

Modular features of motor control and learning

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Major advances

The focus on complex motor behaviors has highlighted the role of modular representations in the planning and in the execution of actions. Recent findings suggest the presence of functional modules within a variety of neural structures. Computational investigations are now addressing the issue of how these modules may act concurrently to generate a wide repertoire of behaviors.

Introduction

The most exciting advances in the study of the motor system have been brought about by a shift of the attention from simple to complex behaviors. Indeed, the class of behaviors that we elect to consider drastically affects our perspective on neural computation. When the investigations focus on the rich repertoire of actions in which living organisms engage, the number of states and of motor commands to be represented appears to be tremendously large. Then, computational analyses may provide valuable insights on constraints that must be satisfied by the neural circuits of the brain. The focus on complex dynamical behaviors has also been a feature of recent progress in the control of artificial systems. There too, the attention has moved from highly constrained manipulations to tasks such as controlling a bouncing ball with a paddle [1*], guiding objects by pushing and rolling [2,3] and, more generally, handling objects without grasping them [4*]. Understanding how this complex yet ordinary motor competence may be represented and implemented in robots is of great value in the study of the biological motor system. This review describes some of the advances that have been recently brought about in neurobiology by dealing with the complexity of 'real' motor behaviors. Among these advances is the formulation of new hypotheses on the building blocks, or "modules" that the central nervous system (CNS) may use to form useful representations for planning and control of actions [5].

The acquisition of complex skills is facilitated by internal models of dynamics.

The ability to generate a variety of complex behaviors cannot be attained by just storing somewhere the control signals for each action and recalling these signals when subsequently needed [6,7]. Simple considerations about the geometrical space of meaningful behaviors are sufficient to establish that this approach would be inadequate [8]. To achieve its typical competence, the motor system must take advantage of experience for going beyond experience itself, by constructing internal representations of the controlled dynamics. These representations allow us to generate new behaviors and to handle situations that have not yet been encountered. A vivid illustration of this is offered by recent work of Atkeson and Schaal [9-11*] who studied the task of balancing an inverted pendulum on the hand of a robotic arm. The balancing task can be accomplished by humans without much effort. Therefore, the simplest way to execute the same task

with a robot arm seemed to be that of copying with the robot every movement of a human expert. When Atkeson and Schaal tried this direct imitation approach they found that it failed: even if the hand movements were carefully copied by the robot, the smallest amount of uncertainty associated with sensing and acting did not allow the pendulum to remain balanced. This does not mean that imitation of successful behavior is not a valid strategy [12-14]. Quite on the contrary, the robot learned to act successfully when the data from the observed demonstrations were used not to mimic the expert's movements but to build an internal representation of the dynamics associated with the task. Such a representation may be constructed by a computational method called a search procedure. Search procedures start from some arbitrary initial model that specifies which action should be taken at every possible state. Then, the data from experience of trials and errors are used to iteratively update the model parameters until some optimal or, at least, satisfactory performance is attained. It turns out that in most cases, search procedures are effective only if the starting point - the initial assumptions about the dynamic model - is not too far from the correct representation. The work of Atkeson and Schaal shows that imitation is a useful strategy when it provides the learner with a good starting point for the subsequent development of an internal model by a search procedure.

The term "internal model" refers to two distinct mathematical transformations: 1) the transformation from a motor command to the consequent behavior and 2) the transformation from a desired behavior to the corresponding motor command [15-20]. A model of the first kind is called a "forward model". Forward models provide the controller with the means not only to predict the expected outcome of a command, but also to estimate the current state in the presence of feedback delays [21]. A representation of the mapping from planned actions to motor commands is called an "inverse model". Studies by Kawato, Wolpert and Miall [22**,23] have proposed that the neural structures within the cerebellum perform sensory-motor operations equivalent to a combination of multiple forward and inverse models. Strong experimental evidence for the biological and behavioral relevance of internal models has been offered by numerous recent experiments [16,24-28*,29]. Some experiments involved the adaptation of arm movements to a perturbing force field generated by an instrumented manipulandum. The major findings of these studies are as follows: 1) when exposed to a complex but deterministic field of velocity-dependent forces, arm movements are first distorted and, after repeated practice, the initial kinematics are recovered; 2) if, after adaptation, the field is suddenly removed, after effects are clearly visible as mirror

images of the initial perturbations [16,24]; 3) adaptation is achieved by the CNS through the formation of a local map that associates the states (positions and velocities) visited during the training period with the corresponding forces [30,31**]; 4) after adaptation this map - that is the internal model of the field - undergoes a process of consolidation [25]. In order to generate the appropriate command for a desired movement of the arm, an inverse model must take into account that multi-joint inertia depends on limb position and velocity. Therefore, an inverse model must be informed about the current state of motion of the limb. This information may come in one of two ways: 1) from the input to the inverse model that specifies where the limb should be or 2) from a prediction of the current state based on based on delayed sensory feedback and on the past history of motor commands. Bhushan and Shadmehr [32**] have found compelling evidence for the second way. Their experimental results are consistent with the hypothesis that we learn to compensate changes in limb dynamics by a process that involves the combined adaptation of a forward and of an inverse model of the limb.

What are internal models made of? The concept of motor receptive fields.

Once established that the motor system creates internal representations of complex multi-joint dynamics, it remains to determine how these representations may come about. As pointed out by Marr [33], any mathematical transformation may be carried out in different ways depending upon which elementary building blocks or "primitives" are employed. To identify a set of possible primitives one may proceed in two directions: a) top-down, based on the nature of the problem to be solved or b) bottom-up based on the properties of the motor output. As detailed below, these views lead to opposite conclusions about an important feature of motor primitives.

The goal of a control system is to define a *policy* [34]: a function that assigns to every possible state of the system and its relevant environment a specific action, for example the force to be produced by the limb muscles. Schaal and Atkeson [35**] demonstrated that complex policies can be learned by tuning the parameters of local controllers. Their approach to motor learning falls within the broad mathematical framework of function approximation [36]. The construction of an optimal (or, simply, of a "good") policy from experience is equivalent to the reconstruction of an unknown function from a set of sampled data- in this case the combinations of states and actions experienced during training. These data are used for tuning the parameters of

predetermined *basis functions* - local linear controllers in [35], radial basis function in [37] or Gaussian fields in [38]. A local controller operates only over a limited region of state space, that is called a *receptive field* in analogy with visual and somatosensory receptive fields. The computational analysis of Schaal and Atkeson shows that on-line learning of complex behaviors is successful only when the receptive fields are sufficiently small. If each local controller had a large region of influence, the tuning of its parameters might interfere disruptively with neighboring regions.

In contrast to the top-down analysis, the bottom-up analysis has revealed the existence of motor primitives with large receptive fields. Electrophysiological studies involving the stimulation of muscles and of the spinal cord in spinalized frogs [39,40] indicated a) that the focal stimulation of a site in the lumbar spinal cord results into the activation of multiple muscles acting on the ipsilateral leg; b) that synergistic muscle recruitment generates a field of viscoelastic forces over a broad region of the leg workspace and, c) that the simultaneous activation of multiple spinal sites leads to the vectorial summation of the corresponding force fields. The hypothesis that interneuronal circuits in the spinal cord organize a set of well-defined muscle synergies was recently supported by a computational analysis of electromyographic (EMG) activities induced in frogs by cutaneous stimulation of the leg [41**]. Taken together, these studies indicate that motor commands are not directed at controlling the forces of individual muscles or single joint torques. Instead, the descending commands that are directed to spinal interneurons modulate the viscoelastic force fields produced by specific sets of muscles [42]. These force fields have influence over broad regions of the limb state space as each active muscle within a synergy contribute a significant force over a large range of positions and velocities. Simulation studies showed that broadly-tuned nonlinear force fields similar to those elicited by stimulation of the spinal cord can generate - by linear combination - the kinematic and dynamic repertoire of reaching movements [38]. However, as shown by Schaal and Atkeson, broadly tuned force fields would lead to negative interference if one were to modify their parameters so as to optimize locally one movement at a time. In this respect it is worth to point out that human subjects display a significant degree of negative interference when adapting to a novel force field [16]: after adaptation is completed in a region of workspace, aftereffects are clearly observable in different regions.

The tradeoff between learning and stability

As pointed out by Hogan, another critical issue in defining the properties of motor primitives is the issue of stability [43,44]. A controlled behavior is stable when errors induced either by inaccuracies in planning or by unexpected perturbations are automatically corrected so that the behavior is rapidly restored. A number of experimental and theoretical studies have supported the hypothesis - known as the equilibrium point hypothesis- according to which reaching movements as well as other behaviors are obtained by the CNS shifting the static equilibrium of a limb along a continuous trajectory [45]. From a mechanical standpoint, this theory emphasizes stability: movements are constructed and represented as smooth transitions among stable postures. In this respect, the hypothesis that the CNS combines spinal force fields to generate stable behaviors is an extension of the equilibrium-point hypothesis. Lohmiller and Slotine [46**] have applied an elegant paradigm from nonlinear fluid dynamics to show that in the control of a nonlinear system, such as a multijoint arm, the linear combination of stable dynamical primitives leads to stable behaviors. The force fields generated by muscle synergies are indeed stable primitives within regions that correspond to the receptive field defined above: these are regions within which external perturbations are compensated by elastic forces. From this analysis it follows that stable behaviors are enforced over broad domains of a limb's state space by combining stable synergies with large receptive fields.

Higher order primitives.

While the internal representation of limb dynamics is vital for the execution of complex tasks, movements are planned in ways that may be independent from the details of movement execution. The computational modules that are needed for movement planning may indeed have features that are distinct from the modules for movement control. In early groundbreaking work, Georgopoulos and coworkers investigated the activities of motor cortical neurons in relation to the direction of hand movements [47]. They found that the firing rates of individual neurons are broadly tuned about preferred hand directions and that the linear combinations of preferred directions weighted by the cell activities provide a good estimate of movement direction. The importance of Georgopoulos' approach lies in the attempt to establish a direct relation between neural activities and kinematic variables related to movement planning [48,49]. These findings, however, have been controversial as they may be consistent both with coding of

variables related to movement execution, such as muscle activities, as well as with coding of variables related to movement planning, such as hand kinematics [50,51]. While some observations suggest a strict relation of motor cortical activity with the action of muscles [52-54], other experiments have shown dissociation between cortical activity and movement execution [55,56**,57**].

The presence of separate neural representations for movement planning and movement execution opens interesting issues concerning the relationships between these representations. Rizzolatti and Fadiga [58] suggest that the representation of action supported by "mirror neurons" in area F5 is a representation of action goals rather than of motor outputs. If these neurons form the basis for a "vocabulary" of actions [59**], that is if they support planning modules, then, it is of great importance to understand how the words of this vocabulary may be combined with each other by the brain to span a repertoire of purposeful behaviors. At present, we know that force fields implementing the execution of motor commands are combined by vectorial superposition. However, the rules that govern the combination of goals appear to be more complex. If there is a system of high order primitives that code for goals, then it remains to be established how these goals may be translated into movements so that their concurrent activation lead to meaningful results.

Conclusions

The latest progress in the study of the motor system has been characterized by an increased focus on complex dynamics of natural task in conjunction with the development of new experimental paradigms for the investigation of motor learning. There is a convergence of theoretical and experimental studies on the concept that complex control problems may be solved by a combination of independent modules. From a functional perspective, these modules implement control policies by associating an action to each experienced state. From a neurophysiological perspective, these modules organize specific synergies of muscles. Finally, from a mechanical perspective, these modules generate force fields upon the controlled limbs. The range of action of a module has been defined a receptive field. There is a significant trade off between on one side the demands for stability and the mechanics of muscles which both lead to broad receptive fields and, on the other side, the demands of learning which suggests narrow receptive fields in the interest of reducing unwanted interference

across the workspace. . This tradeoff defines an important area for future investigations of the interactions between higher and lower centers of the motor system.

REFERENCES

- [1]* Burridge R, Rizzi A, Koditschek D: **Sequential composition of dynamically dexterous robot behaviors.** *International Journal of Robotics Research* 1999, **18**: 534-555.

The paper describes both in formal and in intuitive terms an elegant approach to the issue of combining specialized local controllers to handle a broad problem domain. Their approach consists in dividing the state into smaller overlapping regions. In each region, there is a simple controller that is competent to bring reliably the system at a specified state within the region. The key idea is to combine these local controllers so that the system will eventually move toward the final goal. The work makes use of the formalism of differential geometry to develop this idea.

- [2] Mason M: **Mechanics and planning of manipulator pushing operations.** *International Journal of Robotics Research* 1986, **5**: 53-71.

- [3] Bicchi A, Sorrentino R: **Dexterous manipulation through rolling.** In *Proceedings of the IEEE International Conference on Robotics and Automation*, Washington, DC., 1995: 425-457

- [4]* Lynch K, Mason M: **Dynamic nonprehensile manipulation: Controllability, Planning and Experiments.** *International Journal of Robotics Research* 1999, **18**: 64-92.

Conventional robot manipulators establish a rigid contact with the manipulated object. This simplifies the geometrical relation between object and manipulator coordinates. However, this also constrains the range of possible operations. Humans and other animals operate by establishing 'nonprehensile' contacts: contacts that allow slipping or rolling of the object. This complicates the mathematical description but it also offers a broader repertoire of control policies. The paper provides a mathematically insightful approach to the problem together with some impressive demonstration

- [5] Ghahramani Z, Wolpert D: **Modular decomposition in visuomotor learning.** *Nature* 1997, **386**: 392-5.

- [6] Marr D: **A theory of cerebellar cortex.** *Journal of Physiology* 1969, **202**: 437-470.

- [7] Albus J: **The theory of cerebellar function.** *Mathematical Biosciences* 1971, **10**: 25-61.

- [8] Bizzi E, Mussa-Ivaldi FA: **The acquisition of motor behavior.** *Daedalus* 1998, **127**: 217-232.

- [9] Schaal S: **Learning from demonstration.** In *Advances in Neural Information Processing Systems*. Edited by M. Mozer, M. Jordan, and T. Petsche. Cambridge, MA: MIT Press; 1997: 1040-1046.

- [10] Atkeson C, Schaal S: **Robot learning from demonstration.** In *Machine Learning: Proceedings of the fourteenth international conference (ICML '97)*, 1997: 12-20

- [11]* Schaal S: **Is imitation learning the route to humanoid robots?** *Trends in Cognitive Sciences* 1999, **3**: 233-242.

In earlier work Schaal and Atkeson demonstrated that learning by imitation is most effective when the demonstration data are used to prime an internal model. In this paper, Schaal compares

a variety of different approaches to learning by imitation including model-based learning, symbolic approaches and direct learning of control policies.

- [12] Whiten A: **Imitation of the sequential structure of actions by chimpanzees (Pan troglodytes).** *Journal of Comparative Psychology* 1998, **112**: 270-281.
- [13] Byrne R, Russon A: **Learning by imitation: a hierarchical approach.** *Behavioral and Brain Sciences* 1998, **21**: 667-684.
- [14] Mataric M, Pomplun M: **Fixation behavior in observation and imitation of human movement.** *Brain Research. Cognitive Brain Research* 1998, **7**: 191-202.
- [15] Jordan M, Rumelhart D: **Forward models: supervised learning with a distal teacher.** *Cognitive Science* 1992, **16**: 307-354.
- [16] Shadmehr R, Mussa-Ivaldi FA: **Adaptive representation of dynamics during learning of a motor task.** *Journal of Neuroscience* 1994, **14**: 3208-3224.
- [17] Johansson R: **Sensory input and control of grip.** *Novartis Foundation Symposium* 1998, **218**: 45-59.
- [18] Kawato M, Wolpert D: **Internal models for motor control.** *Novartis Foundation Symposium* 1998, **218**: 291-304.
- [19] McIntyre J, Berthoz A, Lacquaniti F: **Reference frames and internal models.** *Brain Research Brain Research Reviews* 1998, **28**: 143-54.
- [20] Blakemore S, Goodbody S, Wolpert D: **Predicting the consequences of our own actions: the role of sensorimotor.** *Journal of Neuroscience* 1998, **18**: 7511-8.
- [21] Miall R, Wolpert D: **Forward models for physiological motor control.** *Neural Networks* 1996, **9**: 1265-1279.
- [22]** Wolpert D, Kawato M: **Multiple paired forward and inverse models for motor control.** *Neural Networks* 1998, **11**: 1317-1329.

This paper describes a computational architecture in which motor commands are generated by a collection of paired forward and inverse models. The approach is similar to the ‘mixture of experts’ proposed earlier by Jordan and Jacobs. Here, different forward models generate independent state estimations. Comparison of these predictions with the actual state is used to establish the degree to which each corresponding inverse model should contribute to the motor output.

- [23] Wolpert D, Miall R, Kawato M: **Internal models in the cerebellum.** *Trends in Cognitive Sciences* 1998, **2**: 338-347.
- [24] Flash T, Gurevich I: **Arm stiffness and movement adaptation to external loads.** *Proceedings of the Annual Conference on Engineering in Medicine and* 1992, **13**: 885-886.
- [25] Brashers-Krug T, Shadmehr R, Bizzi E: **Consolidation in human motor memory.** *Nature* 1996, **382**: 252-255.
- [26] Gottlieb G: **On the voluntary movement of compliant (inertial-viscoelastic) loads by parcellated control mechanisms.** *Journal of Neurophysiology* 1996, **76**: 3207-3229.
- [27] Flanagan J, Wing A: **The role of internal models in motion planning and control: evidence from grip force adjustments during movements of hand-held loads.** *Journal of Neuroscience* 1997, **17**: 1519-1528.
- [28] Sabes P, Jordan M, Wolpert D: **The role of inertial sensitivity in motor planning.** *Journal of Neuroscience* 1998, **18**: 5948-57.

The authors demonstrate that when an obstacle must be circumvented in a reaching movement of the hand, the hand trajectory is planned so that the point of minimum distance to the object is reached with the largest inertia in the direction between hand and obstacle. This choice insures that when the hand is closest to the object there is a minimal sensitivity to perturbations that could cause a collision. This work provides evidence that internal models of limb dynamics are used in movement planning.

[29] Hore J, Ritchie R, Watts S: **Finger opening in an overarm throw is not triggered by proprioceptive feedback from elbow extension or wrist flexion.** *Experimental Brain Research* 1999, **125**: 301-312.

[30] Conditt MA, Gandolfo F, Mussa-Ivaldi FA: **The motor system does not learn the dynamics of the arm by rote memorization of past experience.** *Journal of Neurophysiology* 1997, **78**: 554-560.

[31] Conditt MA, Mussa-Ivaldi FA: **Central representation of time during motor learning.** *Proceedings of the National Academy of Sciences* 1999, **In press**:

Earlier studies showed that the motor system compensates a perturbing force field by representing the dependence of the experience force upon the position and velocity of the limb. This work demonstrates that when the experimental force depends explicitly upon time instead of position or velocity, the internal representation is not accurate. Forces are still compensated as if they depended upon limb state. As a consequence adaptation does not generalize correctly to different movements.

[32]** Bhushan N, Shadmehr R: **Computational nature of human adaptive control during learning of reaching movements in force fields.** *Biological Cybernetics* 1999, **81**: 39-60.

This paper provides the first compelling evidence suggesting the joint operation of a forward and inverse model of arm dynamics during the adaptation to a novel force field. The authors suggest that a forward model is needed to provide the motor system with the opportunity to produce a mental rehearsal of new dynamics following a limited period of practice. This rehearsal would allow the consolidation of an inverse model, a process that has been observed in subjects after an initial exposure to a novel force field.

[33] Marr D: **Vision.** San Francisco, CA: W.H. Freeman and Co. ; 1982.

[34] Sutton R, Barto A: **Reinforcement learning: An introduction.** Cambridge, MA: MIT Press ; 1998.

[35]** Schaal S, Atkeson C: **Constructive incremental learning from only local information.** *Neural Computation* 1998, **10**: 2047-2084.

The authors describe a learning model, Receptive Field Weighted regression, in which simple locally linear elements are combined to reconstruct unknown functions in parallel with the collection of input-output data. This is called on-line learning to be distinguished from batch learning methods in which all the data are first acquired and then used subsequently. The authors show that the receptive fields of the linear elements can be rapidly adapted to minimize the amount of negative interference between different regions of the input space. It is worthwhile to observe that the local linear elements of this model correspond mathematically to the Gaussian fields in [38]

- [36] Bishop C: **Neural networks for pattern recognition**. Oxford University Press ; 1996.
- [37] Platt J: **A resource-allocating network for function interpolation**. *Neural Computation* 1991, **3**: 213-225.
- [38] Mussa-Ivaldi FA: **Nonlinear force fields : a distributed system of control primitives for representing and learning movements**. In *Proceedings of the 1997 IEEE International Symposium on Computational Intelligence in Robotics and Automation*, 1997: 84-90
- [39] Giszter S, Mussa-Ivaldi FA, Bizzi E: **Convergent force fields organized in the frog's spinal cord**. *Journal of Neuroscience* 1993, **13**: 467-491.
- [40] Mussa-Ivaldi FA, Giszter S, Bizzi E: **Linear combinations of primitives in vertebrate motor control**. *Proceedings of the National Academy of Sciences of the United States of America* 1994, **91**: 7534-7538.
- [41]** Tresch M, Saltiel P, Bizzi E: **The construction of movement by the spinal cord**. *Nature Neuroscience* 1999, **2**: 162-167.

These authors used a gradient descent technique to fit electromyographic data obtained after cutaneous stimulation of several sites of the frog hindlimb. They found that the linear combination of only four muscle synergies was sufficient to reproduce 126 EMG activities induced on 9 muscles by electrically stimulating the leg in 14 different locations. These results are consistent with the hypothesis that the neural circuits of the spinal cord implement a small number of independent muscle synergies.

- [42] D'Avella A, Bizzi E: **Low dimensionality of supraspinally induced force fields**. *Proceedings of the National Academy of Sciences of the United States of America* 1998, **95**: 7711-7714.
- [43] Hogan N: **The mechanics of multi-joint posture and movement control**. *Biological Cybernetics* 1985, **52**: 315-31.
- [44] Won J, Hogan N: **Stability properties of human reaching movements**. *Experimental Brain Research* 1995, **107**: 125-36.
- [45] Bizzi E, Hogan N, Mussa-Ivaldi FA, Giszter S: **Does the nervous system use equilibrium-point control to Guide single and multiple joint movements?** *Behavioral and Brain Sciences* 1992, **15**: 603-613.
- [46] Lohmiller W, Slotine J-J: **On contraction analysis for nonlinear systems**. *Automatica* 1998, **34**: 683-696.

This paper describes an approach to the stability of a control system based on a paradigm from nonlinear fluid dynamics. The approach is centered on the definition of a contraction region as a region where the Jacobian of the dynamics equations is uniformly negative definite. The analysis of the contraction regions of a dynamic system allows one to make strong inferences about the exponential convergence of the system toward a nominal trajectory.

- [47] Georgopoulos AP, Kalaska JF, Camintini R, Massey JT: **On the relations between the direction of two dimensional arm Movements and cell discharge in primate motor cortex**. *Journal of Neuroscience* 1982, **2**: 1527-1537.
- [48] Georgopoulos A, Lurito J, Petrides M, Schwartz A, Massey J: **Mental rotation of the neuronal population vector**. *Science* 1989, **243**: 234-236.
- [49] Georgopoulos A, Taira M, Lukashin A: **Cognitive neurophysiology of the motor cortex**. *Science* 1993, **260**: 47-52.

- [50] Mussa-Ivaldi F: **Do neurons in the motor cortex encode movement direction? An alternative hypothesis.** *Neuroscience Letters* 1988, **91**: 106-111.
- [51] Sanger T: **Theoretical considerations for the analysis of population coding in motor cortex.** *Neural Computation* 1994, **6**: 12-21.
- [52] Caminiti R, Johnson P, Urbano A: **Making arm movements within different parts of space: dynamic aspects in.** *Journal of Neuroscience* 1990, **10**: 2039-58.
- [53] Sergio L, Kalaska J: **Systematic changes in directional tuning of motor cortex cell activity.** *Journal of Neurophysiology* 1997, **78**: 1170-4.
- [54] Scott S, Kalaska J: **Reaching movements with similar hand paths but different arm.** *Journal of Neurophysiology* 1997, **77**: 826-52.
- [55] Fetz E, Finocchio D: **Operant conditioning of isolated activity in specific muscles and precentral cells.** *Brain Research* 1972, **40**: 19-23.
- [56] Carpenter A, Georgopoulos A, Pellizzer G: **Motor cortical encoding of serial order in a context-recall task.** *Science* 1999, **283**: 1752-7.

This is a study of motor cortical activity during a context-recall task. In this task a monkey was instructed to look at a sequence of targets and then it was cued to exert a force in a particular direction. A significant number of cells were found to modulate their activity exclusively in relation to the serial order of a target, regardless of its spatial location. This indicates a role of motor cortex in higher order planning of motor sequences.

- [57] Chapin J, Moxon K, Markowitz R, Nicolelis M: **Real-time control of a robot arm using simultaneously recorded neurons in the motor cortex.** *Nature Neuroscience* 1999, **2**: 664-670.

These investigators used the cortical and thalamic signals associated to a movement of the forelimb for controlling a motorized lever that performed the same task as the forelimb by releasing a water reward. As the action was transferred from the limb-operated lever to the motorized lever, the limb ceased to move while the neural activities remained correlated with the task performed by the artificial mechanisms. This study provides a strong demonstration that cortical activity patterns may be dissociated from the action of muscles.

- [58] Rizzolatti G, Fadiga L: **Grasping objects and grasping action meanings: the dual role of monkey rostroventral premotor cortex (area F5).** In *Novartis Foundation Symposium.*, 1998: 81-95
- [59**] Rizzolatti G, Arbib M: **Language within our grasp.** *Trends in Neurosciences* 1998, **21**: 188-194.

This is a thought provoking interpretation of the mirror neurons observed in several experiments by Rizzolatti's group. Considering the correspondence of monkey's area F5 with Broca's area in human, Rizzolatti and Arbib suggest that mirror neurons provide the foundation for the development of symbolic and linguistic processing in humans. This idea is based on the observation that language evolved not from animal calls but, more likely, from the mechanisms of communication associated with imitative behaviors.