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COMMENTARIES

Getting a Grasp of Theories of Sensorimotor Control of the Hand: Identification of Underlying Neural Mechanisms

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The target article nicely introduces important biomechanical and neural features that make the hand a very complex system, yet a very powerful model for gaining insight into fundamental principles of sensorimotor control. The article also presents an overview of the reference configuration (RC) hypothesis as a general framework to address experimental findings from studies of multidigit force coordination. The appeal of the RC-hypothesis is its (apparent) simplicity as well as its practical applications in robotics, e.g., controlling compliant artificial hands (Bicchi et al., 2011). This commentary argues for the need to (a) quantify the underlying physiological mechanisms, as well as (b) integrate mechanisms responsible for sensorimotor transformations, planning, and learning.

Linking Behavioral Experimental Findings and Neural Mechanisms

Over the past few decades, behavioral studies of hand-object interactions have provided many insights into the control of hand kinematics and manipulative forces. Examples include the early work by Marc Jeannerod (Jeannerod 1981, 1984) that paved the way for a wide variety of kinematic studies of hand preshaping and fingertip trajectories, and the pioneering work of Roland Johansson and his group on the control of grasp forces (Westling & Johansson 1984; Johansson & Westling 1988) and underlying sensory mechanisms (Johansson & Westling 1987; Westling & Johansson 1987). Although important insights have also been provided by studies examining neural mechanisms for grasp control (for review see Alstermark and Isa, 2012), some important questions remain. Specifically, and as summarized in a recent review article (Santello et al., 2013), the hypothesized neural correlates of important and well-described phenomena discussed in the target article, such as finger force and movement enslaving, the relation between ‘good’ and ‘bad’ variance captured by the uncontrolled manifold approach, synergies, or the theoretical model of virtual fingers, remain to be experimentally validated.

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At the most basic level of force control, i.e., motor units, it has been suggested that relatively stable organization and branching of neural inputs to motor unit pools of hand muscles might constrain the activation of intrinsic and extrinsic muscles as quantified by motor unit synchrony and coherence (for review see Santello, 2014). Nevertheless, although we can quantify and describe how neural inputs are distributed to hand muscles, such analysis of peripheral mechanisms cannot address how inputs are selected, distributed, or 'assembled' and retrieved at higher levels of the central nervous system (CNS), e.g., cortical premotor, motor, and association areas. Below I describe recent attempts at addressing this gap and argue for the need to better integrate expertise in neuroscience and biomechanics in future research.

Planning and Execution of Grasping Movements: Neural Mechanisms

Studies of grasping in human and nonhuman primates have identified a number of cortical areas, the so-called 'grasp circuit', involved in the control of grasping and manipulation (for review see Davare et al., 2011). This circuit, that includes anterior intraparietal sulcus, premotor ventral and dorsal areas, and primary motor and sensory areas, appears to be involved with several important aspects of grasp control, such as predictive and reactive scaling of digit forces (Ehrsson et al., 2001; Chouinard et al., 2005; Nowak et al., 2005; Berner et al., 2007; Dafotakis et al., 2008).

These findings are important for guiding future research that could help bridging the gap between the above-described behavioral findings and their underlying neural mechanisms. As several neurological disorders can severely affect dexterous control of the hand (see target article), a better understanding of the causal relations among brain areas would greatly benefits efforts aimed at improving or restoring sensorimotor hand function through noninvasive brain stimulation as well as brain-machine interfaces.

High-Level Representations of Hand Actions

As pointed out by the target article, establishing causal links between behavior and mechanism is a daunting task. This is particularly true when considering the large number of elements that must be accurately coordinated in a system as complex as the human hand. Nevertheless, understanding how the CNS represents motor actions, as well as how such representations are built through motor practice, is critical to (a) understanding how these representations are decomposed into motor commands, and (b) the extent to which these representations drive the interplay between predicted and actual sensory feedback for regulating ongoing motor actions.

Sensorimotor learning has been extensively studied using protocols that require subjects to adapt to unfamiliar task conditions, e.g., force fields or visuomotor rotations (for review, see Wolpert et al., 2011). Until recently, however, most of these studies have focused on the control of arm movements. Studies of manipulation with virtual and physical objects have revealed important features about high-level representations of learned manipulations, as well as the factors that prevent or enable their generalization. For example, subjects are able to compensate—in an anticipatory fashion (before object lift onset)—for trial-to-trial variability of digit placement on an object by modulating digit forces. This phenomenon enables subjects to generate the desired torque necessary to lift an object straight (Fu et al., 2010). In a similar task, subjects can transfer the learned manipulation by generating the same target torque even when asked to use digits that were not used to learn the task (Fu et al., 2011). Subjects' ability to adapt digit forces to variable digit position, tested by changing object width with and without visual feedback of the object, further confirms the role of high-level or task representations of learned manipulation (target torque) for modulating digit forces to variable digit placement (Fu and Santello, 2014). Importantly, learned manipulations are not always transferable to different contexts, as revealed by subjects' inability to manipulate the object after it has been rotated (e.g., Salimi et al., 2000; Bursztyn & Flanagan 2008; Zhang et al., 2010) or when grasping a different part of the same object (Fu & Santello 2012). These observations point to the need of further defining the boundaries of the space within which the CNS is able to flexibly build high-level representation of dexterous manipulation for effector-independent control, but outside of which these representations cannot be generalized to different manipulation contexts (e.g., Ingram et al. 2010, 2011).

To summarize, the complexity of the hand sensorimotor system requires multidisciplinary approaches for unraveling its control mechanisms. The target article title asks whether we will ever understand how the hand works. This commentary suggests that a possible answer to that question may depend on our ability to examine, in a comprehensive fashion, the neural correlates of the large body of experimental evidence from behavioral studies of hand-object interaction. Open questions that should be addressed range from defining high-level representations of learned motor tasks to their interactions with sensory feedback. As a critical mass of research tools and experimental paradigms becomes available to movement scientists, so does the need to better integrate biomechanics and neuroscience for addressing important gaps in our understanding of neural control of the hand.

References

Alstermark, B., & Isa, T. (2012). Circuits for skilled reaching and grasping. *Annual Review of Neuroscience*, *35*, 559–578. PubMed doi:10.1146/annurev-neuro-062111-150527

Berner, J., Schönfeldt-Lecuona, C., & Nowak, D. (2007). Sensorimotor memory for fingertip forces during object lifting: the role of the primary motor cortex. *Neuropsychologia*, *45*, 1931–1938. PubMed doi:10.1016/j.neuropsychologia.2006.11.011

Bicchi, A., Gabiccini, M., & Santello, M. (2011). Modeling force distribution in natural and artificial hands with soft synergies. *Philosophical Transactions B*, *366*, 3153–3161. doi:10.1098/rstb.2011.0152

Bursztyn, L.L., & Flanagan, J.R. (2008). Sensorimotor memory of weight asymmetry in object manipulation. *Experimental Brain Research*, *184*, 127–133. PubMed doi:10.1007/s00221-007-1173-z

Chouinard, P., Leonard, G., & Paus, T. (2005). Role of the primary motor and dorsal premotor cortices in the anticipation of forces during object lifting. *The Journal of Neuroscience*, *25*, 2277–2284. PubMed doi:10.1523/JNEUROSCI.4649-04.2005

Davare, M., Kraskov, A., Rothwell, J.C., & Lemon, R.N. (2011). Interactions between areas of the cortical grasping network. *Current Opinion in Neurobiology*, *21*, 565–570. PubMed doi:10.1016/j.conb.2011.05.021

Dafotakis, M., Sparing, R., Eickhoff, S.B., Fink, G.R., & Nowak, D. (2008). On the role of the ventral premotor cortex and anterior intraparietal area for predictive and reactive scaling of grip force. *Brain Research*, *1228*, 73–80. PubMed doi:10.1016/j.brainres.2008.06.027

Ehrsson, H.H., Fagergren, E., & Forssberg, H. (2001). Differential fronto-parietal activation depending on force used in a precision grip task: an fMRI study. *Journal of Neurophysiology*, *85*, 2613–2623. PubMed

Fu, Q., Hasan, Z., & Santello, M. (2011). Transfer of learned manipulation following changes in degrees of freedom. *The Journal of Neuroscience*, *31*, 13576–13584. PubMed doi:10.1523/JNEUROSCI.1143-11.2011

Fu, Q., Zhang, W., & Santello, M. (2010). Anticipatory planning and control of grasp positions and forces for dexterous two-digit manipulation. *The Journal of Neuroscience*, *30*, 9117–9126. PubMed doi:10.1523/JNEUROSCI.4159-09.2010

Fu, Q., & Santello, M. (2012). Context-dependent sensorimotor memory interferes with visuomotor transformations for manipulation planning. *The Journal of Neuroscience*, *32*, 15086–15092. PubMed doi:10.1523/JNEUROSCI.2468-12.2012

Fu, Q., & Santello, M. (2014).Coordination between digit forces and positions: interactions between anticipatory and feedback control. *Journal of Neurophysiology*. *111*(7), 1519–1528 PubMed

Ingram, J.N., Howard, I.S., Flanagan, J.R., & Wolpert, D.M. (2010). Multiple grasp-specific representations of tool dynamics mediate skillful manipulation. *Current Biology*, *20*, 618–623. PubMed doi:10.1016/j.cub.2010.01.054

Ingram, J.N., Howard, I.S., Flanagan, J.R., & Wolpert, D.M. (2011). A single-rate context-dependent learning process underlies rapid adaptation to familiar object dynamics. *PLoS Computational Biology*, *7*, e1002196. PubMed doi:10.1371/journal.pcbi.1002196

Salimi, I., Hollender, I., Frazier, W., & Gordon, A.M. (2000). Specificity of internal representations underlying grasping. *Journal of Neurophysiology*, *84*, 2390–2397. PubMed

Jeannerod, M. (1981). Intersegmental coordination during reaching at natural visual objects. In J. Long & A. Baddeley (Eds.), *Attention and Performance IX* (pp. 153–168). Hillsdale: Erlbaum.

Jeannerod, M. (1984). The timing of natural prehension movements. *Journal of Motor Behavior*, *16*, 235–254. PubMed doi:10.1080/00222895.1984.10735319

Johansson, R.S., & Westling, G. (1988). Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. *Experimental Brain Research*, *71*, 59–71. PubMed

Johansson, R.S., & Westling, G. (1987). Signals in tactile afferents from the fingers eliciting adaptive motor responses during precision grip. *Experimental Brain Research*, *66*, 141–154. PubMed doi:10.1007/BF00236210

Nowak, D., Voss, M., Huang, Y-Z., Wolpert, D.M., & Rothwell, J.C. (2005). High-frequency repetitive transcranial magnetic stimulation over the hand area of the primary motor cortex disturbs predictive grip force scaling. *The European Journal of Neuroscience*, *22*, 2392–2396. PubMed doi:10.1111/j.1460-9568.2005.04425.x

Santello, M. (2014). Synergistic control of hand muscles through common neural input. In: *The Human Hand as an Inspiration for Robot Hand Development.* (Eds. R Balasubramanian, VJ Santos), Springer Tracts in Advanced Robotics (STAR) series, vol. 95, Springer, Heidelberg: Germany.

Santello, M., Baud-Bovy, G., & Jörntell, H. (2013). Neural bases of hand synergies. Invited contribution to Research Topic on Modularity in Motor Control. *Frontiers in Computational Neuroscience*, *7*, 23. PubMed doi:10.3389/fncom.2013.00023

Westling, G., & Johansson, R.S. (1984). Factors influencing the force control during precision grip. *Experimental Brain Research*, *53*, 277–284. PubMed doi:10.1007/BF00238156

Westling, G., & Johansson, R.S. (1987). Responses in glabrous skin mechanoreceptors during precision grip in humans. *Experimental Brain Research*, *66*, 128–140. PubMed doi:10.1007/BF00236209

Wolpert, D.M., Diedrichsen, J., & Flanagan, J.R. (2011). Principles of sensorimotor learning. *Nature Reviews. Neuroscience, 12,* 739–751. PubMed

Zhang, W., Gordon, A.M., Fu, Q., & Santello, M. (2010). Manipulation after object rotation reveals independent sensorimotor memory representations of digit positions and forces. *Journal of Neurophysiology*, *103*, 2953–2964. PubMed doi:10.1152/jn.00140.2010