Computational Models of Cognitive and Motor Control

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Abstract

Most of the earliest work in both experimental and theoretical/computational systems neuroscience focused on sensory systems and the peripheral (spinal) control of movement. However, over the last three decades, attention has turned increasingly towards "higher" functions related to cognition, decision-making and voluntary behavior. Experimental studies have shown that specific brain structures – the prefrontal cortex, the premotor and motor cortices, and the basal ganglia – play a central role in these functions, as does the dopamine system that signals reward during reinforcement learning. Because of the complexity of the issues involved and the difficulty of direct observation in deep brain structures, computational modeling has been crucial in elucidating the neural basis of cognitive control, decision making, reinforcement learning, working memory and motor control. The resulting computational models are also very useful in engineering domains such as robotics, intelligents agents and adaptive control. While it is impossible to encompass the totality of such modeling work, this chapter provides an overview of significant efforts in the last 20 years. It also outlines many of the theoretical issues underlying this work, and discusses significant experimental results that motivated the computational models.

1. Introduction

Mental function is usually divided into three parts: Perception, cognition, and action – the so-called *sense-think-act cycle*. Though this view is no longer held dogmatically, it is useful as a structuring framework for discussing mental processes. Several decades of theory and experiment have elucidated an intricate, multi-connected functional architecture for the brain (Fuster, 2006, 2008) – a simplified version of which is shown in Figure 1. While all regions and functions shown – and many not shown – are important, this figure provides a summary of the main brain regions involved in perception, cognition and action. The highlighted blocks in Figure 1 are discussed in this chapter, which focuses mainly on the higher-level mechanisms for the control of behavior.

The control of action (or behavior) is, in a real sense, the primary function of the nervous system. While such actions may be voluntary or involuntary, most of the interest in modeling has understandably focused on voluntary action. This chapter will follow this precedent.

It is conventional to divide the neural substrates of behavior into "higher" and "lower" levels. The latter involves the musculoskeletal apparatus of action (muscles, joints, etc.) and the neural networks of the spinal cord and brainstem. These systems are seen as representing the actuation

component of the action system, which is controlled by the higher-level system comprising cortical and sub-cortical structures. This division between a controller (the brain) and the plant (the body and spinal networks), which parallels the models used in robotics, has been criticized as arbitrary and unhelpful (Turvey, 1990; Sternad and Turvey, 1996), and there has recently been a shift of interest towards more embodied views of cognition (Pfeifer et al., 2007; Chemero, 2011). However, the conventional division is useful for organizing material covered in this Chapter, which focuses primarily on the higher-level systems, i.e., those above the spinal cord and the brainstem.
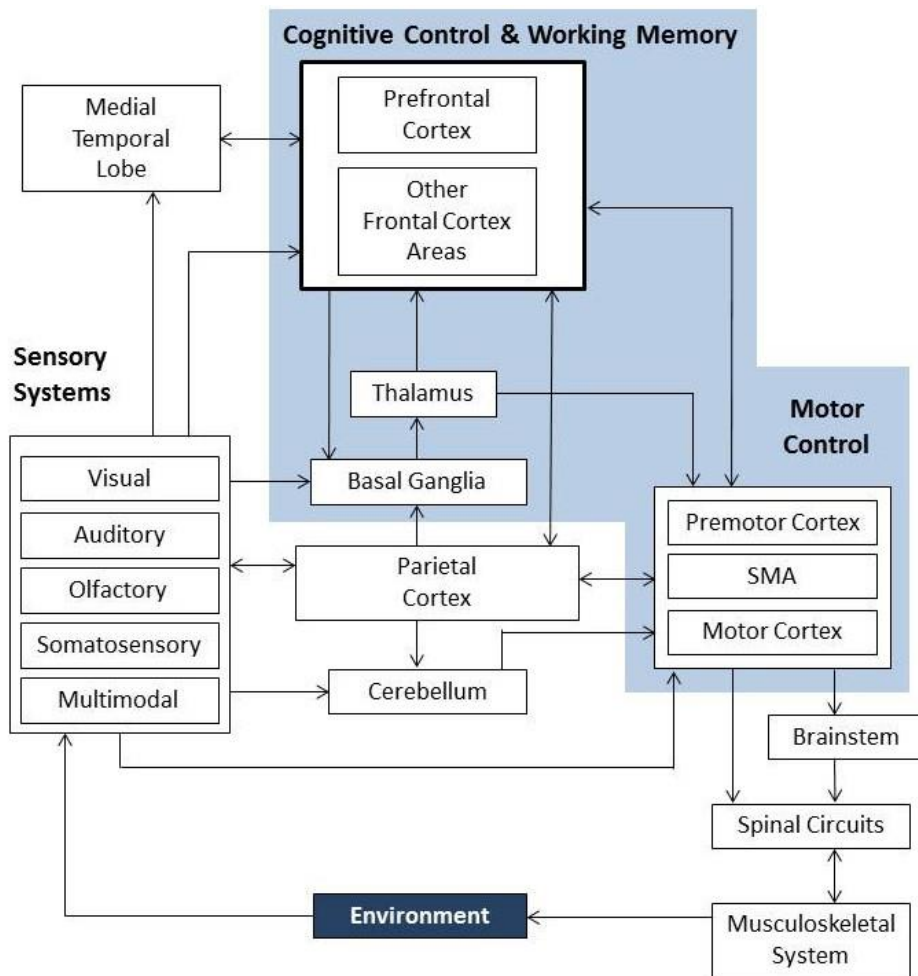

Figure 1: A general schematic of primary signal flow in the nervous system. Many modulatory regions and connections, as well as several known connections, are not shown. The shaded areas indicate the components covered in this Chapter.

The higher-level system can be divided further into a *cognitive control* component involving action selection, configuration of complex actions, and the learning of appropriate behaviors through experience, and a *motor control* component that generates the control signals for the

lower-level system to execute the selected action . The latter is usually identified with the motor cortex (M1), premotor cortex (PMC) and the supplementary motor area (SMA), while the former is seen as involving the prefrontal cortex (PFC), basal ganglia (BG), the anterior cingulate cortex (ACC) and other cortical and subcortical regions (Houk and Wise, 2005). With regard to the generation of actions *per se*, an influential viewpoint for the higher-level system is summarized by Doya (1999). It proposes that higher-level control of action has three major loci: The cortex, the cerebellum, and the basal ganglia. Of these, the cortex – primarily the motor cortex – provides a self-organized repertoire of possible actions that, when triggered, generate movement by activating muscles via spinal networks, the cerebellum implements fine motor control configured through error-based supervised learning (Kawato and Gomi, 1992), and the basal ganglia provide the mechanisms for selecting among actions and learning appropriate ones through reinforcement learning (Graybiel, 1995, 1997, 2005; Humphries et al., 2006). The motor cortex and cerebellum can be seen primarily as motor control (though see Houk, 2005) whereas the basal ganglia falls into the domain of cognitive control and working memory. The PFC is usually regarded as the locus for higher-order choice representations, plans, goals, etc. (Hoshi et al., 2000; Miller and Cohen, 2001; Rougier et al, 2005; Tanji and Hoshi, 2008), while the ACC is thought be involved in conflict monitoring (Botvinick et al., 2004; Brown and Braver, 2005; Botvinick, 2008).

2. Motor Control

Given its experimental accessibility and direct relevance to robotics, motor control has been a primary area of interest for computational modeling (Marr, 1969; Albus, 1975; Dickinson et al, 2008). Mathematical, albeit non-neural, theories of motor control were developed initially within the framework of dynamical systems. One of these directions led to models of action as an emergent phenomenon (Haken et al., 1985; Saltzman and Kelso, 1987; Kugler and Turvey, 1987; Turvey, 1990; Schöner, 1990; Kelso, 1995; Morasso et al., 1997; Scholz and Schöner, 1999; Riley and Turvey, 2002; Riley et al., 2011a) arising from interactions among preferred coordination modes (Goldfield, 1995). This approach has continued to yield insights (Kelso, 1995) and has been extended to multi-actor situations as well (Kelso et al., 2009; Riley et al., 2011b; Ramenzoni et al., 2012). Another approach within the same framework is the *equilibrium point hypothesis* (Feldman and Levin, 2009; Latash, 2010), which explains motor control through the change in the equilibrium points of the musculoskeletal system in response to neural commands. Both these dynamical approaches have paid relatively less attention to the neural basis of motor control and focused more on the phenomenology of action in its context. Nevertheless, insights from these models are fundamental to the emerging synthesis of action as an embodied cognitive function (Pfeifer et al., 2007; Chemero, 2011).

A closely related investigative tradition has developed from the early studies of gaits and other rhythmic movements in cats, fish and other animals (Sherrington, 1906, 1910a,b; Grillner et al., 1995; Whelan, 1996; Grillner, 2003), leading to computational models for *central pattern generators* (CPGs), which are neural networks that generate characteristic periodic activity patterns autonomously or in response to control signals (Grillner, 2006). It has been found that rhythmic movements can be explained well in terms of CPGs – located mainly in the spinal cord – acting upon the coordination modes inherent in the musculoskeletal system. The key insight to

emerge from this work is that a wide range of useful movements can be generated by modulation of these CPGs by rather simple motor control signals from the brain, and feedback from sensory receptors can shape these movements further (Grillner et al., 1995). This idea was demonstrated in recent work by Ijspeert et al. (2007)m showing how the same simple CPG network could produce both swimming and walking movements in a robotic salamander model using a simple scalar control signal.

While rhythmic movements are obviously important, computational models of motor control are often motivated by the desire to build humanoid or biomorphic robots, and thus need to address a broader range of actions – especially aperiodic and/or voluntary movements. Most experimental work on apreiodic movement has focused on the paradigm of manual reaching (Georgopoulos et al., 1982, 1983, 1984, 1988, 1992; Ashe and Georgopoulos, 1994; Schwartz et al., 1988; Bullock and Grossberg, 1988; Bullock et al., 1993, 1998; Scott and Kalaska, 1995, 1997; Morasso et al., 1997; Moran and Schwartz, 1999a; Shadmehr and Wise, 2005; d'Avella et al., 2006, 2008; Muceli et al., 2010). However, seminal work has also been done with complex reflexes in frogs and cats (Mussa-Ivaldi and Giszter, 1992; Giszter et al., 1993; Tresch et al., 1999; Kargo and Giszter, 2000; d'Avella et al., 2003; d'Avella and Bizzi, 2005; Ting and Macpherson, 2005; Torres-Oveido et al., 2006), isometric tasks (Sergio and Kalaska, 2003; Ajemian et al., 2008), ball-catching (Cesqui et al., 2012), drawing and writing (Morasso and Mussia-Ivaldi, 1982; Schwartz, 1992, 1993, 1994; Moran and Schwartz, 1999; Paine et al., 2004) and postural control (Ting and MacPherson, 2005; Torres-Oveido et al, 2006, 2008; Torres-Oveido and Ting, 2007; Ting and McKay, 2007).

A central issue in understanding motor control is the *degrees of freedom problem* (Bernstein, 1967), which arises from the immense redundancy of the system – especially in the context of multi-joint control. For any desired movement – such as reaching for an object – there are an infinite number of control signal combinations from the brain to the muscles that will accomplish the task (see Neilson and Neilson (2010) for an excellent discussion). From a control viewpoint, this has usually been seen as a problem because it precludes the clear specification of an objective function for the controller. To the extent that they consider the generation of specific control signals for each action, most computational models of motor control can be seen as direct or indirect ways to address the degrees of freedom problem.

2.1 Cortical Representation of Movement

It has been known since the seminal work by Penfield and Boldrey (1937) that stimulation of specific locations in the motor cortex elicit motor responses in particular locations on the body. This has led to the notion of a motor homunculus – a map of the body on the motor cortex. However, the issue of exactly what aspect of movement is encoded in the response of individual neurons is far from settled. A crucial breakthrough came with the discovery of *population coding* by Georgopoulos (Georgopoulos et al., 1982). It was found that the activity of specific neurons in the hand area of the motor cortex corresponded to reaching movements in particular directions. While the tuning of individual cells was found to be rather broad (and had a sinusoidal profile), the joint activity of many such cells with different tuning directions coded the direction of movement with great precision, and could be decoded through neurally plausible estimation mechanisms. Since the initial discovery, population codes have been found in other

regions of the cortex that are involved in movement (Georgopoulos *et al*., 1982; Schwartz *et al*., 1988; Schwartz, 1992, 1993, 1994; Ashe and Georgopoulos, 1994; Sanger, 1994; Moran and Schwartz, 1999a,b). Population coding is now regarded as the primary basis of directional coding in the brain, and is the basis of most brain-machine interfaces (BMI) and brain-controlled prosthetics (Chapin et al., 1999; Lebedev and Nicolelis, 2006). Neural network models for population coding have been developed by several researchers (Salinas and Abbott, 1995, 1996; Pouget and Sejnowski, 1994, 1997), and population coding has come to be seen as a general neural representational strategy with application far beyond motor control (Pouget and Snyder, 2000). Excellent reviews are provided by Pouget et al. (2000, 2003). Mathematical and computational models for Bayesian inference with population codes are discussed by Ma et al. (2006) and Beck et al. (2008).

An active research issue in the cortical coding of movement is whether it occurs at the level of *kinematic variables*, such as direction and velocity, or in terms of *kinetic variables*, such as muscle forces and joint torques. From a cognitive viewpoint, a kinematic representation is obviously more useful, and population codes suggest that such representations are indeed present in the motor cortex (Georgopoulos et al., 1982; Schwartz *et al*., 1988; Schwartz, 1992, 1993, 1994; Ashe and Georgopoulos, 1994; Moran and Schwartz, 1999a,b; Ajemian et al., 2000, 2001) and prefrontal cortex (Hoshi et al., 2000; Averbeck et al., 2002). However, movement must ultimately be constructed from the appropriate kinetic variables, i.e., by controlling the forces generated by specific muscles and the resulting joint torques. Studies have indicated that some neurons in the motor cortex are indeed tuned to muscle forces and joint torques (Caminiti et al., 1990; Graham et al., 2003; Scott & Kalaska, 1995, 1997; Sergio & Kalaska, 2003; Ajemian et al., 2008). This apparent multiplicity of cortical representations has generated significant debate among researchers (Ajemian et al., 2008). One way to resolve this issue is to consider the kinetic and kinematic representations as dual representations related through the constraints of the musculoskeletal system. However, Shah et al. (2004) have used a simple computational model to show that neural populations tuned to kinetic or kinematic variables can act jointly in motor control without the need for explicit coordinate transformations.

Graziano et al (2005) studied movements elicited by sustained electrode stimulation of specific sites in the motor cortex of monkeys. They found that different sites led to specific complex, multi-joint movements such as bringing the hand to the mouth or lifting the hand above the head regardless of the initial position. This raises the intriguing possibility that individual cells or groups of cells in the motor cortex encode goal-directed movements that can be triggered as units. The study also indicated that this encoding is not open-loop, but can compensate – at least to some degree – for variation or extraneous perturbations. The motor cortex and other related regions (e.g., the supplementary motor area and the premotor cortex) appear to encode spatially organized maps of a few "canonical" complex movements that can be used as basis functions to construct other actions (Graziano et al., 2005; Graziano, 2006, Graziano, 2008). A neurocomputational model using self-organized feature maps has been proposed by Aflalo and Graziano (2006) for the representation of such canonical movements.

In addition to rhythmic and reaching movements, there has also been significant work on the neural basis of sequential movements, with the finding that such neural codes for movement sequences exist in the supplementary motor area (Shima and Tanji, 1998; Sohn and Lee, 2007),

cerebellum (Mushiake and Strick, 1995), basal ganglia (Mushiake and Strick, 1995) and the prefrontal cortex (Averbeck et al., 2002). Coding for multiple goals in sequential reaching has been observed in the parietal cortex (Baldauf et al., 2008).

2.2 Synergy-Based Representations
A rather different approach to studying the construction of movement uses the notion of motor primitives, often termed *synergies* (Flash and Hochner, 2005; Bizzi et al., 2008; Kelso, 2009). Typically, these synergies are manifested in coordinated patterns of spatiotemporal activation over groups of muscles, implying a force field over posture space (Mussa-Ivaldi, 1988,1992). Studies in frogs, cats and humans have shown that a wide range of complex movements in an individual subject can be explained as the modulated superposition of a few synergies (Mussa-Ivaldi and Giszter, 1992; Giszter et al., 1993; Tresch et al., 1999; Kargo & Giszter, 2000; d'Avella et al., 2003; d'Avella and Bizzi, 2005; Flash and Hochner, 2005; Ting and Macpherson, 2005; Torres-Oveido et al., 2006; Bizzi et al., 2008; d'Avella and Pai, 2010). Given a set of n muscles, the n-dimensional time-varying vector of activities for the muscles during an action can be written as:

$$\boldsymbol{m}^q(t) = \sum_{k=1}^{N} c_k^q \boldsymbol{g}_k(t - t_k^q)$$

where $\boldsymbol{g}_k(t)$ is a time-varying synergy function that takes only non-negative values, c_k^q is the gain of the kth synergy used for action q, and t_k^q is the temporal offset with which the kth synergy is triggered for action q (d'Avella et al., 2003). The key point is that a broad range of actions can be constructed by choosing different gains and offsets over the same set of synergies, which represent a set of hard-coded basis functions for the construction f movements. Even more interestingly, it appears that the synergies found empirically across different subjects of the same species are rather consistent (Tresch et al., 1999; Torres-Oveido and Ting, 2006), possibly reflecting the inherent constraints of musculoskeletal anatomy. Various neural loci have been suggested for synergies, including the spinal cord (Tresch et al., 1999; Graziano, 2008; Hart, 2010), the motor cortex (Drew et al., 2008) and combinations of regions (Neilson and Neilson, 2005, 2010).

Though synergies are found consistently in the analysis of experimental data, their actual existence in the neural substrate remains a topic for debate (Kutch et al., 2008; Tresch and Jarc, 2009). However, the idea of constructing complex movements from motor primitives has found ready application in robotics (Ijspeert et al., 2001, 2002a,b, 2003; Schaal et al., 2003, 2007), as discussed later in this Chapter. A hierarchical neurocomputational model of motor synergies based on attractor networks has recently been proposed by Byadarhaly and Minai (2011, 2012).

2.3 Computational Models of Motor Control
Motor control has been modeled computationally at many levels and in many ways, ranging from explicitly control-theoretic models through reinforcement-based models to models based on emergent dynamical patterns. This section provides a brief overview of these models.

As discussed above the motor cortex (M1), premotor cortex (PMC) and the supplementary motor area (SMA) are seen as providing self-organized ``codes'' for specific actions, including

information on direction, velocity, force, low-level sequencing, etc., while the prefrontal cortex provides higher-level codes needed to construct more complex actions. These codes, comprising a *repertoire* of actions (Graybiel, 1995; Graziano, 2006), arise through self-organized learning of activity patterns in these cortical systems. The basal ganglia (BG) system is seen as the primary locus of selection among the actions in the cortical repertoire. The architecture of the system involving the cortex, basal ganglia and the thalamus, and in particular the internal architecture of the basal ganglia (Alexander et al, 1986), makes this system ideally suited to selectively disinhibiting specific cortical regions, presumably activating codes for specific actions (Graybiel et al., 1994; Graybiel, 1995; Grillner et al., 2005). The BG system also provides an ideal substrate for learning appropriate actions through a dopamine-mediated reinforcement learning mechanism (Schultz et al., 1997; Schultz, 2000; Schultz and Dickinson, 2000; Montague, 2004).

Many of the influential early models of motor control were based on control-theoretic principles (Wolpert and Kawato, 1998; Kawato, 1999; Wolpert and Ghahramani, 2000), using forward and inverse kinematic and dynamic models to generate control signals (Kawato et al., 1987; Bullock and Grossberg, 1988; Shadmehr and Mussa-Ivaldi, 1994; Wolpert et al., 1995; Karniel and Inbar, 1997, 2000; Bullock et al., 1998; Burnod et al, 1999) – see Shadmehr and Wise (2005) for an excellent introduction. These models have led to more sophisticated ones, such as MOSAIC (Modular Selection and Identification for Control) (Haruno, 2001) and AVITEWRITE (Adaptive Vector Integration to Endpoint Handwriting) (Paine et al., 2004). The MOSAIC model is a mixture-of-experts, consisting of many parallel modules, each comprising three sub-systems. These are: a forward model relating motor commands to predicted position, a responsibility predictor that estimates the applicability of the current module, and an inverse model that learns to generate control signals for desired movements. The system generates motor commands by combining the recommendations of the inverse models of all modules weighted by their applicability. Learning in the model is based on a variant of the EM algorithm. The model by Bullock et al. (1998) is a comprehensive neural model with both cortical and spinal components, and builds upon the earlier VITE model by Bullock and Grossberg (1988). The AVITEWRITE model (Paine et al., 2004), which is a further extension of the VITE model, can generate the complex movement trajectories needed for writing by using a combination of pre-specified phenomenological motor primitives (synergies). A cerebellar model for the control of timing during reaches has been presented by Barto et al., (1999).

The use of neural maps in models of motor control was pioneered by Ritter et al. (1989) and Martinetz et al. (1990). These models used self-organized feature maps (SOFMs) (Kohonen, 1982) to learn visuomotor coordination. Baraduc et al. (2001) presented a more detailed model that used multiple maps to first integrate posture and desired movement direction and then to transform this internal representation into a motor command. The maps in this and most subsequent models were based on earlier work by Salinas and Abbott (1995, 1996) and Pouget and Sejnowski (1994, 1997). An excellent review of this approach is given by Pouget and Snyder (2000). A more recent and comprehensive example of the map-based approach is the SURE-REACH (Sensorimotor, Unsupervised, Redundancy-resolving Control Architecture) model by Butz et al. (2007) which focuses on exploiting the redundancy inherent in motor control (Bernstein, 1967). Unlike many of the other models, which use neutrally implausible error-based learning, SURE-REACH relies only on unsupervised and reinforcement learning.

Maps are also the central feature of a general cognitive architecture called ERA (Epigenetic Robotics Architecture) by Morse et al.

Another successful approach to motor control models is based on the use of motor primitives, which are used as basis functions in the construction of diverse actions. This approach is inspired by the experimental observation of motor synergies as described above. However, most models based on primitives implement them non-neurally, as in the case of AVITEWRITE (Paine et al., 2004). The most systematic model of motor primitives has been developed by Schaal and colleagues (Ijspeert et al., 2001, 2003; Schaal et al., 2003, Schaal et al, 2007). In this model, motor primitives are specified using differential equations, and are combined after weighting to produce different movements. Recently, Matsubara et al. (2011) have shown how the primitives in this model can be learned systematically from demonstrations. Drew et al. (2008) proposed a conceptual model for the construction of locomotion using motor primitives (synergies) and identified the characteristics of such primitives experimentally. A neural model of motor primitives based on hierarchical attractor networks has been proposed recently by Byadarhaly et al. (2011, 2012) and Byadarhaly and Minai (in press), while Neilson and Neilson (2005, 2010) have proposed a model based on coordination among adaptive neural filters.

Motor control models based on primitives can be simpler than those based on trajectory tracking because the controller typically needs to choose only the weights (and possibly delays) for the primitives rather than specifying details of the trajectory (or forces). Among other things, this promises a potential solution to the degrees of freedom problem (Bernstein, 1967) since the coordination inherent in the definition of motor primitives reduces the effective degrees of freedom in the system. Another way to address the degrees of freedom problem is to use an optimal control approach with a specific objective function. Researchers have proposed objective functions such as minimum jerk (Flash and Hogan, 1985), minimum torque (Uno et al., 1989), minimum acceleration (Ben-Itzhak and Karniel, 2008) or minimum energy (Neilson and Neilson, 2010), but an especially interesting idea is to optimize the distribution of variability across the degrees of freedom in a task-dependent way (Harris and Wolpert, 1998; Wolpert and Ghahramani, 2000; Todorov and Jordan, 2002; Todorov, 2004; Valero-Cuevas et al., 2009). From this perspective, motor control trades off variability in task-irrelevant dimensions for greater accuracy in task-relevant ones. Thus, rather than specifying a trajectory, the controller focuses only on correcting consequential errors. This also explains the experimental observation that motor tasks achieve their goals with remarkable accuracy while using highly variable trajectories to achieve the same goal. Trainin et al. (2007) have shown that the optimal control principle can be used to explain the observed neural coding of movements in the cortex. Biess et al. (2007) have proposed a detailed computational model for controlling an arm in 3-dimensional space by separating the spatial and temporal components of control. This model is based on optimizing energy usage and jerk (Flash and Hogan, 1985), but is not implemented at the neural level.

An alternative to these prescriptive and constructivist approaches to motor control is provided by models on based on dynamical systems (Haken et al., 1985; Saltzman and Kelso, 1987; Kugler and Turvey, 1987; Turvey, 1990; Kelso, 1995; Scholz and Schöner, 1999; Riley and Turvey, 2002; Riley et al., 2011a). The most important way in which these models diverge from the others is in their use of emergence as the central organizational principle of control. In this

formulation, control programs, structures, primitives, etc., are not preconfigured in the brain-body system, but emerge under the influence of task and environmental constraints on the affordances of the system (Riley et al., 2011a). Thus, the dynamical systems view of motor control is fundamentally ecological (Gibson, 1977), and like most ecological models, is specified in terms of low-dimensional state dynamics rather than high-dimensional neural processes. Interestingly, a correspondence can be made between the dynamical and optimal control models through the so called "uncontrolled manifold" concept (Latash et al., 2007, 2010; Scholz and Schöner, 1999; Riley et al., 2011a). In both models, the dimensions to be controlled and those that are left uncontrolled are decided by external constraints rather than internal prescription, as in classical models.

3. Cognitive Control and Working Memory

A lot of behavior – even in primates – is automatic, or almost so. This corresponds to actions (or internal behaviors) so thoroughly embedded in the sensorimotor substrate that they emerge effortlessly from it. In contrast, some tasks require significant cognitive effort for one or more reason, including:

1. An automatic behavior must be suppressed to allow the correct response to emerge, e.g., in the Stroop task (Dehaene et al., 1998).

2. Conflicts between incoming information and/or recalled behaviors must be resolved (Botvinick et al., 2004; Botvinick, 2008).

3. More contextual information – e.g., social context – must be taken into account before acting.

4. Intermediate pieces of information need to be stored and recalled during the performance of the task, e.g., in sequential problem solving.

5. The timing of subtasks within the overall task is complex, e.g., in delayed-response tasks or other sequential tasks (Botvinick and Plaut, 2004).

Roughly speaking, the first three fall under the heading of *cognitive control*, and the latter two of *working memory*. However, because of the functions are intimately linked, the terms are often subsumed into each other.

3.1 Action Selection and Reinforcement Learning
Action selection is arguably the central component of the cognitive control process. As the name implies, it involves selectively triggering an action from a repertoire of available ones. While action selection is a complex process involving many brain regions, a consensus has emerged that the basal ganglia (BG) system plays a central role in its mechanism (Graybiel, 1995; Graybiel, 2005; Houk, 2005). The architecture of the BG system and the organization of its projections to and from the cortex (Alexander et al., 1986; Middleton and Strick, 2000, 2002)

make it ideally suited to function as a state-dependent gating system for specific functional networks in the cortex. As shown in Figure 3, the hypothesis is that the striatal layer of the BG system, receiving input from the cortex, acts as a pattern recognizer for the current cognitive state. Its activity inhibits specific parts of the globus pallidus (GPi), leading to disinhibition of specific neural assemblies in the cortex – presumably allowing the behavior/action encoded by those assemblies to proceed (Graybiel, 1995). The associations between cortical activity patterns and behaviors are key to the functioning of the BG as an action selection system, and the configuration and modulation of these associations is thought to lie at the core of cognitive control. The neurotransmitter dopamine (DA) plays a key role here by serving as a reward signal (Schulz et al, 1997; Schulz and Dickinson, 2000; Schulz, 2000) and modulating reinforcement learning (Sutton and Barto, 1998; Sutton 1988) in both the BG and the cortex (Montague et al., 2004; Daw et al., 2005; Frank and O'Reilly, 2006; Gruber et al., 2006).

3.2 Working Memory

All non-trivial behaviors require task-specific information, including relevant domain knowledge and the relative timing of subtasks. These are usually grouped under the function of *working memory* (WM). An influential model of working memory by Baddeley (1986) identifies three components in WM: 1) A *central executive*, responsible for attention, decision-making and timing; 2) A *phonological loop*, responsible for processing incoming auditory information, maintaining it in sort-term memory, and rehearsing utterances; and 3) A *visuospatial sketchpad*, responsible for processing and remembering visual information, keeping track of `what' and `where' information, etc. An *episodic buffer* to manage relationships between the other three components is sometimes included (Baddeley, 2000). Though already rather abstract, this model needs even more generalized interpretation in the context of many cognitive tasks that do not directly involve visual or auditory data. Working memory function is most closely identified with the prefrontal cortex (PFC) (Goldman-Rakic, 1995; Goldman-Rakic et al., 1996; Duncan, 2001).

Almost all studies of working memory consider only short-term memory, typically on the scale of a few seconds (Ratcliff and McKoon, 2008). Indeed, one of the most significant – though lately controversial – results in working memory research is the finding that only a small number of items can be "kept in mind" at any one time (Miller, 1956; Lisman and Idiart, 1995). However, most cognitive tasks require context-dependent repertoires of knowledge and behaviors to be enabled collectively over longer periods. For example, a player must continually think of chess moves and strategies over the course of a match lasting several hours. The configuration of context-dependent repertoires for extended periods has been termed *long-term working memory* (Ericsson and Kintsch, 1995).

3.3 Computational Models of Cognitive Control and Working Memory

Several computational models have been proposed for cognitive control, and most of them share common features. The issues addressed by the models include action selection, reinforcement learning of appropriate actions, decision-making in choice tasks, task sequencing and timing, persistence and capacity in working memory, task switching, sequence learning and the configuration of context-appropriate workspaces. Most of the models discussed below are neural with a range of biological plausibility. A few important non-neural models are also mentioned.
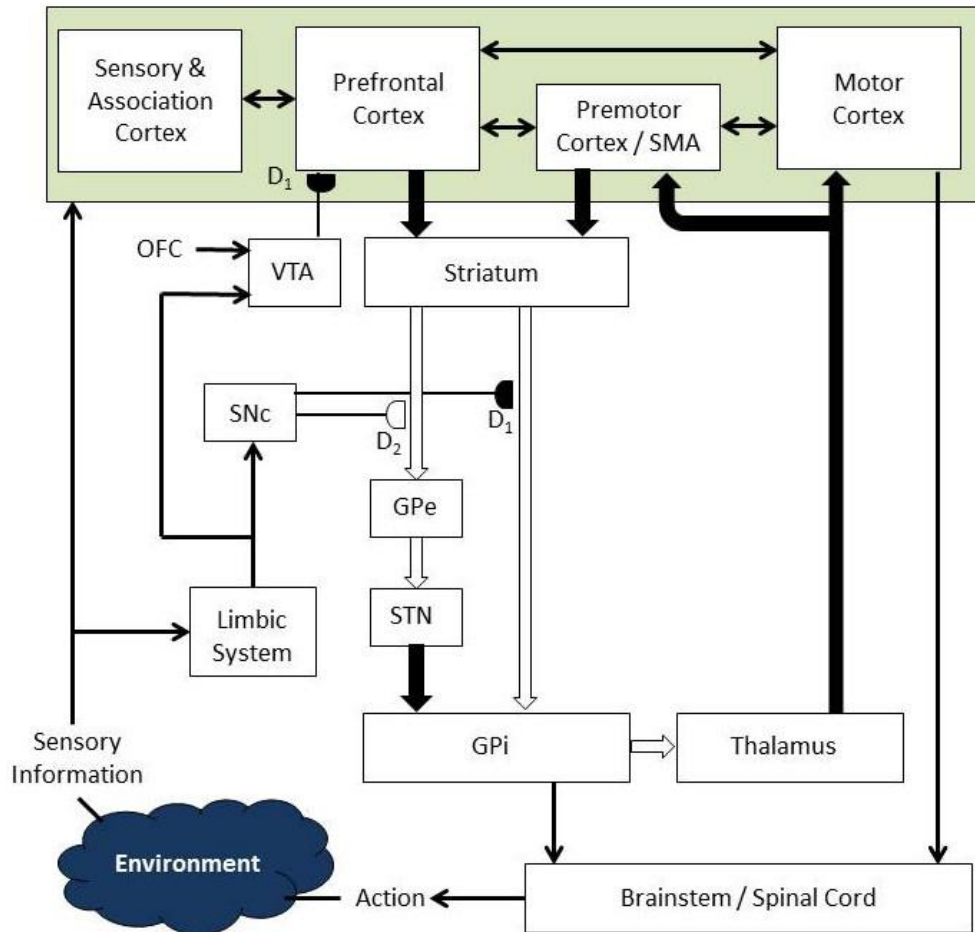
Figure 3: The action selection and reinforcement learning substrate in the basal ganglia. Wide filled arrows indicate excitatory projections while wide unfilled arrows represent inhibitory projections. Linear arrows indicate generic excitatory and inhibitory connectivity between regions. The inverted D-shaped contacts indicate modulatory dopamine connections that are crucial to reinforcement learning. Abbreviations: SMA = supplementary motor area; SNc = substantia nigra pars compacta; VTA = ventral tegmental area; OFC = orbitofrontal cortex; GPe = globus pallidus (external nuclei); GPi = globus pallidus (internal nuclei); STN = subthalamic nucleus; D_1 = excitatory dopamine receptors; D_2 = inhibitory dopamine receptors. The primary neurons of GPi are inhibitory and active by default, thus keeping all motor plans in the motor and premotor cortices in check. The neurons of the striatum are also inhibitory but usually in an inactive "down" state (Wilson, 1995). Particular subgroups of striatal neurons are activated by specific patterns of cortical activity (Flaherty and Graybiel, 1994), leading first to disinhibition of specific actions via the direct input from striatum to GPi, and then by re-inhibition via the input through STN. Thus the system gates the triggering of actions appropriate to current cognitive contexts in the cortex. The dopamine input from SNc projects a "reward" signal based on limbic system state, allowing desirable context-action pairs to be reinforced (Graybiel, 1998) – though other hypotheses also exist (Houk, 2005). The dopamine input to PFC from the VTA also signals reward and other task-related contingencies.

A comprehensive model using spiking neurons and incorporating many biological features of the BG system has been presented by Humphries et al. (2002, 2006). This model focuses only on the BG and explicitly on the dynamics of dopamine modulation. A more abstract but broader model of cognitive control is the `agents of the mind' model by Houk (2005), which incorporates the cerebellum as well as the basal ganglia. In this model, the basal ganglia provide the action selection function while the cerebellum acts to refine and amplify the choices. A series of interrelated models have been developed by O'Reilly, Frank and their colleagues (O'Reilly and Munakata, 2000; Frank et al., 2001; Rougier et al., 2005; Hazy et al., 2006; Frank and O'Reilly, 2006; O'Reilly and Frank, 2006, Frank and Claus, 2006; O'Reilly, 2006). All these models use the adaptive gating function of the BG in combination with the working memory (WM) function of the prefrontal cortex to explain how executive function can arise without explicit top-down control – the so-called `homunculus' (O'Reilly and Frank, 2006; Hazy et al., 2006). A comprehensive review of these and other models of cognitive control is given in O'Reilly et al. (2010). Models of goal-directed action mediated by the PFC have also been presented in Hasselmo (2005) and Hasselmo and Stern (2006). Reynolds and O'Reilly (2009) have proposed a model for configuring hierarchically organized representations in the PFC via reinforcement learning. Computational models of cognitive control and working have also been used to explain mental pathologies such as schizophrenia (Braver et al., 1999).

An important aspect of cognitive control is switching between tasks at various time-scales (Monsell, 2003; Braver et al., 2003). Imamizu et al. (2004) compared two computational models of task switching – a mixture-of-experts (MoE) model and MOSAIC – using brain imaging. They concluded that task switching in the PFC was more consistent with the MoE model and that in the parietal cortex and cerebellum with the MOSAIC model.

An influential abstract model of cognitive control is the *interactive activation model* by Cooper and Shallice (2000, 2006). In this model, learned behavioral schemata contend for activation based on task context and cognitive state. While this model captures many phenomenological aspects of behavior, it is not explicitly neural. Botvinick and Plaut (2004) present an alternative neural model that relies on distributed neural representations and the dynamics of recurrent neural networks rather than explicit schemata and contention. Dayan (2006, 2008) has proposed a neural model for implementing complex rule-based decision-making where decisions are based on sequentially unfolding contexts. A partially neural model of behavior based on the CLARION cognitive model has been developed by Helie and Sun (2010).

Recently, Grossberg and Pearson (2008) have presented a comprehensive model of working memory called LIST PARSE. In this model, the term `working memory' is applied narrowly to the storage of temporally ordered items, i.e., lists, rather than more broadly to all short-term memory. Experimentally observed effects such as recency (better recall of late items in the list) and primacy (better recall of early items in the list) are explained by this model, which uses the concept of *competitive queuing* for sequences. This is based on the observation (Averbeck et al., 2002; Rhodes et al., 2004) that multiple elements of a behavioral sequence are represented in the PFC as simultaneously active codes with activation levels representing the temporal order. Unlike the WM models discussed in the previous paragraph, the working memory in LIST PARSE is embedded within a full cognitive control model with action selection, trajectory generation, etc. Many other neural models for chains of actions have also been proposed (Ans,

1994; Bapi and Levine, 1994; Taylor and Taylor, 2000; Cooper, 2003; Rhodes et al., 2004; Nishimoto and Tani, 2004; Dominey, 2005; Salinas, 2009; Vasa et al., 2010; Chersi et al., 2011; Silver et al., 2011).

Higher level cognitive control is characterized by the need to fuse information from multiple sensory modalities and memory to make complex decisions. This has led to the idea of a *cognitive workspace*. In the *global workspace theory* (GWT) developed by Baars (1988), information from various sensory, episodic, semantic and motivational sources comes together in a global workspace that forms brief, task-specific integrated representations that are broadcast to all sub-systems for use in working memory. This model has been implemented computationally in the *Intelligent Distribution Agent* (IDA) model by Franklin (Baars and Franklin, 2003; Franklin and Patterson, 2006). A neurally implemented workspace model has been developed by Dehaene and colleagues (Dehaene and Changeaux, 1991; Dehaene et al., 1998; Dehaene and Naccache, 2001) to explain human subjects' performance on effortful cognitive tasks (i.e., tasks that require suppression of automatic responses), and the basis of consciousness. The construction of cognitive workspaces is closely related to the idea of long-term working memory (Ericsson and Kintsch, 1995). Unlike short-term working memory, there are few computational models for long-term working memory. Neural models seldom cover long periods, and implicitly assume that a chaining process through recurrent networks (e.g., Botvinick and Plaut, 2004) can maintain internal attention. Iyer et al. (2009, 2010) have proposed an explicitly neurodynamical model of this function, where a stable but modulatable pattern of activity called a *graded attractor* is used to selectively bias parts of the cortex in context-dependent fashion. An earlier model was proposed by Doboli et al. (2000) to serve a similar function in the hippocampal system.

Another class of models focuses primarily on single decisions within a task, and assume an underlying stochastic process (Ratcliff, 1978; Ashby, 1983; Busemeyer and Townsend, 1993; Ratcliff and McKoon, 2008). Typically, these models address two-choice short-term decisions made over a second or two (Ratcliff and McKoon, 2008). The decision process begins with a starting point and accumulates information over time resulting in a diffusive (random walk) process. When the diffusion reaches one of two boundaries on either side of the starting point, the corresponding decision is made. This elegant approach can model such concrete issues as decision accuracy, decision time and the distribution of decisions without any reference to the underlying neural mechanisms, which is both its chief strength and its primary weakness. Several connectionist models have also been developed based on paradigms similar to the diffusion approach (McClelland and Rumelhart, 1981; Rumelhart and McClelland, 1982; Usher and McClelland, 2001). The neural basis of such models has been discussed in detail by Gold and Shadlen (2007). A population-coding neural model that makes Bayesian decisions based on cumulative evidence has been described by Beck et al. (2009).

Reinforcement learning (Sutton and Barto, 1998) is widely used in many engineering applications, but several models go beyond purely computational use and include details of the underlying brain regions and neurophysiology (Montague et al., 2004; Khamassi et al., 2005). Excellent reviews of such models are provided by Daw and Doya (2006), Dayan and Niv (2008), and Doya (2008). Recently, models have also been proposed to show how dopamine-mediated

learning could work with spiking neurons (Izhikevich, 2007) and population codes (Urbanczik and Senn, 2009).

Computational models that focus on working memory *per se* (i.e., not on the entire problem of cognitive control) have mainly considered how the requirement of selective temporal persistence can be met by biologically plausible neural networks (Durstewitz et al., 2000, 2002). Since working memories must bridge over temporal durations (e.g., in remembering a cue over a delay period), there must be some neural mechanism to allow activity patterns to persist selectively in time. A natural candidate for this is attractor dynamics in recurrent neural networks (Hopfied, 1982; Amit and Brunel, 1995), where the recurrence allows some activity patterns to be stabilized by reverberation (Amit and Brunel, 1997). The neurophysiological basis of such persistent activity has been studied by Wang (1999). A central feature in many models of working memory is the role of dopamine in the PFC (Durstewitz et al., 1999; Brunel and Wang, 2001, Cohen et al., 2002). In particular, it is believed that dopamine sharpens the response of PFC neurons involved in working memory (Servan-Schreiber et al., 1990) and allows for reliable storage of timing information in the presence of distractors (Durstewitz et al., 2000). The model by Durstewitz et al., (1999, 2000) includes several biophysical details such as the effect of dopamine on different ion channels and its differential modulation of various receptors. More abstract neural models for working memory have been proposed by Hochreiter and Schmidhuber (1997) and Moody et al., (1998).

An especially interesting type of attractor network uses so-called *bump attractors* – spatially localized patterns of activity stabilized by local network connectivity and global competition (Hahnloser et al., 1999). Such a network has been used in a biologically plausible model of working memory in the PFC by Compte et al. (2000), which demonstrates that the memory is robust against distracting stimuli. A similar conclusion is drawn by Gruber et al. (2006) based on another bump attractor model of working memory. They show that dopamine in the PFC can provide robustness against distractors, but robustness against internal noise is achieved only when dopamine in the BG locks the state of the striatum. Recently, Mongillo et al., (2008) have proposed the novel hypothesis that the persistence of neural activity in working memory may be due to calcium-mediated facilitation rather than reverberation through recurrent connectivity.

4. Conclusion

This chapter has attempted to provide an overview of neurocomputational models for cognitive control, working memory, and motor control. Given the vast body of both experimental and computational research in these areas, the review is necessarily incomplete, though every attempt has been made to highlights the major issues, and to provide the reader with a rich array of references covering the breadth of each area.

The models described in this chapter relate to several other mental functions including sensorimotor integration, memory, semantic cognition, etc., as well as to areas of engineering such as robotics and agent systems. However, these links are largely excluded from the chapter – in part for brevity, but mainly because most of them are covered elsewhere in this Handbook.

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