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Comment

A physicist's view on biological synergies
Comment on "Hand synergies: Integration of robotics and neuroscience for understanding the control of biological and artificial hands" by Marco Santello et al.

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The review by Marco Santello and his colleagues [1] presents a comprehensive treatment of a number of central concepts in the fields of motor control and robotics. In this brief commentary, I focus not on aspects where I completely agree with the authors (> 95% of the review!) but rather on concepts that, in my opinion, could be developed better with an emphasis on specific features of biological movement that make it different from movement of inanimate objects, including robots. *Motor control* can be defined as a field of science searching for laws of nature describing interactions within the body and between the body and the environment that lead to natural movements [2]. This definition makes motor control a subfield of the physical approach to biological movement (cf. [3,4]).

A physicist typically starts with definitions. Here is one for *living system*: A living system is a system able to: (1) unite universal physical laws (those common for all objects) into chains and clusters leading to new stable and pervasive relations among physical variables and involving new parameters; and (2) modify these parameters in a purposeful way. In other words, living systems create *biology-specific physical laws* (BSPLs) and then modify parameters of those new laws to achieve their goals. (At this time, the origin of the goals is beyond my comprehension.)

I agree with Santello and colleagues that the neural control of movement is organized in a hierarchical way. Within the current set of terms, this means that BSPLs that define behavior at a higher hierarchical level use hierarchically lower BSPLs as the basis. For example, pointing movement by an arm may be described at the level of its end-effector (e.g., the hand, [5,6]), joint rotations, and also at the level of muscle involvement as a combination of BSPLs defined

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by the stretch reflex mechanisms for each of the muscles [7]. Within such a hierarchy, the number of parameters describing action at higher levels is typically smaller than the number of parameters describing the same action at lower levels.

The review defines synergy as a set of performance variables (degrees-of-freedom, DOFs) changing together, possibly reflecting time changes in a single higher-order variable. Within this definition, the main purpose of synergy is viewed as reducing the number of DOFs manipulated by the central nervous system (CNS) helping to alleviate the famous problem of redundancy [8]. This idea has been supported by many experimental studies using matrix factorization techniques ([9–12], reviewed in [13]). Note, however, that such higher-order variables (synergies or *modes*) have shown flexibility in their composition with modification of tasks [14] and, moreover, some of the mode sets may not reduce the number of DOFs (e.g., finger modes, [15]).

The review does not consider an alternative view that the problem of motor redundancy exists in the minds of researchers, not in biological systems. The apparently redundant design of the human body may be better addressed as *abundant* [2,16]. It is not a source of computational problems for the CNS but a purposeful design. One of its purposes is ensuring *stability of performance* with respect to salient variables; different variables can be stabilized by the same set of effectors depending on the task [17]; this idea has been confirmed and developed in later studies [18,19]. The hierarchical neural organization of multi-effector system can be characterized by (a) sharing seen in the average across trials trajectories of the effectors (addressed in the review [1]); and (b) stability of performance reflected in such characteristics as structure of inter-trial variance.

Within this alternative view, the purpose of modes is not reducing DOFs *per se* (although this may happen frequently) but the creation of a basis that facilitates ensuring stability of performance with respect to salient variables. Note that stability is crucial for success of movements given the varying and unpredictable internal states and external forces. Note also that stability has to be controlled; it makes little sense to ensure high stability of a variable that the person plans to change quickly (reflected in the phenomenon of *anticipatory synergy adjustments*, ASAs, [20]). A computational apparatus to address this topic has been developed within the *uncontrolled manifold hypothesis* [21]. It uses analysis of inter-trial variance in different directions within the space of elemental variables as well as analysis of displacements caused by quick actions in that space [22–24].

Where do synergies come from? The authors review a body of literature on the role of different neurophysiological structures in synergies, but this problem has to be considered at a physical level first, before looking for a substrate. A useful framework is offered by the idea of *control with referent coordinates* (RCs) for salient variables addressed as the RC hypothesis [25], which is a natural development of the *equilibrium-point hypothesis* [7]. According to this view, the CNS specifies spatial RCs for salient variables at all levels of the assumed hierarchy, while performance variables (such as forces, displacements, and muscle activations) emerge given the actual external conditions. For example, a task of moving the endpoint of a limb to a target may be associated with defining a time course of the vector of endpoint referent coordinates, $\mathbf{RC}_{\text{TASK}}$. At the joint level, for each axis of rotation, two RCs are specified, addressed as the reciprocal and co-activation commands, $\{r(t); c(t)\}$ [26]. At the muscle level, each $\{r(t); c(t)\}$ pair is mapped on a set of variables, $\lambda_i(t)$ corresponding to changes in the tonic stretch reflex thresholds for each muscle i. Each transformation is formally redundant (abundant!). The authors mention "reference hand" in their review and invoke the notions of mechanical compliance of the hand and impedance control, but they stop short of defining RCs and referent body configurations and developing the concept of synergies within the framework offered by the RC hypothesis.

If the goal is to understand how synergies are organized in the human body (not only to build a robot that emulates certain features of the human behavior), one has to look for synergies in the spaces of control variables, i.e. those involved in the mentioned of $\mathbf{RC}_{\text{TASK}}(t) \Rightarrow \{r(t); c(t)\} \Rightarrow \lambda(t)$ transformations. This is not a trivial task because the salient variables are not directly measurable; however, several studies have shown that such variables can be reconstructed for systems of different complexity [27–29]. Recently, synergies within the $\mathbf{RC}_{\text{TASK}}(t) \Rightarrow \{r(t); c(t)\}$ transformation have been studied experimentally during one-finger force production tasks [30]. While this task is non-redundant mechanically, it is abundant at the level of two control variables, $\{r; c\}$, that define the fingertip force in isometric conditions. The experiment has shown that humans use wide ranges of r and c values that co-vary to produce a required fingertip force level with high accuracy. To my knowledge, this is the first demonstration of a synergy at a level of analysis that is as close to the neural control level as it if feasible in non-invasive studies.

The comprehensive review of possible relations between specific neurophysiological structures and synergies in the review [1] is very impressive. It is possible, however, that synergic control may not be substrate specific. Earlier