Comment

The competitive and multi-faceted nature of neural coding in motor imagery
Comment on "Muscleless motor synergies and actions without movements: From motor neuroscience to cognitive robotics" by V. Mohan et al.

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The tight interplay of motor imagery and actual motor production has been one of the fundamental driving concepts in modern motor neuroscience [1,2] and computational modelling of cognitive and sensorimotor functions [3]. Jeannerod originally gathered into the single name of *S-states* a variety of cognitive situations which, while involving cortical motor areas, did not end up in an overt motor action.

The activation of sensory and motor cortex areas in association with actions that are not actually performed supports the existence of simulation mechanisms by which all, or at least part of, neural processing aimed at action production is recruited, but the final motor release is held, so no movements are really executed. Mohan et al. [4] provide a means of unifying the neural representation of performed and imagined actions, building on the assumption that they both share the same internal motor simulation resources. Very noticeably, they also offer a valid account for a plausible solution to the inverse kinematics problem.

It appears indeed ecologically sound, and coherent with mainstream cognitive science knowledge, to propose that a single, relatively simple neural mechanism is at the base of a number of related phenomena. On the other hand, S-states differ substantially from each other according to their neural activation, and to their relation with overt action execution [2]. While some S-states are substantially covered and explained by the internal simulation account, some cases are more difficult to reconcile with a simple one to one matching between simulated and performed actions.

Observation of actions performed by others, and of objects affording those same actions, elicit activation of only partially overlapping networks, not only at the visual level, as it would be expected, but also at the pre-motor level, indicating a different motor value for these conditions [5]. In particular, action observation has been found to be associated to alternative incompatible sensorimotor responses, depending on additional contextual information [6]. Observation of a certain grasping action, performed by a potential partner, elicits either a mirroring (repeating the partner's action) or a complementing response (perform a different action which is socially compatible with the partner's), according to the social value of the action. The type of response changes when the partner starts a hand

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movement towards an object located close to the observer, and once the social stage of the action begins, the observer neural response, by all means a type of S-state activity, instantly switches from mirroring to complementing [6]. This phenomenon supports the importance of two neural mechanisms that are not yet encompassed within the model by Mohan et al. [4], i.e. the simulation multiplicity, through a competitive framework, and its faceted nature in complex interactive tasks.

The simultaneous activation of mutually incompatible motor plans, which compete for the control of the subject motor system, is a well recognised mechanism [3,7], and computational models of action selection based on it have been around for a quite long time [8], being successfully applied to real robotic applications [9]. Interestingly, current competitive models of action representations are also based on inverse models, thus sharing a fundamental common background with the discussed proposal. The two approaches are not incompatible: Mohan et al. focus on generating the most appropriate motor pattern suitable to achieve a certain goal, implicitly solving the inverse kinematics problem, whilst the competitive framework deals with the issue of contextually selecting among alternative potential goals. It is very plausible that multiple simulations with mutually exclusive goals run in parallel, competing to achieve control of the motor system. Only one at a time can access motor control, but the others are ready to quickly get in charge if circumstances change.

It has also been shown that alternative plans are not totally segregated, and that motor interference may happen when attention cannot be allocated entirely to one plan, or if a sudden switch in focus is required [10]. The neural counterparts of attractor dynamics, as suggested by Mohan et al., might contribute to goal selection in such a competitive framework, acting as a referee in the simulation race, before it gets to an overt status. The body schema is in fact a "task-agnostic middleware" and can serve multiple simulations simultaneously, since resources can safely be shared at the cortical level, until projection to the peripheral nervous system is required.

Experiments specifically designed to clarify the faceted role of neural response during action observation [6] showed that the winning simulation, the one found to elicit muscle pre-activation, can be of different natures, being aimed either at action interpretation or at actual voluntary response. The two are mutually exclusive regarding their access to action execution, but not during planning, and the instantaneous switch observed between them suggest that their respective simulations can indeed run in parallel. As appropriately stated by Mohan et al. [4], "people recruit motor representations as if they were themselves acting", but this is not the whole story, since a totally different action, aimed at correctly complementing the observed movement when interpreted socially, is ready to kick in in the matter of milliseconds if the context requires it.

Even though it is not specifically formulated for it, the proposed framework [4] could be extended to work in the context of action observation during social interactions. As explained above, this is a particular S-state in which simulations referred to a subject own actions run in parallel with simulations matching and interpreting the goals of a partner. Moreover, we have recently showed [11] that action observation involves a multiplicity of neural coding scenarios, in which mirroring of the observed action (kinematic coding), anticipation of the forthcoming events (predictive coding) and the preparation of a socially congruent action (response coding) coexist and modulate each other. Extending the proposed model [4] with a competitive component among multiple simulations would also partly address the issue of multiple coding, since active parallel simulations may be referred to one or another motor coding alternatives. In fact, competitive models showed that it is possible to run competitive simulations that take into account both predictive and response coding, hence interpreting a partner movement while preparing a possible compatible response [12].

The neural mechanisms behind sensorimotor control, and the multiplicity of responses linked to overt and simulated motor activities are extremely complex, and we are only starting to understand their multi-faceted nature. Mohan et al. provide a very necessary and highly convincing step towards a more grounded interpretation of such mechanisms, and towards their emulation in computational models and practical applications in modern autonomous robotics. Merging their model with related efforts aimed at clarifying the competitive nature of neural simulation and the issue of multiple neural coding seems the most promising way forward to shed further light on the nature of motor control and motor imagery.

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