009). Sakagami & Pan (2007) suggest that this information is further integrated with sensory signals from the ventral visual stream to provide an es-

timate of the behavioral relevance of potential actions in the ventrolateral prefrontal cortex (VLPFC), which then projects to the DLFPC and premotor regions to influence action selection.

Because action selection is a fundamental problem faced by even the most primitive vertebrates, it likely involves structures that were prominently developed long ago and have been conserved in evolution. The basal ganglia are promising candidates (Kalivas & Nakamura 1999, Mink 1996, Redgrave et al. 1999). The basal ganglia may form a central locus in which excitation that arrives from different motor systems competes, and a winning behavior is selected while others are inhibited through projections back to the motor systems (Brown et al. 2004, Leblois et al. 2006, Mink 1996, Redgrave et al. 1999). Afferents to the input nuclei of the basal ganglia (the striatum and subthalamic nucleus) arrive from nearly the entire cerebral cortex and from the limbic system, converge onto the output nuclei (substantia nigra and globus pallidus), and project through the thalamus back to the cerebral cortex. This cortico-striatal-pallido-thalamo-cortical loop is organized into multiple parallel channels, which runs through specific motor regions as well as through regions implicated in higher cognitive functions (Alexander & Crutcher 1990a, Middleton & Strick 2000). In agreement with the hypothesis of basal ganglia selection, cell activity in the input nuclei is related to movement parameters (Alexander & Crutcher 1990a) but is also influenced by the expectation of reward (Schultz et al. 2000, Takikawa et al. 2002). During learning of arbitrary visuomotor mappings, striatal activity evolves in concert with PMd activity to indicate the selected movement (Buch et al. 2006). The inactivation of cells in output nuclei disrupts movement speed in a manner consistent with the proposal that the inhibition of competing motor programs is disrupted (Wenger et al. 1999). Furthermore, the finding that the basal ganglia connect with prefrontal regions, in a manner similar to their connections with premotor cortex, suggests that basal ganglia innervation of prefrontal regions also

Key stimulus: a particular feature of the environment which, when detected, elicits a specific action

mediates selection but on a more abstract level (Hazy et al. 2007). This is also consistent with motor and cognitive aspects of basal ganglia diseases (Mink 1996, Sawamoto et al. 2002).

Parallel Operation

Continuous interactive behavior often does not allow one to stop to think or to collect information to build a complete knowledge of one's surroundings. The demands of survival in an ever-changing environment drove evolution to endow animals with an architecture that allows them to partially prepare several courses of action simultaneously, so that alternatives can be ready for release at short notice. Such an ecological view of behavior suggests that the processes of action selection and specification normally occur simultaneously and continue even during the overt performance of movements, which allows animals to switch to another option if they change their mind (Resulaj et al. 2009). That is, sensory information that arrives from the world is continuously used to specify several currently available potential actions, in parallel, while other kinds of information are collected to select the one that will be released into execution at a given moment (Cisek & Kalaska 2005, Glimcher 2003, Gold & Shadlen 2007, Kalaska et al. 1998, Kim & Shadlen 1999, Shadlen et al. 2008). From this perspective, behavior is viewed as a constant competition between internal representations of conflicting demands and opportunities.

Suppose that an animal is endowed with this kind of parallel architecture, adapted for continuous real-time interaction with a natural environment. What would happen if we remove that animal from its natural environment and place it in a neurophysiological laboratory? In this highly controlled and impoverished setting, time is broken into discrete trials, each starting with the presentation of a stimulus and ending with the production of a response (and if the response is correct, a reward). Furthermore, unlike in natural behavior, most features of the sensory input are deliberately made independent from the animal's actions—the response

in a given trial usually does not determine the stimulus in the next trial. Of course, animals are capable of dealing with this artificial scenario and able to learn which responses yield the best rewards. The question addressed here is the following: What would a parallel architecture such as that of **Figure 1** predict about the time course of processing in such a situation?

When the stimulus is first presented, we should expect an initial fast feedforward sweep of activity along the dorsal stream, crudely representing the potential actions that are most directly specified by the stimulus. Indeed, Schmolesky et al. (1998) showed that neural responses to simple visual flashes appear quickly throughout the dorsal visual system and engage putatively motor-related areas such as FEF in as little as 50 ms. This is significantly earlier than some visual areas such as V2 and V4. In general, even within the visual system neural activation does not appear to follow a serial sequence from early to late areas (Paradiso 2002). In a reaching task, population activity in PMd responds to a learned visual cue within 50 ms of its appearance (Cisek & Kalaska 2005). Such fast responses are not purely visual because they reflect the context within which the stimulus is presented. For example, they reflect whether the monkey expects to see one or two stimuli (Cisek & Kalaska 2005), reflect anticipatory biases or priors (Coe et al. 2002, Takikawa et al. 2002), and can be entirely absent if the monkey already knows what action to take and can ignore the stimulus altogether (Crammond & Kalaska 2000) (**Figure 3**). In short, these phenomena are compatible with the notion of a fast dorsal specification system that quickly uses novel visual information to specify the potential actions most consistently associated with a given stimulus (Gibson 1979, Milner & Goodale 1995).

After the initial options are quickly specified, slower selection processes should begin to sculpt the neural activity patterns by introducing a variety of task-relevant biasing factors. Indeed, extrastriate visual areas MT and 7a respond to a stimulus in approximately 50 ms but begin to reflect the influence of attention in 100–120 ms (Constantinidis & Steinmetz 2001,
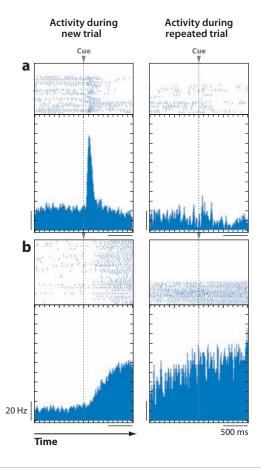
Activity during new trial

Activity during repeated trial

Cue

Cue

a

b

20 Hz

Time

500 ms

(*a*) Pooled activity of three phasic PMd neurons during trials in their preferred direction, aligned on cue onset. The left panel shows activity during trials in which a novel and unpredictable cue is presented, instructing the monkey about the required reaching movement. The right panel shows activity from trials that follow errors and repeat the same cue at the same location. Because the monkey has learned from experience that the same target will be presented in trials following an error, the presentation of the target stimulus provides it with no new salient information about movement and does not evoke a neural response. (*b*) Pooled activity of three tonic PMd neurons, same format. Note that in trials following errors, the directionally tuned activity is already present before the cue appears. This reflects the retention of prior knowledge about the imminent presentation of the same target after an error. Reprinted with permission from Crammond & Kalaska (2000).

Treue 2001). FEF neurons respond to the onset of a stimulus in 50 ms (Schmolesky et al. 1998), but detect the singleton of a visual-search array with a median of approximately 100 ms and discriminate pro- versus antisaccades in approximately 120 ms (Sato & Schall 2003). LIP neurons respond to stimulus onset in approximately

50 ms and discriminate targets from distracters in 138 ms (Thomas & Pare 2007). Neurons in dorsal premotor cortex respond to the locations of cues instructing two potential movements in 70 ms but begin to predict the monkey's choice in 110–130 ms (Cisek & Kalaska 2005).

A recent study by Ledberg et al. (2007) provides an overall picture of the time course observed in all of the experiments described above. These authors simultaneously recorded local field potentials (LFPs) from up to 15 cerebral cortical regions of monkeys that performed a conditional Go/NoGo task (**Figure 4*a***). Through an elegant experimental design, Ledberg and colleagues identified the first neural events that responded to the appearance of a stimulus, those which discriminated its identity, as well as those that predicted the monkey's chosen response (**Figure 4*b***). In agreement with earlier studies (c.f. Schmolesky et al. 1998), they observed a fast feedforward sweep of stimulus onset-related activity appearing within 50–70 ms in striate and extrastriate cortex and 55–80 ms in FEF and premotor cortex. Discrimination of different stimulus categories occurred later, within approximately 100 ms of onset in prestriate areas and 200 ms in prefrontal sites. The Go/NoGo decision appeared approximately 150 ms after stimulus onset, nearly simultaneously within a diverse mosaic of cortical sites including prestriate, inferotemporal, parietal, premotor, and prefrontal areas.

In summary, when behavior is experimentally isolated in the lab, the continuous and parallel processes critical for interaction appear as two waves of activation: an early wave crudely specifying a menu of options and a second wave that selects among them approximately 120–150 ms after stimulus onset (Ledberg et al. 2007). It appears that the brain can quickly specify multiple potential actions within its fast frontoparietal sensorimotor control system, but it takes approximately 150 ms (in the case of simple tasks) to integrate sufficient information to make a decision between them. However, the apparent serial order of these events is largely a result of the experimental strategy of
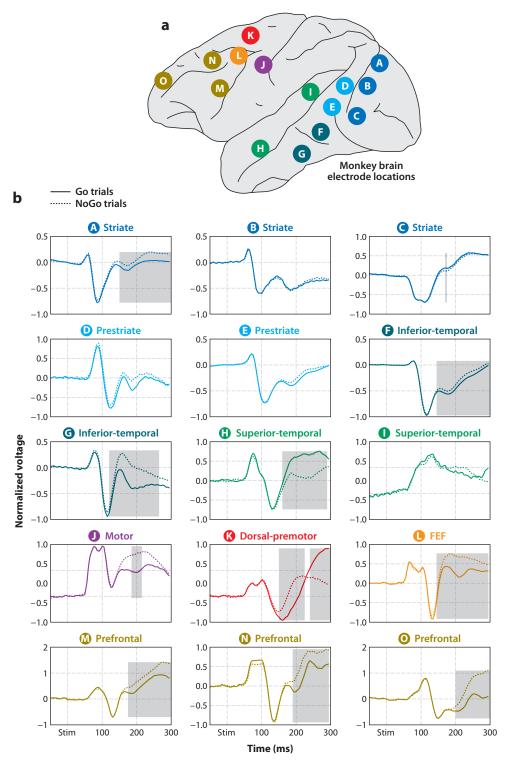
Figure 4

(*a*) Anatomical location of electrodes measuring local-field potentials. (*b*) Time course of average normalized event-related potentials from the electrodes shown in (*a*). (*Solid line*) Potentials during Go trials. (*Dashed line*) Potentials during NoGo trials. Gray-shaded regions highlight epochs of time during which these differ. Note that the earliest responses to stimuli appear throughout the cerebral cortex after approximately 50 ms, and activity begins to predict the monkey's choice after approximately 150 ms in a distributed network that includes parietal and frontal regions. Reprinted with permission from Ledberg et al. (2007).

dividing behavior into a sequence of discrete and independent trials. During natural activity, all of these events presumably occur continuously.

These results are consistent with the hypothesis that decisions emerge through a distributed consensus achieved among reciprocally connected frontoparietal regions, each of which may contain representations of several potential actions. This makes a further prediction: The precise order in which decisions appear across the cerebral cortex will be highly task dependent (Cisek 2006). For example, if the factors that lead to a decision are bottom-up visual features such as stimulus salience, then neural correlates of that decision should appear first in the parietal cortex and then in frontal regions. In contrast, if the biasing factors require the kinds of complex stimulus-rule conjunctions that engage neurons in the prefrontal cortex, then the decision should emerge first in frontal regions before propagating back to the parietal cortex. Recent studies have supported that prediction. For example, when monkeys perform pop-out visual search tasks, neural activity in LIP reflects the choice before FEF, but if the task involves conjunction search then FEF reflects the choice before LIP (Buschman & Miller 2007). Interestingly, during a Go/NoGo task in which monkeys made decisions on the basis of cognitive rules, activity that predicted the response appeared in PMd even before the prefrontal cortex (PFC) (Wallis & Miller 2003). It is as if, at least in that kind of task, a decision may be influenced by noisy neural votes arriving from the PFC but is determined by a consensus that is reached in a frontoparietal network that includes the PMd (Pesaran et al. 2008).

FUTURE DIRECTIONS

We conclude this article by returning to several practical issues. If we hypothesize that the functional architecture of the brain consists of simultaneous competing sensorimotor control systems and distributed selection mechanisms—how should we proceed to study these processes? Clearly, neurophysiological

experiments must be conducted in a careful and quantitative manner to allow the interpretation of resulting data. But how can one quantitatively study natural behavior, which is inherently variable and unconstrained?

One approach is to continue as before. There is no reason why data obtained in a classical laboratory setting cannot still be interpreted in the broader context of natural behavior. For example, the study of Ledberg et al. (2007) on the timing of cortical processes was done with head-fixed animals that were observing an impoverished stimulus and making a single Go/Nogo response, but its results can still be used to gain valuable insights into the organization of a flexible parallel system for interactive behavior. In fact, all of the studies discussed above are still relevant and amenable to interpretation in terms of interactive behavior. However, we should not mistake our experimental method for the outline of a theory.

Controlled laboratory experiments can also be designed to be inspired by natural behavior. For example, visual-search tasks capture many aspects of natural foraging activity, which requires animals to discriminate food (targets) within a cluttered environment (distracters). Recent studies by Michael Dorris and colleagues take the analogy further, by presenting monkeys with a visual foraging task in which they can explore their environment through unconstrained saccades, making tradeoffs between harvesting rewards by looking at one stimulus versus searching for better payoffs among other stimuli (Kan & Dorris 2009).

Finally, technical and mathematical advances are starting to make it possible to study truly unconstrained behavior while still yielding solid and interpretable data. For example, d'Avella & Bizzi (2005) studied motor control in frogs by allowing them to freely move around their environment—swimming, jumping, and walking without constraints—while EMG activity was chronically recorded from 13 hindlimb muscles. Through a careful analysis of muscular patterns, they extracted the motor synergies that appear to underlie these natural behaviors. A still more ambitious approach

is to implant wireless multielectrode arrays in the brains of rats (Sodagar et al. 2007) or monkeys (Chestek et al. 2009) and record ensemble activity during free behavior. However, unconstrained behavior requires novel ways of analyzing and thinking about our data. In particular, we need methods that move away from the standard approach of averaging over similar trials and toward analyzing behavior and the neural firing patterns of many of neurons during each individual action (Yu et al. 2009).

CONCLUSIONS

One of the major goals of neuroscience research is to reveal the brain's functional architecture to build a theoretical framework that bridges the brain and behavior (Schall 2004). In recent decades, an influential framework has been based on concepts developed in cognitive psychology, which were originally intended to explain human abstract problem solving behavior. These led to a functional architecture of information processing stages that can be roughly categorized as perceptual, cognitive, and motor control modules. However, as we review above, a growing number of neurophysiological studies in nonhuman primates appear difficult to interpret from this perspective. This motivates us to consider alternative theoretical frameworks. Above, we consider proposals developed for many decades in fields such as ethology, ecological psychology, and autonomous robotics research, which were designed to explain the original and still primary purpose of the brain—to endow organisms with the ability to adaptively interact with their environment. We discuss diverse neurophysiological data on the control of voluntary behavior that, in our opinion, appear to be more compatible with these alternative frameworks. This leads to the claim that perhaps they provide a better foundation for interpreting neural data and designing future experiments. We acknowledge that similar claims have been made many times in the past, but limitations of space and our own knowledge make it impossible to list all

of the contributors to these views. Our purpose here is to draw attention to how recent neurophysiological experiments lend strong support to these alternative ways of thinking about the brain.

The proposals we review above address interactive sensorimotor behavior and are not meant to constitute a general theory of all brain function. Clearly, tasks such as writing an email or playing chess involve processes that are far removed from simple sensorimotor control. Nevertheless, theories of embodied cognition have suggested, following Piaget, that cognitive abilities may have evolved within the context of ancestral abilities for interacting with the world (Hendriks-Jansen 1996, Pezzulo & Castelfranchi 2009, Powers 1973, Thelen et al. 2001, Toates 1998). For example, Toates (1998) proposed that primitive switching mechanisms, which mediate between different stimulus-response associations, have become elaborated through evolution into the cognitive systems that now allow us to make complex and sophisticated decisions. Pezzulo & Castelfranchi (2009) suggest that our ability to think about the world results from the internalization of the processes of predicting the consequences of actions. Their cognitive leverage hypothesis proposes that as the sensorimotor control system gradually evolved, it began to predict increasingly abstract consequences of behavior. This eventually allowed the mental rehearsal of entire sequences of acts and evaluation of their potential outcomes, without overt motor activity. Their hypothesis is consistent with the close relationship between mental imagery and the systems for motor preparation (Cisek & Kalaska 2004, di Pellegrino et al. 1992, Rizzolatti & Craighero 2004, Umilta et al. 2001) and potentially explains how an organism may go beyond merely reacting to properties of the immediate environment and act in a goal-directed manner. In conclusion, the neural systems that mediate the sensorimotor behavior of our ancient ancestors may have provided the foundations for modern cognitive abilities, and their consideration may shed light on the neural mechanisms that underlie human thought.

SUMMARY POINTS

1. Brains evolved for sensorimotor control and retained much of that architecture—even the neocortex is still part of that old circuit.

2. Natural interactive behavior requires sensorimotor control and selection systems to operate continuously and in parallel.

3. Distinctions between perceptual, cognitive, and motor processes, although descriptively useful, might not reflect the natural categories of the brain's functional organization.

4. Decisions appear to be made through a distributed consensus that emerges in competitive populations.

5. Neurophysiological data may be more readily interpreted from the perspective of interactive behavior than from the perspective of serial information processing.

FUTURE ISSUES

1. What are possible experimental approaches for studying behavior without constraining its interactive nature? Although some behavioral abilities are already studied in a relatively natural setting (e.g., locomotion), other systems demand new technologies for wireless multi-unit recording and new methods for analyzing data.

2. For a deeper understanding of the evolution of modern behavioral abilities, we would like to reconstruct the sequence of phylogenetic elaborations of a given system along a particular branch of the evolutionary tree. This calls for comparative neurophysiological studies of a diverse set of related species. However, this poses a significant challenge, not only because homologies are difficult to establish but also because practical matters motivate scientists to study particular species whose brains are already well mapped (e.g., rats, cats, and macaques).

3. From a theoretical standpoint, we need models that explain how sensorimotor control systems could have become elaborated to implement more sophisticated behavior. For example, if action selection takes place within a space defined by movement parameters (e.g., reach direction), what are the parameter spaces in which high-level decisions are made? Do these high-level spaces maintain topology, similar to the somatotopy and spatial maps useful for action selection?

4. How can an advanced agent discover the high-level opportunities afforded within its behavioral niche and link them with long-term goals?

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