Motor Control, Biological and Theoretical

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Introduction

Biological motor control can be characterized as a problem of controlling nonlinear, unreliable systems whose states are monitored with slow and sometimes low-quality sensors. In response to changing sensory inputs, internal goals, or motor errors, the motor system must solve several basic problems: selection of an appropriate action and transformation of control signals from sensory to motor coordinate frameworks; coordination of the selected movement with other ongoing behaviors and with postural reflexes; and monitoring the movement to ensure its accuracy. These stages may be interlinked, so that separation of any one particular problem into these individual stages may not be possible. This article describes some of the ways we think that biological motor systems solve these tasks, based on principles (and terminology) whose origins are in engineering and cybernetics. The field of cybernetics has developed from Norbert Wiener's initial ideas on communication and control theory in complex mechanical and biological systems, which focused on feedback mechanisms.

A motor control system acts by sending motor commands to a controlled object, often called the "plant," which in turn acts on its local environment (Figure 1). The plant or the environment has one or more variables that the motor system attempts to regulate, either to maintain them at a steady reference level in the face of disturbances (a "regulator") or to follow some changing reference value (a "controller"). The motor control system may make use of sensory signals from the environment, from its reference inputs, and from the plant to determine what actions are required. Sensory inputs from the plant can provide information about the *state* of the controlled object. Here, the state can be considered as all relevant variables that adequately describe the controlled object. But note that the sensory inputs to the controller do not necessarily provide direct measures of the true state of the system: They may be inaccurate or delayed, as discussed later. If controller output is based on signals that are unaffected by the plant output, it is said to be a *feedforward controller*: The feedforward control path is the thick line from left to right in Figure $1A_1$, which requires no return signals. If the controller output is instead based on a comparison between the reference and the controlled variables, it is a *feedback controller* (Figure $1B_1$): The control pathway is a closed loop. One can add more complex control strategies to these simple systems (Figure $1A_2$, $1B_2$), as described in more detail below.

The advantage of feedforward control is that it can, in the ideal case, give perfect performance with no error between the reference and the controlled variable. The main disadvantages for biological systems include the potential difficulty in generating an accurate controller for a complex system and the lack of error corrections. If the controller is not accurate, if the plant is unreliable, or if unexpected external disturbances occur, output errors go unchecked. Since no biological system can be both perfectly accurate and perfectly free of external disturbances, error correction is usually necessary. In contrast, the major advantage of negative feedback control lies in its very simple, robust strategy. The controller drives the plant so as to cancel the feedback error signaled by the comparator. Because it constantly seeks to cancel the error, it operates well, even without exact knowledge of the controlled object and despite internal or external disturbances. But feedback control strategies also have disadvantages: Errors cannot be avoided but must occur and be corrected, and feedback control—especially in biological systems—tends to be slow.

Feedback Control

The design criteria for negative feedback control are dominated by the closed-loop gain. Gain is defined as the ratio of a system's

67   output to its input. For a linear servo controller, the gain should be
68   close to unity, so that a given input (the reference value) evokes
69   an output of almost equal magnitude. In a feedback circuit (Figure
70    $1B_1$), one can define both open-loop and closed-loop gains. The
71   open-loop gain K_o is given by the ratio of the response to the error;
72   it gives the response expected if the feedback path shown in Figure
73    $1B_1$ is cut, thus opening the loop. The closed-loop gain K_c is given
74   by the ratio of response to reference amplitudes. The closed-loop
75   gain K_c is determined by the open-loop gain where $K_c = K_o/(1 +$
76    $K_o)$. For ideal control, K_c should be unity under all conditions; thus
77   the open-loop gain K_o should be as high as possible, ensuring that
78   K_c approaches unity. In practice, K_o is usually frequency dependent
79   and can never reach infinity; hence K_c is also frequency dependent
80   and less than unity.
81   The design of nonlinear and multidimensional feedback systems
82   is beyond the scope of this article, except to note that, in many
83   instances, complex control problems can be simplified and linear-
84   ized around the current state of the system. This may be particularly
85   true of biological systems, in which control is often only
86   approximate.
87   Notice that the comparison of the reference value with the con-
88   trolled variable to give an error signal (Figure $1B_1$) is affected by
89   the dynamics of the motor control and sensory systems. When a
90   command is issued by the controller, its effects are not immediately
91   apparent to the comparator, but are delayed by the plant and sensor
92   dynamics and by transport delays on both the forward and feedback
93   paths. In biological systems, where sensor delays are inevitable,
94   the comparison is always out of date. Hence in any feedback system
95   there will be a frequency at which these delays combine to impart
96   a 180° phase lag. The open-loop gain K_o at that frequency now only
97   needs to be unity (instead of very large) to make $K_c > 1.0$, forcing
98   the system into instability. Any small error or disturbance will be
99   overcorrected and result in even bigger errors, leading to yet bigger
100   corrections. Human examples of instability are indeed seen when
101   control delays are artificially increased in man-machine interfaces
          AQ=1
102   (Miall and Wolpert, 1996) or as a result of increased neural trans-
103   port delays in neuropathies such as multiple sclerosis.

104   *Physiological Feedback Circuits*

105   Although feedback control circuits are found throughout physiol-
106   ogy, let us consider just two examples from vertebrate motor sys-
107   tems. The major tension-producing fibers of the vertebrate muscle,
108   known as extrafusal fibers, contract following excitation by alpha
109   motor neurons. However, the amount of tension produced by the
110   muscle in response to a motor command varies with the length of
111   the muscle, its speed of contraction, level of fatigue, and so on.
112   The muscles are therefore provided with numerous sensory struc-
113   tures, muscle spindles, that signal back to the CNS the length and
114   rate of stretch of the muscle. Spindles are complex sensorimotor
115   structures combining contractile elements (intrafusal fibers, excited
116   by specialized gamma motor neurons) with a central stretch-
117   sensitive region. Their axons project onto alpha motor neurons in
118   the spinal cord which serve the same muscle and synergistic mus-
119   cles. This circuit (the stretch reflex) is a feedback controller for
120   muscle length. If the muscle is stretched, the spindles respond,
121   exciting the alpha motor neurons, and the resulting reflex contrac-
122   tion of the extrafusal fibers restores the muscle to its original length,
123   silencing the spindles again. Thus the spindles signal a deviation
124   from their regulated length, and the controller (the alpha motor
125   neuron) acts to cancel the error. The muscles also contain Golgi
126   tendon organs (GTOs), which are attached to the tendons of muscle
127   and respond to increased tension in the tendon. They excite inter-
128   neurons which inhibit motor neurons of that muscle and other mus-
129   cles acting around the same joint, and also act in a feedback man-
130   ner. If muscle tension increases due to an external load, for
131   example, the GTOs are activated and, via the inhibitory interneu-
132   ron, inhibit the motor neurons, causing the muscle to relax. This
133   reduces tension, and thus the negative feedback loop serves to
134   maintain a controlled level of tension. This description of the spin-
135   dle and GTO is oversimplified, ignoring aspects such as control of
136   muscle stretch velocity, but emphasizes their basic control prop-
137   erties. Together, they act to maintain a muscle in its current state:

138 Changes in length or in tension will be automatically opposed.

Feedforward Control

140 Feedforward control schemes may be grouped as those based on
141 direct control and those based on indirect control using internal
142 models. Here, direct control means control without *explicit* knowl-
143 edge of the behavior of the plant (see REINFORCEMENT LEARNING
144 IN MOTOR CONTROL). In practice, a controller that can store and
145 issue appropriate motor programs must have implicitly, if not ex-
146 plicitly, captured knowledge of the plant. Hence feedforward con-
147 trollers must be matched to the properties of the plant they control.
148 As a physiological example, the equilibrium point hypothesis (see
149 EQUILIBRIUM POINT HYPOTHESIS) makes use of the spring-like
150 properties of muscles. For any set of springs pulling across the
151 multiple joints of a limb, there will be a stable position into which
152 the limb passively settle. Thus, the CNS could define the "end-
153 point" muscle tensions and the limb would move to the desired
154 position without the controller's knowing either its starting position
155 or its behavior during the movement. An alternative direct scheme
156 is to generate the appropriate commands—a temporal sequence of
157 required changes in muscle force, acquired and stored as a motor
158 program—but again without any explicit knowledge of the plant.
159 In the limit one could use a memorized lookup table to store ap-
160 propriate motor commands for each input–output pair. However,
161 the memory demands grow explosively if a motor command is
162 stored for every possible pairing. Some form of generalization is
163 assumed to avoid this problem (see SENSORIMOTOR LEARNING)
164 such that a coarse-grained representation is achieved, with
165 interpolation.

Physiological Feedforward Control

167 Muscle spindles and GTOs are used to ensure that actions occur as
168 planned. By sending motor commands both to the alpha and to the
169 gamma motor neurons, both the force-producing extrafusal fibers
170 of the muscle and the much weaker intrafusal fibers of the spindle
171 co-contract. If the joint fails to move fast enough owing to an un-
172 expected load, the spindle contractile elements shorten within the
173 main muscle, the stretch-sensitive sensory region is stimulated, and
174 additional excitatory drive is reflexively added to the spinal alpha
175 motor neurons to overcome the load. The original position control
176 theory proposed by Merton has had to be supplemented by tension
177 and velocity control; but this simple description, while incomplete,
178 highlights the main principles. Note that by co-activating alpha and
179 gamma motor neurons, the reference values of the feedback circuit
180 described earlier are predictively modified. Thus for the supraspinal
181 centers driving the movement, the spinal circuits can be treated as
182 a feedforward controller, autonomously regulating the muscles
183 without the need for feedback to these higher centers. Of course,
184 if errors become large, cortical control can be invoked. This dem-
185 onstrates an important principle: Biological motor circuits are often
186 hierarchical, with lower levels regularizing the behavior of the con-
187 trolled object and higher systems providing increasingly indirect
188 control (Loeb, Brown, and Cheng, 1999).
189   Another example of feedforward control is found in the oculo-
190 motor system (see COLLICULAR VISUOMOTOR TRANSFORMATIONS
191 FOR SACCADES). Human eye muscles have muscle spindles, but
192 they do not seem to have a functional stretch reflex: Passive move-
193 ments of the eyes are not reflexively adjusted, and even seem to be
194 ignored. As Helmholtz noted, if one pushes on the side of one's
195 own eye, the resulting retinal movement is reported by the visual
196 system as movement of the external world. The reason the oculo-
197 motor system may be able to operate in feedforward mode is that
198 the mechanical load (the spherical eyeball) is relatively constant,
199 unaffected by external weights or gravity, and is therefore more
200 easily controlled than a multi-jointed limb. Functionally, of course,
201 there is powerful *visual* feedback: If the eyes drift from the target
202 of gaze, the error is reported as slip of the visual image over the
203 retina. Retinal slip drives "on-line" corrective velocity adjustment
204 during smooth eye movement. Because saccades are of short du-
205 ration, errors are corrected "off-line" with a secondary saccade.
206 Consistent saccadic under- or overshooting errors lead to long-term

207 changes in the feedforward controller, an example of adaptive
208 control.

Adaptive Control and Internal Models

Adaptive Control

211 Adaptive control (see ADAPTIVE CONTROL) relies on monitoring
212 performance over a longer time scale than that used by negative
213 feedback control to generate a measure of average performance
214 rather than of moment-to-moment error. The adaptive controller is
215 then used to adjust the motor responses, for example, by modulat-
216 ing the feedforward controller as indicated in Figure $1A_2$ or by
217 modulating the open-loop gain of a feedback controller. The ad-
218 vantage of adaptive control is that it can compensate for gradual
219 changes in the motor performance of the controlled object. Con-
220 trollers can also be designed to track predictable changes in the
221 reference value. Because the performance of physiological systems
222 (as well as the goals of behavior) changes over time, all biological
223 control systems are to some extent adaptive through mechanisms
224 as diverse as evolutionary change, growth, or learning and memory.
225 In control of eye movements, there is good evidence that the cer-
226 ebellum is involved in adaptation (Robinson and Fuchs, 2001).

Internal Models

228 Two forms of internal model can be distinguished. An ideal feed-
229 forward controller will ensure that the plant output (the controlled
230 variable) is always identical to the reference value. Thus it inputs
231 the reference value (and often also the state signals, Figure $1A_1$)
232 and outputs a motor command; the motor command shifts the plant
233 into a new state, which should equal the reference value. Thus one
234 can describe the ideal feedforward controller as an *inverse* of the
235 plant: The plant translates commands into states whereas the in-
236 verse controller translates desired states into commands. If the
237 transfer function of the plant is represented as P, its inverse is P^{-1},
238 and the transfer function of the complete system (from reference
239 value to controlled variable) is $P \cdot P^{-1} = 1$. Again, this implies
240 that the perfect system has a gain of unity. Inverse modeling is
241 covered in more detail in Jordan (1994).
242   The alternative type of internal model is known as a forward
243 model of the plant (Figure $1B_2$). Its inputs are a copy of the motor
244 command being sent to the plant and also the current feedback of
245 the plant state, and its output is an estimate of the next state of the
246 plant or of the controlled variables. This estimate is available to
247 the feedback controller more rapidly than actual feedback. Thus,
248 the external feedback loop can be replaced by an internal loop,
249 which avoids the feedback delays mentioned above. A negative
250 feedback loop with negligible delay and a high open-loop gain will
251 rapidly and accurately drive its plant in a direction to minimize the
252 comparator error. Thus, a fast internal loop including a forward
253 model is functionally equivalent to an inverse dynamic model. Of
254 course, viewed from outside the loop, it functions as a feedforward
255 controller: It disregards the actual feedback and hence is no longer
256 error correcting. The oculomotor feedforward controller may be an
257 inverse model like that shown in Figure $1A_2$ (Krauzlis and Lisber-
258 ger, 1989); an alternative proposal suggests an internal forward
259 model as in Figure $1B_2$ (Robinson, 1975).
260   Schemes that combine feedback with feedforward control (Hoff
261 and Arbib, 1992; Miall et al., 1993) depend on estimation of the
262 expected feedback signal, including its delay. Recent theories have
263 proposed combined forward and inverse models, working in pairs
264 for system identification, control, and adaptation (Wolpert, Miall,
265 and Kawamoto, 1998).

Physiological Internal Models

267 Visual guidance of the human arm is based on sensory information
268 from the visual system with processing delays of up to 100 ms.
269 Motor commands issued by the CNS may take 50 ms to initiate
270 muscle contraction, and these changes are signaled by vision and
271 by proprioceptors with delays of perhaps 50 to 100 ms. So feedback
272 signals from the environment will lag significantly behind the issue

of each motor command. Despite this, we control our limbs skillfully and accurately with movement durations of well under half a second. Thus, our motor control cannot be based entirely on feedback signals; we also employ feedforward control. It is likely (although not yet certain) that control is based on internal representations of the motor system—internal models (Miall and Wolpert, 1996).

Can we identify these internal models in the brain? The cerebellum is a strong contender for internal model representations (Ito, 1984; Wolpert et al., 1998). The model should receive as inputs either the motor goal or an efferent copy of the motor command, and also receive proprioceptive information about the current state of the body. There must be a mechanism to allow the model to adapt to predict accurately the behavior of the limb, i.e., a neural learning mechanism. And the output of the model must form either the motor command or a sensory prediction of the action outcome. The cerebellum can satisfy all these constraints, but this alone is not proof. Other possible sites are the motor cortex, parietal cortex, and the spinal cord, although a spinal representation would probably be more closely related to individual muscles than a model of the whole arm.

There are strong connections from the motor cortical areas and posterior parietal cortex to the lateral hemispheres of the cerebellum, and from there, ascending paths back to premotor and motor cortices or descending to brainstem nuclei. Spino-cerebellar tracts provide a large array of proprioceptive signals, updating the cerebellum on the current state of the limb. For adaptation, we know that coincident activity in climbing fiber and parallel fiber inputs to Purkinje cells results in a sustained change in the strength of the parallel fiber:Purkinje cell synapse (see LTD MECHANISMS OF CEREBELLUM). Some researchers therefore suspect that the cerebellum acts as an adaptive inverse model on the feedforward control pathway (Figure $1A_2$; Ito, 1984; Kawato and Gomi, 1992). Ito viewed the cerebellum as an adaptive side path to the descending systems, modulating the feedforward commands issued by cerebral control centers. Kawato views it as an alternative to these cerebral systems, replacing their control function. The alternative forward model-based scheme (Figure $1B_2$) is also valid; hence the cerebellum may represent an adaptive forward model on a feedback pathway (Miall et al., 1993). This Smith predictor theory places the forward model within the closed cerebro-cerebellar loop as the controller and incorporates feedback via an adaptive delay module. Each module is learned independently, with different time courses. It is difficult to distinguish between inverse dynamics models (Figure $1A_2$) and internal feedback loops containing forward models (Figure $1B_2$) unless one can get access to their internal structure. One might block the internal feedback loop needed for a forward model or decoding the input and output signals. However, many recent psychophysical, electrophysiological and functional imaging experiments have generated strong evidence of the use of internal models for motor control, for state estimation, and for planning and interpretation of actions.

Roadmap: Mammalian Motor Control; Robotics and Control Theory
Related Reading: Action Monitoring and Forward Control of Movements; Cerebellum and Motor Control; Optimization Principles in Motor Control; Sensorimotor Learning

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358

A1

reference variable(s) → Feedforward controller → motor command → Controlled object → Environment → controlled variable(s)

Sensors ← state variables

B1

error → Feedback controller → Controlled object → Environment

+ −

Sensors

feedback

A2

Adaptive controller ← Sensors

Feedforward controller → Controlled object → Environment

B2

Sensors

Internal model

Feedback controller → Controlled object → Environment

+ − −

Sensors