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The Bliss of Motor Abundance

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Abstract

Motor control is an area of natural science exploring how the nervous system interacts with other body parts and the environment to produce purposeful, coordinated actions. A central problem of motor control – the problem of motor redundancy – was formulated by Nikolai Bernstein as the problem of elimination of redundant degrees-of-freedom. Traditionally, this problem has been addressed using optimization methods based on a variety of cost functions. This review draws attention to a body of recent findings suggesting that the problem has been formulated incorrectly. An alternative view has been suggested as the principle of abundance, which considers the apparently redundant degrees-of-freedom as useful and even vital for many aspects of motor behavior. Over the past ten years, dozens of publications have provided support for this view based on the ideas of synergic control, computational apparatus of the uncontrolled manifold hypothesis, and the equilibrium-point (referent configuration) hypothesis. In particular, large amounts of "good variance" – variance in the space of elements that has no effect on the overall performance – have been documented across a variety of natural actions. "Good variance" helps an abundant system to deal with secondary tasks and unexpected perturbations; its amount shows adaptive modulation across a variety of conditions. These data support the view that there is no problem of motor redundancy; there is bliss of motor abundance.

Keywords

motor redundancy; principle of abundance; synergy; referent configuration

Preamble

Over ten years ago, a brief Editorial was published in *Motor Control* with the title "There is no motor redundancy in human movements. There is motor abundance." (Latash 2000). In that paper, it was claimed that the formulation of the classical problem of motor redundancy – the MR problem – (Bernstein 1967) was misleading. There are good reasons to re-visit the redundancy-abundance issue. First, many researchers are still focusing their efforts on the MR problem in its original formulation. Second, much experimental data have been collected supporting the claim that the apparently redundant design of the human neuromotor system is not a source of computational problems for the central nervous system (CNS). For the purpose of this brief review, I would like to define motor control as an area of natural science (physics, including physiology) exploring how the nervous system interacts with other body parts and the environment to produce purposeful, coordinated movements. Motor control is not a subfield of control theory and/or engineering trying to decipher software in the brain that has to control the poorly designed body plagued with the hosts of complex interactions among body parts and between the body and the environment.

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So, this mini-review accepts as an axiom that the goal of motor control is to find a set of laws of physics that bring about observed patterns of physiological and behavioral variables.

Classical formulation of the MR problem

At any level of analysis of the system for movement production, there are more variables produced by elements (elemental variables) than constraints associated with typical tasks (Bernstein 1967). For example, for the task of reaching a target in the three-dimensional space, the number of arm joint rotations is typically more than three. For the task of producing a certain magnitude of joint torque, there are typically several muscles that span the joint. For the task of producing a certain level of muscle activation, there are numerous motor units that can be recruited at different frequencies. So, the CNS seems to always confront problems of choice from an infinite number of possibilities, similar to solving n equations with m unknowns, $n < m$.

The most common approach to the MR problem has been looking for a solution that optimizes (typically, minimizes or maximizes) a cost function (reviewed in Nelson 1983; Prilutsky and Zatsiorsky 2002). Cost functions have been selected rather arbitrarily, based on engineering principles or reasonable considerations from physiology, psychology, mechanics, and other areas. Best known examples include minimum jerk (Flash and Hogan 1985), minimum torque-change (Uno et al. 1989), minimum effort (Hasan 1986), minimum discomfort (Cruse and Brower 1987), as well as more complex cost functions (Rosenbaum et al. 2001). Recently, there have been a few attempts at reconstructing unknown cost functions based on sets of experimental observations using inverse optimization (Botasso et al. 2006; Terekhov et al. 2010).

Among more recent approaches to the MR problem is optimal feedback control (Todorov and Jordan 2002). Optimal control is a branch of mathematics developed to find ways to control a system, which changes in time, such that certain criteria of optimality are satisfied. The model of Todorov and Jordan minimizes the weighted sum of the squared difference between a function of the effector outputs and its required value and the effort defined as the variance of the control signals. This approach does not view MR as a problem (Diedrichsen et al. 2010). It suggests a particular method of producing flexible behaviors leading to a desired goal, which is one of the trademarks of voluntary movements. The approach is based on assuming computations within the central nervous system, an assumption that goes against the main axiom formulated in the first paragraph.

Roots of the MR problem

The classical formulation of the MR problem is deeply rooted in Newtonian mechanics and control theory. This formulation is based on an implicit (sometimes explicit) assumption that, to produce a movement, the controller has to make sure that all the involved elements produce certain outputs, in particular that all muscles produce requisite force time profiles (Hinder and Milner 2003; for review see Shadmehr and Wise 2005). If one starts with this assumption, a whole sequence of MR problems become unavoidable. These problems are inherent, for example, to the field of internal models based on an idea that neural structures compute/predict effects of the interactions among parts of the body and between the body and the environment (reviewed in Kawato 1999). A different view on internal models assumes that these models represent neural structures that map the realized effector system changes on expected perceptual consequences (Hommel et al. 2001). This definition is close in spirit to the notion of neural representations and does not allow the degree of formalization afforded by the former definition.

Early facts that spoke against the MR problem

One of the first classical studies by Nikolai Bernstein produced results that were already sufficient to claim that no unique, optimal solution is found for typical MR problems. Bernstein (1930) studied professional blacksmiths using his original motion analysis system (kimocyclograph) and discovered that high variability in the joint angle space across repetitive trials was associated with low variability of the hammer trajectory. Note that the subjects in that study were as well trained as one could possibly imagine for the task they performed: hitting the chisel with the hammer. So, if there were such a thing as an optimal solution for the problem of kinematic redundancy, these subjects were in the best position to discover it. Nevertheless, they showed “repetition without repetition” (Bernstein 1967), that is repetitive solutions of the task with variable means. A number of later studies provided more evidence for variable solutions used by humans (and animals) in tasks that involved motor redundancy, even following extensive practice (Jaric and Latash 1999; Latash et al. 2002; Yang and Scholz 2005).

The principle of abundance

Consider the following problem: When an action potential is generated on the membrane of a neuron, a huge number of Na^+ ions cross the membrane. There are many more ions in the vicinity of the site where the action potential is being generated. How does the CNS decide which ions should cross the membrane? This is a problem with zillions of unknowns. Likely, 100% of the readers would agree that the CNS does not micromanage at such a level. It does not care which particular ions participate in the process. The laws of physics make sure that about the right number of ions cross the membrane.

Consider now the aforementioned problem of defining a motor unit recruitment pattern for a desired level of muscle activation. Does the CNS care about specific patterns of recruitment or does it allow laws of physics – including the size principle (Henneman et al. 1965) – solve the problem? In this context, “physics” implies classical physics, chemistry, and physiology; however, it does not imply computation. Does the CNS care about specific solutions for the problems of sharing joint torque among the muscles and sharing fingertip trajectory among the joints of the limb? There will be less agreement among researchers with respect to these questions.

An alternative view on the apparently redundant design of the neuromotor system was suggested as the principle of abundance (Gelfand and Latash 1998). According to this principle, the CNS facilitates families of solutions equally able to solve the task. It does so by imposing (time-varying) constraints on the system “body+environment” (cf. Hu and Newell 2011) and allowing solutions to emerge given the actual state of this system (which never repeats exactly over repetitive trials). In other words, laws of physics define behavior of the neuromotor system at any level just like they define motion of Na^+ during the action potential generation. The phrase “CNS imposes constraints” should also be viewed as a reflection of our current lack of knowledge of physical processes underlying decision making by the brain. For remarkable reviews and insights on this issue see Kugler and Turvey (1987) and Strepp and Turvey (2010).

Evidence that motor abundance is a bliss

Over the past ten years, dozens of publications have provided support for the view that there is no MR problem but instead there is bliss of motor abundance. One such direction of research has been associated with the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999; Latash et al. 2007; Martin et al. 2009). The UCM hypothesis assumes that physical processes associated with performing a movement by a redundant system can be adequately expressed as creating a sub-space (UCM) in the space of elemental variables corresponding to a desired value of an important performance variable to which all the elements contribute. Note that elemental variables are not ‘controlled’ in any sense. It is important that there is theoretical availability and actual use of numerous (infinite number of) solutions in typical tasks. Variance along the UCM does not affect performance and has been addressed as “good” (V_{GOOD}), while variance orthogonal to that space is “bad” (V_{BAD}). Large amounts of V_{GOOD} have been documented in studies of multi-joint kinematic tasks, multi-digit kinetic tasks, and multi-muscle tasks (reviewed in Latash et al. 2007). Note that V_{GOOD}, by definition, has no effect on performance and, therefore, cannot be predicted by any approach looking for single optimal solutions for the MR problems. V_{GOOD} emerges in optimal feedback control schemes that allow numerous solutions to emerge; these approaches look for both optimal solutions and a feedback law around them (Todorov and Jordan 2002).

V_{GOOD} is not simply a by-product of the imperfect system design, “neuromotor noise”. Several studies have shown that the CNS increases the relative amount of V_{GOOD} (and sometimes even its absolute magnitude) in conditions of possible changes in the target location (de Freitas et al. 2007), practice in an unusual force field (Yang et al. 2007), practice of a novel task (Latash et al. 2002; Yang and Scholz 2005), and fatigue of one of the elements (Singh et al. 2010). V_{GOOD} has been shown to help an abundant system to deal with secondary tasks (Zhang et al. 2008) and unexpected perturbations (Gorniak et al. 2009; Mattos et al. 2011).

The equilibrium-point (referent configuration) hypothesis

According to the opinion of the author, currently there is only one theory of motor control that is based on the physical approach to movement production and is compatible with the known physiology of the neuromotor system, the equilibrium-point hypothesis (Feldman 1966, 1986). Originally this hypothesis was developed for one-muscle and one-joint systems. It suggested that the very complex system of reflex pathways controlling a muscle (which involves many apparent MR problems) can be adequately described with setting just one parameter, threshold ( ) of muscle activation to length. This method of control is an example of applying the principle of abundance to a particular subsystem within the body. The controller imposes a constraint on the system (sets a value of), which facilitates numerous patterns of neuronal activation, including motor unit firing patterns, for any task, for example, moving a constant external load to a new location.

Recently, the equilibrium-point hypothesis has been generalized for multi-joint action in the form of the referent configuration (RC) hypothesis (Feldman 2009). The RC hypothesis may be viewed as reflecting a hierarchical system, where at the upper level of the hierarchy, subthreshold depolarization of a neuronal pool defines a RC of the body (given external force field) in terms of task related variables. RC is a configuration at which all muscles are at thresholds of their activation. RC may not be attainable due to external and anatomical constraints; as a result, an equilibrium state may emerge with non-zero levels of muscle activation reflecting the difference between the actual configuration and RC. After a RC is established, a sequence of few-to-many mappings leads to inputs into -motoneuronal pools that define thresholds of the tonic stretch reflex for the involved muscles (Latash 2010). At each step of the hierarchy, the system functions according to the principle of abundance: No MR problems are being solved but task-specific constraints are imposed by the controller thus affording the system flexibility of getting to acceptable solutions.

Two aspects of synergies: Sharing and variable solutions

Recent developments of the principle of abundance have led to the idea of synergies as neural organizations that ensure task-specific co-variation of elemental variables providing for desired stability properties of an important output (performance) variable. Imagine a simple task involving a redundant system, for example pressing with two fingers to produce a specific total force magnitude, F_{TASK}. Any point that belongs to the line $F_1 + F_2 = F_{TASK}$ solves the task. Imagine now that a subject performs this task many times and the data for each trial are plotted as points on the force-force plane (Fig. 2). Two major characteristics of the data distribution can be introduced: (1) the location of the center of the distribution; and (2) the shape of the distribution. For simplicity, in Fig. 2 it is assumed that the distribution forms a perfect ellipse, and its center is on the line of perfect performance.

The method developed within the UCM hypothesis can be used to quantify the amount of V_{GOOD} (along the dashed line in Fig. 2) and V_{BAD} (orthogonal to this line). The other characteristic, the location of the center of the data distribution, may indeed be formally described as following an optimization principle. Note that in this context optimization is used not to define a single optimal solution for the task (in Fig. 2 the task is always the same but the solutions obviously vary) but the center of a distribution of solutions. Recent attempts at computing cost function based on experimental observations, inverse optimization (Terekhov et al. 2010), have been promising but interpretation of the reconstructed cost functions is still at its infancy and does not go beyond rather simplistic biomechanical considerations (Park et al. 2011a,2011b).

Generalization of the principle of abundance

While the MR problem explicitly refers to *motor* redundancy, such problems are inherent to other aspects of the functioning of the CNS. For example, the idea of sensory abundance and sensory synergies has been discussed (Latash 2008). Indeed, information on the person's own body and external world is delivered by receptors of different modalities, and the task of the brain in to construct a single, coherent picture of the body in the world based on all these signals (and preconceptions). This picture is stable if one or a few of the sensory signals become unavailable, for example when a person closes the eyes or puts on earphones. Recent studies on sensory re-weighting suggest that the CNS uses sensory signals of different modalities with weights that depend on the reliability and availability of those signals (Maurer et al. 2006). Regularities in linguistic tasks involving picture description have been demonstrated despite the variability across individual trials (Latash et al. 2011). In general, any decision making is typically based on abundant information; the recent idea of Feldman (2011) that control with thresholds for activation of neuronal pool may be involved in all cognitive processes is compatible with the main message of this mini-review: We are blessed with abundance; so, let us not waste time trying to eliminate it.

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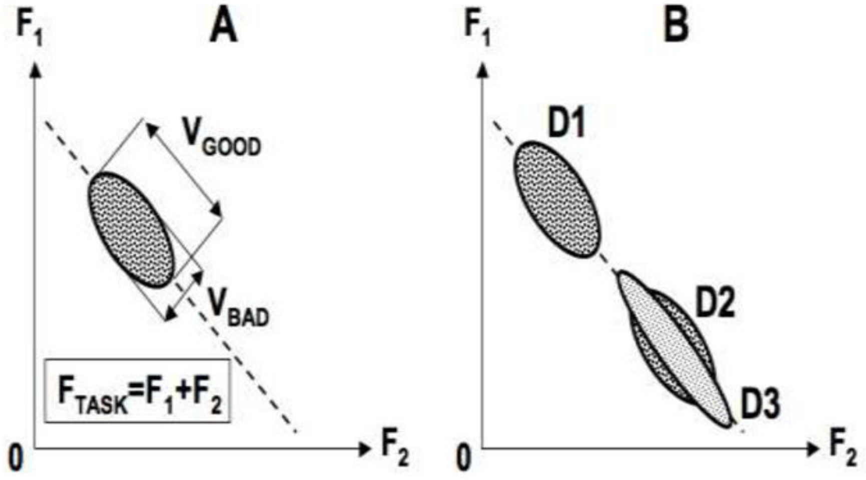

Figure 1.

A: An illustration of the notions of “good” and “bad” variance for the task of producing a magnitude of total force by pressing with two index fingers on individual force sensors. The dashed line shows the sub-space corresponding to perfect task execution. B: For the same task different data distributions are illustrated corresponding to different sharing patterns (different locations of the centers of the distributions, cf. D1 and D2) and different co-variation (different relative amounts of “good” and “bad” variance, cf. D2 and D3).