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Comment

The role of synergies within generative models of action execution and recognition: A computational perspective

Comment on "Grasping synergies: A motor-control approach to the mirror neuron mechanism" by A. D'Ausilio et al.

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Controlling the body – given its huge number of degrees of freedom – poses severe computational challenges. Mounting evidence suggests that the brain alleviates this problem by exploiting "synergies", or patterns of muscle activities (and/or movement dynamics and kinematics) that can be combined to control action, rather than controlling individual muscles of joints [1–10].

D'Ausilio et al. [11] explain how this view of motor organization based on synergies can profoundly change the way we interpret studies of action recognition in humans and monkeys, and in particular the controversy on the "granularity" of the mirror neuron system (MNs): whether it encodes either (lower) kinematic aspects of movements, or (higher) goal representations, or both but at different hierarchical levels [12]. Here we offer a complementary, computational perspective on the role of synergies for action recognition and the MNs.

In computational modeling and robotics, it is widely assumed that a control scheme using synergies simplifies movement planning and execution. This scheme permits to use elemental behaviors or primitives as "building blocks" to be composed (e.g., combined linearly, sequenced) to produce more complex behaviors, thus controlling relatively few degrees of freedom [13–15].

Do synergies yield equivalent benefits for action recognition? To answer this question from a computational viewpoint, we frame the concept of synergies within *generative architectures* of action execution and recognition [16–20].

According to two leading theories of motor control, optimal feedback control [21] and active inference [22], the motor system can be conceptualized as a (hierarchical) generative model, which encodes a (probabilistic) mapping between "task goals" specified at a higher level (e.g., grasping a cup) and states of the "plant" to be controlled (i.e.,

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the musculoskeletal system) such as the position of the fingers around the cup, the corresponding joint configurations, etc.[1]

Within the generative scheme, synergies (which encode for example "*the shape of the fingertip trajectory over a short period of time*") might provide a "middle layer" between abstract representations of goals and detailed representations of plant states, and might simplify motor control, in the same way *visual features* (which are extensively used in perceptual processing) simplify the recognition of visual scenes [24].

Using synergies yields two useful forms of abstraction compared to the control of individual muscles or plant states: *spatial abstraction*, because a synergy specifies only some relevant aspects of the state of the plant (e.g., only the fingertip positions over time, not all the joint angles), and *temporal abstraction*, because a synergy corresponds to a period of time [24].

To discuss why these two forms of abstraction are useful in action observation domains (not only motor control), we next consider computational architectures of action recognition and MNs that use the same generative scheme elucidated earlier [16–20]. These architectures can support different computations required for action recognition: the high-level task of recognition of the action goals (proximal and/or distal) and the low-level task of action prediction.

One way to perform goal recognition is "inverting" the generative model: the inference runs from the observed sensory stimuli (e.g. noisy hand movements) to the goals that might have generated them (e.g., grasping an object with a precision grip). Using synergies as an intermediate layer can simplify the inversion of the generative model, analogous to the way *visual features* are often used in computational approaches to simplify perceptual processing. A generative model augmented with synergies can reuse them as "building blocks" and search the linear combination of these known elements that provides the "best explanation" of the perceptual stimuli – which is far more easier than computing a complete description of the problem (e.g., reconstructing the whole sequence of the observed limb positions or joint angles) [25]. Here, the system benefits from *spatial abstraction*, or the fact that the dimensionality of the action/goal recognition space is smaller than the full sensory stimuli – while at the same time, despite the dimensionality reduction, synergies retain the "right" dimensions to correctly produce and recognize ethologically relevant actions.[2]

Synergies can be used to facilitate the *prediction* of the observed action, too, as shown for example in [25]. In the same way synergies can be composed and sequenced to produce a coherent unfolding of actions in time (see, for example, [26]), they can be used within an *action simulation* scheme to provide top-down predictions of observed actions. Thanks to temporal abstraction, they are like (dynamical) "perceptual templates" that help predicting how low-level (e.g., kinematic) patterns of ethologically valid actions unfold in time [27].[3] These "templates" can have an internal structure; for example, a tree-like structure in which some (higher) elements are shared among multiple actions and some (lower) elements are action-specific, permitting to identify and predict their distinctive (e.g., kinematic) features [26].

Conceptualizing synergies as a "middle layer" in generative models of action execution and recognition has three main implications for the arguments of D'Ausilio et al. [11]. First, here synergies are incorporated within a hierarchical scheme rather than replacing it. Even if motor control is essentially based on synergies, this does not prevent the architecture from making inferences at other hierarchical levels (e.g., of action goals or movement kinematics) when necessary. Importantly, although we have discussed these inferences separately, in generative schemes they influence one another and all depend on task demands and prior information [16].

This brings us to a second important point. Even if we assume that the MNs mechanism is better described at the level of *whole-hand movement synergies* [11] than at the level of goals or kinematics, it would not be a bottom-up (reconstruction) process that proceeds solely from sensory inputs (e.g., *the visual appearance of others' grasping actions*). Rather, in generative schemes, synergies would be inferred by coherently orchestrating all the available sources of evidence, bottom-up and top-down (e.g., sensory stimuli, prior knowledge of task and action goals) and

[1] Both optimal feedback control and active inference theories use hierarchical generative schemes but disagree on what the organization of the control architecture (feedback control or predictive coding) is, what the motor system computes (motor commands or proprioceptive predictions), and how is action optimized (using cost functions or free energy minimization) [23]. These differences are crucial to understand motor control but are not discussed here for brevity.

[2] Note that learning synergies (like extracting visual features in perceptual processing) is not a trivial task for the brain, but it could bring significant adaptive advantages, e.g., simplifying the burdening problem of inversion of the generative model [24].

[3] In this respect, an important difference with visual features is that synergies are intrinsically dynamical.

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weighting them depending on their reliability or precision [20]. This fact could explain why the information provided to an observer modulates mirror responses and corticospinal excitability [28].

As a third, related point, given that generative models use feedback, predictions, and a cascade of bottom-up and top-down information streams, one should expect a mixture of high- and low-level features of the (performed or observed) motor task at every level [29]. These features might not necessarily reflect the variables that a set of neurons (e.g., MNs) preferentially code or their "granularity", but the information that the brain area/network is processing and integrating (e.g. top-down, goal related information and visual feedback/predictions as examples of high-level features, and bottom-up, kinematic-related information and proprioceptive feedback/predictions as examples of low-level features), which varies depending on the task demands. In the system-level perspective of generative models the question of "what variables MNs represent" (e.g., goals or kinematic variables of a task) is ancillary to the question of "what neural control scheme MNs are part of". Here, predictive coding/active inference models offer a slightly unusual answer: one in which MNs discharge during action observation because they are part of a generative model that *predicts* the sensory (exteroceptive and proprioceptive) consequences of the action and possibly its synergies, not because they are driven by sensory inputs or because they code goals [18,20].

More broadly, the arguments sketched here suggest the importance of establishing a tighter link between experimental findings on MNs and computational motor control models, possibly based on synergies. Improving our current models of motor control and MNs is equally important. To this aim, an open challenge is to precisely specify synergies at the neuro-computational level, given that they have been defined in different ways and linked to coordination patterns at different levels, kinematic, kinetic, and neural [30]. Another outstanding question is assessing whether and how synergies map to neuronal "domains" and are organized around ecologically relevant behaviors in (pre)motor brain areas and beyond (e.g., posterior parietal cortex) [5,31,32]. This question is important to understand to what extent synergies can be composed to realize complex behaviors, and whether there are aspects of motor control that are *not* based on synergies or require the integration of synergies with other, more fine-grained forms of control [33].

It is interesting to remark that, if one assumes that the action representation is the same in action execution and observation [34], experiments designed to study "mirror" phenomena can ultimately help understand the neuronal code and granularity of (pre)motor areas.

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