Granularity within the mirror system is not informative on action perception - Comment on "Grasping synergies: A motor-control approach to the mirror neuron mechanism" by D'Ausilio et al.

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The present work [1] reviews a part of the now vast literature on visuomotor stimulus-response associations in the domain of action observation, commonly referred to as mirror mechanism or mirror system. The aim of the study is to propose a solution to a currently debated problem, namely in what frame of reference are mirror neurons coding movement. The solution proposed here is that, if the mirror system is part of the motor system, then the motor responses to action observation must be in the same frames of reference as that generally observed in the production of voluntary actions. This idea is part of the very first conceptualizations of the mirror system ("Each time an individual sees an action done by another individual, neurons that represent that action are activated in the observer's premotor cortex. This automatically induced, motor representation of the observed action corresponds to that which is spontaneously generated during active action and whose outcome is known to the acting individual" [2]) and has been explicitly proposed earlier [3] in the attempt of reconciling the very different findings in the literature on the mirror system's frames of reference. The novelty of the present approach is the explicit reference to the 'motor synergy' theory of voluntary hand movements. This theory states that the high number of degrees of freedom intrinsic to hand anatomy is reduced by the motor system to few principal components named motor synergies that are the building blocks of voluntary behavior [4]. I am enthusiastic about two points proposed by D'Ausilio in the present review and I am skeptical about some other points.

I fully agree with the proposal that TMS-evoked motor responses are much better described in terms of TMSevoked movements rather than in terms of electromyographic activity of single muscles. Optimal characterization of motor behavior by means of EMG requires several different recording sites [5,6]. Unfortunately, most works on humans with motor cortex TMS record only one or two muscles. There are obvious dangers to this approach. Take for example the work of Cavallo et al. [7] in which only a pair of agonist muscles was recorded. The authors concluded very sharply that on the basis of their data only movements are represented in the mirror system. In a subsequent independent work [3] the complexity of the recordings was dimensionally improved by adding an antagonist muscle. The new data overlapped with those of Cavallo et al. as far as the single flexor muscles are concerned but the conclusions drawn from the complete dataset including flexor and extensor muscles contradicted entirely those of Cavallo et al. The use of the kinematics of evoked movement rather than EMG recordings completely bypasses this problem. The downside to this is that recording TMS-evoked kinematics is a non-standardized procedure. As such it requires very skillful prior validation within each body segment in terms of timing of the response. The knowledge of the timing of the TMS-evoked phenomena is a necessary step for their measurement. TMS-evoked electromyographic activity (the motor evoked potential) occurs at predictable timing with respect to the TMS pulse (for example, it appears around 20 ms from TMS in the distal upper limb). On the contrary, when to expect TMS-evoked movements is largely unknown. Electromechanical delay in skeletal muscles varies between individual muscles by even tens of milliseconds [8]. Other factors such as muscle viscosity and joint resistance also contribute to the onset time of TMS-evoked movements. In general it is advisable to carefully assess the TMS-movement delay in individual body segments prior to any experiment that uses TMS-evoked kinematics as an experimental measure. In the paper by D'Ausilio et al. illustrated here [9] for example, an electromechanical delay of less than 10 ms in tongue muscles is assumed, but such assumption probably requires more extensive preliminary investigations. For example in our previous work [10] using kinematics of TMS-evoked movements we estimated on the basis of a preliminary study on a significant population of subjects a delay between electrical and mechanical TMS-evoked responses of at least 30 ms for forearm muscles.

I am in general enthusiastic about the motor synergy model and its applications in motor control. However it should be kept in mind that, as other motor control theories, it is based on the recording and analysis of movements and not on direct measurements from the central nervous system. The site within the central nervous system where motor commands take the form of motor synergy is not known and is of little interest to the theory. However, it is likely to be at least in part located in the spinal cord [4]. Therefore, any strong link between the motor synergy theory and specific cortical functions such as the mirror one, which is mainly supported by the premotor and parietal cortices, should be made with caution. Additionally, I am skeptical about the way the literature data on the granularity of mirror motor representations are presented here. The fact that in different experimental conditions different motor representations emerge does not mean that these are mutually exclusive. Actually, it is likely that joint displacements, movements and actions are simultaneously represented as mirror images in the observer's motor system, but that single experiments and measurements privilege one or the other aspect. In a study on the motor-visual aftereffect [11] we actually demonstrated something similar to this latter hypothesis: the interplay between the observer's motor system and observed movements occurred at the level of joint displacements, of movements and of actions, without any apparent interaction between the three levels of motor representation.

A second concern is that the motor synergy model seems to be particularly efficient in describing voluntary movements. On the contrary the movements produced by the mirror mechanism are far from being voluntary. In fact, most literature on stimulus-response compatibility effects in action observation (among others see [12–14]) including our recent research [15] suggest that voluntary movements are produced by a completely different neural system, independent from the mirror one. Of course, the development of the mirror stimulus-response association is very likely to be based on previous voluntary action, however this issue should be explicitly addressed.

Finally, I am doubtful about the general idea that this approach can define whether the mirror system is used by the brain for "action perception". If the term "perception" is used here at the physical/representational level [16], i.e. as the capacity of the brain to produce non-random neural activity associated with the characteristics of a stimulus, then mirror neurons are by definition endowed with "action perception" properties. It would be tautological to state that neurons that fire when observing specific actions (i.e. mirror neurons) are capable of firing when observing specific actions. On the contrary if the term "perception" is used here at a computational level, then describing a lower-level feature such as its granularity is of no help. This limitation is obviously inherent to all physical/representational levels of knowledge and not only to the present one. For example, the fact that the mirror system can encode observed action goals [3,17] is not informative on what may be the higher level process for which the mirror system has been selected. So the first thing to do is probably to define what is the computational goal that is to be achieved by means of the mirror system and such computational goal is identified in [1] as the perception of actions. While there is clear evidence that movements can influence action perception to a certain degree [11,18] it is unlikely that the computational goal subserved by the mirror system is action perception. In my opinion the most likely goal of the mirror system is that of producing behavior [19], by acting together with other parallel systems that transform vision of others' actions into motor responses [10,15]. In this perspective studying the granularity of mirror responses can produce valuable information on brain-behavior relations.

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