Published in final edited form as: *Phys Life Rev.* 2015 March ; 12: 129–130. doi:10.1016/j.plrev.2015.01.006.

The (un)coupling between action execution and observation: Comment on "Grasping synergies: A motor-control approach to the mirror neuron mechanism" by D'Ausilio, Bartoli and Maffongelli

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When we observe actions performed by others, our motor system resonates along with that of the observed agent [1]. The exact features of this resonant motor response, however, are unclear. Do we mirror the goal of others' actions or rather the low-kinematic features of their movements? D'Ausilio et al. suggest that this is an ill-defined problem: the mirror system plausibly replicates the same computational mechanisms implicated by motor control. Accordingly, motor synergies may not only constitute a pervasive element of motor control, but also form the fundamental unit of action observation.

While we applaud D'Ausilio et al.'s attempt to draw from methods and models developed for motor control, at the same time, we are concerned that the idea that "the granularity of the mirror system cannot be any different from that of the motor system" may overlook important differences between action execution and observation. In the following, we focus on two aspects that, in consideration of these differences, may need further development.

Representation level: goal vs. kinematics. In execution, goals and intentions guide action planning and control. Conversely, in action–perception, goals and intentions have to be understood from the observed motor behavior. Hence, the question: Is MEP pattern of movement recruitment linked to the features of the observed movement or to the estimated action goal? [2].

The synergy-based approach suggests that mirror activity needs to be probed by recording TMS-evoked kinematics [3] or TMS-evoked activity in a large number of muscles [4]. The problem, however, remains: Is synergic activity in the observer linked to the kinematics features of the observed movement (i.e., the observed motor synergy) or to the object-directed goal (i.e., the most appropriate motor synergy to achieve the goal of the action)?

In agreement with the prevailing view, D'Ausilio et al. assume that kinematics provides lowlevel details of the implementation of the movement. Recent work, however, has shown that i) action goals are encoded in movement kinematics [5]; ii) observers may use subtle

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changes in movement kinematics to discriminate between movements performed with different intents [6] and [7]. It is thus likely that simulating the kinematics of an observed action permits estimation of higher-level goal features. In this regard, the problem of kinematics vs. goal coding is ill-posed not because "the appropriate level of granularity of the mirror mechanism is neither that of low-level movement features nor that of object-directed goal representation", but rather because kinematics and goal are not independent of each other.

Returning to the problem of representational level, the question is not whether we should look at motor synergies rather than at low/high-level features; the question is what specific methodological contribution the synergic approach may make to improve our understanding of the perception–action coupling mechanism (i.e., how visual information from an observed action maps onto the observer's own motor system).

Inhibition. A second pivotal network difference between action execution and observation is inhibition of covert movements [8]. In everyday life, observers almost never actively mirror the movements of the people they observe. This implies that, in comparison to action execution, action observation needs to recruit an additional inhibitory neural process to prevent overt movements. Direct evidence of this inhibitory process is provided by recent studies showing that, although many pyramidal tract neurons (PTN) in the primary motor cortex (M1) exhibit a mirror-like activity, EMG activity is completely absent during action observation [9] and [10]. The clue seems to lie in the activity of PTNs themselves: not only is the majority of facilitation mirror neurons half as active for action observation as for action execution, but at least one third of mirror neurons in M1 (referred to as suppression mirror neurons) reverse their activity pattern during observation. As a result, M1 output to spinal interneurons and motoneurons involved in generating movements could be strongly disfacilitating, helping monkeys (and presumably humans) to withhold unwanted movements during action observation [10]. In line with this, Lago and Fernandez-del-Olmo [11] found a decreased corticospinal excitability in humans during action observation. This brings up a specific concern regarding the use of TMS-evoked kinematics proposed by D'Ausilio et al. to measure motor synergies: If mirror neurons can be modulated by action observation with absolutely no movement resulting, then overt movement may not be the optimal window to study the mirror response to observed actions.

In sum, the synergy-based approach proposed by D'Ausilio et al. may provide important methodological guidelines for the investigation of the mirror response in humans. The notion that the mirror system shares the same computational mechanisms implicated by motor control, however, may be an oversimplification and much further work is required to understand how these mechanisms apply to action observation.

Acknowledgements

This work received funding from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007–2013)/ERC grant agreement No. 312919.

Phys Life Rev. Author manuscript; available in PMC 2016 September 28.

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