

Moving to a different beat

R Christopher Miall & Richard Ivry

Many primitive movements, such as swimming or scratching, are rhythmic. An imaging study now suggests that complex discrete movements may simply be a special case of rhythmic movements, in which they are stopped after only one cycle.

How is waving to a friend different from swatting at an annoying fly? Is running on the spot simply the repetition of a single step? In this issue, Stefan Schaal *et al.*¹ use functional magnetic resonance imaging (fMRI) to explore these questions, examining the neural systems engaged during discrete and rhythmic wrist movements.

They begin by noting a fundamental division in current research on motor control between two camps that rarely interact. One camp works on rhythmic behaviors, building on the idea that complex actions in humans are likely to have their roots in phylogenetically primitive movements. The neural elements underlying locomotor and feeding behaviors—chewing, walking, swimming, flying or scratching—are quite well understood, especially in invertebrates, where the central pattern-generating circuits that can produce these rhythmic actions have been documented in considerable detail^{2,3}. In humans, periodic movements not only are a prominent feature of basic actions such as walking or chewing, but also are manifest in more complex behaviors such as dancing, writing and many sports—as was evident in the recent Olympic games. The other camp has focused on more discrete actions, with reaching serving as the paradigmatic task for understanding the computations required to successfully interact with the environment. The emphasis here has been on problems related to coordinate transformations and the control of kinematic and dynamic variables that allow us to move from one discrete state to another⁴.

An implicit, yet untested, assumption in each school of thought [AU: OK as edited?] is that there is considerable overlap in the neural structures required to control discrete and rhythmic actions. Rhythmic arm movement

may be no more than the repetition of discrete movements. Hence one might expect that rhythmic wrist actions would activate the same neural circuits involved in discrete movement control, perhaps with stronger activity owing to the greater demand on the circuitry. Alternatively, discrete movements may simply be rhythmic movements that have been stopped after a single cycle, or half a cycle. In that case, we might expect the neural centers generating rhythms to be supplemented by some ‘start and stop’ circuitry.

To test this assumption, subjects were scanned when making wrist movements of one arm, either by smoothly alternating between flexion and extension or by pausing between each flexion and extension phase. In the latter condition, the subjects were explicitly told to avoid initiating each cycle in a periodic manner. Despite the overall similarity between the two conditions in terms of movement requirements and kinematics, the activation patterns were strikingly different. In the rhythmic condition, the activation was restricted to cerebral areas contralateral to the moving hand, including primary sensorimotor areas, premotor and supplementary motor areas (SMA [AU: Correct? Or spell out “pre-SMA” below]), cingulate cortex and ipsilateral cerebellum. Activation was much more widely distributed in the discrete movement condition. It included all these areas, plus dorsal premotor cortex, prefrontal, posterior parietal cortex, rostral cingulate cortex and contralateral cerebellum. Control experiments suggest that the activity in some of these areas was related to movement initiation and/or termination. However, when these parameters were matched for the two movement conditions, dorsal premotor cortex, pre-SMA, prefrontal and parietal regions (Brodmann’s areas 6, 47, 7 and 40) were selectively recruited in the discrete condition, along with the contralateral cerebellum. These results indicate that rhythmic movements should not be considered as the concatenation of a series of discrete movements. However, it is possible that the control of discrete movements might be superimposed on neural systems required for the control of rhythmic movements (Fig. 1) [AU: OK to insert figure callout here?].

There are several important issues still to be resolved. If we take these results at face value, we need to ask, What is the extra neural activity observed during discrete movement actually doing? First, the discrete condition does place additional demands on decision processes. In the main experiment, the subjects have to decide when to initiate each movement as well as monitor the passage of time to meet the requirement that they do not produce the discrete movements in a periodic manner. Although movement initiation was controlled by auditory cues in one of the control experiments, the discrete task does require the subject to monitor finger position and select movement direction for each successive gesture. These requirements may, at least in part, account for some of the activations observed in prefrontal, premotor and parietal areas.

Second, the extra neural activity may be related to demands associated with timing the actions in the discrete conditions. Timing may be needed to directly control the discrete movements; for example, such control would be needed if discrete movements are produced by starting and stopping rhythm generators. Alternatively, the subjects may need to time the intervals between each discrete action. The latter is a parameter of the task that was under the participants’ control in two of the three experiments reported, and it would have been difficult for the participants to avoid timing the events, either implicitly or explicitly, in the third, externally paced, experiment. There is a striking similarity to the cortical areas activated in the discrete condition to the areas activated in a number of studies of discrete human interval timing⁵. Moreover, timing of repetitive actions or the discrimination of simple rhythms activates the same lower-level sensorimotor systems that were active in the rhythmic conditions of Schaal’s study¹. Thus one could argue that the pattern of results seen by the authors mainly reflects the differential timing constraints of the rhythmic and discrete tasks used.

Third, the logical questions posed in the Schaal *et al.* study assume that the appropriate division of tasks is between rhythmic and discrete movements. This is, of course,

Chris Miall is in the Department of Behavioural Brain Sciences, School of Psychology, University of Birmingham, B15 2TT, UK. Richard Ivry is in the Department of Psychology and Helen Wills Neuroscience Institute, University of California, Berkeley, California 94720, USA.
e-mail: r.c.miall@bham.ac.uk or ivry@socrates.berkeley.edu

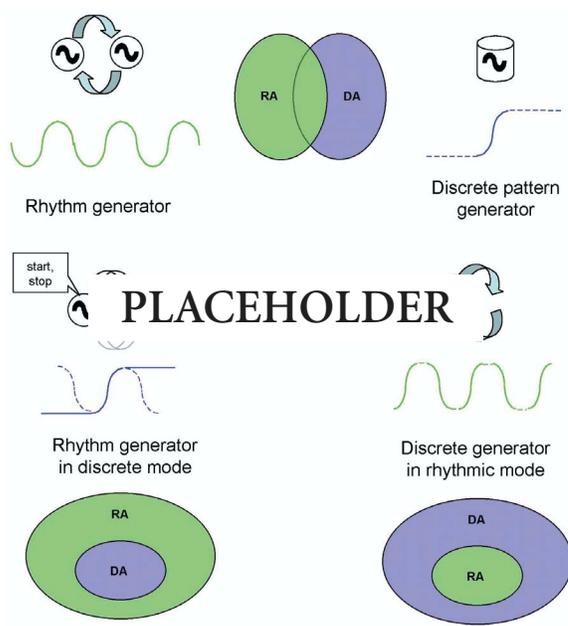


Figure 1 Possible models for the control of rhythmic and discrete movements. (a) In the first model, separate neural circuits control rhythmic and discrete movements, with the former involving the control of central pattern generators (left) and the latter involving generation of a discrete motor program (right). In this case, functional imaging would reveal activation of separate regions for each task, as well as shared regions (middle). (b) In a second model, discrete action activates the rhythm circuitry plus other regions required to start and stop rhythm generators. Imaging would also reveal additional activity contributing to the decision processes associated with this form of control. (c) In the third model, rhythmic action results from the repetitive use of circuits involved in the control of discrete actions. Schaal *et al.*¹ report more widespread activation during discrete movement, including left premotor, parietal and cerebellar areas, consistent with the model in (b). They do not see more widespread activity in the rhythmic condition, ruling out the model in (c). [AU: OK as edited?]

only one way to divide the pie. Within the class of rhythmic actions, control requirements also differ between movements that are made in a continuous manner and those that involve discontinuities. In one study, subjects were asked to rhythmically flex and extend the index finger, either by switching from one movement to the other in a continuous manner or by inserting a brief pause before each flexion cycle⁶. Patients with lesions of the cerebellum showed an increase in temporal variability only in the latter condition, and this deficit could not be accounted for by the greater initiation and termination requirements in the discrete condition⁷. Moreover, when subjects perform the task bimanually, the movements of split-brain patients remain temporally coupled in the discrete condition, whereas the two fingers become temporally uncoupled in the continuous condition⁸ [AU: sentence OK as edited?]. These studies suggest that subcortical mechanisms are essential for the temporal control and coordination of discontinuous rhythmic movements. In contrast, cortical structures are essential for the control of continuous rhythmic movements, perhaps operating in the manner of central pattern generators as envisioned by Schaal *et al.* It would be interesting to see the activation patterns for a

hybrid rhythm condition in which the individual movement cycles were discrete.

Some existing data are not easy to fit into the theoretical framework proposed by Schaal *et al.*¹. For example, some reports of rhythmic action show more extensive activation patterns than seen here^{5,9}. Hence the argument that rhythms are simple and automatic, whereas discrete actions are more cognitively controlled, may not hold true under all conditions. Furthermore, there is no guarantee that the overlapping areas of activity seen in an fMRI experiment comparing rhythmic and discrete actions actually involve the same neural circuits, rather than separate but spatially coincident circuits. Behavioral evidence of interactions between the two control systems has been interpreted both ways^{10,11}. However, there is little evidence as yet to suggest that central pattern generators exist in the cerebral cortex. Cortical areas may be involved in controlling rhythmic actions by their descending control of spinal circuits. If so, it would be extremely interesting to repeat these experiments but with a spinal field of view¹², to measure the contribution of pattern generators to discrete actions. We might expect to see greater spinal activity during rhythmic than during discrete movement, even if the amount of movement in the two conditions

were carefully equated; it might even be possible to visualize spinal pattern-generator activity during discrete actions.

As a last thought, the two camps of neuroscientists mentioned previously are not the only ones working on primate motor control. Would researchers working on ocular motor control, or control of tongue movements, have an opinion on the question of rhythmic action? Neither of these two systems is likely to have any phylogenetic connection with pattern generators, and so either would provide a powerful test of the separation of discrete and rhythmic control.

1. Schaal, S., Sternad, D., Osu, R. & Kawato, M. *Nat. Neurosci.* **7**, aaa-bbb (2004).
2. Burke, R.E. *Adv. Neurol.* **87**, 11–24 (2001).
3. Marder, E. & Calabrese, R.L. *Physiol. Rev.* **76**, 687–717 (1996).
4. Wolpert, D.M. & Ghahramani, Z. *Nat. Neurosci.* **3** (Suppl.), 1212–1217 (2000).
5. Lewis, P.A. & Miall, R.C. *Curr. Opin. Neurobiol.* **13**, 250–255 (2003).
6. Spencer, R.M., Zelaznik, H.N., Diedrichsen, J. & Ivry, R.B. *Science* **300**, 1437–1439 (2003).
7. Spencer, R.M., Ivry, R. & Zelaznik, H.N. *Exp. Brain Res.* in the press. [AU: any update available?]
8. Kennerley, S.W., Diedrichsen, J., Hazeltine, E., Semjen, A. & Ivry, R.B. *Nat. Neurosci.* **5**, 376–381 (2002).
9. Lewis, P.A., Wing, A.M., Pope, P.A., Praamstra, P. & Miall, R.C. *Neuropsychol.* **42**, 1301–1312 (2004).
10. Sternad, D., Dean, W.J. & Schaal, S. *Hum. Move. Sci.* **19**, 627–665 (2000).
11. de Rugy, A. & Sternad, D. *Brain Res.* **994**, 160–174 (2003).
12. Stroman, P.W. & Ryner, L.N. *Magn. Reson. Imaging* **19**, 27–32 (2001).