Journal Club

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On the Origins of Modularity in Motor Control

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Review of Hart and Giszter

The control of movement is highly complex because of the biomechanical redundancy of the musculoskeletal system (Bernstein, 1967). To cope with the large number of degrees of freedom, humans and animals likely rely on a modular control architecture. In other words, the CNS may activate flexible combinations of motor primitives instead of controlling each muscle independently, a motor primitive being a premotor drive generated by some neuronal population (for example, in the spinal cord) that recruits a covarying group of muscles that remain in a fixed relationship during recruitment (Hart and Giszter, 2010). Hence, motor primitives may represent the building blocks of movement organization. An important direction for research is to investigate the neural basis of this organization in the spinal cord, i.e., the neural mechanisms that select the muscle activation patterns required to achieve a behavioral goal.

In a recent study published in *The Journal of Neuroscience*, Hart and Giszter (2010) addressed this question in an innovative way, by developing a new methodology linking the neural input to the motor output. They supported the hypothesis that modularity is directly embodied

in the neural circuitry of the spinal cord. The authors performed simultaneous recordings of muscle and neural activities of anesthetized spinal bullfrogs. Using three types of stimulation (muscle palpation, light touch stimulation, and manipulation of limb position), each one involving a different sensorimotor reflex pathway, they recorded EMGs from the bullfrog right hindlimb and neural data from three sites (depths) of the spinal cord.

Hart and Giszter (2010) extracted primitives from the EMG data using the linear statistical method of independent component analysis (ICA). Using the standard assumption that the components accounting for the most EMG variance represent estimates of motor primitives (Ivanenko et al., 2005), they proceeded to investigate how the recorded neural activity was related to the extracted components and to the original EMG recordings. If neuronal firing correlated significantly better with component-based than with EMG representations of motor activity, such a result would be a strong argument in favor of the hypothesis that specific neural activities associate with primitives. A novelty of this study was the use of information-theoretic measures, which quantify associations between random variables, including dependencies that cannot be captured by linear regression methods. Hart and Giszter used the mutual information coefficient (MI), measuring the amount of information that the firing rate shared with the independent components or EMG values. This method suggested that neuronal firing

was more closely related to independent components than to contraction of individual muscles [Hart and Giszter (2010), their Fig. 4].

Hart and Giszter (2010) also showed that the correlation between neuronal firing and motor components occurred for neurons in a specific region of the spinal cord [the intermediate zone (IZ)] (see their Fig. 3B). The neurons in the IZ depths (700–800 μm) thus qualified as putative interneurons and consequently, were selected for further analysis. The authors also looked at the neural activity in the shallowest depth (400–500 μm) and demonstrated that firing of neurons at that level were also uniformly better related to independent components than EMGs [Hart and Giszter (2010), their Fig. 3D], but only for firing in response to light touch stimulation: such a preference for independent components was not observed in responses to the other two types of stimuli [Hart and Giszter (2010), their Fig. 3C,E]. This finding indicates that some neurons might be specifically related to primitives selected by a particular stimulus type. Support for this argument has also been provided by other studies (Todorov et al., 2005; Lockhart and Ting, 2007), suggesting that the activity of motor primitives can be correlated to task parameters. Hence, it could be useful to investigate how behavioral goals are transformed into detailed patterns of muscle activation, and more significantly, to examine the neural control mechanisms that underlie the production of task-level functions.

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In a final phase of analysis, Hart and Giszter (2010) performed spike-triggered averaging to reveal direct relationships between neural spiking and muscle recruitment. Neurons in the IZ showed significant postspike facilitations to groups of muscles [Hart and Giszter (2010), their Fig. 6B]. Moreover, these postspike facilitations closely matched the independent component weights (extracted from the EMGs) both qualitatively and quantitatively. Therefore, evidence that neural activity is associated with motor primitives was provided in two steps: First, there are sets of interneurons dedicated to produce specific patterns of activity, and second, these patterns closely match motor primitives detected by other means (ICA on EMG data).

Besides representing a huge step toward understanding the neural underpinnings of motor primitives, the findings described above provide matter for other points of discussion. One of them concerns the assumptions of the ICA method for EMGs. To be more precise, the assumed spatial independence of the underlying components is not guaranteed a priori and mainly is not intuitive considering the biomechanical structure of humans and animals. Additionally, restricting the components to add linearly is a commonly used method but may not be able to incorporate higher-order dependencies that are intrinsic in the neural structure. Hence, a nonlinear dimensionality reduction method (e.g., support vector machines) should be considered in future studies.

Another point that deserves particular attention stems from the observation that kinematic parameters of the movement are uniquely determined by populations of neurons rather than individual ones (Georgopoulos et al., 1986). In this work, a relation of motor primitives to neurons in the IZ of the spinal cord has been established, but the effect of interactions

between these neurons has not been examined. Since the brain is thought to typically make decisions on single events by evaluating the activity of large neuronal populations (Quiari Quiroga and Panzeri, 2009), it is worth investigating the information carried by a population of neurons as a whole for performing motor tasks.

Finally, another question inspired by the results of the study reviewed here is that of understanding the origins of the modular features observed in natural motor behaviors and determining the fundamental output controlled by the CNS (Tresch and Jarc, 2009). There are arguments for constructing primitives early in development and even for hardwiring primitives. In other words, the flexible combination of groups of muscles may be an innate mechanism attributable to evolutionary constraints. Another, probably complementary, interpretation for this modular structure is that motor primitives may provide a way for the CNS to simplify the approximately optimal control of movements (Todorov et al., 2005). This control scheme could be learned on a faster timescale. The work by Hart and Giszter (2010) in particular demonstrated that, if such optimal control strategies drive modularity, then their physiological outcome may be a focused selection of a set of premotor neurons. To obtain more insights on these interpretations, more experimental work should be done on relating neural activity to muscle activation patterns and the physiological properties of the neurons recorded should be examined. Furthermore, it could be of interest to investigate the effect of motor learning on developing a wide repertoire of movements. For this purpose, we should look directly at the variations in motor primitive composition during learning motor tasks.

In conclusion, Hart and Giszter offered important new insights into the

neural mechanisms regulating motor control. Their work goes much further than most previous studies trying to characterize the relationships between neural discharges and movement-related variables, suggesting strongly that the CNS does control movement using motor primitives. Evidence that discharge of individual neurons in the primary motor cortex encodes the activity of functional groups of muscles during voluntary movements was previously found (Holdefer and Miller, 2002). In contrast, the study by Hart and Giszter focused not on voluntary but on reflex behaviors. Thus, in the future, further experiments should confirm whether the neural basis for motor primitives holds also for goal-directed movement.

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