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Comment

The representational nature of the body schema Comment on "Muscleless motor synergies and actions without movements: From motor neuroscience to cognitive robotics" by V. Mohan et al.

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Traditional accounts of motor control have focused on feedback and feed-forward signals to explain motor behavior [1]. Models which posit the existence of a continuous sensory-motor interchange have many advantages: they explain behavior in closed-loop and open-loop situations – that is, when error signals are or are not available –, predict adaptation of the motor response to spatial, temporal or force perturbations, are capable of learning and are compatible with the notion of a predictive brain [2]. Feed-forward and feedback mechanisms of motor control strongly depend on frontoparietal circuits connecting the dorsal parietal and premotor cortex. However, the same brain regions are also involved in the simulation of actions [3], mirroring processes triggered when participants merely observe other's actions [4,5] as well as other purely cognitive faculties such as working memory, mental rotation and spatial attention [6]. In their review Mohan et al. [1] correctly point out that a complete understanding of motor control should also explain these additional properties of the motor system. They propose that a body schema is shared by real and imagined actions, and thus provides a critical link between motor programming and motor imagery. Interestingly, their computational models of simple or more complex kinematic chains implement a straightforward version of a 'limb space', reduced to two essential properties: one node representing force, and a second node representing displacement. Critically, the same elements are repeated across different limb spaces (hand space, arm space, waist space and tool space) and different levels of complexity, which eventually results in the construction of a plastic, configurable and adaptable representation of the body. The authors show that this conception is sufficient to characterize the behavior of a robot performing simple unimanual actions, or its performance during bimanual coordination and when its action space is extended through the use of tools.

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These findings are convincing demonstrations of how relatively simple building blocks of cognition that are repeated at different spatial scales may predict motor performance. However, can this model reliably reproduce the complex representational nature of the body schema? A good theory of simulation [3] should specify the necessary biological constraints of an action production system, be it involved in overt action, action simulation, or both. A muscle that contracts without knowledge of its effects is of no biological utility. Similarly, an action system that has no measure to characterize the space within which it produces its effects will have a very limited impact on the environment. Imagined action must take place in a spatial and temporal medium. A rudimentary representation of the spatial coordinates that characterize the body space and its surrounding action space must therefore be an essential constituent of the frontoparietal action planning system. For example, though they fail when executing movements that require complex intersegmental coordination deafferented patients are still capable of producing accurate single joint movements in the absence of vision [7]. A rudimentary, low-resolution body schema is thus an inherent property of the motor system and must not be seen as a separate (and possibly independent) module dedicated to the representation of the body.

Nevertheless, I do agree with the authors that more complex multi-joint and multi-limb movements cannot rely on this low-level body schema, but require a spatially more accurate and adaptable representation of the body. Studies of brain-injured patients with specific neuropsychological impairments suggest that this high-level body schema has several cognitive components. Damage to the right temporo-parietal or insular cortex leads to *somatoparaphrenia*, the feeling that individual body parts do not belong to one's own body, have been distorted or even added [8,9]. This disturbance of body ownership differs from *personal neglect* (the unawareness of one's own contralesional limb, which is not explained by sensory loss) [10,11] and *anosognosia* (the denial of paralysis), which may be observed after injury to premotor or insular cortex [12,13]. Damage to the right temporo-parietal junction may result in the *out-of-body experience*, feelings that the subjective 'self' is located outside the body space [14]. Finally, inferior parietal damage may lead to *tactile apraxia*, the failure to identify objects through active tactile exploration [15]. Although their precise underlying neural and cognitive mechanisms are subject to speculation, these disparate clinical phenomena all exemplify the variety of computational and representational components of the body schema. For example, somatoparaphrenia appears to reflect a specific sense of body ownership, which can be modulated through vestibular, but not tactile or visual stimulation [9]. In contrast, patients with anosognosia for hemiplegia generate motor programs (e.g., the intention to lift their paralyzed arm) despite the fact that their limb is clearly not moving [16]. These motor programs are rationally interpreted as real movements, leading to the conviction that the affected limb is not paralyzed. Yet another cognitive mechanism underlies tactile apraxia: impaired integration of tactile and proprioceptive feedback during active exploration, which leads to a failure to identify the explored object through touch alone. Together, these findings suggest a conclusion that might guide future approaches to the study of body representations and their role in motor control: we should move away from the idea that the body schema is a purely afferent representation of the body, which is decoupled from the motor system. Instead, it emerges as a result of predictions and the constant integration of motor and multisensory signals into a representation of the body as a space for action, somatosensation and the self.

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