

tual, motor, and conceptual processes in a common theoretical framework. Along with influential proposals by Damasio (1989), Barsalou (1999), and others, Grush is making a strong case for the importance of on-line and off-line simulation. His emulation theory extends previous work by emphasizing the role of efference copies and on-line, dynamic use of the feedback information. Further, he precisely specifies the characteristics of the control process and proposes some possible neural mechanisms. In our commentary, we focus mostly on the unique conceptual gains offered by the proposal, and highlight its fit to empirical data. However, we also suggest that more work is needed for the theory to achieve a respectable level of neurological plausibility.

Grush builds his main arguments around the motor system. Although the traditional simulation theories all highlight the general correspondences between the mechanisms underlying motor imagery and motor execution, the emulation theory, with its emphasis on on-line, efferent feedback, offers a more precise account of empirical data. This can be illustrated with a study that investigated the temporal relation between the physical and visualized performances of springboard dives (Reed 2002a). The study included participants across three skill levels (novice, intermediate, expert) and measured performance of different components within a dive (e.g., approach, hurdle). This design allows for a test of different predictions offered by the simulation and emulation accounts. The traditional simulation theory predicts that skill differences should manifest themselves only during the *first component* of the dive, during motor program selection. In contrast, emulation theory predicts that the skill differences continue throughout *all stages* of the dive, because the emulator would assess the consequences of each motor program selection as dives progress. Specifically, experts should use emulator corrections of their motor execution less because their motor programs are highly accurate and their selection is largely automatic. Novices cannot use the emulator for fine corrections because they simply lack motor programs with which to correct the errors. However, intermediates use the emulator the most to correct their selections of motor programs. The empirical data are consistent with emulation theory. Intermediate performers not only were comparatively slowest in the visualizations, but also showed predicted skill differences throughout the dives. Thus, emulation theory provides insight into the mechanisms underlying complex motor-skill imagery.

The gains offered by the emulation theory extend beyond the motor system. This can be illustrated by research on “embodiment” of emotion processing. Grush offers a useful idea that the “visceral/emotional emulator” helps not only in off-line processing (e.g., providing efferent feedback based on past decisions), but also in on-line processing of emotional material. Several findings not only support this general notion, but also highlight that the emulation process can be impaired on the “brain” level as well as the muscular level. Adolphs et al. (2000) observed that damage to right somatosensory-related cortices impairs recognition of emotion from facial expressions. Niedenthal et al. (2001) showed that participants required to hold a pen in their mouth (blocking efferent feedback) performed worse at detecting changes in emotional facial expression than participants allowed to mimic the expressions freely. Finally, a provocative study discussed by Zajonc and Markus (1984) found that participants who watched novel faces while chewing gum (motor-blocking condition) later performed worse on a recognition test than either participants who encoded by mimicking faces (muscular-facilitation condition) or participants who squeezed a sponge (motor-control condition). This finding is particularly important for the emulation theory because it shows that to benefit cognition, the emulator needs feedback from a specific effector, not just any sensory feedback.

There are many more findings like the ones just mentioned. In fact, a recent review of the social-psychological and emotion literature revealed a number of phenomena that can be explained by the ideas of simulation (emulation) and embodiment (Niedenthal et al., in press). In short, theories such as Grush’s, as well as Barsalou’s and Damasio’s, offer much promise not only when it comes

to accounting for specific problems in motor control, imagery, or emotion, but also as general theories of cognition, including social and emotional cognition.

However, to take advantage of the potential explanatory power of emulation theory, research must clarify how emulators are neurally instantiated. Grush ventures that the emulator for his prototypical system, the musculoskeletal system (MSS), is contained in the cerebellum. Since Grush’s theory explains imagery to be a product of emulation, this proposal predicts that damage to the cerebellum would disrupt motor imagery. However, in contrast to lesions in other brain regions such as the striatum, frontal lobes, and parietal lobes, cerebellar lesions are not known to induce deficits in motor imagery. For example, patients with Parkinson’s disease show selective deficits on motor imagery tasks, but patients with cerebellar atrophy do not (Reed & O’Brien 1996). This suggests either that emulation is not necessary for imagery or that there is more to MSS emulation than the cerebellum. In general, we suggest that emulators may not be discrete structures, but instead, capitalize on multiple subsystems of the brain.

In sum, emulation theory moves us beyond the current simulation theories by providing more mechanistic explanations and specific predictions. In its emphasis on the critical role of efferent feedback in efficient processing, emulation also gives current theories a good functional reason for why perception, cognitive, and motor systems are so tightly intertwined. Despite these strengths, the neural instantiation of such an emulator must be developed further so that it can incorporate multiple cognitive and motor functions. Further, the emulator, rather than being its own module, should be conceived as a general brain mechanism that permits feedback to multiple existing neural systems that have more or less direct relationships to the motor system. In short, the emulation theory requires some additional development before it fully filters down from armchair to laboratory.

## Emulation of kinesthesia during motor imagery

Norihiro Sadato<sup>a</sup> and Eiichi Naito<sup>b</sup>

<sup>a</sup>Department of Cerebral Research, Section of Cerebral Integration, National Institute for Physiological Sciences, Myodaiji, Okazaki 444–8585, Japan;

<sup>b</sup>Faculty of Human Studies, Kyoto University, Sakyo-ku, Kyoto 606–8501, Japan. sadato@nips.ac.jp

eiichi.naito@neuro.mbox.media.kyoto-u.ac.jp

**Abstract:** Illusory kinesthetic sensation was influenced by motor imagery of the wrist following tendon vibration. The imagery and the illusion conditions commonly activated the contralateral cingulate motor area, supplementary motor area, dorsal premotor cortex, and ipsilateral cerebellum. This supports the notion that motor imagery is a mental rehearsal of movement, during which expected kinesthetic sensation is emulated by recruiting multiple motor areas, commonly activated by pure kinesthesia.

It is uncertain whether motor imagery could generate expected kinesthetic sensation, although it has been considered a mental rehearsal of movement. It is empirically known that many people can experience vivid motor imagery, mostly involving a kinesthetic representation of actions (Feltz & Landers 1983; Jeannerod 1994; Mahoney & Avenier 1987). In movement control, the musculoskeletal system is subject to the measurement of proprioceptive and kinesthetic information generated by actual movement and relayed as feedback sensory signals. One of the important predictions of Grush’s “emulation theory” in motor imagery is that the emulator will output the sensory signal in “mock” proprioceptive format in response to motor control signals (efferent copy), resulting in kinesthetic sensation. This is in contrast to the “simulation theory” in motor imagery, in which only efferent copies are supposed to be generated. If the emulation theory is correct, one may identify the output sensory signals generated by the emula-

tor by detecting their interaction with pure kinesthetic sensation without movement.

It is known that pure kinesthesia without movement can be elicited by vibration of the tendon with a specific frequency (83 Hz; Craske 1977; Goodwin et al. 1972a; 1972b; Naito et al. 1999). Using this fact, Naito et al. (2002) showed that motor imagery affected pure kinesthetic sensation, generated by tendon vibration without overt movement. They found that the motor imagery of palmar flexion, or dorsiflexion of the right wrist, psychophysically influenced the sensation of illusory palmar flexion elicited by tendon vibration. Motor imagery of palmar flexion psychophysically enhanced the experienced illusory angles of palmar flexion, whereas dorsiflexion imagery reduced it in the absence of overt movement. This finding indicates that the emulator, driven by the mental imagery, outputs the “mock” sensory signals in a proprioceptive format, which interferes with the real (but artificially generated) proprioceptive sensory information from the musculoskeletal system.

Another prediction of Grush’s emulation theory is that the articulated emulator is a functional organization of components (articulants), whose interaction is comparable to that within the musculoskeletal system, and hence their neural representations are expected to be common. This point was also demonstrated by the study of Naito et al. (2002). Regional cerebral blood flow was measured with O-15 labeled water ( $H_2^{15}O$ ) and positron emission tomography in ten subjects. The right tendon of the wrist extensor was vibrated at 83 Hz (ILLUSION) or at 12.5 Hz with no illusion (VIBRATION). Subjects kinesthetically imagined doing wrist movements of alternating palmar and dorsiflexion at the same speed with the experienced illusory movements (IMAGERY). A REST condition with eyes closed was included. The researchers identified common active fields between the contrasts of IMAGERY versus REST and ILLUSION versus VIBRATION. Motor imagery and the illusory sensation commonly activated the contralateral cingulate motor areas, supplementary motor area, dorsal premotor cortex, and ipsilateral cerebellum. The researchers concluded that kinesthetic sensation associated with imagined movement was generated during motor imagery by recruiting multiple motor areas, which were also activated by the kinesthetic sensation generated by tendon vibration. These commonly activated areas may constitute the articulants of the emulator driven by the efferent copy during motor imagery.

In conclusion, generation of kinesthetic sensation during motor imagery, and its neural representation common to kinesthesia without movement, can be interpreted as “emulated kinesthetic sensation” in the framework of the emulation theory by Grush.

## Modality, quo vadis?

K. Sathian

Department of Neurology, Emory University School of Medicine, WMRB 6000, Atlanta, GA 30322. ksathia@emory.edu

**Abstract:** Grush’s emulation theory comprises both modality-specific and amodal emulators. I suggest that the amodal variety be replaced by multisensory emulators. The key distinction is that multisensory processing retains the characteristics of individual sensory modalities, in contrast to amodal processing. The latter term is better reserved for conceptual and linguistic systems, rather than perception or emulation.

Grush develops his emulation theory as a unified account of perception, imagery, and motor control, with the prospect of extension to diverse other neural functions. This theory is an advance over previous, less systematic formulations of simulation and imagery as being important in sensorimotor function. It makes the claim that particular neural elements work together in an emulation of perceptual or motor tasks, running in a special mode in which they are disconnected from external inputs/outputs. Vari-

ous emulations differing in their characteristics can hence be run, based on which the organism can select the best one to implement in interaction with the environment. The appeal of the theory stems from its unifying potential, and hence its success will be measured to a large extent by how well its binding of seemingly disparate streams of thought bears up over time. In this commentary, I focus on the relationship between the proposed sensorimotor emulator and sensory modality.

Grush argues for modality-specific as well as amodal emulators in the nervous system. Modality-specific emulators are relatively easy to understand, in terms of the operation of modality-specific sensory or motor systems. For instance, the findings reviewed in section 4.3 of the target article are compatible with a role for a motor emulator during visual imagery. However, the concept of a strictly amodal emulator, one that is entirely independent of any sensory “tags,” is less clear.

Let me make it absolutely clear that I am not arguing against amodal representations in the brain. Such representations must exist for abstract concepts that can be encoded linguistically, or “propositionally,” rather than directly in the workings of sensory systems. Indeed, as a vital part of human thought and communication, they are among the most important abilities that evolution has conferred on our species, compared to the other species that live or have lived on this planet. It is the characterization of abstract, amodal representations as imagery, and, by extension, as substrates of emulation strategies, that I am not comfortable with. Rather than “amodal” emulators, I suggest invoking “multisensory” emulators to provide the link between modality-specific systems and between these systems and abstract representations. I must emphasize that this is not a merely semantic distinction. By “multisensory,” I mean a system that receives inputs from more than one sensory modality. The existence of multisensory processes is well established, as is their neural implementation. The functions of multisensory processing include integration between the senses, cross-modal recruitment of sensory cortical regions, and coordinate transformation. Each of these functions has been studied in some detail.

Coordinate transformation in multisensory neurons of the posterior parietal cortex (PPC) has been intensively studied by Andersen and colleagues. This work indicates that multiple reference frames are represented in different regions of the PPC (Buneo et al. 2002; Cohen & Andersen 2002; Snyder et al. 1998). Reference frames may be allocentric, as in Brodmann’s area 7a; eye-centered, as in the lateral intraparietal area (LIP) and parietal reach region (PRR); body-centered, as in LIP; and both eye- and hand-centered, as in Brodmann’s area 5. Further, the eye-centered neuronal responses in LIP and PRR are gain-modulated by a variety of other factors such as eye, head, body, or hand position (Cohen & Andersen 2002). This effectively allows for a distributed representation of multiple reference frames simultaneously, and hence, for the coordinate transformations that are required for particular tasks, for example, between the retinocentric reference frame of visual stimuli or the head-centered reference frame of auditory stimuli and the body-centered reference frame of reaching arm movements, so that motor outputs may be appropriately directed. Multisensory emulators, then, could be engaged for specific coordinate transformations to allow planning of motor behavior as dictated by the organism’s current goals.

Another function of multisensory neurons is to integrate perceptual processes across the different senses. Such multisensory integration has been studied at the level of single neurons in the superior colliculus (Stein & Meredith 1993) and more recently in human cerebral cortex using functional neuroimaging. A case in point is the integration of auditory and visual information during perception of speech, which appears to depend importantly on cortex in the superior temporal sulcus (Calvert 2001). Moreover, Freides (1974) suggested three decades ago that, regardless of the modality of sensory input, the task at hand, especially if it is complicated, will recruit the sensory system that is most adept at the kind of processing required.