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A comparative approach to closed-loop computation

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Neural computation is inescapably closed-loop: the nervous system processes sensory signals to shape motor output, and motor output consequently shapes sensory input. Technological advances have enabled neuroscientists to close, open, and alter feedback loops in a wide range of experimental preparations. The experimental capability of manipulating the topology—that is, how information can flow between subsystems—provides new opportunities to understand the mechanisms and computations underlying behavior. These experiments encompass a spectrum of approaches from fully open-loop, restrained preparations to the fully closed-loop character of free behavior. Control theory and system identification provide a clear computational framework for relating these experimental approaches. We describe recent progress and new directions for translating experiments at one level in this spectrum to predictions at another level. Operating across this spectrum can reveal new understanding of how low-level neural mechanisms relate to high-level function during closed-loop behavior.

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Introduction

In his seminal 1948 book entitled ''Cybernetics,'' Norbert Wiener proffered that neural computation is a fundamentally closed-loop process [1]:

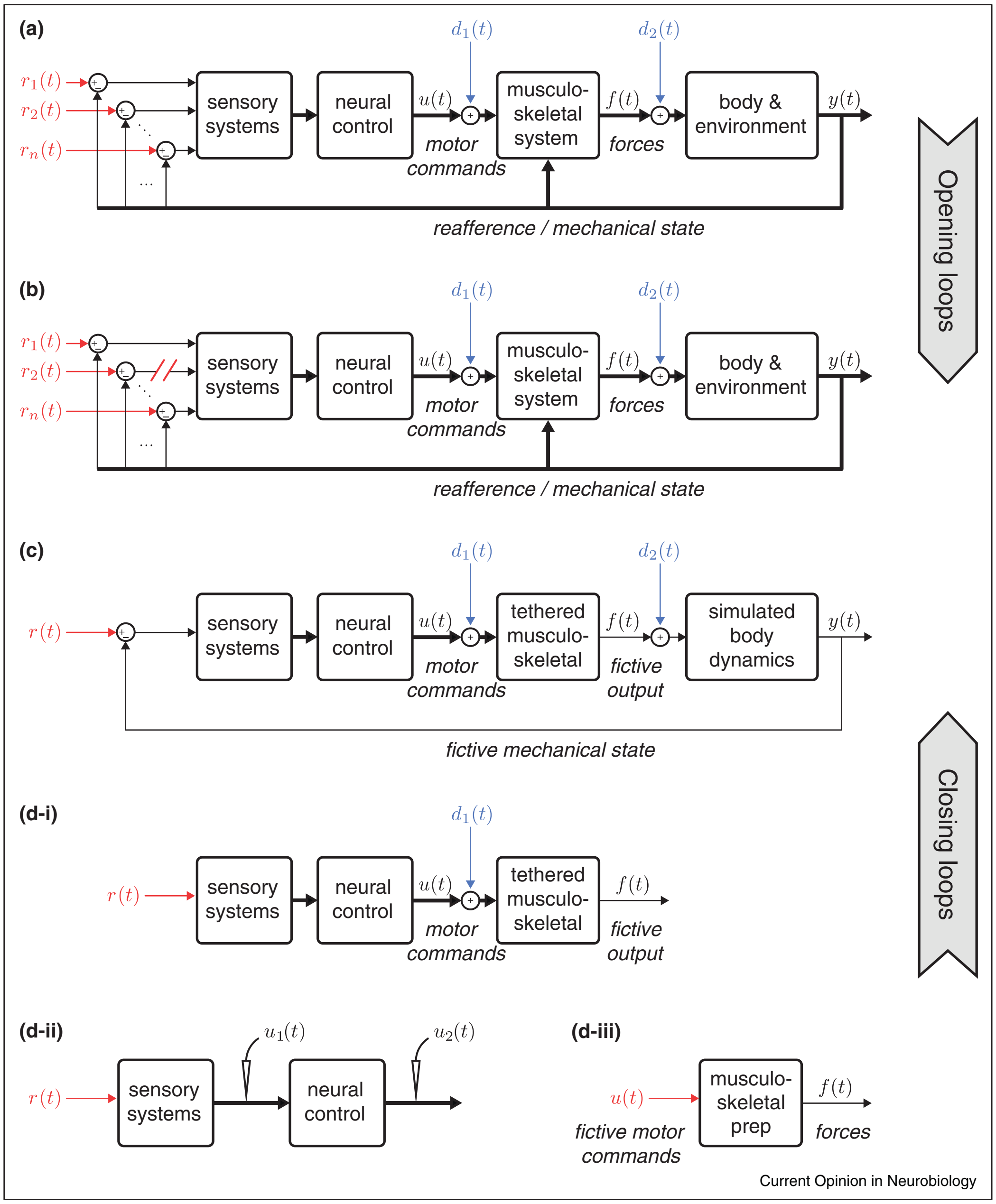
> The central nervous system no longer appears as a self-contained organ, receiving inputs from the senses and discharging into the muscles. On the contrary, some of its most characteristic activities are explicable only as circular processes, emerging from the nervous system into the muscles, and re-entering the nervous system through the sense organs. . .

This circular process is *closed-loop feedback*; sensing governs action, action changes the state of the animal in its environment, and these changes are perceived via sensing. This contrasts with *open-loop* processes, where information flows unidirectionally and the output of the system does not influence the sensory inputs. Understanding how behavior arises from the physiological complex of sensory, neural, and motor subsystems requires an understanding of how information flows through this network that is inescapably closed loop.

Technological limitations have historically required a focus on open-loop responses of individual mechanisms or subsystems within the nervous system. Recent progress has enabled unprecedented access to physiological signals across a spectrum of experimental conditions, spanning open-loop neurophysiology to artificially closed-loop preparations to perturbed free behavior (Figure 1). But, there remains a gap: the primary mathematical tools in computational neuroscience are statistics, information theory, and dynamical systems theory. Largely absent from that list is feedback control theory. Control theory can be thought of as a subfield of dynamical systems theory—after all, the addition of feedback loops merely alters the dynamics of a system. However, feedback control is a general and flexible means to achieve goal-directed ends, reject task-irrelevant disturbances, and govern system-level behavior. The dynamics of a feedback-controlled system can bear little resemblance to the open-loop response. Feedback can render fragile systems robust and unstable systems stable. For example, in human postural control, the body acts as an inverted pendulum (which is unstable), but under the control of the nervous system, the dynamic response shares the stable character of a hanging pendulum [2••].

Control theory furnishes a common language for quantifying and interpreting behavior of the whole animal or its subsystems in the closed-loop context. In what follows, we describe approaches to experimentally opening and closing feedback loops (Figure 1), present a control theoretic framework for interpreting and interrelating results across this spectrum of experimental paradigms, and then provide concrete examples showing how to use empirical results from one configuration to make quantitative predictions about system behavior in another.

Figure 1



A spectrum of experimental topologies. At all levels of the spectrum, we can record a variety of signals, including motor output, $u(t)$, force output, $f(t)$, and mechanical state, $y(t)$. We can perturb the system to modify behavior via modulations to reference signals $r_i(t)$ (red) or disturbances $d_i(t)$ (blue), which can be injected to motor commands or added to musculoskeletal forces. Thin lines represent signals with one (or very few) dimensions, while heavier lines represent potentially high-dimensional signals. **(a)** Free, intact behavior has multiple closed loops. The animal's movement (change in its mechanical state) is fed back via multiple sensory modalities. Only relative motion is measured by the nervous system, so self motion is intrinsically subtracted from exogenous reference signals $r_1(t)$ through $r_n(t)$ that represent these different sensory modalities (e.g. vision, olfaction, mechanoreception). **(b)** Working down the spectrum, if an individual sensory modality is inhibited, then the topology changes and the corresponding feedback loop is opened. **(d)** The bottom of the spectrum includes many fully open-loop conditions from rigidly tethered behavioral experiments (d-i) to reduced electrophysiological (d-ii) and *ex vivo* musculoskeletal (d-iii) preparations. **(c)** Working up the spectrum, we close the loop around these preparations in an individual modality by simulating the changes in the mechanical state of the body (fictive mechanical state), feeding that signal back, and subtracting it from the reference signal.