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Models for the control of grasping

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Summary

This chapter underlines the multifaceted nature of reach and grasp behavior by reviewing several computational models that focus on selected features of reach-to-grasp movements. An abstract meta-model is proposed that subsumes previous modeling efforts, and points towards the need to develop computational models that embrace all the facets of reaching and grasping behavior.

Introduction

Hand transport and hand (pre)shaping are basic components of primate grasping. The different views on their dependence and coordination lead to different explanations of human control of grasping. One can view these two components as being controlled independently but coordinated so as to achieve a secure grasp. The alternative view is that the hand and the arm are taken as a single limb and controlled using a single control mechanism. Needless to say, this distinction is not very sharp; but it becomes a choice to be made by a control engineer when it is necessary to actually implement a grasp controller. The experimental findings so far point towards the view that human grasping involves independent but coordinated control of the arm and the hand (see Jeannerod *et al.*, 1998) (see also Chapter 10). However, reports against this view do exist as it has been suggested that human grasping is a generalized reaching movement that involves movement of digits so as to bring the fingers to their targets on the object surface (Smeets & Brenner, 1999, 2001). Although theoretically both control mechanisms are viable, from a computational viewpoint, the former is more likely. Learning and/or optimization of a single gigantic controller is very difficult; dealing with smaller and simpler controllers (i.e. for the hand and the arm) and coordinating them according to the task requirements seems more plausible (Kawato & Samejima, 2007).

Monkey neurophysiology and human brain-imaging studies help us delineate the brain regions that are involved in grasp planning and execution (see Chapters 4, 6, 7 and 8); however, it is far from known *how* exactly these regions work together to sustain a grasping mechanism that exhibits the range of properties observed in adult or infant reach and grasp.

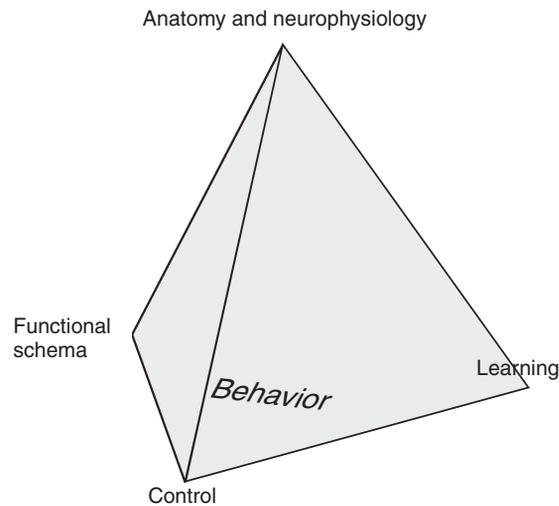


Figure 9.1. The conceptual tetrahedron illustrating the multitude of ways of approaching primate reach-to-grasp.

The computational studies often focus on a selected subset of the properties of primate grasping. Among these, many consider an adult grasping system that is modeled with a low-to-moderate level of biological realism so as to match the experimental, mostly behavioral, data. Some other studies attempt to explain how the skill of grasping can be attained via learning, often employing techniques from machine learning. It is unfortunate that, to date, there are no computational models that can explain the full extent of reach and grasp movements in terms of development, neural mechanisms and behavioral markers in a single framework. So, here we propose a meta-model that considers those previous studies as points inside (or on) the conceptual tetrahedron (see Figure 9.1) whose corners are identified by (1) anatomy and neurophysiology, (2) schemas representing brain function, (3) learning (infant to adulthood transition of grasping) and (4) control (the optimization and control principles of reach-to-grasp).

In what follows, we review existing modeling efforts that can be considered to be representatives for the corners of the conceptual tetrahedron shown in Figure 9.1. First, we briefly review the cortical areas involved in grasp control (anatomy and neurophysiology) and introduce the FARS model that addresses the neural ingredients of reach-to-grasp in terms of functional schemas (Fagg & Arbib, 1998). Then, we move to the models that attempt to explain the learning aspect of grasping. We present a developmentally oriented model that learns finger configurations for stable grasping (Oztop *et al.*, 2004), and a model that synthesizes human-like grasp using human motion capture data (Uno *et al.*, 1995; Iberall & Fagg, 1996). For the control aspect of grasping, we first present the Hoff–Arbib model that explains the coordination of the timing of transport and preshape (Hoff & Arbib, 1993), and an internal model explanation of the load-force–grip-force coupling (Kawato, 1999).

Neurophysiological considerations and the FARS model

Neurophysiological data indicate that the parietal cortex is involved in visuomotor aspects of manual manipulative movements (Wise *et al.*, 1997). In particular, the anterior intraparietal area (AIP) of macaque monkeys discharges in response to viewing and/or grasping of 3D objects representing object features relevant for grasping (Sakata *et al.*, 1995, 1998) (see also Chapters 6, 7 and 13). Area AIP has strong recurrent connections with the rostral part of the ventral premotor cortex (area F5) in the macaque (Luppino *et al.*, 1999). The ventral premotor cortex is involved in grasp planning and execution (Rizzolatti *et al.*, 1990), and projects to motoneurons that control finger muscles (Dum & Strick, 1991). The activity of neurons in the primary motor cortex (area F1) when contrasted to the premotor activity suggests that the primary motor cortex may be more involved in dynamic aspects of movement, executing “instructions” sent by the premotor cortex. Thus, it is generally accepted that the anterior intraparietal area–ventral premotor cortex–primary motor cortex network (AIP–F5–F1 circuit in short) is responsible for grasp planning and execution (Gallese *et al.*, 1994; Jeannerod *et al.*, 1995; Fagg & Arbib, 1998; Fogassi *et al.*, 2001). Cerebral cortex coordinates the execution of the AIP–F5–F1 circuit with the transport of the hand, which is mediated via a similar parietal-to-motor pathway. For representation of the space for action the areas in and around the intraparietal sulcus play a key role. Ventral, medial and lateral intraparietal areas represent the space in different coordinate frames (Colby & Duhamel, 1996; Duhamel *et al.*, 1998; Colby & Goldberg, 1999). Although MIP appears to be the main area responsible for the representation of a reach target, we hold that LIP and VIP should be involved in representing targets as well (e.g. it is likely that the goal of a slapping action triggered by a mosquito bite is registered in area VIP). Therefore we take the liberty of collectively using VIP/MIP/LIP (ventral/medial/lateral intraparietal areas) as the regions responsible for reach target representation. This representation is used by the caudal part of the ventral premotor cortex (area F4) for planning and executing the transport phase of the grasping action. In short we have a (VIP/MIP/LIP)–F4–F1 pathway for reaching and AIP–F5–F1 for grasping (see Figure 9.2A) in macaque monkeys. Strong evidence suggests that the human brain has a similar organization for reaching and grasping, with homologous areas (Culham *et al.*, 2006; Culham & Valyear, 2006). The human homolog¹ of macaque AIP appears to be the area located at the junction of the anterior part of the intraparietal sulcus and the inferior postcentral sulcus (see Culham *et al.*, 2006 and citations therein). The other macaque intraparietal areas also have their homologs in or around the human intraparietal sulcus although these are not as well established as AIP (Culham *et al.*, 2006). There is strong evidence that the human area 44 is the homolog of the monkey F5 (the rostral part of the ventral premotor cortex) with similar motor and cognitive functions (Rizzolatti *et al.*, 2002). The homology of monkey area F4 is not well established yet, however a likely candidate is the ventral part of area 6 neighboring area 44.

Based on the properties of the summarized parietofrontal reach and grasp areas, Fagg & Arbib (1998) proposed a schema model of grasp planning and execution (FARS,

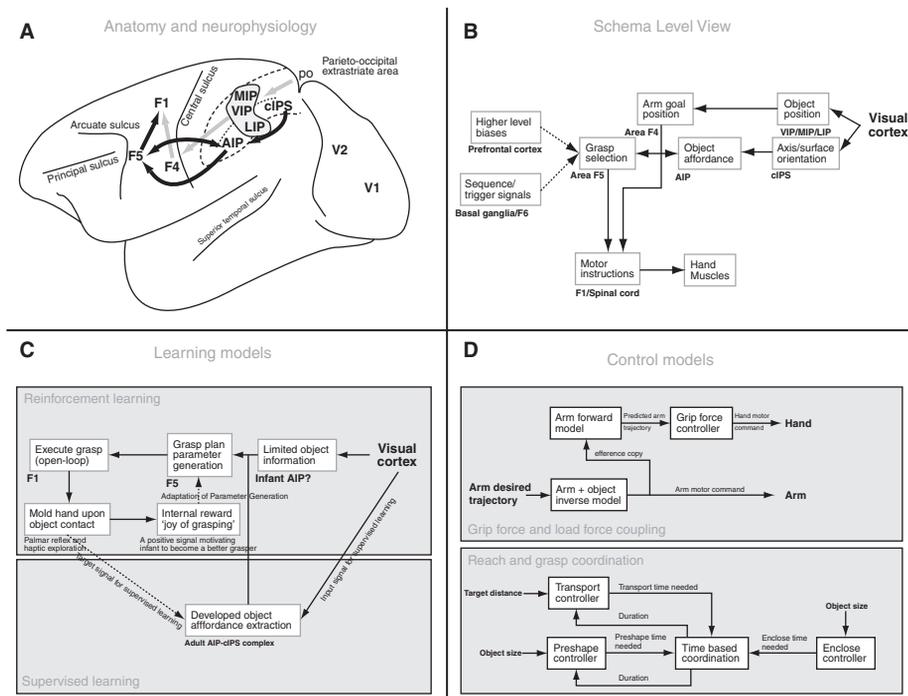


Figure 9.2. A. The cortical organization of reach and grasp pathways are shown. The darker arrows indicate the grasp-related visuomotor transformation pathways, whereas the lighter arrows indicate the projections mediating the transport component. B. The schema-level organization of grasping according to the FARS model (Fagg & Arbib, 1998). C. Upper panel: According to the ILGM model (Oztop *et al.*, 2004) infant grasp development is mediated by the internal reward generated when an object is grasped. Lower panel: How the result of ILGM learning can bootstrap visuomotor development (Oztop *et al.*, 2006). D. Upper panel: How the central nervous system adjusts the grip force according to the predicted load force using inverse and forward models (Kawato, 1999). Lower panel: How the ‘time-to-completion’ signal can be used for coordinating transport and hand controllers (Hoff & Arbib, 1993)

Fagg–Arbib–Sakata–Rizzolatti model). According to the model (see Figure 9.2B), AIP converts the information relayed by the dorsal and ventral visual stream into a set of representations, called the “object affordances.” These affordances then are forwarded to area F5, which selects the suitable affordance given task constraints. Then the selected affordance is reported back to AIP, virtually establishing a memory. The execution then unfolds with a sequencing mechanism that monitors phases of the grasp action (such as “maximum aperture reached” and “object contact”). The sequencing is postulated to be implemented by basal ganglia and the presupplementary motor area (area F6) via inhibition and disinhibition mechanisms. Figure 9.2B illustrates the FARS model’s main functional units (schemas) and their interrelation.

Learning: grasp development in infants

On the one hand, there are many experimental studies on the attributes of adult and infant reaching; on the other, there are several models of reaching to grasp (Arbib & Hoff, 1994) and robotic grasp synthesis techniques (Shimoga, 1996). However, there are few computational models that combine the empirical data on infant motor development relating to cortical structures. In this direction, Oztop *et al.* (2004) has proposed the Infant learning to grasp model (ILGM) that attempts to give an account of infant grasp learning that could be mapped onto cortical structures and capture infant motor development data.

Infants exhibit a crude ability to reach at birth (von Hofsten, 1982) (see also Chapter 17), that transforms into better controlled reaching and simple grasping by 4–5 months, and adult-like reaching and grasping by 9 months, achieving precision grasping by 12–18 months (von Hofsten, 1984). Infants 12 weeks of age make hand contact with glowing and sound-making objects under lighted and dark conditions with similar frequency, and the onset of successful grasping under these two conditions takes place at approximately the same age of 15–16 weeks (Clifton *et al.*, 1993). This indicates that reaches of the neonate elicited by vision of an object (counter intuitively) can be executed without vision of the hand. Between 9–13 months of age, reaches become better matched to the target object, with earlier hand orientation and anticipatory grasp closure relative to object orientation and size (Lockman *et al.*, 1984; von Hofsten & Ronnqvist, 1988; Newell *et al.*, 1993). These data suggest that infants initially use an open-loop control (i.e. ballistic) strategy that transports the hand to the target object followed by a haptic grasping phase (molding of the hand to match the object shape). Perhaps, later in development, the initial open-loop grasping provides the training stimuli for development of a visual feedback grasping circuit that is prerequisite for delicate manipulation (see Oztop *et al.*, 2006).

In the ILGM, a grasp plan is defined with the triplet (p , r , v) generated by the computational modules of Hand position (p), Wrist rotation (r) and Virtual fingers (v). The triplet (p , r , v) represents a minimal set of kinematic parameters specifying basic grasp actions. The movement execution mechanism first transports the hand to the location p while the wrist is rotated according to r . After this phase, the hand is transported towards the object center. So, p in effect determines the “approach direction” of the grasping movement. On contact with the object, the fingers specified with v enclose the object simulating the palmar reflex (when simulating infants of 4–6 months old, v engages all the fingers). If this enclosure results in a stable grasp, a positive reward stimulus is relayed back to the computational modules that generated p , r , v parameters. The connection weights among the modules are updated so to encourage such output next time a similar object is presented. A failure to contact with the object or an unstable grasp produces a negative reward signal that causes changes in the connection weights to discourage such p , r , v output. Thus, during learning, the ILGM discovers which orientations and approach directions are appropriate for a particular object.

The ILGM not only captures some interesting features of infant grasp development, but also maps the modules of the model to the brain areas that might be involved in the

associated functions.² The ILGM is a systems-level model based on the broad organization of the primate visuomotor network, where visual features are extracted by the parietal cortex, and used by the premotor cortex to generate high-level motor signals that drive the lower motor centers for movement generation (see Figure 9.2C, upper panel). The feedback arising from the object contact is used to modify grasp generation mechanisms within the premotor cortex. The model consists of four modules: the Object Information/Input module, the Grasp Learning/Generation module, the Movement Execution module, and the Grasp Evaluation module. The Grasp Learning/Generation module contains the aforementioned computational layers that generate the grasp plan (*Virtual finger*, *Hand position* and *Wrist rotation*). These layers are motivated by the *Preshape*, *Approach vector* and *Orient* grasping schemas proposed by Iberall & Arbib (1990). The Object Information module is postulated to be located in the parietal cortex (probably AIP; Sakata *et al.*, 2005), with the function of extracting object affordances. The affordances are relayed to the Grasp Learning module that is postulated to be located in the ventral premotor cortex that is known to be involved in grasp programming (Jeannerod *et al.*, 1995; Luppino *et al.*, 1999). The grasp plan output by the Grasp Learning module is then used by the Movement Execution module for actual grasp execution. The primary motor cortex and spinal motor circuitry is postulated to undertake the actual execution task. The Movement Execution module also implements the palmar reflex upon object contact. The sensory stimuli generated by the execution of the grasp plan are integrated and evaluated by the Movement Evaluation module that is postulated to be located in the primary somatosensory cortex. Output of the somatosensory cortex, the reinforcement signal, is used to adapt the parietal-premotor circuit's internal parameters. Grasp evaluation is implemented in terms of grasp stability: a grasp attempt that misses the target or yields an unstable object enclosure produces a negative reinforcement signal.

The ILGM simulations showed that a limited set of behaviors (reaching and grasp reflex) coupled with simple haptic feedback (holding of object) was enough for a goal-directed trial and error learning mechanism to yield an interesting set of grasping behaviors. The experiments with the model showed that power grasping would be the dominant mode of grip in the early stages of learning, and as learning progresses several different type of grips would be added to the infant's grasp repertoire (Oztop *et al.*, 2004). In addition, the simulations showed that the task constraints and the environment shape the infant grasp repertoire: when the ILGM was simulated in a situation where only small objects on top of a table were presented, precision pinch became the dominant mode of grasping, as a tiny object over a hard surface could not be picked up by power grasping (Oztop *et al.*, 2004).

Learning: hand configurations suitable for the target object

Grasping an object in one's hand requires at least two forces to be applied to the object. Iberall *et al.* (1986) used the term opposition to describe basic forms of force application patterns. (1) Pad opposition occurs when an object is held between a set of fingers and the thumb, as in holding a peanut with the index finger and the thumb. (2) Palm opposition

occurs when an object is held with fingers opposing the palm, as in holding a large hammer. (3) Side opposition occurs when the thumb's volar surface opposes radial sides of the fingers, as in holding a key. This classification, in effect, transforms a complex, high degree-of-freedom problem into a lower dimensional problem of (1) determining which opposition(s) to be used for a given object, and (2) implementing the selected opposition(s), in terms of how many fingers should be involved and what forces to be produced. The set of fingers, thumb or the palm surface that is involved in providing oppositional forces are called the virtual fingers (Iberall *et al.*, 1986; see also Chapter 3 and Baud-Bovy & Soechting, 2001). Within this framework grasping proceeds as follows: (1) object properties are perceived, (2) object is located in space, (3) opposition to be used is determined, (4) the virtual fingers are set up (i.e. which fingers to involve are decided), (5) hand aperture is determined, (6) the grasp is executed (preshape and enclose). Experimental evidence suggests that the choice of fingers to use depends on many factors including object properties, the manipulation required after the grip, environmental constraints and the anatomy of the forearm. Iberall used a feedforward neural network to determine which opposition to use for a given set of task requirements (object properties + force and precision requirements), and which fingers to contribute in the selected opposition (see Iberall & Fagg 1996 and citations therein). After training the neural network could produce the opposition necessary for the given object properties and task requirements as input.

A conceptually similar, but more advanced approach to train an artificial neural network for producing the "right" finger configuration given an object was proposed by Uno *et al.* (1995). The neural network proposed was a five-layer information compression network that was trained to reproduce the given input at the output (i.e. an identity mapping was to be learned). In this kind of network, when the number of units in the middle layer is chosen less than the input, the middle layer acts as a bottle neck so that the network effectively performs a non-linear principal component analysis.³ The input and output consisted of visual (object information) and motor information (joint angles). The input and output training set was prepared by recording a set of successful grasping actions of a human actor. After the network was trained it formed a compressed, and thus a multimodal representation of the grasping actions that "encoded" compatible object properties and finger configurations. The grasp generation was performed by an optimization process where for a given visual input (x) a complementary motor code (y) was searched so that the network retained its identity mapping property (that is (x, y) would be mapped to (x, y)) and a specified optimization criterion was satisfied, which could tilt the bias towards certain grasp types (i.e. precision pinch vs. power grasp). The simulations showed that the network can not only produce the taught grasps but also generalize to objects with different dimensions as well.

The concept of multimodal representation appears to be a promising and a logical target for modeling as it is supported by monkey electrophysiology. The neurons in the monkey anterior intraparietal area (AIP) are involved in grasp planning and have multimodal responses, encoding a mixture of object features (i.e. object affordances) and executed grasp properties (Sakata *et al.*, 1995, 1998; Murata *et al.*, 1996, 2000). A classic view related to synaptic plasticity and learning in the brain is Hebbian learning ("when an axon of cell A

is near enough to excite a cell B and repeatedly or persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A's efficiency, as one of the cells firing B, is increased.”). A similar mechanism may lead to emergence of multimodal representation in the cerebral cortex (Keysers & Perrett, 2004; Oztop *et al.*, 2005a; Chaminade *et al.*, 2008).

Uno *et al.*'s model requires a set of successful grasping examples to become functional. Therefore, from a developmental perspective, we can say that it models the stage where infants grasp objects with a rudimentary grasping circuit (4–6 months of age). So, the Infant learning to grasp model (Oztop *et al.*, 2004) presented above and Uno *et al.*'s model are complementary in that ILGM learning provides the successful examples that Uno *et al.*'s model requires to form multimodal representations and to function as a more elaborate grasp-planning circuit. In the same vein, Oztop *et al.* (2006) also proposed a neural network model of AIP neurons, where a combination of self-organizing map and a three-layer feedforward network “learned” from the performance of the rudimentary grasping ability provided by ILGM.

Control: coordination of reach and grasp

One of the characteristics of reach-to-grasp movement is that during the execution of the movement when the target location is suddenly changed not only the transport phase of the movement but also the kinematics and timing of the preshape are altered (Paulignan *et al.*, 1991a, 1991b; Roy *et al.*, 2006; see also Chapters 2 and 10). Likewise, when the target object size is suddenly changed not only the finger kinematics but also the transport phase of the movement is affected (Paulignan *et al.*, 1991a, 1991b; Roy *et al.*, 2006). The Hoff–Arbib model attempts, and to a large extent succeeds in explaining the temporal relation of hand transport kinematics with the finger aperture kinematics observed during reach-to-grasp movements. Hoff & Arbib (1993) have postulated the existence of a higher-level schema that coordinates the controllers (“schemas”) for reach and grasp. The overall control of the movement is achieved by a modular decomposition of (1) transport, (2) preshape and (3) enclose controllers as shown in the lower panel of Figure 9.2D. The higher-level schema receives “time-to-completion” information from the reach and grasp schemas. The schema that needs a longer time to complete is allowed its time, whereas the others are slowed down. Although the controllers were built upon the minimum-jerk model, the key is the coordination of the controllers rather than the particular choice for the actual implementation of each controller. Perhaps the model would predict human grasping behavior better when one of the more recent models e.g. “minimum variance” (Harris & Wolpert, 1998) or the “TOPS” (Miyamoto *et al.*, 2004) model was used instead of the minimum-jerk model. The Hoff–Arbib model accounts for the smooth corrections in response to sudden position and object size alterations observed in human reach-to-grasp movements. Moreover, the Hoff–Arbib model, although originally developed for reach and grasp, seems to account for the temporal invariance property observed in bimanual actions that require complex hierarchical and temporal coordination (Weiss & Jeannerod, 1998; Weiss *et al.*, 2000).

Control: internal models and load force – grip force coupling

Internal models when used in the context of the central nervous system, refer to neural mechanisms that mimic input–output relationships of the limbs and external objects. A forward internal model predicts the sensory consequences of a given motor command (i.e. corollary discharge), thus provides a mechanism to overcome the delay (that is undesirable for control) involved in sensing the actual sensory outcome using sensory receptors. Forward models also can be used in mental simulation (Oztop *et al.*, 2005b) of actions as well as attenuating the sensory stimulus generated by one's own movement (Blakemore *et al.*, 1998). An inverse model starts from a desired sensory state and outputs the motor command that will achieve the desired state. Experimental evidence from human neuroimaging and monkey neurophysiology indicate that the cerebellum is involved in acquiring inverse models through motor learning (Flanagan & Wing, 1997; Imamizu *et al.*, 2000; Kawato *et al.*, 2003; Bursztyn *et al.*, 2006; Kawato, 2008; see also Chapter 26). The so-called “grip force–load force coupling” (Johansson, 1996) that is observed when the hand is moved voluntarily while an object is being held by finger(s) opposing the thumb demonstrates that the central nervous system employs forward models in sensory motor control. Since the movement of the hand induces varying load forces on the held object, the central nervous system has to adjust the grip force such that the object does not slip and an unnecessarily large force is avoided. So the grip force modulation has similar temporal waveform as the load force and is usually associated with a phase advance indicating that the grip-force modulation is anticipatory. This is so because the sensory delays in relaying the change in load force to the central nervous system is of the range 50–100 ms.

Kawato (1999) proposed a control model that explains the “grip-force–load-force coupling.” Imaging studies verified that the components of the model can be located in the cerebellum and cerebral cortex; in particular it was shown that right and superior cerebellum may be the locus of the forward model that allows an anticipatory grip force modulation to occur (Kawato *et al.*, 2003). In addition, a PET imaging study by Boecker *et al.* (2005) indicated the existence of modular representations for predictive force coupling in the cerebellum, which are applicable to different environmental contexts (see also Nowak *et al.*, 2007 and Chapter 26). According to Kawato's model, there are at least three key computational elements (see Figure 9.2D, upper panel): the Arm controller, the Grip controller, and the Forward model. The Arm controller controls the arm, hand and the object held. This is usually considered an inverse model that produces feedforward motor commands given a desired arm trajectory.⁴ The Grip controller produces hand motor commands to keep the object firm in the hand by computing the grip force necessary given the arm trajectory: first the load force is derived using the arm trajectory,⁵ and then the grip force is easily estimated from the load force using the friction coefficient (this depends on the object/finger contact, here it is assumed to be known) and a safety margin scale factor. The Forward model uses the efference copy of the command sent to the arm muscles and predicts the arm state in the future. This future state is relayed to the Grip controller which calculates the required grip force *at the right time*, that is, before the object

actually experiences the load force that the motion of the arm will cause. In this way, the central nervous system guarantees the stability of the object even when the hand movements are very fast, where a feedback grip force controller would fail to react fast enough, and thus lose the grip on the object. This conceptual model will work fine for a single object as long as the forward model and the inverse models embedded in the controllers can be learned. In fact, there are various computational architectures that can satisfy these learning requirements and handle multiple objects. One particularly well suited to this context is the Modular selection and identification for control (MOSAIC) model (Wolpert & Kawato, 1998; Wolpert *et al.*, 2003). MOSAIC is a modular adaptive controller that can learn the dynamics of the controlled limb and multiple objects with different dynamic properties (Haruno *et al.*, 2001). Therefore it removes the multiple object limitation, and can be used to implement the model outlined above (Kawato, 1999).

Discussion

In primates, including humans, the brain areas that contribute to planning and execution of reach and grasp movements are relatively well known. Yet, the question of “how” still remains to be answered. This is the point where computational modeling comes into play. If a proposed working mechanism (conceptual model) can not be spelled out in computational terms and implemented on a computer, then it is very likely that the proposal is wrong, or missing critical components. (Of course, this argument is rather philosophical; one may be spiritual or believe that the way the brain computes cannot be emulated with a Turing-machine.)

Grasping and reaching being a complex behavior, it is not trivial to model in its entirety. Adult behavior gives us clues about the intrinsic optimizations carried on by the cerebral cortex in planning grasping and reaching. Detailed experimentation with the growing infant tells us about the phases of neural and motor development. First, the random-looking reaches of the newborn become directed towards visual and auditory stimuli by 2 months. The occasional contact of the hand with the objects in the environment triggers the palmar reflex. Infants use these “coincidental” grasps to learn how to orient or preshape his/her hand for a small set of objects by 6 months of age. These early grasps become more adult-like grasps by the age of 9 months; the transport phase now reflects the effects of the target object: during the transport the hand is preshaped and oriented according to the target size and orientation.

But then, how is the intrinsic optimization that appears to be central to adult reaching and grasping acquired together with infants’ motor development? Are development and tuning for optimal behavior mediated by different cortical mechanisms that follow different time courses? Motor development stabilizes after childhood; but obviously we retain our ability to learn new skills such as using new tools and inventing new grasping skills. So, how does the adult motor learning ability compare with the infant motor learning? One speculation is that the immature motor apparatus (for the hand and the arm) – the hardware – of an infant imposes restrictions on the “motor learning and optimization mechanisms” – the software – that undertakes the tasks of (1) learning to grasp, (2) learning to act optimally, (3) staying adaptive for new task requirements (i.e. what is “optimal” is not fixed, but can be redefined by

context). The corticospinal system is the main neural substrate for independent finger control (Triggs *et al.*, 1998). In infant primates, the development of corticospinal projections terminating in the ventral horn on motor neurons innervating hand muscles is essential for independent finger control (Bortoff & Strick, 1993), and lesion of the corticospinal tract prevents the development of independent finger movement (Lawrence & Hopkins, 1976). The myelination of the corticospinal tract and the enlargement of the diameter of the corticospinal axons (which both contribute to the conduction velocity) are main components of the cortical motor maturation. Therefore, the myelination and the enlargement of the diameter of the corticospinal axons might be a mechanism by which the “motor learning and optimization mechanism” are forced to follow a temporarily staged learning regime as seen in the developing infant. In fact, myelination of the corticospinal tract is far from complete by the end of the second postnatal year, and the increase in the conduction velocity of the corticospinal tract goes well beyond childhood (see Lemon *et al.*, 1997 and citations therein).

Although considerable knowledge has been gathered on individual properties of human grasping (i.e. at corners of the conceptual tetrahedron), we do not have a single and concise picture of human grasping. We believe that it is only when we can combine the (1) development of grasping, (2) the intrinsic optimality principles and (3) the adaptation capability of human reach and grasp within a neurophysiologically plausible computational model, will it be possible to make predictions that may shed light on the impairments of reach and grasp, and mediate the development of smart prosthetics and brain-machine interfaces.

Notes

- 1 We use homology in a somewhat loose sense; in the text it generally indicates functional equivalence rather than the strict definition adopted in evolutionary biology.
- 2 With the assumption that monkey and human grasp development follow similar paths, the model is specified in terms of macaque monkey nomenclature. In the macaque monkey, a specialized circuit in the parietal area AIP extracts object affordances relevant to grasping (Sakata *et al.*, 1998; Murata *et al.*, 1996, 2000) and relays this information to the premotor cortex where contextual and intention-related bias signals are also integrated for grasp selection/execution (see Fagg & Arbib, 1998). It is very likely that a similar circuit exists in the human (see Jeannerod *et al.*, 1995) and is adapted during infancy for subsequent acquisition of adult grasp skills.
- 3 Here it is assumed that the network activation functions are non-linear (e.g. sigmoidal activation function).
- 4 The net motor command arriving at the muscles is a summation of the feedforward command and the signals from the feedback loops at the cortical and subcortical structures. However for simplicity we talk about a single inverse dynamic controller for the arm.
- 5 Note that it is also possible to split the Grip force controller into two modules, the first one computing the load force based on the arm trajectory, and the second one deriving a grip force based on the output of the first module, the load force (see Kawato *et al.*, 2003).

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