

perspective. They first learn physical abacus operations, and then they train themselves to operate on a mental abacus image, moving their fingers as if they were pushing imaginary abacus beads. Once they fully develop the mental calculation skill, they usually do not bother to move their fingers while performing mental calculation. Figure 1 illustrates a control theory of physical and mental abacus operations from the “emulationist” viewpoint adapted from Grush’s Figure 7 in the target article. Based on this theory, mental abacus operations correspond to offline, conscious manipulation of an imaginary abacus supported by a modality-specific emulator. To achieve this, however, amodal imagery is probably working in the background by emulating rules that govern expert abacus interaction and monitoring what is going on in the virtual space.

The neural substrates during mental abacus operations included the rostral PMd, posterior parietal cortex, and the posterior cerebellum, bilaterally (Hanakawa et al. 2003b). Notably, control nonexperts also showed activity in the left rostral PMd and posterior parietal cortex, in addition to the language areas, during mental calculation. This result further supports the amodal nature of imagery computed in the rostral motor areas.

Conclusions. The above-mentioned rostral motor area activities coexist with activity in the posterior parietal cortex and also the cerebellum, to which Rick Grush has tentatively assigned the neural correlates of the “emulator.” Taken together, therefore, rostral motor areas may constitute a part of the neural network representing the “emulators,” particularly of amodal imagery. An alternative explanation for the amodal functions of rostral motor areas may be that these areas correspond to one of the key structures representing the “controllers” for both motor and cognitive operations, as we show in Figure 1.

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The size-weight illusion, emulation, and the cerebellum

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Abstract: In this commentary we discuss a predictive sensorimotor illusion, the size-weight illusion, in which the smaller of two objects of equal weight is perceived as heavier. We suggest that Grush’s emulation theory can explain this illusion as a mismatch between predicted and actual sensorimotor feedback, and present preliminary data suggesting that the cerebellum may be critical for implementing the emulator.

If a person compares the weight of a large object with that of a small object of identical physical weight, the latter will feel substantially heavier, even though the person is explicitly asked to compare the weight rather than the density. This effect – the so-called “size-weight illusion” – is a striking demonstration of the principle that perception is predictive and does not simply involve a passive response to sensory inputs (Charpentier 1891; Ross & Gregory 1970). Traditionally, it has been suggested that the brain expects the bigger object to be much heavier and sets the muscle

tension accordingly, and so when the larger object is lifted it feels surprisingly light (Ross 1966; Ross & Gregory 1970), indeed lighter than a small object of identical weight. However, recent evidence has shown that the size-weight illusion (SWI) persists despite adaptation of these peripheral lifting movements (Flanagan & Beltzner 2000), suggesting that the source of the illusion may be a central mismatch between the expected and actual sensory feedback. We therefore suggest that the source of the mismatch in the SWI may be an internal sensory prediction, which, after a lifetime of experience, generates an erroneous weight prediction, yielding a sensory residual and the corresponding illusion (Hubbard et al. 2000; in preparation).

One prediction that we made on the basis of this hypothesis is that patients with damage to the cerebellum, which has been implicated in weight perception (see Holmes 1917; 1922), may also show reductions in the SWI, even in the absence of impairments in weight perception. A number of researchers (e.g., Kawato 1990; Wolpert et al. 1995; and Grush in the present target article) have suggested that predicting the sensory consequences of motor actions may be a function of portions of the cerebellum, especially the dentate nucleus. These speculations led us to wonder whether the cerebellum may be involved not only in overt movement, but also in cognitive simulation prior to movement, functioning as a “Grush emulator” (Grush 1995; target article), or forward model (Jordan & Rumelhart 1992). This line of reasoning is also supported by the observation that neurons in the lateral cerebellar cortex (specifically lobules V and VI) respond to the anticipated sensory consequences of an action (Miall 1998).

To test this prediction, we tested six control subjects and seven cerebellar patients. Cerebellar patients of varying etiologies were referred to us by physicians on the basis of neurological assessment. Patients showed typical signs of cerebellar dysfunction including intention tremor, past pointing, and dysdiadochokinesia.

To assess weight discrimination, subjects were presented with a pair of weights differing in weight by 50 grams and were asked to state which of the two cans was heavier. We used both a pair of large cans (300 g, 350 g) and a pair of small cans (150 g, 200 g). Each subject was tested twice. After assessing weight discrimination, we assessed the magnitude of the SWI by asking subjects to determine which of 10 small cans (ranging from 100–275 g) matched the apparent weight of the large 300-gram can. Each subject was tested four times.

The six control subjects showed accurate weight discrimination. Subjects made errors on a total of four out of 24 trials, and no subject made more than one error. However, when asked to match the weight of the large 300-gram can, control subjects showed a clear SWI, matching the large can with a can that weighed substantially less (mean 151.04 g). The magnitude of the illusion is far greater than the minimum difference that can be discriminated – the illusion is not due to an inability to discriminate the weight of the cans.

On the other hand, five of seven cerebellar patients showed a reduction of the SWI, despite intact weight discrimination. The first patient, a middle-aged woman showing acute unilateral cerebellar signs (left hand) caused by secondary tumor metastasis in the brain, showed the most dramatic effect. She was mentally lucid, intelligent, and articulate. She showed cerebellar signs – intention tremor, past pointing, and dysdiadochokinesia – only in the left hand. Her ability to estimate subtle differences in weight was identical in both hands. However, the left hand showed no SWI, whereas the right hand showed the illusion in full strength. She expressed considerable surprise that the two hands were producing different results on the task. There was some recovery from cerebellar signs on the following day, and this time the left hand showed the illusion, but still it was substantially smaller than in the normal, right hand.

The subsequent six patients had bilateral cerebellar damage caused by injury, infarction, and electrocution (one patient). Unlike the first patient, they were seen weeks to months after the on-

set of the lesion. Two of these showed the full SWI, despite florid bilateral cerebellar signs. The other four showed a small reduction of the illusion (mean 175 g in the four patients who showed the effect, with almost 210 g in one of them, compared to the 300 g standard).

These experiments provide some preliminary evidence that the cerebellum may be involved in sensory predictions of overt motor behavior and thereby contributes to the SWI. However, these results are not conclusive. Future research should be conducted with additional cerebellar patients to distinguish between three hypotheses: (1) a specific part of the cerebellum serves as a Grush emulator and this was severely damaged in Patient One but less damaged in the others; (2) Patient One may have had some other metastatic lesion causing the reduction of the SWI, for example, a zone in the basal ganglia or frontal lobes that receives information from the cerebellum rather than in the cerebellum itself; or (3) the loss of the SWI may be seen only acutely (as in Patient One) and, given the cerebellum's remarkable adaptive capacities, may have recovered substantially in the other patients. These findings suggest that the cerebellum may be involved in perceptual and cognitive predictions, functioning as a Grush emulator or forward model for internal simulations before performing certain tasks.

The role of “prespecification” in an embodied cognition

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Abstract: Grush makes extensive use of von Holst and Mittelstaedt's (1950) efference copy hypothesis. Although his embellishment of the model is admirably more sophisticated than that of its progenitors, I argue that it still suffers from the same conceptual limitations as entailed in its original formulation.

Efference-copy models tend to be based on a sensory-motor distinction in which the terms “sensory” and “motor” imply functionally orthogonal halves of an organism (Jordan 2003). This habit has its scientific roots in the Bell-Magendie law – the discovery that the spinal cord entails separate ascending and descending tracts (Boring 1950). It was this neurological fact, along with others, that motivated Pavlov's and Sherrington's reflexologies, as well as von Holst and Mittelstaedt's (1950) control theoretic critique of such stimulus–response (S–R) based approaches. And although the efference-copy hypothesis offered a seemingly workable alternative to S–R approaches, it still entails a commitment to functional orthogonality implied in the terms “sensory” and “motor.”

The problem with such proposed orthogonality is that more and more data indicate the nervous system does not function in this way. And what is more, Grush himself touches upon the most robust data in support of this point as he discusses the role the cerebellum might play in his emulator model. In traditional models of the “motor-control” hierarchy, a desired behavior, expressed in body coordinates, is fed from association cortex to the motor cortex. It is then converted into the actual motor command, that is, the torque to be generated by the muscles. This motor command is then sent to both the musculoskeletal system and the spinocerebellum–magnocellular red nucleus system (SMRN). The SMRN system has access to both the motor command and its immediate sensory effects. The SMRN uses these sources of information to generate what Kawato et al. (1987) refer to as a motor-error signal. Because the cerebro-cerebellar loop is faster (10–20 msec; Eccles 1979) than the cerebro-spinal loop, the use of anticipated motor error, or “virtual feedback” as Clark (1997) refers to it, affords control at much finer time scales than that allowed via the “real” feedback obtained through the cerebro-spinal loop.

Though this description makes it sound appropriate to refer to this hierarchical system as a motor-control system, the model itself challenges such language. Specifically, in addition to inputs from the association cortex, the motor cortex also receives input from the SMRN. This SMRN signal, however, defies definition via terms such as “motor” or “sensory.” It is neither, yet at the same time, both. For all intents and purposes, it is best described as Clark described it: as a “virtual feedback” or a virtual effect. Given that this virtual effect figures into the content of the actual motor command, the motor command also defies definition via terms such as “motor” and “sensory.” For all intents and purposes, it is perhaps best described as a specified virtual effect. Perhaps at the motor-cortex level of the hierarchy, this virtual effect is expressed in terms of anticipated or intended torque, whereas at the association-cortex level of the hierarchy, the virtual effect is expressed in terms of a more distal, environmental consequence. The point is that at all levels within this hierarchy, what are being prespecified (i.e., commanded), detected, and controlled, are effects (i.e., feedbacks) that play themselves out at different spatiotemporal levels for different systems.

Grush himself indirectly addresses this point when he argues that sensation and perception both constitute control systems. They both utilize prespecifications (i.e., “goals”) and control feedback. If this is truly the case, however, it means that control systems control their input (i.e., feedback), not their output (Powers 1973). When this notion of prespecified/controlled input is applied to Grush's account of motor control, a contradiction is generated between the notions of prespecified input and an efferent-motor command, for the efference copy is traditionally modeled as a prespecified motor output. Hershberger (1976) was aware of this contradiction and coined the concept “afference copy” to address the fact that control systems prespecify, monitor, and control inputs (i.e., effects/feedback). Hershberger's notion of “afference copy” makes it clear that all of the prespecifications (i.e., goals, control signals, and efference copies) in the system are prespecifications of effects (i.e., input/feedback). The entire system, therefore, seems more appropriately modeled as an effect-control hierarchy.

In addition to overcoming some of the conceptual problems engendered by the efference-copy hypothesis, the notion of effect-control also provides a means of potentially integrating ecological and representational approaches to perception. Grush's model is firmly entrenched in the representational camp. His model begs representationalism because he begins by conceptually dividing the problem into organisms and environments. Given this dualism, the task becomes one of determining how it is that organisms build models of the environment in their brains in order to get around in the world. This then sets the stage for the introduction of yet another dualism – efference and afference.

The notion of effect control provides a means of avoiding such dualisms, for it begins by recognizing that the common denominator among environments, organisms, brains, and neurons, is regularities. Every aspect of an organism, including its nervous system, can be coherently modeled as an embodiment (Jordan 1998; 2000) or encapsulation (Vandervert 1995) of environmental regularities. The implications of this notion are straightforward. There is no need to divide an organism's nervous system into biological and informational properties. Nervous systems are, by necessity, embedded, embodied regularities. The control dynamics of such systems, therefore, need not be modeled via terms such as “sensory,” “motor,” “afferent,” and/or “efferent.” Such terms are used because of our historical commitment to the input-output orthogonality inherent in the Bell-Magendie law. What control systems do is to prespecify and control effects.

Once such an embodied controller is in place, its own regularities become available for further embodiment. Grush acknowledges this point when he argues that because his emulators are neural systems, any and all of their relevant states can be directly tapped. Tapping into such regularities affords an organism the ability to control effects at increasing spatiotemporal scales. At every point in this phylogenetic bootstrapping process, regulari-