Overcomplete Musculature or Underspecified Tasks?

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The number of muscles in the body is actually fairly close to the number required to control completely all its degrees of freedom. The apparent need for a coordinating principle arises from the experimental practice of asking subjects to perform simple movements and assuming that they make no implicit assumptions about other constraints. Natural activities include implicit constraints that differ greatly for different tasks and circumstances and that would be met best by a nervous system free of a priori principles.

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Ever since Bernstein (1947; English translation 1967) pointed out the problem of having "overcomplete" or "redundant" muscles, biomechanists have been trying to guess the principle employed by the brain to decide which muscles to use. For some reason (foolish consistency?), they usually start by assuming that there is one such principle that is applied all of the time for all of the tasks. Boris Prilutsky has amassed much of the pertinent literature on muscle coordination in the limbs in support of Crowninshield and Brand's general principle. He concludes that it accounts well for a fair amount of the data, but he notes several exceptions that seem to require additional, ad hoc principles. Is the cup half-full or half-empty?

Perhaps we should think again about whether there is a cup to be filled. Do we really have more muscles than we need? Prilutsky starts with the assertion that "the number of skeletal muscles in animal and human limbs exceeds the number of kinematic degrees of freedom (DOF) in the joints." Let's do the math. Each human arm has about 25 DOF (including the scapula as 2 and counting each digit as only 3). Because muscles can pull but not push, there should be at least two muscles for each DOF, making 50. The human head-neck system from skull to the T1 vertebra includes 8 separate joints, each with 2 DOF, requiring 32 muscles overall. (The range of motion at each joint may be less dramatic than in the limb [Selbie et al., 1992], but any controlled motion still requires muscles.) The actual number of muscles controlling the neck or each arm alone is difficult to delimit because their mechanical actions overlap where they meet on the trunk, but the total for the neck plus two arms is not far from 132. From this perspective, the musculature may actually be incomplete rather than overcomplete, depending on

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how we count muscles with neuromuscular compartments that may or may not be independently controllable.

Perhaps what the biomechanists really mean is that there are more muscles than we need to perform the highly restricted tasks to which they set their subjects. If we imagine that the brain sees tasks in the same way that investigators describe them in their papers (e.g., "dorsiflex the ankle"), then there usually are many more muscles potentially involved than experimental DOF. But suppose that the brain, with its vast experience with more complex (not to say interesting) tasks, makes inferences about specifications that the investigator left ambiguous. Perhaps the subject infers that "dorsiflex the ankle" includes the notion of doing so without everting the ankle or wiggling the toes or without straining against the straps holding the thigh in place in the apparatus. Perhaps the subject understands that he or she will have to conserve energy to complete the 200 repetitions required by the experimental protocol. These inferred parameters provide reasons to perform the task using a particular combination of muscles, but a different set of explicit instructions might have caused the same ankle dorsiflexion to be produced by different patterns of muscle recruitment.

In real life, motor tasks normally come with even more sophisticated and variable specifications having to do with stability and accuracy in the face of perturbations. The pattern of elbow and shoulder muscle activation that you might use to hold a gun in your hand would likely depend greatly on whether or not you intended to fire it and whether it was pointed down, up, or horizontal (Brown & Loeb, 1999). This is because the intrinsic properties of the muscles are very useful for resisting perturbations (particularly the force-velocity component responsible for the viscous component of "stiffness"). The ability of the musculoskeletal system to resist generalized perturbations is best described by an impedance vector containing length, velocity, and accelerational terms (Hogan, 1984). In this two-joint system with monoarticular and biarticular agonists and antagonists, both the magnitude and direction of this impedance is strongly dependent on the distribution of activity in the various muscles. A biomechanist might note correctly that there are many more muscles than needed to produce the static torques at elbow and shoulder required to offset the weight of the forearm and the gun, but the brain knows that the task is much more complex. In fact, it can be performed optimally by only one pattern of cocontraction distributed among all of the available muscles. That pattern will be seen only if the subject actually understands the task fully and has had sufficient practice with it to have learned that optimal pattern.

The perturbations that cause the brain to select one of what appears to be an infinite number of equally valid motor strategies may not even be apparent to the investigator. The nervous system is plagued by internal computational and transmission noise arising from the stochastic summation of asynchronous post-synaptic potentials and the generation of all-or-none action potentials (Loeb & Marks, 1985; Scott & Loeb, 1994; Stein, 1967). This noise manifests itself in tremors and imprecision of posture and movement. The brain can minimize such adverse consequences via a combination of strategies, including adopting a stable posture, cocontracting antagonist muscles, setting fusimotor sensitivity and adjusting reflex gains (Loeb et al., 1999). The brain's assessment of what constitutes an adverse consequence may depend on conditions that are implicit in the way the task is presented (but perhaps overlooked by the investigator). Recently, Sabes et al. (1997) demonstrated that subjects tend to select particular trajectories of the hand

when going around a via point, apparently because those trajectories take advantage of the inertia of the forearm to stabilize the critical part of the trajectory against stochastic fluctuations in muscle activation produced by the nervous system.

Given all of the above considerations, it is surprising and therefore useful to note that a relatively simple optimization scheme accounts for a fairly large body of experimental data. For those interested in how the brain works, the question is whether this accounting reflects a fundamental principle of motor planning or coincidental similarities in an impoverished and ill-posed set of experimental paradigms. My personal bias is to be highly suspicious of any principle of motor planning that forecloses the use of any physically realizable strategy that might be useful under a particular set of circumstances. From this perspective, no general theory of muscle coordination could possibly take into account all of the relevant circumstances, and any overlooked parameter represents an opportunity to falsify the theory with a cleverly designed experiment.

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