

COMMENTARY

Transforming abstract plans into concrete actions

Melvyn A. Goodale^{a,b,1}

Most of us, at one time or another, will have used a pen to sign our name on a check or legal document—or written our name on a white board with a magic marker. Some of us may even remember writing our name in the air with a sparkler in our younger years, or in the wet sand of a beach using our toe. What is striking is that the strokes and swirls we produce in writing our name in these various ways are remarkably similar, even though the muscles that are recruited to make the movements are quite different. The ability to generate the same pattern of movements with entirely different sets of muscles suggests that, somewhere in the brain, there must be an abstract high-level representation of the required action that transcends the recruitment of a particular limb or group of muscles. The fact that we can generate the same actions with different limbs and muscles is often referred to as “motor equivalence.”

Although handwriting and other complex sequences of movements constitute the most common examples in the literature, simpler goal-directed movements such as pointing, reaching, and grasping also show motor equivalence. For example, we are able to point toward an object of interest with our finger, with our foot, or with a stick or some other implement (Fig. 1). Despite the large differences in the muscles that are recruited, however, the kinematics of the different pointing movements are often quite similar—and the goal and function of the movements are certainly the same. Again, it seems, some sort of abstract representation of even a simple action such as pointing is encoded in the brain and is independent of the particular limb or muscles that are used to perform the action. But where in the brain are these abstract representations encoded? In a neuroimaging study, Liu et al. (1) address this question by looking at the patterns of brain activation in people born without arms as they reached toward or grasped objects using their toes. The authors then compare these patterns of activation with the activation that emerged in the brains of other individuals who reached toward or grasped those same objects with their hands.



Fig. 1. Functional equivalence in different actions. We can indicate an object of interest by pointing to it with our hand, our foot, or a handheld stick.

Liu et al. (1) are not the first to look for the neural substrates of abstract representations of the same action performed with different effectors. The study of motor equivalence has a long history in psychology and neuroscience (2–6), and, since the advent of reliable neuroimaging, investigators have been searching for its neural signature. In a pioneering study carried out more than 20 years ago, Rijntjes et al. (7) used functional magnetic resonance imaging (fMRI) to identify activation in common areas of the brain when people signed their name in the air with their index finger or with their big toe. Not surprisingly, they found that, in regions where there are relatively stable topographic maps of the body, such as primary motor and somatosensory cortex, separate areas were activated for hand vs. toe movements. In other brain regions, however, similar and overlapping networks were activated whether participants used their hand or their toe to write their name, suggesting that, in these brain regions, there are effector-independent representations of the motor plan. In other words, the action representations in these brain regions, which include the premotor cortex, supplementary motor cortex, the posterior parietal cortex, the cerebellum, and various thalamic nuclei, do not seem to care what limb is used—as long as the pattern and sequence of the movements are the same.

In a more recent fMRI study, Heed et al. (8) asked participants to move their hand or their foot toward the location of a remembered visual target. They focused their analysis on activity in the posterior parietal cortex, in regions that have been demonstrated to

^aBrain and Mind Institute, The University of Western Ontario, London, ON, Canada N6A 5B7; and ^bDepartment of Psychology, The University of Western Ontario, London, ON, Canada N6A 5C2

Author contributions: M.A.G. wrote the paper.

The author declares no competing interest.

Published under the [PNAS license](#).

See companion article, “Evidence for an effector-independent action system from people born without hands,” [10.1073/pnas.2017789117](https://doi.org/10.1073/pnas.2017789117).

¹Email: mgoodale@uwo.ca.

First published November 11, 2020.

play a central role in the visual control of action (9, 10). Again, they found overlapping regions for pointing movements made with the hand and pointing movements made with the foot, suggesting that the posterior parietal cortex follows a functional rather than a strict effector-based organization. Importantly, they found that eye movements directed to the same remembered targets activated a region in the posterior parietal cortex that was segregated from the shared hand and foot area. The authors speculated that the high-level representations that are engaged in the planning of target-directed hand and foot movements share common computational constraints that are different from those involved in planning eye movements. This idea is consistent with observations of individuals with damage to the parietal lobe who show deficits in visually guided movements of both the hand and foot on the side of the body contralateral to the lesion (11) but, at the same time, are often able to move their eyes to targets they cannot point to with their limbs (12, 13).

Although the neuroimaging studies provide support for the existence of overarching and abstract neural representations of movement that can account for motor equivalence, the experimental paradigms that were used are not without problems. For one thing, there is the question of whether or not the findings can be explained by motor imagery. It is possible that, when people are asked to use their foot to point to something or to sign their name, they imagine using their hand and try to emulate the imagined movement with their foot. There is certainly evidence that imagining a particular motor act will activate the same neural networks that are engaged in programming that act (14). Thus, the apparent “overlap” in the networks that mediate similar movements in the hand and foot could simply reflect activation of the hand network by real and imagined movements of the hand. Another problem is that, in many studies, participants performed only one kind of functional action, such as pointing. Thus, the common activation that was observed for the same movement made with the foot and the hand could have been related to some other feature of the task rather than the shared function of the movements made with the two limbs.

Liu et al. (1) are able to rule out these possible alternative explanations, by looking at brain activation associated with reaching and grasping movements made with the toes in people with developmental dysplasia who were born without hands and arms—and comparing the pattern of activation in their brains with that observed in participants with a normal developmental trajectory using their hand to perform the same actions. People who are born without hands and arms often become quite adept at reaching out and grasping objects using their feet. Some, such as Italian artist Simona Atzori (<https://simonarte.com/simona>), have even learned to paint using brushes held between their toes. Importantly, the brain activation associated with skilled movements made with the toes and feet in such individuals cannot be due to imagining doing the same actions with the fingers and hand. After all, they have never had hands—and even if they picture hand movements being made by others in their “mind’s eye,” such imagined observations of movements are known to activate visual areas rather than the motor areas normally recruited in the performance of these movements (15). In short, the brain activation associated with reaching and grasping in people with upper limb dysplasia is uncontaminated by the recruitment of neural networks mediating real or imagined hand movements—and is

likely to reflect both activity specific to the foot and the effector-independent brain activity similar to that observed in people without dysplasia making corresponding movements with their hand.

By looking in detail at the patterns of activation for the two separate functional actions (reaching vs. grasping), Liu et al. are able to investigate whether or not the two kinds of action have separate effector-independent representations: one for reaching with either the hand or the foot and another for grasping with either the hand or the foot.

Finally, by looking in detail at the patterns of activation for the two separate functional actions (reaching vs. grasping), Liu et al. (1) are able to investigate whether or not the two kinds of action have separate effector-independent representations: one for reaching with either the hand or the foot and another for grasping with either the hand or the foot. If there are separate representations, then this would mean that the overlapping activation for the same action made by the foot and hand truly reflects the nature of the action rather than some other aspect of the task.

As was the case in the earlier studies, Liu et al. (1) find separate areas of activation for movements of the hand and foot in primary sensorimotor cortex, in areas corresponding to the classic somatotopic organization of this brain region. In addition, this effector-specific activation showed some selectivity for the action (reaching vs. grasping) that was performed. But, in premotor cortex, as well as in the posterior parietal cortex, basal ganglia, and cerebellum, they observed something quite different. In these brain regions, there were distinct patterns of activation that corresponded to the functional actions that were performed rather than to the effector that was used. In other words, reaching with the foot in the individuals with dysplasia or with the hand in the control participants activated the same areas in these brain regions—and the patterns of activation associated with reaching were anatomically distinct from those related to grasping with the foot or the hand. All of this suggests that the information encoded in these brain regions reflects some high-level representation of the action rather than a specific effector that might be used to perform those actions.

When Liu et al. (1) carried out a more detailed analysis of the activation, they found that there was a distinct anterior–posterior gradient from effector-independent to effector-specific activation within premotor cortex, with the more effector-based regions closer to primary sensorimotor cortex, as one might expect. The presence of this gradient almost certainly reflects the existence of a hierarchical network in which the intention to make a particular action, such as grasping an object or signing one’s name, is eventually transformed into a specific set of motor commands. The nature of that transformation depends on the effector to be used and the setting in which the action is to be performed. It is likely that there are critical recurrent connections within this network, but the nature of the circuitry and the constraints operating on the underlying cascade of computations have yet to be specified. But one thing is clear: There is, indeed, an effector-independent representation of an action plan, and that representation can be linked to any one of many different effector-specific circuits in the motor system. To put it another way, the same tune can be played on many different instruments.

-
- 1 Y. Liu, G. Vannuscorps, A. Caramazza, E. Striem-Amit, Evidence for an effector-independent action system from people born without hands. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 28433–28441 (2020).
 - 2 K. S. Lashley, Basic neural mechanisms in behavior. *Psychol. Rev.* **37**, 1–24 (1930).
 - 3 D. O. Hebb, *The Organization of Behavior: A Neuropsychological Theory* (Wiley, 1949).
 - 4 P. A. Merton, How we control the contraction of our muscles. *Sci. Am.* **226**, 30–37 (1972).
 - 5 G. E. Stelmach, V. A. Diggles, Motor equivalence and distributed control: Evidence for nonspecific muscle commands. *Behav. Brain Sci.* **5**, 566–567 (1982).
 - 6 A. M. Wing, Motor control: Mechanisms of motor equivalence in handwriting. *Curr. Biol.* **10**, R245–R248 (2000).
 - 7 M. Rijntjes *et al.*, A blueprint for movement: Functional and anatomical representations in the human motor system. *J. Neurosci.* **19**, 8043–8048 (1999).
 - 8 T. Heed, S. M. Beurze, I. Toni, B. Röder, W. P. Medendorp, Functional rather than effector-specific organization of human posterior parietal cortex. *J. Neurosci.* **31**, 3066–3076 (2011).
 - 9 M. A. Goodale, A. D. Milner, Separate visual pathways for perception and action. *Trends Neurosci.* **15**, 20–25 (1992).
 - 10 M. A. Goodale, Transforming vision into action. *Vision Res.* **51**, 1567–1587 (2011).
 - 11 P. Rondot, J. de Recondo, J. L. Dumas, Visuomotor ataxia. *Brain* **100**, 355–376 (1977).
 - 12 G. Riddoch, Visual disorientation in homonymous half-fields. *Brain* **58**, 376–382 (1935).
 - 13 G. Ratcliff, G. A. B. Davies-Jones, Defective visual localization in focal brain wounds. *Brain* **95**, 49–60 (1972).
 - 14 M. Jeannerod, J. Decety, Mental motor imagery: A window into the representational stages of action. *Curr. Opin. Neurobiol.* **5**, 727–732 (1995).
 - 15 A. Guillot *et al.*, Brain activity during visual versus kinesthetic imagery: an fMRI study. *Hum. Brain Mapp.* **30**, 2157–2172 (2009).