

Cortical mechanisms of action selection: The affordance competition hypothesis¹

Paul Cisek
University of Montréal
Department of physiology
C.P. 6128 Succursale Centre-ville
Montréal, QC H3C 3J7 CANADA
paul.cisek@umontreal.ca

At every moment, the natural world presents animals with two fundamental pragmatic problems: selection between actions that are currently possible, and specification of the parameters or metrics of those actions. It is commonly suggested that the brain addresses these by first constructing representations of the world on which to build knowledge and make a decision, and then by computing and executing an action plan. However, neurophysiological data argues against this serial viewpoint. In contrast, it is proposed here that the brain processes sensory information to specify, in parallel, several potential actions that are currently available. These potential actions compete against each other for further processing, while information is collected to bias that competition until a single response is selected. The hypothesis suggests that the dorsal visual system specifies actions which compete against each other within the fronto-parietal cortex, while a variety of biasing influences are provided by prefrontal regions and the basal ganglia. A computational model is described which illustrates how that competition may take place in the cerebral cortex. Simulations of the model capture qualitative features of neurophysiological data and reproduce various behavioural phenomena.

KEYWORDS

Decision-making, action selection, cerebral cortex, computational modelling.

¹ This chapter is a new version of an earlier publication (Cisek, 2007) which appeared in *Philosophical Transactions of the Royal Society B*. The present version expands upon that earlier article with some discussion of recent experimental results.

1. INTRODUCTION

At every moment, the natural environment presents animals with many opportunities and demands for action. The presence of food offers an opportunity to satiate hunger, while the appearance of a predator demands caution or evasion. An animal cannot perform all of these behaviours at the same time because they often share the same effectors (you only have two hands; you can only transport yourself in one direction at a time, etc.). Thus, one fundamental issue faced by every behaving creature is the question of action *selection*. That question must be resolved, in part, by using external sensory information about objects in the world, and in part, by using internal information about current behavioural needs.

Furthermore, the animal must tailor the actions it performs to the environment in which it is situated. Grasping a fruit requires accurate guidance of the hand to the location of the fruit, while evading a predator requires one to move in an unobstructed direction that leads away from the threat. The *specification* of the parameters of actions is a second fundamental issue faced by behaving creatures. Specification of actions also must use sensory information from the environment. In particular, it requires information about the spatial relationships among objects and surfaces in the world, represented in a coordinate frame relative to the orientation and configuration of the animal's body.

Traditional cognitive theories propose that these two questions are resolved in a serial manner, that we select "what to do" before specifying "how to do it". According to this view, the perceptual system first collects sensory information to build an internal descriptive representation of objects in the external world (Marr 1982). Next, this information is used along with representations of current needs and memories of past experience to make judgments and decide upon a course of action (Shafir & Tversky 1995, Newell & Simon 1972, Johnson-Laird 1988). The resulting plan is then used to generate a desired trajectory for movement which is finally realized through muscular contraction (Miller et al. 1960, Keele 1968). In other words, the brain first builds knowledge about the world using representations which are independent of actions, and this knowledge is later used to make decisions, compute an action plan, and finally execute a movement.

However, studies of the cerebral cortex have encountered difficulties in interpreting neural activity in terms of distinct perceptual, cognitive, or motor systems. For example, visual processing diverges in the cortex into separate systems sensitive to object identity and spatial location

(Ungerleider & Mishkin 1982), with no single representation of the world (Stein 1992), leading to the question of how these disparate systems are bound together to form a unified percept (von der Malsburg 1996, Cisek & Turgeon 1999). Cells in the posterior parietal cortex appear to reflect a mixture of sensory (Andersen 1995, Colby & Goldberg 1999), motor (Snyder et al. 1997), and cognitive information (Platt & Glimcher 1999), leading to persistent debates on their functional role. A recent review of data on the parietal cortex has suggested that “current hypotheses concerning parietal function may not be the actual dimensions along which the parietal lobes are functionally organized; on this view, what we are lacking is a conceptual advance that leads us to test better hypotheses” (Culham & Kanwisher 2001 pp. 159-160). In other words, perhaps the concepts of separate perceptual, cognitive, and motor systems, which theoretical neuroscience inherits from cognitive psychology, are not appropriate for bridging neural data with behaviour.

Even stronger concerns regarding cognitive psychology’s suitability as a bridging framework are raised by considerations of evolutionary history (Sterelny 1989, Hendriks-Jansen 1996). Brain evolution is strikingly conservative and major features of modern neural organization can be seen in the humble *Haikouichthys*, a primitive jawless fish that lived during the early Cambrian epoch over 520 million years ago (Shu et al. 2003). Since the development of the telencephalon, the basic outline of the vertebrate nervous system has been strongly conserved throughout its phylogenetic history (Holland & Holland 1999, Katz & Harris-Warrick 1999, Butler & Hodos 2005). The basic topology of neural circuitry is analogous across very diverse species (Karten 1969) and even recently-elaborated structures such as the mammalian neocortex have homologues among non mammalian species (Medina & Reiner 2000). Although the idea that brain evolution consists of new structures being added on top of old structures (e.g. the “Triune Brain” (MacLean 1973)) is still popular among non-specialists, it has been rejected in recent decades of comparative neuroanatomical work (Butler & Hodos 2005, Deacon 1990). Brain evolution consists of the differentiation and specialization of existing structures (Krubitzer & Kaas 2005), shifts in existing axonal projection patterns (Deacon 1990), and modifications of developmental “morphogenetic fields” (Gilbert et al. 1996), not through the addition of new structures. Thus, the basic anatomical and functional organization of the primate brain reflects an ancient architecture which was well-established by the time of the earliest terrestrial tetrapods. This architecture could not have been designed to serve the needs of higher cognitive abilities, which did not exist, but must have been laid down so as to best address the needs of simple, interactive behaviour.

An emphasis on the brain's role in interactive behaviour is by no means novel. Similar ideas have for a long time been central to theories in ethology (Hinde 1966, Ewert et al. 2001), and have recently led to several new viewpoints on cognition (Clark 1997, Thelen et al. 2001, Núñez & Freeman 2000, Beer 2000, Adams & Mele 1989), and interactive behaviour (Brooks 1991, Prescott et al. 1999, Hendriks-Jansen 1996, Seth this volume). All of these are similar to several lines of thought that are much older (Ashby 1965, Merleau-Ponty 1945, Powers 1973, Powers 1973, Gibson 1979, Maturana & Varela 1980, Mead 1938) in some cases by over a hundred years (Bergson 1896, Dewey 1896, Jackson 1884). Most of these viewpoints emphasize the pragmatic aspects of behaviour (Gibson 1979, Millikan 1989, Piaget 1967), a theme that underlies several proposals regarding representation (Dretske 1981, Gallese 2000, Hommel et al. 2001), memory (Ballard et al. 1995, Glenberg 1997), and visual consciousness (O'Regan & Noë 2001). Here, it is proposed that these views, which emphasize the brain's role in controlling behaviour in real time (Cisek 1999), provide a better basis for interpreting neurophysiological data than the traditional framework of cognitive psychology (Cisek 2001).

Continuous interaction with the world often does not allow one to stop to think or to collect information and build a complete knowledge of one's surroundings. To survive in a hostile environment, one must be ready to act at short notice, releasing into execution actions which are at least partially prepared. These are the fundamental demands which shaped brain evolution. They motivate animals to process sensory information in an action-dependent manner, to build representations of the potential actions which the environment currently affords. In other words, the perception of a given natural setting may involve not only representations which capture information about the identity of objects in the setting, but also representations which specify the parameters of possible actions that can be taken (Gibson 1979, Fadiga et al. 2000, Cisek 2001). With a set of such potential actions partially specified, the animal is ready to quickly perform actions if circumstances demand. In essence, it is possible that the nervous system addresses the questions of specification ("how to do it") *before* performing selection ("what to do"). Indeed, for continuous interactive behaviour, it may be best to perform both specification and selection processes at all times, to enable continuous adjustment to the changing world.

The proposal made here is that *the processes of action selection and specification occur simultaneously*, and continue even during overt performance of movements. That is, sensory information arriving from the world is continuously used to specify several currently available

potential actions, while other kinds of information are collected to select from among these the one that will be released into overt execution at a given moment (Glimcher 2001, Gold & Shadlen 2001, Kalaska et al. 1998, Kim & Shadlen 1999, Platt 2002, Cisek & Kalaska 2005, Gold & Shadlen 2001, Platt 2002, Glimcher 2001, Kalaska et al. 1998, Cisek 2001, Fagg & Arbib 1998). From this perspective, behaviour is viewed as a constant competition between internal representations of conflicting demands and opportunities, of the potential actions that Gibson (1979) termed “affordances”. Hence, the framework presented here is called the “affordance competition” hypothesis.

It is not proposed that complete action plans are prepared for all of the possible actions that one might take at a given moment. First, only actions which are *currently* available are specified in this manner. Second, many possible actions are eliminated from processing by selective attention mechanisms which limit the sensory information that is transformed into representations of action. Finally, complete action planning is not proposed even for the final selected action. Even in cases of highly practiced behaviours, no complete pre-planned motor program or entire desired trajectory appears to be prepared (Kalaska et al. 1998, Cisek 2005).

2. THE AFFORDANCE COMPETITION HYPOTHESIS

The view of behaviour as a competition between actions has been common in studies of animal behaviour and the interpretation of subcortical circuits (Ewert 1997, Ewert et al. 2001, Prescott et al. 1999). However, it is more rarely used to explain the activity of cerebral cortical regions, perhaps due to an assumption that the cortex is a new structure concerned with new, cognitive functions. However, as discussed above, that assumption is not justified. The organization of the cerebral cortex has been conserved for a long time, motivating one to interpret it, like subcortical circuits, in terms of interactive behaviour. Figure 1 outlines a proposal on how the affordance competition hypothesis may be used to interpret neural data from the primate cerebral cortex during visually-guided behaviour.

The visual system is organized into two parallel processing pathways: an occipito-temporal “ventral stream” in which cells are sensitive to information about the identity of objects, and an occipito-parietal “dorsal stream” in which cells are sensitive to spatial information (Ungerleider & Mishkin 1982). From the traditional cognitive perspective, the ventral stream builds a representation of “what” is in the environment, while the dorsal stream builds a representation of

“where” things are. However, the dorsal stream does not appear to contain any unified representation of the space around us, but rather diverges into a number of sub-streams each specialized toward the needs of different kinds of actions (Stein 1992, Andersen et al. 1997, Colby & Goldberg 1999, Matelli & Luppino 2001, Wise et al. 1997). For example, the lateral intraparietal area (LIP) is concerned with the control of gaze (Snyder et al. 2000b, Snyder et al. 1997), represents space in a body-centred reference frame (Snyder et al. 1998b), and is strongly interconnected with parts of the oculomotor system including the frontal eye fields (FEF) and the superior colliculus (Paré & Wurtz 2001). In contrast, the medial intraparietal area (MIP) is involved in arm reaching actions (Cui & Andersen 2007, Pesaran et al. 2008, Scherberger & Andersen 2007, Ferraina & Bianchi 1994, Kalaska & Crammond 1995, Snyder et al. 1997), represents target locations with respect to the current hand location (Buneo et al. 2002, Graziano et al. 2000), and is interconnected with frontal regions involved in reaching, such as the dorsal premotor cortex (PMd) (Johnson et al. 1996, Marconi et al. 2001). The anterior intraparietal area (AIP) is involved in grasping (Baumann et al. 2009), is sensitive to object size and orientation, and is interconnected with the grasp-related ventral premotor cortex (PMv) (Rizzolatti & Luppino 2001, Nakamura et al. 2001).

These observations are consistent with the proposal that the major role of the dorsal visual stream is not to build a unified representation of the world, but rather to mediate various visually-guided actions (Goodale & Milner 1992). It may therefore be part of the system for action specification (Cisek & Turgeon 1999, Cisek 2001, Kalaska et al. 1998, Fagg & Arbib 1998, Passingham & Toni 2001), processing visual information to specify potential actions of various kinds: LIP cells specify potential saccade targets; MIP cells specify possible directions for reaching, etc. Furthermore, the dorsal stream represents not only a single unique movement that has already been selected, but rather offers a variety of options to choose from, including multiple saccade targets (Kusunoki et al. 2000, Platt & Glimcher 1997) as well as multiple reaching movements (Cisek et al. 2004). It does not, of course, represent all possible movements. As one proceeds further along the dorsal stream, one finds an increasing influence of attentional modulation, with information from particular regions of interest enhanced while information from other regions is suppressed (Desimone & Duncan 1995, Treue 2001). The result is that the parietal representation of external space becomes increasingly sparse as one moves away from striate cortex (Gottlieb et al. 1998). In other words, only the most promising targets for movements make

it so far as to be represented in the parietal cortex. From this perspective, the phenomenon of selective attention is seen as an early mechanism for action selection (Allport 1987, Tipper et al. 1998, Tipper et al. 1992, Neumann 1990), reducing the volume of information that is transformed into action-related representations.

As mentioned, parietal cortical areas are strongly and reciprocally interconnected with frontal regions involved in movement control. LIP is interconnected with FEF, MIP with PMd and primary motor cortex (M1), AIP with ventral premotor cortex (PMv), etc. (Matelli & Luppino 2001). As a result, the fronto-parietal system may be viewed as a set of loops spanning over the central sulcus, each processing information related to a different aspect of movement (Jones et al. 1978, Pandya & Kuypers 1969, Marconi et al. 2001). If these regions are involved in representing potential actions, as assumed here, then they appear to do so in tandem. For example, potential reaching actions are represented together by both MIP and PMd (Cisek & Kalaska 2005, Cisek et al. 2004). It is proposed that the competition between potential actions plays out in large part within this reciprocally interconnected fronto-parietal system. Within each cortical area, cells with different movement preferences mutually inhibit each other, creating a competition between distinct potential actions. This competition is biased by excitatory input from a variety of sources, including both cortical and subcortical regions. The influence of all of these biasing factors modulates the activity in frontal and parietal neurons, with information favouring a given action causing activity related to that action to increase, while information against an action causes it to decrease.

Indeed, neurophysiological evidence for the modulation of fronto-parietal activity by “decision factors” is very strong. For example, recent studies of decision-making show that LIP activity correlates not only with sensory and motor variables, but also with decision variables such as expected utility (Platt & Glimcher 1999), local income (Sugrue et al. 2004), hazard rate (Janssen & Shadlen 2005), relative subjective desirability (Dorris & Glimcher 2004), and log-likelihood estimates (Yang & Shadlen 2007). More generally, variables traditionally considered as sensory, cognitive, or motor, appear to be mixed in the activity of individual cells in many regions, including prefrontal cortex (Hoshi et al. 2000, Constantinidis et al. 2001), premotor cortex (Cisek & Kalaska 2005, Romo et al. 2004), FEF (Coe et al. 2002, Gold & Shadlen 2000, Thompson et al. 1996), LIP (Coe et al. 2002, Platt & Glimcher 1997, Shadlen & Newsome 2001), and the superior colliculus (Basso & Wurtz 1998, Horwitz et al. 2004). Such mixing of variables is difficult to

interpret from the perspective of distinctions between sensory, motor, and cognitive systems, and it has led to persistent debates about the functional role of specific cortical regions. For example, some studies have shown that neurons in area LIP respond only to stimuli which capture attention, leading to its interpretation as a “saliency map” (Bisley & Goldberg 2003, Colby & Goldberg 1999, Kusunoki et al. 2000). However, other studies have shown that these activities are stronger when the stimulus serves as the target of a saccade (as opposed to a reach), leading to the interpretation of LIP as a representation of intended saccades (Snyder et al. 1997, 2000a, 1998a). These competing interpretations have been the subject of a long and vibrant debate. However, from the perspective of the affordance competition hypothesis, both interpretations are correct: Neural activity in fronto-parietal regions correlates with sensory and motor variables because it is involved in the specification of potential actions using sensory information, and it is modulated by decision variables (including saliency/attention) because a competition between potential actions is influenced by various sources of biasing inputs.

There are many potential sources from which biasing inputs might originate. Because action selection is a fundamental problem faced by even the most primitive of vertebrates, it likely involves neural structures which developed very early and have been conserved in evolution. A promising candidate is the basal ganglia (Kalivas & Nakamura 1999, Mink 1996, Redgrave et al. 1999, Hazy et al. this volume, Frank et al. this volume, Leblois et al. 2006), which are strongly interconnected with specific cortical areas (Middleton & Strick 2000, Alexander & Crutcher 1990a) and exhibit activity that is related both to movement parameters (1990c, Alexander & Crutcher 1990b) and decision variables such as reward (Schultz et al. 2000) and expectation (Lauwereyns et al. 2002). However, it is also likely that action selection involves brain structures which have become particularly developed in recent evolution, such as the prefrontal cortex of primates. The prefrontal cortex is strongly implicated in decision-making (Bechara et al. 1998, Kim & Shadlen 1999, Fuster et al. 2000, Miller 2000, Tanji & Hoshi 2001, Rowe et al. 2000), which may be viewed as an aspect of advanced action selection. 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 (di Pellegrino & Wise 1991, Hoshi et al. 1998, Kim & Shadlen 1999, Quintana & Fuster 1999, Rainer et al. 1998). Prefrontal decisions appear to evolve through the collection of “votes” for categorically selecting one action over others, as demonstrated by studies of saccade target and reach target selection

(Kim & Shadlen 1999, Tanji & Hoshi 2001). Of course, the prefrontal cortex is not a homogeneous system but a diverse collection of specialized regions, including some which appear to be involved in aspects of working memory (Bechara et al. 1998, Fuster & Alexander 1971, Petrides 2000, Rowe et al. 2000). Here, we include only a very simplified account of one particular subregion of PFC, the dorsolateral prefrontal cortex.

What role might the ventral visual stream play within the functional architecture of Figure 1? Cell responses in anterior inferotemporal (IT) cortex are sensitive to features of a currently-viewed stimulus (Tanaka et al. 1991, Desimone et al. 1984), and to the behavioural context in which that stimulus is presented (Eskandar et al. 1992). These results have been taken to implicate IT in object recognition. However, it may also serve a more humble role. Studies of animal behaviour over the last hundred years have shown that many kinds of behaviours are elicited by simple combinations of particular stimulus features, what ethologists referred to as “sign stimuli” (Tinbergen 1950, Hinde 1966). Neural responses in IT cortex are compatible with a putative role in sign stimulus detection, which could serve as a front-end input to action selection via direct projections from temporal cortex to prefrontal regions (Saleem et al. 2000). Thus, an early role of what is now the ventral stream may have been the detection of the stimulus combinations that were relevant for selection of actions in a particular behavioural context, and this may have eventually evolved into the sophisticated object recognition ability of modern mammals.

In the view schematized by Figure 1, specification and selection processes operate in parallel. As an animal interacts with its world, sensorimotor processing in the dorsal stream is continuously fine-tuning an ongoing action even while it continues to build egocentric representations of alternative potential actions that could be performed. Meanwhile, selection mechanisms vote for which of those actions progress furthest in sensorimotor processing and whether the animal will switch behaviour from its ongoing task to a new one which might become more immediately relevant. For example, while a monkey is feeding on some fruit that is within reach, its parietal system can continue to represent nearby branches as potential escape routes in case its ventral stream detects evidence that a leopard has appeared.

Although during natural behaviour the processes of specification and selection will occur simultaneously, we can still make predictions about what would happen if an animal endowed with such a parallel architecture was placed in a neurophysiological laboratory. In this highly controlled setting, time is broken up into discrete trials, each starting with the presentation of a stimulus and

ending with the production of a response. What would the architecture of Figure 1 predict about the time-course of neural events?

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 responses to simple visual flashes appear very quickly throughout the dorsal visual system, and engage putatively motor-related areas like FEF in as little as 50ms. 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 discriminates the direction of the cue within 50ms of its appearance (Cisek & Kalaska 2005). These fast responses are not purely visual, as 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). In short, these phenomena are compatible with the notion of a fast dorsal specification system that quickly uses visual information to specify the potential actions most consistently associated with a given stimulus. The speed of that system also allows us to quickly adjust ongoing movements to perturbations (Day & Lyon 2000, Desmurget et al. 1999).

After the initial options are quickly specified, we expect that slower selection processes will 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 about 50ms but begin to reflect the influence of attention in 100-120ms (Constantinidis & Steinmetz 2001, Treue 2001). FEF neurons respond to the onset of a stimulus in 50ms (Schmolesky et al. 1998), but detect the singleton of a visual-search array with a median of about 100ms and discriminate pro- vs. anti-saccades in about 120ms (Sato & Schall 2003). LIP neurons respond to stimulus onset in about 50ms and discriminate targets from distractors in 138ms (Thomas & Pare 2007). Neurons in dorsal premotor cortex respond to a visual cue in 50ms but begin predict the monkey’s choice in 110-130ms (Cisek & Kalaska 2005).

A recent study by Ledberg and colleagues (2007) provides an overall picture of the time-course observed in all of the experiments described above (Figure 5). These authors

simultaneously recorded local field potentials (LFPs) from up to 15 cerebral cortical regions of monkeys performing a conditional Go/NoGo task. Because LFPs are believed to reflect the summed dendritic input to an area, they are an excellent measure of processing onset latency. Through an elegant experimental design, Ledberg and colleagues were able to detect the first neural events that responded to the presence of a stimulus, those which discriminated its identity, as well as those predicting the monkey's chosen response. In agreement with earlier studies (c.f. Schmolesky et al. 1998), they observed a fast feedforward sweep of stimulus onset-related activity appearing within 50-70ms in striate and extrastriate cortex, and 55-80ms in FEF and premotor cortex. Discrimination of different stimulus categories occurred later, within about 100ms of onset in prestriate areas and 200ms in prefrontal sites. The Go/NoGo decision appeared about 150ms 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 discriminates between them about 120-150ms after stimulus onset (Ledberg et al. 2007). In summary, it appears that the brain can very quickly specify multiple potential actions within its fast fronto-parietal sensorimotor control system, but it takes approximately 150ms to integrate information sufficiently in order to make a decision between them.

3. A COMPUTATIONAL MODEL OF REACHING DECISIONS

The broad concepts outlined in the previous section can be translated into more concrete and testable hypotheses through a mathematical model of the neural processes which may implement action specification and selection in the mammalian cerebral cortex. A model of the cortical mechanisms which specify reaching movements and select between them has been described by Cisek (2006b) and it is summarized briefly here.

Figure 2a illustrates the circuit model and suggests how its elements may correspond to specific cortical regions. Because the model focuses on visually-guided reaching actions, it includes some of the main cortical regions involved in reaching behaviour, such as the posterior parietal cortex (PPC), dorsal premotor cortex (PMd), primary motor cortex (M1), and prefrontal cortex (PFC). These were chosen as a subset of the complete distributed circuits for reaching control, sufficient to demonstrate a few central concepts. Other relevant regions not currently

modelled are the supplementary motor areas, somatosensory cortex, and many subcortical structures including the basal ganglia, red nucleus, etc. The input to the model consists of visual information about target direction and a signal triggering movement onset (GO signal), and the output is the direction of movement. The control of the overt movement is not simulated here (for compatible models of execution, see Bullock et al. 1998, Bullock & Grossberg 1988, Cisek et al. 1998, Houk et al. 1993, Kettner et al. 1993, McIntyre & Bizzi 1993).

In the model, each neural population was implemented as a set of 90 mean-rate leaky-integrator neurons each of which is broadly tuned to a particular direction of movement. All of the weights are fixed to resemble the known anatomical connections between the modelled regions. Within each population, neurons with similar tuning excite each other while neurons with dissimilar tuning inhibit each other. Between populations, neurons with similar tuning excite each other through reciprocal topological connections. Noise is added to all neural activities. See Cisek (2006a) for details of the model's implementation.

In the model, neural populations do not encode a unique value of a movement parameter (such as a single direction in space) but can represent an entire distribution of potential values of movement parameters (e.g. many possible directions represented simultaneously). This proposal is related to the attention model of Tipper et al. (2000), the "decision field" theory of Erlhagen and Schöner (2002), and the "Bayesian coding" hypothesis (Dayan & Abbott 2001, Sanger 2003, Knill & Pouget 2004). It suggests that given a population of cells, each with a preferred value of a particular movement parameter, one can interpret the activity across the population as something akin to a probability density function of potential values of that parameter. Sometimes, the population may encode a range of contiguous values defining a single action, and at other times, several distinct and mutually exclusive potential actions can be represented simultaneously as distinct peaks of activity in the population (Fig. 2b). The strength of the activity associated with a particular value of the parameter reflects the likelihood that the final action will have that value, and it is influenced by a variety of factors including salience, expected reward, estimates of probability, etc. This hypothesis predicts that activity in the population is correlated with many decision variables, as observed in frontal (Coe et al. 2002, Gold & Shadlen 2000, Hoshi et al. 2000, Kim & Shadlen 1999, Roesch & Olson 2004, Romo et al. 2004) and parietal cortex (Coe et al. 2002, Glimcher 2003, Platt & Glimcher 1999, Shadlen & Newsome 2001, Sugrue et al. 2004, Janssen & Shadlen 2005, Dorris & Glimcher 2004).

The model suggests that sensory information in the dorsal visual stream is used to specify the spatial parameters of *several* currently available potential actions in parallel. These potential actions are represented simultaneously in frontal and parietal cortical regions, appearing as distinct peaks of activity in the neural populations involved in sensorimotor processing (Cisek & Kalaska 2005, Cisek et al. 2004, Platt & Glimcher 1997) (Figure 2b). Whenever multiple peaks appear simultaneously within a single frontal or parietal cortical region, they compete against each other through mutual inhibition. This is related to the biased competition mechanism in theories of visual attention (Desimone 1998, Boynton 2005). To state it briefly, cells with similar parameter preferences excite each other while cells with different preferences inhibit each other. This basic mechanism can explain a variety of neural phenomena, such as the inverse relationship between the number of options and neural activity associated with each (Basso & Wurtz 1998, Cisek & Kalaska 2005), narrowing of tuning functions with multiple options (Cisek & Kalaska 2005), and relative coding of decision variables (Roesch & Olson 2004).

Because neural activities are noisy, competition between distinct peaks of activity cannot follow a simple “winner-take-all” rule or random fluctuations would determine the winner each time, rendering informed decision-making impossible. To prevent this, small differences in levels of activity should be ignored by the system. However, if activity associated with a given choice becomes sufficiently strong, it should be allowed to suppress its opponents and conclusively win the competition. In other words, there should be a threshold of activity above which a particular peak is selected as the final response choice. This is consistent with sequential sampling models of decision-making (Usher & McClelland 2001, Reddi et al. 2003, Mazurek et al. 2003, Smith & Ratcliff 2004, Bogacz et al. 2006) which propose that decisions are made when neural activity reaches some threshold. In the model, this threshold emerges from the nonlinear dynamics between competing populations of cells (Grossberg 1973, Cisek 2006b).

Finally, the model suggests that the competition which occurs between potential actions represented in the fronto-parietal system is biased by a variety of influences from other regions, including the basal ganglia (Redgrave et al. 1999, Leblois et al. 2006, Brown et al. 2004) and PFC (Miller 2000, Tanji & Hoshi 2001) which accumulate evidence for each particular choice (Figure 1). Here, only the influence of PFC is modelled, although it is likely that basal ganglia projections play a significant role in action selection (Frank et al. this volume, Hazy et al. this volume, Houk et al. this volume; Stafford and Gurney this volume). Several studies have shown that some cells in

lateral prefrontal cortex (PFC) are sensitive to conjunctions of relevant sensory and cognitive information (Miller 2000, Rainer et al. 1998, Tanji & Hoshi 2001, White & Wise 1999), and that they gradually accumulate evidence over time (Kim & Shadlen 1999). Many studies have suggested that orbitofrontal cortex and the basal ganglia provide signals which predict the reward associated with a given response (Schultz et al. 2000), which could also serve as input to bias the fronto-parietal competition.

The operation of the model can be most easily understood in the context of a particular task. For example, Fig. 3a shows a reach-decision task in which the correct target was indicated through a sequence of cues: during the spatial-cue period (SC), two possible targets were presented, and during a subsequent colour-cue period (CC), one of these was designated as the correct target. In the model, the appearance of the spatial cue causes activity in two groups of cells in PPC, each tuned to one of the targets. Mutual excitation between nearby cells creates distinct peaks of activity, which compete against each other through the inhibitory interactions between cells with different preferred directions. Because of the topographic projections between PPC and PMd, two peaks appear in PMd as well, although they are weaker in the lower PMd layers (compare layers PMd¹ and PMd³). These two peaks continue to be active and to compete against each other even after the targets vanish, due to the positive feedback between layers. At the same time, activity accumulates in the PFC cells selective for the particular location-colour conjunctions. The colour cue is simulated as uniform excitation to all PFC cells preferring the given colour (in this case, PFC^R), and it pushes that group of PFC cells toward stronger activity than the other. This causes the competition in PMd to become unbalanced, and one peak increases its activity while the other is suppressed. In the model, this is equivalent to a decision. Finally, once the GO signal is given, activity is allowed to flow from PMd³ into M1, and the peak of the M1 activity is taken to define the initial direction of the movement.

The simulation reproduces many features of neural activity recorded from the dorsal premotor and primary motor cortex of a monkey performing the same reach-decision task (Cisek & Kalaska 2005). As shown in Fig. 3a, PMd cells tuned to both spatial targets were active during the SC, and then during the CC, one of these became more strongly active (predicting the monkey's choice), while the other was suppressed. Note how the activity was weaker while both options were present, consistent with the hypothesis that the two groups of cells exert an inhibitory influence on each other. As in the model, these phenomena were seen more strongly in the rostral

part of PMd than in the caudal part. The model also exhibits sustained activity (“working memory”) because after the targets are removed (second black line in the simulation images) target information is maintained in both PPC and PMd (Fig. 3a,b).

Figure 3c shows a variation of the task in which the CC is presented before the SC. In this case, no directionally-tuned activity appears in PMd during the colour-cue period, and after the spatial targets are presented there is sustained activity corresponding only to the correct target. Thus, the neural activity is determined not by the sensory properties of the stimulus (which are the same as in Fig. 3a) but by the movement information specified by the stimulus. However, note that immediately after the SC, there is a brief burst toward the incorrect target, in both the neurons in rostral PMd and in the PMd¹ population in the model (Fig. 3c). One might be tempted to classify this as a pure “sensory” response. However, at least in the model, this burst is more correctly described as a brief representation of a potential action, aborted quickly in light of the prior information provided by the colour-cue. Again, this is seen most strongly in the rostral part of PMd, in both the data and the model.

Figure 4 shows some predictions about the context-dependent timing of cortical responses. As discussed above, studies on the timing of attentional and decisional processes suggest that action selection occurs in 120-150ms after stimulus presentation in a distributed network of regions (Ledberg et al. 2007, Constantinidis & Steinmetz 2001, Treue 2001, Sato & Schall 2003, Thomas & Pare 2007, Cisek & Kalaska 2005). This is compatible with the model, but we can make a further prediction. While the distributions of latencies should be similar across cortical regions, we predict that they are not identical, and that they will follow a specific context-dependent trend. In particular, consider the case when a decision is made on the basis of cognitive information, such as a learned color cue (as in the two-target task described above). Because such cues are collected by prefrontal regions which project into rostral PMd, the bias introduced by the cue will begin to unbalance the PMd competition directly, which will then in turn (through fronto-parietal connections) cause the PPC competition to become unbalanced. Therefore, a decision made on the basis of such cognitive cues will first be expressed in frontal cortex and then, a very short time later, in parietal regions. This is indeed what was observed during neural recordings in the two-target task, which showed that PMd neurons tended to reflect the decision about 80 ms before PPC neurons (Cisek et al. 2004). This phenomenon is simulated in Figure 4a. In particular, note that just after the color cue is presented (green circle) the neural activity tuned to the selected target begins

to diverge from the activity tuned to the unselected target first in PMd (blue lines), and then shortly afterwards in PPC (red lines).

In contrast, consider a situation in which the decision is made on the basis of a more direct sensory signal, such as the reappearance of one of the targets. This information will first be available in parietal cortex, and will cause the PPC competition to become unbalanced, which will then in turn unbalance the PMd competition. Therefore, a decision made on the basis of the reappearance of a stimulus will first be expressed in parietal cortex and then very soon after appear in PMd. Figure 4b simulates this phenomenon. Note that just after the target reappears (green circle), the activity in PPC (red lines) reflects this event slightly before the activity in PMd (blue lines). Although such conditions have not been directly tested in neurophysiological recording experiments, the model predicts that the sequence by which decision-related activity spreads across the cerebral cortex is dependent upon the nature of the information which guides the choice that is made.

Recent neurophysiological studies have supported these predictions. For example, when monkeys perform pop-out visual search, neural activity in LIP reflects the choice before FEF and PFC, but if the task involves conjunction search then it is FEF and PFC which reflect the choice before LIP (Buschman & Miller 2007). Assumptions about expected actions (priors) influence activity in SEF before FEF and LIP (Coe et al. 2002, Pesaran et al. 2008). Interestingly, in a Go/Nogo task in which monkeys made decisions on the basis of cognitive rules, activity predicting the response appeared in PMd *even before PFC*, which presumably processes the rule information (Wallis & Miller 2003). It is as if, at least in that kind of task, a decision may be *influenced* by noisy neural votes arriving in part from PFC but is *determined* by a consensus that is reached in PMd.

In addition to reproducing qualitative features of neural activity during various action selection tasks, the model produces important psychophysical results on the spatial and temporal characteristics of human motor decisions. For example, it is well-known that reaction times in choice-tasks increase with the number of possible choices. This can be explained by the model (see Fig. 5a), because the activity associated with each option is reduced as the number of options is increased (compare model PMd activity in Fig. 3a vs. Fig. 3b), and it therefore takes longer for the activity to reach the decision threshold. Furthermore, it has also been shown that reaction time is not only determined by the number of targets but also by their spatial configuration. For example,

Bock & Eversheim (2000) showed that reaction time in a reaching task is similar with two or five targets as long as they subtend the same spatial angle, but shorter if two targets are closer together. This finding is difficult to account for with models in which the options are represented by discrete groups of neurons, but is easily reproduced in a model such as the present one, in which movements are specified by a continuous population (see Fig. 5b). The model also reproduces the important finding that reducing the quality of evidence for a given choice, makes reaction times longer and more broadly distributed. The model produces this (see Fig. 5c), through the same mechanism proposed by other models which involve a gradual accumulation to threshold: that with weaker evidence, the rate of accumulation is slower and the threshold is reached later in time, and therefore variability in accumulation rate produces broader distributions of reaction times (Carpenter & Williams 1995, Ratcliff et al. 2003, Smith & Ratcliff 2004).

The model also explains several observations on the spatial features of movements made in the presence of multiple choices. For example, Ghez and colleagues (1997) showed that when subjects are forced to make choices quickly, they move to targets randomly if they are spaced further than 60° apart (“discrete mode”), and in-between them if the targets are close together (“continuous mode”), as shown in Fig. 6a. The model reproduces all of these results (Fig. 6b). When two targets are far apart, they create multiple competing peaks of activity in the PMd-PPC populations, and the decision is determined by which peak happens to fluctuate higher when the signal to move is given. However, if the targets are close together, then their two corresponding peaks merge into one because of the positive feedback between cells with similar parameter preferences (A similar explanation has been proposed by Erlhagen & Schoner 2002). In a related experiment, Favilla (1997) demonstrated that the discrete and continuous modes can occur at the same time when four targets are grouped into two pairs that are far apart but each of which consists of two targets close together (see Fig. 6c). This is also reproduced by the model (Fig. 6d) (except for an additional central bias exhibited by human subjects). With four targets, peaks corresponding to targets within each pair merge together and then the two resulting peaks compete and are selected discretely.

4. DISCUSSION

This manuscript describes a theoretical framework called the “affordance competition hypothesis”, which suggests that behaviour involves a constant competition between currently

available opportunities and demands for action. It is based on the idea that the brain's basic functional architecture evolved to mediate real-time interaction with the world, which requires animals to continuously specify potential actions and to select between them. This framework is used to interpret neural data from the primate cerebral cortex, suggesting explanations for a number of important neurophysiological phenomena. A computational model is presented to illustrate the basic ideas of the hypothesis and to suggest how neural populations in the cerebral cortex may implement a competition between representations of potential actions.

The mathematical model presented above shares a number of features with existing models of decision-making. For example, it is similar to a class of models called "sequential sampling models" (Bogacz et al. 2006, Roe et al. 2001, Usher & McClelland 2001, Reddi et al. 2003, Mazurek et al. 2003, Smith & Ratcliff 2004), which propose that decisions are made by accumulating information for a given choice until it reaches some threshold. In some models, the evidence is accumulated by a single process (e.g. Smith & Ratcliff 2004), in some it is collected by separate processes which independently race toward the threshold (Reddi et al. 2003, Roe et al. 2001), and in some the independent accumulators inhibit each other (Usher & McClelland 2001). Some models separate the decision process into serial stages (e.g. Mazurek et al. 2003) and in some it occurs when a single population exhibits a transition from biased competition to binary choice (Wang 2002, Machens et al. 2005). While the present model shares similarities with these, it extends their scope in an important way. In all of the models of decision-making described above, the choices are predefined and represented by distinct populations, one per choice. In contrast, the present model suggests that the choices themselves emerge within a population of cells whose activity represents the probability density function of potential movements. In other words, the model describes the mechanism by which the choices are defined using spatial information. In this sense, it is related to the models of Erlhagen & Schöner (2002) and Tipper et al. (2000), which also discuss continuous specification of movement parameters within a distributed representation. To summarize, the present model may be seen as combining three lines of thought: (1) sequential sampling models of accumulation of evidence to a threshold; (2) models of a phase transition from encoding options to binary choice behaviour (Cisek 2006a); and (3) models of action specification within a distributed population. It also suggests a plausible manner in which these concepts can be used to interpret neural data in specific cortical regions.

The model presented here makes a number of predictions which distinguish it from many other models of decision-making. First, it focuses on decisions about actions (as opposed to sensory discrimination) and suggests that these are made within the very same neural circuits that control the execution of those actions. These circuits are distributed among a large set of brain regions. In the case of visually-guided reaching, decisions are made within the fronto-parietal circuit that includes both PMd and parietal area MIP. In the specific mathematical formulation described above, the competition between actions uses information from PFC, but the decision first appears in PMd, in agreement with data (Wallis & Miller 2003). However, the broader framework of the affordance competition hypothesis does not impose any rigid temporal sequence in which decisions appear in the fronto-parietal system. Each population in the network is proposed to involve competitive interactions, and biasing influences can modulate that competition in different places. Because cortico-cortical connections are bi-directional, if a decision begins to emerge in one region then it will propagate outward to other regions. For example, decisions based on sensory features such as stimulus salience may first appear in parietal cortex and then influence frontal activity. In contrast, decisions based on abstract rules may first be expressed in frontal regions and propagate backward to PPC. Thus, decisions are proposed to emerge as a “distributed consensus” which is reached when a competition between representations of potential actions is unbalanced by the accumulation of evidence in favour of a given choice.

Although the mathematical model presented here is similar in some ways to previous models of decision-making, it is based on a somewhat unusual theoretical foundation. The affordance competition hypothesis, illustrated schematically in Figure 1, differs in several important ways from the cognitive neuroscience frameworks within which models of decision-making are usually developed. Importantly, it lacks the traditional emphasis on explicit representations which capture knowledge about the world. For example, the activity in the dorsal stream and the fronto-parietal system is not proposed to encode a representation of objects in space, or a representation of motor plans, or cognitive variables such as expected value. Instead, it implements a particular, functionally-motivated mixture of all of these variables. From a traditional perspective, such activity appears surprising because it doesn't have any of the expected properties of a sensory, cognitive, or motor representation. It doesn't capture knowledge about the world in the explicit descriptive sense expected from cognitive theories, and has proven difficult to interpret from that perspective (see above). However, from the perspective of affordance competition, mixtures of

sensory information with motor plans and cognitive biases make perfect sense. Their functional role is not to describe the world, but to mediate adaptive interaction with the world.

In summary, instead of viewing the functional architecture of behaviour as serial stages of representation, we view it as a set of competing sensorimotor loops. This is by no means a novel proposal. It is related to several theories which describe behaviour as a competition between actions (Toates 1998, Prescott et al. 1999, Hendriks-Jansen 1996, Ewert et al. 2001, Kornblum et al. 1990), and as discussed above, to a number of philosophical proposals made throughout the last hundred years. The present discussion is an attempt to unify these and related ideas with a growing body of neurophysiological data. It is suggested that a great deal of neural activity in the cerebral cortex can be interpreted from the perspective of a competition between potential movements more easily than in terms of traditional distinctions between perception, cognition, and action (Cisek 2001). It is not suggested that distinctions between perceptual, cognitive, and motor processes be discarded entirely (they are certainly appropriate for interpreting primary sensory and motor regions), but only that other conceptual distinctions may be better suited to understanding central regions.

Figure 7 provides a schematic of the conceptual differences between the affordance competition hypothesis and the traditional frameworks of cognitive neuroscience. Traditional frameworks tend to view brain function as consisting of three basic classes of neural processes (see Fig. 7a): *perceptual systems*, which take sensory information and construct internal representations of the world (e.g. Marr 1982); *cognitive systems*, which use that representation along with memories of past experience to build knowledge, form judgments, and make decisions about the world (Shafir & Tversky 1995, Newell & Simon 1972, Johnson-Laird 1988); and *action systems*, which implement the decisions through planning and execution of movements (Miller et al. 1960, Keele 1968). Each of these broad classes can be subdivided into subclasses. For example, perception includes different modalities such as vision, which can be subdivided further into object recognition, spatial vision, etc. Likewise, cognition includes processes such as working memory storage and retrieval, decision-making, etc. These conceptual classes and subclasses are used to define research specialties, categorize scientific journals, and to interpret the functional role of specific brain regions.

Here, a different taxonomy of concepts is proposed (Fig. 7b). Brain function is seen as fundamentally serving the needs of interactive behaviour, which involves two classes of processes:

action specification processes, which use sensory information to define potential actions and guide their execution on-line; and *action selection processes*, which help to select which potential action will be performed at a given moment. Each of these can be subdivided further. For example, action specification can be divided into the specification of different kinds of actions, such as reaching, which involves spatial vision, inverse kinematics, etc. Action selection includes processes such as visual attention which select information on the basis of sensory properties, as well as decision-making which selects potential actions on the basis of more abstract rules. Note that many of the same concepts appear within both taxonomies, albeit in a different context. For example, vision of space is seen as closely related to object recognition in Fig. 7a, but in Fig. 7b they are thought of as contributing to very different behavioural abilities.

It is proposed here that the taxonomy of Fig. 7b may be better suited to interpret neural activity in many brain regions because it more closely reflects the basic organization of the nervous system. Several aspects of brain anatomy are reflected in Fig. 7b, such as the distinction between tectal and striatal circuits, dorsal and ventral visual streams, and the divergence of parietal processing toward different kinds of actions (Of course, the specification and selection systems are not completely separate: as described above, mechanisms for action selection must influence activity related to specification at many loci of sensorimotor processing throughout the dorsal stream). Furthermore, one may view the relationships between the conceptual classes and subclasses in Fig. 7b as reflecting, at least to some extent, the phylogenetic relationships between them. For example, one can speculate that processes such as “object recognition” evolved as specializations of older mechanisms of decision-making which did not explicitly represent the identity of objects but simply detected particular features, called “sign stimuli” (Tinbergen 1950, Hinde 1966). A classification of concepts which aims to reflect their phylogenetic relationships is important because the conservative nature of neural evolution motivates us to view all brain functions as modifications of ancestral mechanisms. Abilities such as sophisticated cognitive decision-making did not appear from thin air, complete with appropriate anatomical connections and a full developmental schedule. They evolved within an ancestral context of real-time, interactive behaviour. Viewed from this perspective, even the advanced cognitive abilities of higher primates can be understood as serving the fundamental goal of all brain activity – to endow organisms with the ability to interact with their environment in adaptive ways.

ACKNOWLEDGEMENTS

The author wishes to thank Andrea Green and Steve Wise for helpful comments on various versions of this manuscript. This work was supported by the New Emerging Teams grant NET-54000 from the Canadian Institutes of Health Research.

FIGURE LEGENDS

Figure 1: Sketch of the proposed neural substrates 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. Filled dark arrows represent processes of action specification, which begin in the visual cortex and proceed rightward across the parietal lobe, transforming visual information into representations of potential actions. Polygons represent three neural populations along this route: 1) The leftmost represents the encoding of potential visual targets, modulated by attentional selection; 2) The middle represents potential actions encoded in parietal cortex; 3) The rightmost represents activity in premotor regions. Each population is depicted as a map of neural activity, with activity peaks corresponding to the lightest regions. As the action specification occurs across the fronto-parietal cortex, distinct potential actions compete for further processing. This competition is biased by input from the basal ganglia and prefrontal cortical regions which collect information for action selection (double-line arrows). This biasing influences the competition in a number of loci, and because of reciprocal connectivity, these influences are reflected over a large portion of the cerebral cortex. The final selected action is released into execution and causes both overt feedback through the environment (dashed black arrow) and internal predictive feedback through the cerebellum.

Figure 2: Computational model described in Cisek (2006a). **(a)** Each neural layer is depicted by a set of circles representing cells with different preferences for a movement parameter (e.g. direction). Thin arrows represent topographic connections (in most cases reciprocal) between layers involved in action specification. Gray polygons represent the input to and from prefrontal cortex, which is divided into two sub-populations each preferring a different stimulus colour. These projections are also topographic, but with much lower spatial resolution. Visual inputs are

presented to the input layer, and the GO signal gates activity in primary motor cortex. Abbreviations: PPC – posterior parietal cortex; PFC – prefrontal cortex; PMd – dorsal premotor cortex; M1 – primary motor cortex. **(b)** Each population consists of cells with different preferred directions, and their pattern of activity can represent one potential reach direction (top) or several potential directions simultaneously (bottom).

Figure 3: Comparison between neural activity and model simulations in three kinds of tasks. **(a)** Two-target task. During the spatial cue (SC), two possible targets are presented, one red and one blue. During the colour cue (CC), the centre indicates which of these is the correct target. The GO signal instructs the monkey to begin the movement. Neural data (Cisek & Kalaska 2005) is shown from three sets of neurons: rostral PMd, caudal PMd, and primary motor cortex (M1). In each, neural activity is depicted as a 3D coloured surface in which time runs from left to right and cells are sorted by their preferred direction along the left edge. Coloured circles indicate the locations of the two targets. Simulated model activities are depicted in the same format, where black lines indicate behavioural events (spatial cue on, spatial cue off, colour cue on, colour cue off, GO). **(b)** One-target task, same format. **(c)** Matching task, same format.

Figure 4: Simulations of the context-dependent order of neural activation. **(a)** Simulation of the standard two-target task (in which the decision is made on the basis of a color conjunction rule). Black lines show the time course of the average activity of two groups of PMd¹ cells – cells tuned to the selected target (thick line) and cells tuned to the unselected target (thin dotted line). Gray lines show the activity of PPC cells tuned to the selected (thick line) and unselected targets (thin dotted line). Vertical lines indicate the time of SC onset, SC offset, and CC onset. The double circle emphasizes the first activity which reflects the decision made by the network, which appears in PMd prior to PPC. **(b)** Simulation of a task in which instead of a color cue, the decision is made when one of the target stimuli reappears at the time marked as “SC1 on”. In this situation, the decision is reflected first in PPC, before it appears in PMd (note the activity emphasized by the double circle).

Figure 5: Latency effects. **(a)** Simulated reaction time during tasks with one, two, three, or four targets presented for 1.3 seconds, followed by a single correct target for 0.1 seconds, followed by the GO signal. Reaction times were calculated as first time after the GO signal that any neuron in the M1 population exceeded an activity threshold of 1.5. The mean and standard error

are shown for $N=300$ replications in each condition. **(b)** Simulated reaction time when cues are presented for 0.8 seconds followed by a single target for 0.3 seconds prior to the GO. The bars show mean \pm s.e. of reaction time in four conditions: when three cues are presented 80° apart, two cues 160° apart, two cues 80° apart, or no cue at all. $N=100$ in each condition. **(c)** Distributions of decision latency computed during simulations (each with two targets) using a CC cue of different magnitudes. The decision latency was calculated as the time between the CC cue and the first time any PMd³ cell activity exceeded 0.75. $N=200$ for each condition.

Figure 6: Data and simulation of the timed response paradigms of Ghez et al. (1997) and Favilla (1997). **(a)** Behavioural data from the Ghez et al. (1997) task. Each panel shows the distribution of initial directions of force production with respect to two targets (vertical lines). Data is aligned such that the correct target (solid line) is on the right. Different distributions are reported for different delays between target identification and movement onset, and for different angular separations between the targets. **(b)** Simulations of the Ghez et al. (1997) task. Each panel shows the distribution of initial directions, calculated as the preferred direction of the first M1 cell whose activity exceeded a threshold of 1.75. **(c)** Behavioural data from the Favilla (1997) task, in which four targets are shown either all 30° apart or grouped into two pairs that are far apart. Same format as (a). **(d)** Simulations of the Favilla (1997) task, same format as (b).

Figure 7: Two possible conceptual taxonomies of neural processes. **(a)** The taxonomy implied by classical cognitive science, in which brain functions are classified as belonging to perceptual, cognitive, or action systems. **(b)** An alternative taxonomy, in which brain functions are classified as processes aiding either action specification or action selection.

REFERENCES

Literature Cited

- Adams F, Mele A. 1989. The role of intention in intentional action. *Canadian Journal of Philosophy* 19:511-31
- Alexander GE, Crutcher MD. 1990a. Functional architecture of basal ganglia circuits: Neural substrates of parallel processing. *TINS* 13(7):266-71
- Alexander GE, Crutcher MD. 1990b. Neural representations of the target (goal) of visually guided arm movements in three motor areas of the monkey. *J. Neurophysiol.* 64(1):164-78
- Alexander GE, Crutcher MD. 1990c. Preparation for movement: Neural representations of intended direction in three motor areas of the monkey. *J. Neurophysiol.* 64(1):133-50
- Allport DA. 1987. Selection for action: Some behavioral and neurophysiological considerations of attention and action. In *Perspectives on Perception and Action*, ed. H Heuer, AF Sanders, 15:395-419. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Andersen RA. 1995. Encoding of intention and spatial location in the posterior parietal cortex. *Cereb. Cortex* 5:457-69
- Andersen RA, Snyder LH, Bradley DC, Xing J. 1997. Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annual Review of Neuroscience* 20:303-30
- Ashby WR. 1965. *Design for a Brain: The Origin of Adaptive Behaviour*, London: Chapman and Hall.
- Ballard DH, Hayhoe MM, Pelz JB. 1995. Memory representations in natural tasks. *J. Cognitive Neurosci.* 7(1):66-80
- Basso MA, Wurtz RH. 1998. Modulation of neuronal activity in superior colliculus by changes in target probability. *J. Neurosci.* 18(18):7519-34
- Baumann MA, Fluet MC, Scherberger H. 2009. Context-specific grasp movement representation in the macaque anterior intraparietal area. *J Neurosci* 29(20):6436-48
- Bechara A, Damasio H, Tranel D, Anderson SW. 1998. Dissociation of working memory from decision making within the human prefrontal cortex. *J. Neurosci.* 18(1):428-37
- Beer RD. 2000. Dynamical approaches to cognitive science. *Trends. Cogn. Sci.* 4(3):91-9
- Bergson H. 1896. *Matter and Memory*, New York: Macmillan.
- Bisley JW, Goldberg ME. 2003. Neuronal activity in the lateral intraparietal area and spatial attention. *Science* 299(5603):81-6
- Bock O, Eversheim U. 2000. The mechanisms of movement preparation: a precuing study. *Behav. Brain Res.* 108(1):85-90
- Bogacz R, Brown E, Moehlis J, Holmes P, Cohen JD. 2006. The physics of optimal decision making: a formal analysis of models of performance in two-alternative forced-choice tasks. *Psychol. Rev.* 113(4):700-65
- Boynton GM. 2005. Attention and visual perception. *Curr. Opin. Neurobiol.* 15(4):465-9
- Brooks R. 1991. Intelligence without representation. *Artificial Intelligence* 47:139-59
- Brown JW, Bullock D, Grossberg S. 2004. How laminar frontal cortex and basal ganglia circuits interact to control planned and reactive saccades. *Neural Networks* 17(4):471-510

- Bullock D, Cisek P, Grossberg S. 1998. Cortical networks for control of voluntary arm movements under variable force conditions. *Cereb. Cortex* 8:48-62
- Bullock D, Grossberg S. 1988. Neural dynamics of planned arm movements: Emergent invariants and speed-accuracy properties during trajectory formation. *Psychological Review* 95(1):49-90
- Buneo CA, Jarvis MR, Batista AP, Andersen RA. 2002. Direct visuomotor transformations for reaching. *Nature* 416(6881):632-6
- Buschman TJ, Miller EK. 2007. Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science* 315(5820):1860-2
- Butler AB, Hodos W. 2005. *Comparative vertebrate neuroanatomy : evolution and adaptation*, New York: Wiley-Liss.
- Carpenter RH, Williams ML. 1995. Neural computation of log likelihood in control of saccadic eye movements. *Nature* 377(6544):59-62
- Cisek P. 2005. Neural representations of motor plans, desired trajectories, and controlled objects. *Cognitive Processing* 6:15-24
- Cisek P. 2006a. Integrated neural processes for defining potential actions and deciding between them: A computational model. *J. Neurosci.* 26(38):9761-70
- Cisek P. 1999. Beyond the computer metaphor: Behaviour as interaction. *Journal of Consciousness Studies* 6(11-12):125-42
- Cisek P. 2006b. Integrated neural processes for decision-making and movement planning: A computational model. Work. Pap..
- Cisek P. 2001. Embodiment is all in the head. *Behav. Brain Sci.* 24(1):36-8
- Cisek P, Grossberg S, Bullock D. 1998. A cortico-spinal model of reaching and proprioception under multiple task constraints. *J. Cognitive Neurosci.* 10(4):425-44
- Cisek P, Kalaska JF. 2005. Neural correlates of reaching decisions in dorsal premotor cortex: Specification of multiple direction choices and final selection of action. *Neuron* 45(5):801-14
- Cisek P, Michaud N, Kalaska JF. 2004. Integration of motor planning and sensory feedback in area 5. *Society for Neuroscience Abstracts* 30
- Cisek P, Turgeon M. 1999. 'Binding through the fovea', a tale of perception in the service of action. *Psyche* 5(34)
- Clark A. 1997. *Being There: Putting Brain, Body, and World Together Again*, Cambridge, MA: MIT Press.
- Coe B, Tomihara K, Matsuzawa M, Hikosaka O. 2002. Visual and anticipatory bias in three cortical eye fields of the monkey during an adaptive decision-making task. *J. Neurosci.* 22(12):5081-90
- Colby CL, Goldberg ME. 1999. Space and attention in parietal cortex. *Annual Review of Neuroscience* 22:319-49
- Constantinidis C, Franowicz MN, Goldman-Rakic PS. 2001. The sensory nature of mnemonic representation in the primate prefrontal cortex. *Nat. Neurosci.* 4(3):311-6
- Constantinidis C, Steinmetz MA. 2001. Neuronal responses in area 7a to multiple-stimulus displays: I. neurons encode the location of the salient stimulus. *Cereb. Cortex.* 11(7):581-91
- Crammond DJ, Kalaska JF. 2000. Prior information in motor and premotor cortex: activity during the delay period and effect on pre-movement activity. *J. Neurophysiol.* 84(2):986-1005

- Cui H, Andersen RA. 2007. Posterior parietal cortex encodes autonomously selected motor plans. *Neuron* 56(3):552-9
- Culham JC, Kanwisher NG. 2001. Neuroimaging of cognitive functions in human parietal cortex. *Curr. Opin. Neurobiol.* 11(2):157-63
- Day BL, Lyon IN. 2000. Voluntary modification of automatic arm movements evoked by motion of a visual target. *Exp. Brain Res.* 130(2):159-68
- Dayan P, Abbott LF. 2001. *Theoretical Neuroscience*, Cambridge, MA: MIT Press.
- Deacon TW. 1990. Rethinking mammalian brain evolution. *American Zoologist* 30:629-705
- Desimone R. 1998. Visual attention mediated by biased competition in extrastriate visual cortex. *Philos. Trans. R. Soc. Lond B Biol. Sci.* 353(1373):1245-55
- Desimone R, Albright TD, Gross CG, Bruce C. 1984. Stimulus-selective properties of inferior temporal neurons in the macaque. *J. Neurosci.* 4(8):2051-62
- Desimone R, Duncan J. 1995. Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* 18:193-222
- Desmurget M, Epstein CM, Turner RS, Prablanc C, Alexander GE, Grafton ST. 1999. Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nat. Neurosci.* 2(6):563-7
- Dewey J. 1896. The reflex arc concept in psychology. *Psychological Review* 3(4):357-70
- di Pellegrino G, Wise SP. 1991. A neurophysiological comparison of three distinct regions of the primate frontal lobe. *Brain* 114:951-78
- Dorris MC, Glimcher PW. 2004. Activity in posterior parietal cortex is correlated with the relative subjective desirability of action. *Neuron* 44(2):365-78
- Dretske F. 1981. *Knowledge and the Flow of Information*, Oxford: Blackwell.
- Erlhagen W, Schöner G. 2002. Dynamic field theory of movement preparation. *Psychol. Rev.* 109(3):545-72
- Eskandar EN, Richmond BJ, Optican LM. 1992. Role of inferior temporal neurons in visual memory. I. Temporal encoding of information about visual images, recalled images, and behavioral context. *J. Neurophysiol.* 68(4):1277-95
- Ewert J-P. 1997. Neural correlates of key stimulus and releasing mechanism: a case study and two concepts. *TINS* 20(8):332-9
- Ewert J-P, Buxbaum-Conradi H, Dreisvogt F, Glasgow M, Merkel-Harff C et al. 2001. Neural modulation of visuomotor functions underlying prey-catching behaviour in anurans: perception, attention, motor performance, learning. *Comparative Biochemistry and Physiology Part A* 128(3):417-60
- Fadiga L, Fogassi L, Gallese V, Rizzolatti G. 2000. Visuomotor neurons: ambiguity of the discharge or 'motor' perception? *International Journal of Psychophysiology* 35(2-3):165-77
- Fagg AH, Arbib MA. 1998. Modeling parietal-premotor interactions in primate control of grasping. *Neural Netw.* 11(7-8):1277-303
- Favilla M. 1997. Reaching movements: concurrency of continuous and discrete programming. *Neuroreport* 8(18):3973-7
- Ferraina S, Bianchi L. 1994. Posterior parietal cortex: functional properties of neurons in area 5 during an instructed-delay reaching task within different parts of space. *Exp. Brain Res.* 99(1):175-8
- Frank MJ, Scheres A, Sherman SJ. this volume. Understanding decision-making deficits in neurological conditions: insights from models of natural action selection. *This Volume*.

- Fuster JM, Alexander GE. 1971. Neuron activity related to short-term memory. *Science* 173(997):652-4
- Fuster JM, Bodner M, Kroger JK. 2000. Cross-modal and cross-temporal association in neurons of frontal cortex. *Nature* 405(6784):347-51
- Gallese V. 2000. The inner sense of action: Agency and motor representations. *Journal of Consciousness Studies* 7(10):23-40
- Ghez C, Favilla M, Ghilardi MF, Gordon J, Bermejo R, Pullman S. 1997. Discrete and continuous planning of hand movements and isometric force trajectories. *Exp. Brain Res.* 115(2):217-33
- Gibson JJ. 1979. *The ecological approach to visual perception*, Boston: Houghton Mifflin.
- Gilbert SF, Opitz JM, Raff RA. 1996. Resynthesizing evolutionary and developmental biology. *Dev. Biol.* 173(2):357-72
- Glenberg AM. 1997. What memory is for. *Behav. Brain Sci.* 20(1):1-55
- Glimcher PW. 2003. The neurobiology of visual-saccadic decision making. *Annu. Rev. Neurosci.* 26:133-79
- Glimcher PW. 2001. Making choices: The neurophysiology of visual-saccadic decision making. *TINS* 24(11):654-9
- Gold JI, Shadlen MN. 2001. Neural computations that underlie decisions about sensory stimuli. *Trends Cogn. Sci.* 5(1):10-6
- Gold JI, Shadlen MN. 2000. Representation of a perceptual decision in developing oculomotor commands. *Nature* 404(6776):390-4
- Goodale MA, Milner AD. 1992. Separate visual pathways for perception and action. *TINS* 15(1):20-5
- Gottlieb JP, Kusunoki M, Goldberg ME. 1998. The representation of visual salience in monkey parietal cortex. *Nature* 391(6666):481-4
- Graziano MSA, Cooke DF, Taylor CSR. 2000. Coding the location of the arm by sight. *Science* 290(5497):1782-6
- Grossberg S. 1973. Contour enhancement, short term memory, and constancies in reverberating neural networks. *Studies in Applied Mathematics* 52:213-57
- Hazy TE, Frank MJ, O'Reilly RC. this volume. Towards an executive without a homunculus: computational models of the prefrontal cortex/basal ganglia system. *This Volume*.
- Hendriks-Jansen H. 1996. *Catching Ourselves in the Act: Situated Activity, Interactive Emergence, Evolution, and Human Thought*, Cambridge, MA: MIT Press.
- Hinde RA. 1966. *Animal Behaviour: A Synthesis of Ethology and Comparative Psychology*, New York: McGraw-Hill Book Company.
- Holland LZ, Holland ND. 1999. Chordate origins of the vertebrate central nervous system. *Curr. Opin. Neurobiol.* 9(5):596-602
- Hommel B, Müsseler J, Aschersleben G, Prinz W. 2001. The Theory of Event Coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences* 24(5):849-937
- Horwitz GD, Batista AP, Newsome WT. 2004. Representation of an abstract perceptual decision in macaque superior colliculus. *J. Neurophysiol.* 91(5):2281-96
- Hoshi E, Shima K, Tanji J. 2000. Neuronal activity in the primate prefrontal cortex in the process of motor selection based on two behavioral rules. *J. Neurophysiol.* 83(4):2355-73
- Hoshi E, Shima K, Tanji J. 1998. Task-dependent selectivity of movement-related neuronal activity in the primate prefrontal cortex. *J. Neurophysiol.* 80(6):3392-7

- Houk JC, Bastianen C, Fansler D, Fishbach A, Fraser D et al. this volume. Action selection and refinement in subcortical loops through basal ganglia and cerebellum. *This volume*.
- Houk JC, Keifer J, Barto AG. 1993. Distributed motor commands in the limb premotor network. *TINS* 16(1):27-33
- Jackson JH. 1884. Evolution and dissolution of the nervous system. In *Selected writings of John Hughlings Jackson*, ed. J Taylor,45-75. London: Staples Press, 1958.
- Janssen P, Shadlen MN. 2005. A representation of the hazard rate of elapsed time in macaque area LIP. *Nat. Neurosci.* 8(2):234-41
- Johnson PB, Ferraina S, Bianchi L, Caminiti R. 1996. Cortical networks for visual reaching: Physiological and anatomical organization of frontal and parietal arm regions. *Cereb. Cortex* 6(2):102-19
- Johnson-Laird PN. 1988. *The Computer and the Mind: An Introduction to Cognitive Science*, Cambridge, Massachusetts: Harvard University Press.
- Jones EG, Coulter JD, Hendry HC. 1978. Intracortical connectivity of architectonic fields in the somatic sensory, motor and parietal cortex of monkeys. *Journal of Comparative Neurology* 181:291-348
- Kalaska JF, Crammond DJ. 1995. Deciding not to GO: Neuronal correlates of response selection in a GO/NOGO task in primate premotor and parietal cortex. *Cereb. Cortex* 5:410-28
- Kalaska JF, Sergio LE, Cisek P. 1998. Cortical control of whole-arm motor tasks. In *Sensory Guidance of Movement, Novartis Foundation Symposium #218*, ed. M Glickstein,176-201. Chichester, UK: John Wiley & Sons.
- Kalivas PW, Nakamura M. 1999. Neural systems for behavioral activation and reward. *Curr. Opin. Neurobiol.* 9(2):223-7
- Karten HJ. 1969. The organization of the avian telencephalon and some speculations on the phylogeny of the amniote telencephalon. *Annals of the New York Academy of Sciences* 167(1):164-79
- Katz PS, Harris-Warrick RM. 1999. The evolution of neuronal circuits underlying species-specific behavior. *Curr. Opin. Neurobiol.* 9(5):628-33
- Keele SW. 1968. Movement control in skilled motor performance. *Psychological Bulletin* 70:387-403
- Kettner RE, Marcario JK, Port NL. 1993. A neural network model of cortical activity during reaching. *J. Cognitive Neurosci.* 5(1):14-33
- Kim J-N, Shadlen MN. 1999. Neural correlates of a decision in the dorsolateral prefrontal cortex of the macaque. *Nat. Neurosci.* 2(2):176-85
- Knill DC, Pouget A. 2004. The Bayesian brain: the role of uncertainty in neural coding and computation. *Trends Neurosci.* 27(12):712-9
- Kornblum S, Hasbroucq T, Osman A. 1990. Dimensional overlap: Cognitive basis for stimulus-response compatibility - a model and taxonomy. *Psychological Review* 97(2):253-70
- Krubitzer L, Kaas J. 2005. The evolution of the neocortex in mammals: how is phenotypic diversity generated? *Curr. Opin. Neurobiol.* 15(4):444-53
- Kusunoki M, Gottlieb J, Goldberg ME. 2000. The lateral intraparietal area as a salience map: the representation of abrupt onset, stimulus motion, and task relevance. *Vision Res.* 40(10-12):1459-68
- Lauwereyns J, Watanabe K, Coe B, Hikosaka O. 2002. A neural correlate of response bias in monkey caudate nucleus. *Nature* 418(6896):413-7

- Leblois A, Boraud T, Meissner W, Bergman H, Hansel D. 2006. Competition between feedback loops underlies normal and pathological dynamics in the basal ganglia. *J Neurosci* 26(13):3567-83
- Ledberg A, Bressler SL, Ding M, Coppola R, Nakamura R. 2007. Large-scale visuomotor integration in the cerebral cortex. *Cereb. Cortex* 17(1):44-62
- Machens CK, Romo R, Brody CD. 2005. Flexible control of mutual inhibition: a neural model of two-interval discrimination. *Science* 307(5712):1121-4
- MacLean PD. 1973. *A triune concept of the brain and behaviour*, Toronto: University of Toronto Press.
- Marconi B, Genovesio A, Battaglia-Mayer A, Ferraina S, Squatrito S et al. 2001. Eye-hand coordination during reaching. I. Anatomical relationships between parietal and frontal cortex. *Cereb. Cortex*. 11(6):513-27
- Marr DC. 1982. *Vision*, San Francisco: W. H. Freeman.
- Matelli M, Luppino G. 2001. Parietofrontal circuits for action and space perception in the macaque monkey. *Neuroimage*. 14(1 Pt 2):S27-S32
- Maturana HR, Varela FJ. 1980. *Autopoiesis and cognition: the realization of the living*, Boston: D. Reidel.
- Mazurek ME, Roitman JD, Ditterich J, Shadlen MN. 2003. A role for neural integrators in perceptual decision making. *Cereb. Cortex* 13(11):1257-69
- McIntyre J, Bizzi E. 1993. Servo hypotheses for the biological control of movement. *Journal of Motor Behavior* 25(3):193-202
- Mead GH. 1938. *The Philosophy of the Act*, Chicago: The University of Chicago Press.
- Medina L, Reiner A. 2000. Do birds possess homologues of mammalian primary visual, somatosensory and motor cortices? *TINS* 23(1):1-12
- Merleau-Ponty M. 1945. *Phénoménologie de la perception*, Paris: Gallimard.
- Middleton FA, Strick PL. 2000. Basal ganglia and cerebellar loops: motor and cognitive circuits. *Brain Research Reviews* 31(2-3):236-50
- Miller EK. 2000. The prefrontal cortex and cognitive control. *Nature Reviews Neuroscience* 1(1):59-65
- Miller GA, Galanter E, Pribram KH. 1960. *Plans and the Structure of Behavior*, New York: Holt, Rinehart and Winston, Inc.
- Millikan RG. 1989. Biosemantics. *J. Philosophy* 86(6):281-97
- Mink JW. 1996. The basal ganglia: focused selection and inhibition of competing motor programs. *Prog Neurobiol* 50(4):381-425
- Nakamura H, Kuroda T, Wakita M, Kusunoki M, Kato A et al. 2001. From three-dimensional space vision to prehensile hand movements: the lateral intraparietal area links the area V3A and the anterior intraparietal area in macaques. *J. Neurosci.* 21(20):8174-87
- Neumann O. 1990. Visual attention and action. In *Relationships Between Perception and Action: Current Approaches*, ed. O Neumann, W Prinz, 227-267. Berlin: Springer-Verlag.
- Newell A, Simon HA. 1972. *Human Problem Solving*, Englewood Cliffs, NJ: Prentice-Hall.
- Núñez R, Freeman WJ. 2000. *Reclaiming Cognition: The Primacy of Action, Intention and Emotion*, Thorverton: Imprint Academic.
- O'Regan JK, Noë A. 2001. A sensorimotor account of vision and visual consciousness. *Behav. Brain Sci.* 24(5):939-1011
- Pandya DN, Kuypers HGJM. 1969. Cortico-cortical connections in the rhesus monkey. *Brain Research* 13:13-36

- Paradiso MA. 2002. Perceptual and neuronal correspondence in primary visual cortex. *Curr. Opin. Neurobiol.* 12(2):155-61
- Paré M, Wurtz RH. 2001. Progression in neuronal processing for saccadic eye movements from parietal cortex area lip to superior colliculus. *J. Neurophysiol.* 85(6):2545-62
- Passingham RE, Toni I. 2001. Contrasting the dorsal and ventral visual systems: guidance of movement versus decision making. *Neuroimage.* 14(1 Pt 2):S125-S131
- Pesaran B, Nelson MJ, Andersen RA. 2008. Free choice activates a decision circuit between frontal and parietal cortex. *Nature* 453(7193):406-9
- Petrides M. 2000. The role of the mid-dorsolateral prefrontal cortex in working memory. *Exp. Brain Res.* 133(1):44-54
- Piaget J. 1967. *Biologie et Connaissance: Essai sur les Relations Entre les Régulation Organiques et les Processus Cognitifs*, Paris: Editions Gallimard.
- Platt ML. 2002. Neural correlates of decisions. *Curr. Opin. Neurobiol.* 12(2):141-8
- Platt ML, Glimcher PW. 1997. Responses of intraparietal neurons to saccadic targets and visual distractors. *J. Neurophysiol.* 78(3):1574-89
- Platt ML, Glimcher PW. 1999. Neural correlates of decision variables in parietal cortex. *Nature* 400(6741):233-8
- Powers WT. 1973. *Behavior: The Control of Perception*, New York: Aldine Publishing Company.
- Prescott TJ, Redgrave P, Gurney K. 1999. Layered control architectures in robots and vertebrates. *Adaptive Behavior* 7:99-127
- Quintana J, Fuster JM. 1999. From perceptions to actions: Temporal integrative functions of prefrontal and parietal neurons. *Cereb. Cortex* 9(3):213-21
- Rainer G, Asaad WF, Miller EK. 1998. Selective representation of relevant information by neurons in the primate prefrontal cortex. *Nature* 363(6885):577-9
- Ratcliff R, Cherian A, Segraves M. 2003. A comparison of macaque behavior and superior colliculus neuronal activity to predictions from models of two-choice decisions. *J. Neurophysiol.* 90(3):1392-407
- Reddi BAJ, Asrress KN, Carpenter RHS. 2003. Accuracy, information, and response time in a saccadic decision task. *J. Neurophysiol.* 90(5):3538-46
- Redgrave P, Prescott TJ, Gurney K. 1999. The basal ganglia: a vertebrate solution to the selection problem? *Neuroscience* 89(4):1009-23
- Rizzolatti G, Luppino G. 2001. The cortical motor system. *Neuron* 31(6):889-901
- Roe RM, Busemeyer JR, Townsend JT. 2001. Multialternative decision field theory: a dynamic connectionist model of decision making. *Psychol. Rev.* 108(2):370-92
- Roesch MR, Olson CR. 2004. Neuronal activity related to reward value and motivation in primate frontal cortex. *Science* 304(5668):307-10
- Romo R, Hernandez A, Zainos A. 2004. Neuronal correlates of a perceptual decision in ventral premotor cortex. *Neuron* 41(1):165-73
- Rowe JB, Toni I, Josephs O, Frackowiak RS, Passingham RE. 2000. The prefrontal cortex: response selection or maintenance within working memory? *Science* 288(5471):1656-60
- Saleem KS, Suzuki W, Tanaka K, Hashikawa T. 2000. Connections between anterior inferotemporal cortex and superior temporal sulcus regions in the macaque monkey. *J. Neurosci.* 20(13):5083-101
- Sanger TD. 2003. Neural population codes. *Curr. Opin. Neurobiol.* 13(2):238-49
- Sato TR, Schall JD. 2003. Effects of stimulus-response compatibility on neural selection in frontal eye field. *Neuron* 38(4):637-48

- Scherberger H, Andersen RA. 2007. Target selection signals for arm reaching in the posterior parietal cortex. *J. Neurosci.* 27(8):2001-12
- Schmolecky MT, Wang Y, Hanes DP, Thompson KG, Leutgeb S et al. 1998. Signal timing across the macaque visual system. *J. Neurophysiol.* 79(6):3272-8
- Schultz W, Tremblay L, Hollerman JR. 2000. Reward processing in primate orbitofrontal cortex and basal ganglia. *Cereb. Cortex.* 10(3):272-84
- Seth AK. this volume. The ecology of action selection: insights from artificial life. *Philos. Trans. R. Soc. Lond B Biol. Sci.* 362(1485):1545-58
- Shadlen MN, Newsome WT. 2001. Neural basis of a perceptual decision in the parietal cortex (area lip) of the rhesus monkey. *J. Neurophysiol.* 86(4):1916-36
- Shafir E, Tversky A. 1995. Decision making. In *Thinking: An Invitation to Cognitive Science*, ed. EE Smith, DN Osherson, 3:77-100. Cambridge, MA: MIT Press.
- Shu DG, Morris SC, Han J, Zhang ZF, Yasui K et al. 2003. Head and backbone of the Early Cambrian vertebrate Haikouichthys. *Nature* 421(6922):526-9
- Smith PL, Ratcliff R. 2004. Psychology and neurobiology of simple decisions. *Trends Neurosci.* 27(3):161-8
- Snyder LH, Batista AP, Andersen RA. 1998a. Change in motor plan, without a change in the spatial locus of attention, modulates activity in posterior parietal cortex. *J. Neurophysiol.* 79(5):2814-9
- Snyder LH, Batista AP, Andersen RA. 2000a. Intention-related activity in the posterior parietal cortex: a review. *Vision Res.* 40(10-12):1433-41
- Snyder LH, Batista AP, Andersen RA. 2000b. Saccade-related activity in the parietal reach region. *J. Neurophysiol.* 83(2):1099-102
- Snyder LH, Batista AP, Andersen RA. 1997. Coding of intention in the posterior parietal cortex. *Nature* 386:167-70
- Snyder LH, Grieve KL, Brotchie P, Andersen RA. 1998b. Separate body- and world-referenced representations of visual space in parietal cortex. *Nature* 394(6696):887-91
- Stafford, T. and Gurney K. N., this volume.
- Stein JF. 1992. The representation of egocentric space in the posterior parietal cortex. *Behav. Brain Sci.* 15:691-700
- Sterelny K. 1989. Computational functional psychology: Problems and prospects. In *Computers, Brains, and Minds*, ed. P Slezak, WR Albury, 71-93. Dordrecht: Kluwer Academic Publishers.
- Sugrue LP, Corrado GS, Newsome WT. 2004. Matching behavior and the representation of value in the parietal cortex. *Science* 304(5678):1782-7
- Takikawa Y, Kawagoe R, Hikosaka O. 2002. Reward-dependent spatial selectivity of anticipatory activity in monkey caudate neurons. *J. Neurophysiol.* 87(1):508-15
- Tanaka K, Saito H-A, Fukada Y, Moriya M. 1991. Coding visual images of objects in the inferotemporal cortex of the macaque monkey. *J. Neurophysiol.* 66(1):170-89
- Tanji J, Hoshi E. 2001. Behavioral planning in the prefrontal cortex. *Curr. Opin. Neurobiol.* 11(2):164-70
- Thelen E, Schöner G, Scheier C, Smith LB. 2001. The dynamics of embodiment: a field theory of infant perseverative reaching. *Behav. Brain Sci.* 24(1):1-34
- Thomas NW, Pare M. 2007. Temporal processing of saccade targets in parietal cortex area LIP during visual search. *J. Neurophysiol.* 97(1):942-7

- Thompson KG, Hanes DP, Bichot NP, Schall JD. 1996. Perceptual and motor processing stages identified in the activity of macaque frontal eye field neurons during visual search. *J. Neurophysiol.* 76(6):4040-55
- Tinbergen N. 1950. The hierarchical organisation of nervous mechanisms underlying instinctive behavior. *Symposium for the society of experimental biology* 4:305-12
- Tipper SP, Howard LA, Houghton G. 1998. Action-based mechanisms of attention. *Phil. Trans. R. Soc. Lond. B* 353(1373):1385-93
- Tipper SP, Howard LA, Houghton G. 2000. Behavioural consequences of selection from neural population codes. In *Control of Cognitive Processes: Attention and Performance XVIII*, ed. S Monsell, J Driver, 223-245. Cambridge, MA: MIT Press.
- Tipper SP, Lortie C, Baylis GC. 1992. Selective reaching: Evidence for action-centered attention. *Journal of Experimental Psychology: Human Perception and Performance* 18(4):891-905
- Toates F. 1998. The interaction of cognitive and stimulus-response processes in the control of behaviour. *Neuroscience and Biobehavioral Reviews* 22(1):59-83
- Treue S. 2001. Neural correlates of attention in primate visual cortex. *Trends Neurosci.* 24(5):295-300
- Ungerleider LG, Mishkin M. 1982. Two cortical visual systems. In *Analysis of Visual Behavior*, ed. DJ Ingle, MA Goodale, RJW Mansfield, 18:549-586. Cambridge, MA: MIT Press.
- Usher M, McClelland JL. 2001. The time course of perceptual choice: the leaky, competing accumulator model. *Psychol. Rev.* 108(3):550-92
- von der Malsburg C. 1996. The binding problem of neural networks. In *The Mind-Brain Continuum: Sensory Processes*, ed. R Llinás, PS Churchland, 7:131-146. Cambridge, MA: MIT Press.
- Wallis JD, Miller EK. 2003. From rule to response: neuronal processes in the premotor and prefrontal cortex. *J. Neurophysiol.* 90(3):1790-806
- Wang XJ. 2002. Probabilistic decision making by slow reverberation in cortical circuits. *Neuron* 36(5):955-68
- White IM, Wise SP. 1999. Rule-dependent neuronal activity in the prefrontal cortex. *Exp. Brain Res.* 126(3):315-35
- Wise SP, Boussaoud D, Johnson PB, Caminiti R. 1997. Premotor and parietal cortex: corticocortical connectivity and combinatorial computations. *Annu. Rev. Neurosci.* 20:25-42
- Yang T, Shadlen MN. 2007. Probabilistic reasoning by neurons. *Nature* 447(7148):1075-80