How the Brain Solves Redundancy Problems

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In the review, Latash summarizes the many achievements of his group and numerous collaborators in clarifying and experimentally supporting the synergy concept re-defined in the framework of the uncontrolled manifold (UCM) concept. This concept is the basis of an effective method of analysing motor actions, including their anticipatory (“feedforward”) aspects and their deficiencies in the case of neuropathology. In combination with the synergy concept, the UCM notion also represents a theoretical framework that provides some insights on how the brain controls motor actions. I will comment on the second, theoretical aspect of the UCM-synergy approach.

Admittedly, this approach is not sufficient to understand how the brain solves redundancy problems in motor control. Specifically, redundancy in the number of mechanical degrees of freedom (DFs) is the basis for flexible motor behaviour allowing the brain to produce different motor actions to meet motor demands despite changes in the properties of neuromuscular elements (e.g. resulting from muscle fatigue) or external, environmental conditions. Such flexibility likely played a key role in human survival in evolution. On the other hand, flexibility might not be helpful without the ability to quickly initiate a unique action each time the motor goal is clear, while disregarding many other actions leading to the same motor goal. This ability often takes place in the absence of any possibility of repeating and comparing different actions, for example, in sports and especially in threatening situations (Bernstein 1996). This implies that the redundancy (abundance) problem cannot be solved without addressing the question of how the uniqueness of actions is achieved without repetitions. Latash suggests that the UCM-synergy approach should be combined with some optimality criterion or principle to enable a specific action for each motor goal.

Formulated in terms of “elemental” variables that predominantlydescribe effect, rather than cause, the UCM-synergy approach leaves the question of how motor actions are actually controlled and executed unanswered. To overcome this limitation, Latash makes an attempt to place the UCM and synergy concepts into the context of a theory that directly addresses this question. The choice of the advanced formulation of the equilibrium-point (EP) theory to address the control question seems natural. Unlike other conventional theories, it offers a physiologi-
cally feasible solution to several classical action-perception problems, including the fundamental posture-movement problem of how the brain may make movement from a stable posture without evoking resistance of posture-stabilizing mechanisms (Feldman 2009).

I will use the framework of the EP theory to outline solutions of different redundancy problems in the control of motor actions. This may provide the basis for further discussion on how the UCM and synergy concepts can be incorporated into the EP theory.

**Rank-Ordered Recruitment of Neurons and Muscles.** If motor units (MUs) of a muscle were functionally identical and recruited independently of each other, then the same muscle force could be reproduced by recruiting different MUs. The redundancy problem is successfully avoided due to a specific organization — the rank-ordered recruitment of MUs such that, except for the case of fatigue, the same MUs are recruited each time it is necessary to generate the same muscle force (Henneman et al. 1965). In the framework of the EP theory, this rule has been reformulated by suggesting that MUs are recruited depending on their individual threshold lengths (Fig. 1A). The total number of recruited MUs is defined by the tendency to minimize the difference between the actual muscle length ($x$) and the threshold length ($\lambda^*$) of the MU that initiates muscle activation (Feldman and Levin 2009; here and below the asterisk implies that he threshold depends on the velocity of muscle lengthening, inter-muscular interactions and intrinsic or history-dependent properties of motoneurons, see Feldman 2009). This specific example may reflect a general rule: redundancy problems are avoided by the rank-ordered recruitment of neurons and muscles.

**Figure 1** — Examples of avoiding redundancy problems at different levels of motor control.
**Taking Advantage of Natural Physical and Physiological Laws.** This type of solution of redundancy problems can be illustrated by considering the interaction of muscles with an external load (Fig. 1B). By specifying the common threshold joint angle (R) for recruitment of all muscles spanning a joint, the brain chooses a monotonic torque-angle relationship called the invariant characteristic. The points on the ICs are EPs, each of which represents the combination of the static muscle torque and joint angle associated with a steady state of the system. By specifying an invariant characteristic, the system only narrows the set of possible steady states but does not pre-determine which of them will be reached. The nervous system allows the joint to interact with the load to reach a unique EP from this redundant set (Fig. 1A). If, say, the established position is different from the target position, the brain may continuously change the R to nullify the movement error. A more general rule following from this simple analysis is that the brain, in essence, does not solve redundancy problems – it just narrows the amount of redundancy and allows natural interactions of the system to bring about unique actions.

**Constraining Neurons and Muscles To Work in Common Spatial Frames of Reference.** When we want to carry many objects, we usually put them in a box and deal with all of them as if it were a single object. In abstract, mathematical terms, the objects represent a set of elements and the box is a spatial frame of reference (FR) in which these elements are placed. By shifting the FR, we relocate all elements in a FR associated with the environment. In the EP theory, a similar means is used by the brain to control numerous neurons, muscles and DFs without redundancy problems.

In the previous example, the threshold joint angle, R, is just one of numerous forms of threshold position control considered in the EP theory. Each threshold position can be considered as the origin (referent) point in the respective spatial (FR) in which muscles are activated. In particular, the referent arm configuration (R_a) is the origin point in a spatial frame of reference that represents all-possible geometrically defined arm configurations (Q_a). Thereby, the difference between Q_a and R_a* is a global factor that guides recruitment and de-recruitment of each arm muscle.

Another form of threshold position (considered in the review) is the referent body configuration (R_b) for all skeletal muscles. An important implication of the R_b concept is that despite a tremendous number of muscles, the brain does not need to decide which muscles should participate in an action: in the body configurational FR, all skeletal muscles are constrained to act as a coherent unit and each muscle may or may not be involved in the action, depending on the gap between Q_b and R_b*. This implies the absence of any redundancy problem in the control of multiple muscles (Feldman et al. 2007). Note that this control organisation is similar to that of MUs, except that, instead of MUs, the former organization provides rank-ordered recruitment of neurons that deal with different referent body configurations. Thus, by placing neurons and neuromuscular elements in a spatial FR, the brain can control them as if they were a single unit, without any concern about redundancy.

**Hierarchy of Spatial Frames of Reference.** To avoid redundancy problems in dealing with multiple FRs, FRs can be hierarchically organized such that each low-level FR is imbedded into a hierarchically higher FR (a variety of the rank-ordered recruitment principle). At the top of this hierarchy is an FR with
an origin point that represents the referent location ($R_l$) of the whole body in the environment. By shifting the referent body location, the nervous system influences referent body configurations and thus can elicit actions such as taking a step, walking or running depending on the duration, rate and direction of $R_l$ shifts (Fig. 1C; Feldman et al. 2007).

**The Principle of Natural Selection of Actions.** The principle of natural selection of actions unifies the solutions of redundancy problems described above (Feldman et al. 2007; Feldman and Levin 2009). The principle also integrates some elements of the principle of minimal interaction (Gelfand and Tsetlin 1971) nicely discussed by Latash. The name of the principle also implies that actions are selected like species in the process of evolution but on a comparably shorter time span since action selection substantially relies on rapid interactions guided by natural physical and neural laws.

Many, if not all, motor actions can be considered as minimization tasks. For example, by reaching and grasping an object, we minimize the discrepancy between the shapes of the hand and object (Yang and Feldman 2009). A primary purpose of taking a step or walking is to minimize the difference between the actual ($Q_l$) and desired ($Q_{d_l}$) locations of the body in the environment (Fig. 1C). A waiter minimizes the deviation of a tray loaded with dishes from the horizontal plane to avoid them sliding. Different forms of threshold position control can be considered as tools that enable such minimizations. For example, to take a step, the system can shift the referent location, $R_l$, of the body in the environment by influencing neurons that receive visual information about the actual body location, $Q_l$. Activated depending on the gap between $Q_l$ and $R_l^*$, these neurons will also tend to minimize their activity by influencing neurons responsible for shifts in the referent body configuration, $R_b$ (Fig. 1C), presumably accomplished by the central pattern generator for locomotion. These neurons will tend to minimize the difference between the actual ($Q_{d_b}$) and the referent body configuration ($R_{b_l}$) by forcing motoneurons to appropriately change their $\lambda$ s, thus producing a step. The step will not only re-locate the body in the environment but also minimize the difference between the actual ($x$) and threshold muscle length ($\lambda^*$) for each skeletal muscle. The minimization process continues until the desired body location is reached (Fig. 1C).

Reach-to-grasp movement can be guided by neurons responsible for changes in the referent hand shape ($R_{h_l}$) that subordinate neurons responsible for changes in the referent arm configuration, $R_a$. The minimization process brings the hand to the object. Changes in the referent position of the fingers continue such that they begin to virtually penetrate the object (Pilon et al. 2007) until cutaneous receptors signal that the emerging grip force has reached a safety margin for preventing slippage of the object from the fingers. The minimization process attracts all DFs that can contribute to this process. As a consequence, the hand trajectory may remain invariant if the number of DFs involved in the task changes either intentionally, or following mechanical perturbations. This prediction of the minimization strategy has been validated (Adamovich et al. 2001).

The task of carrying a tray loaded with dishes can be governed by neurons responsible for the referent orientation of the hand ($R_{o_l}$). The minimization process in this case resembles that for reach-to-grasp movements, except that in the former case it prevents large deviations of the tray from the horizontal plane. The control is
based on proprioceptive, tactile and visual information reflecting these deviations. This is done without knowledge or imitation of multi-dimensional mechanical equations of motion and torques describing the behaviour.

In light of the fact that there are many forms of threshold position control in addition to the referent body configuration, how the UCM and synergy concepts can be integrated into the EP theory still needs further consideration. The synergy concept also needs further clarification since, defined in the context of the UCM hypothesis, the concept relies on the possibility of action repetitions. While action repetition may be essential for motor learning, the solution of the redundancy problem requires an explanation of how a unique action can be chosen regardless of whether or not it can be repeated (see above). Finally, assuming that actions are repeated, is it possible to derive basic properties of the UCMs from the principle of natural selection of actions?

**Note**

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**References**


