

allied to their experimental work. Since they come from such diverse backgrounds, mathematics to 'wet' zoology, and from different cultures, they approach the field from quite disparate directions and question almost everything you say. We discussed many issues, from the minutiae of channel kinetics and the experimental evidence that the theoreticians need the experimentalists to provide, to the directions that computational neuroscience might take in the future. Contemplation of the work required to initiate, plan and fund such an enjoyable and valuable course and to circumvent myriad minor difficulties as it progressed initiates strong sympathetic activity. Our heartfelt thanks go to Erik De Schutter, Idan Segev, Adonis Moschovakis and Jim Bower for providing a brief rejuvenating respite that reminded us that science and teaching can be fun.

Alex Thomson
Faculty member

I come from a small country, Finland, where computational neuroscience is not

yet a well-established discipline in neuroscience. Having an interdisciplinary background (electrical engineering and electrophysiology), I have found the use of modeling techniques both scientifically and educationally valuable. Before the course, I had some experience in single-cell modeling and had used one simulation software package, but I wanted to gain a deeper understanding of the whole field. I wanted to grasp as much information as possible: What is realistic for us to simulate with our existing tools? At what level and detail should we build our models? How detailed and in what format do we need our experimental data? Where do the pitfalls of the modeling process lie? At the end of the course, my hopes were more than fulfilled.

What did I learn? Every morning two or three distinguished faculty members from all over the world shed light on theories of the brain and available experimental and modeling methods. They used their own work as an example, and managed to place their own results into a larger context. Models can be used to gain insights into

how a system (subcellular, cellular, local or larger network) works as a whole. A systematic approach was taken to introduce all these levels to us and it became obvious to me that studies at all levels are needed. Furthermore, models may suggest new ideas for experiments, and they can also be used as a collective 'database' for a large amount of anatomical and physiological data. Thus, modeling techniques are useful tools towards understanding the brain, but they can never replace the real experiments.

Finally, what was the most fascinating aspect of the course? Clearly the multidisciplinary atmosphere. The students and faculty members represented fields including physics and mathematics, computer science and electrical engineering, neuroscience and the medical sciences. There was no such dilemma as 'what am I – an engineer or a physiologist or what?' Everybody had the same goal – to learn the techniques that might eventually make us understand our own brain!

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RESEARCH NEWS

Motor imagery: never in your wildest dream

Research into motor imagery, the mental rehearsal of a motor act^{1,2}, is providing new insights into the representation of willed action. Motor imagery activates descending motor pathways³, modulates downstream autonomic⁴ and spinal-reflex pathways⁵, and alters the transmission of signals in cortical afferent pathways⁶. Imaging a movement enhances later performance in much the same manner as physical training⁷. Results from a wide range of studies support the notion that motor imagery and execution involve activation of very similar cerebral structures 'at all stages of motor control'⁸ with the proviso that the final motor output is not expressed during motor imagery^{4,7}.

Mental and executed tasks

In two recent articles, Angela Sirigu and her colleagues^{9,10} report several findings that illuminate the nature and locus of central motor representations. Using only a metronome and a stopwatch, they studied patients with lesions located in parietal and precentral motor-cortical areas. Normal subjects and patient groups were asked to perform three different motor tasks and to mentally rehearse doing the same. The crucial variable in both the mental and executed tasks was the duration of move-

ment. In mental chronometry, experimenters depend upon subjects' reliability in faithfully performing mental tasks as instructed and reporting the time of task completion. Sirigu *et al.* used two basic approaches: First, using the metronome, they paced thumb–finger opposition movements in which subjects first touched the tip of the little finger and then each other finger in turn. Starting at 40 beats per minute, subjects either performed this fixed sequence of finger movements or imaged doing so. The metronome beat gradually quickened until subjects reported they were unable to continue moving or to mentally image moving at this rate. Second, subjects made repetitive alternating hand postures or pointing movements. These movements were triggered by a tone and time to completion was measured with the stopwatch.

Using this simple yet elegant experimental design, Sirigu *et al.* found that in naïve, control subjects mentally rehearsed and overtly executed movements have the same temporal characteristics. The fastest speed at which subjects could mentally rehearse the thumb–finger movement sequence nearly equaled the fastest actual movement. Similarly, the times taken to complete sets of alternating hand postures

of varying difficulty and duration were about the same for imaged as for executed ones. Pointing-movement times also increased with decreasing target size for both executed and mentally simulated hand movements. This logarithmic speed–accuracy trade-off (Fig. 1A), known as Fitts' law, remains one of the most robust principles of motor-control theory. These results extend previous work on mentally simulated handwriting¹¹ and walking¹² movements, and suggest that imaged movements are constrained by the same physical laws and physiological limitations that apply to our everyday motor behaviors. We can imagine moving our fingers in a sequence of postures in order to play the piano, but apparently we cannot imagine playing the piano faster than we can actually move our fingers. The basis of this limitation remains unknown, but one conjecture seems plausible, and it is based on the concept of efference copy, also known as corollary discharge. Prediction of the temporal unfolding of a motor act, as reflected in a copy of the efferent motor-command signal sent to CNS structures as a corollary of its transmission to the motor effectors, is one strategy the nervous system might employ to compensate for the sluggish and complex nature of the motor

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system. The factors underlying this sluggishness include central processing and peripheral neural-transmission times, feedback delays, and biomechanical characteristics of the motor plant including the inertia and impedance. This corollary discharge could be compared to the multimodal sensory 'feedback', or 'reafferent', signals reflecting how a behavior actually unfolds. In this view, motor imagery might be the efference copy alone, which would explain why it is constrained by normal motor experience.

Results from lesion studies

But the studies of Sirigu *et al.* go beyond the usual issues to focus on the effects of brain lesions. One patient, with a lesion to the motor cortex (Fig. 1B) and concomitant disruptions of the executive motor system, also managed to perform movements with similar duration in all three tasks whether executed or imagined. In the pointing task, this similarity of timing and the compliance with Fitts' law was preserved bilaterally (Fig. 1B, 'Contra' and 'Ipsi'), even though the imagined and executed movement times for the contralesional hand (Fig. 1B, 'Contra') were increased significantly. The normally parallel timing of simulated and actual movements, and Fitts' law, also applied to parietal-lesioned patients when they pointed with the unaffected, ipsilesional hand (Fig. 1C, 'Ipsi'). However, in comparison to control subjects and to the motor cortex-lesioned patient, parietal-lesioned patients were unable to match their actual movement times during mental imagery. This disability was independent of the nature of the motor task. Specifically, neither the fastest attainable speeds in the imaged metronome-paced task of finger movements nor the time taken to simulate alternating between two hand postures matched the values obtained with comparable executed movements. Moreover, on the contralesional side their movement times were not modulated by changing the size of the target window in the mentally imaged pointing task (Fig. 1C, 'Contra'), as expected from Fitts' law, and, as was the case when pointing movements were executed.

Thus, results from the neurologically impaired patients differ according to lesion site (Fig. 1B,C) and provide insight into the neuronal substrate of motor representations. The patient with a motor-cortex lesion mentally simulated movements of the contralesional limb, which incorporated the same deficit (increased movement times) as was recorded for executed movements of this limb. Parkinsonian¹³ and hemiplegic¹⁴ patients also mentally simulate movements as slow as those actually executed. Thus, it appears that frontal-atrial circuits, including the motor cortex

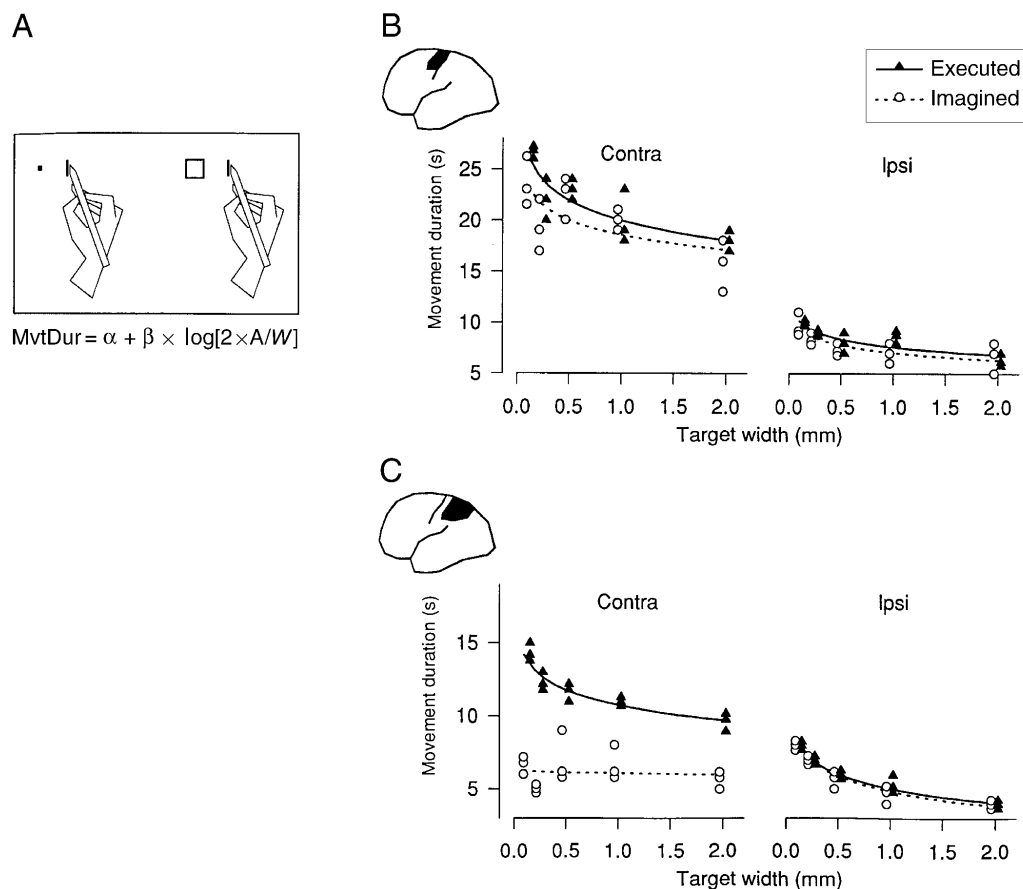


Fig. 1. Executed and imaged movements in cerebral cortex-lesioned patients. (A) Schematic of the pointing task, in which a hand-held stylus was moved from a starting line into a target square of varying widths. Fitts' law (below) describes the linear relationship between movement duration (MvtDur) and the logarithm of task difficulty expressed as movement amplitude (A , constant) divided by target width (W , 1.25–20 mm). (B) Schematic of the site of a rolandic motor-cortex lesion and line drawings of movement duration plotted for pointing into target squares of different widths for this patient performing the task with the contralesional (contra) and ipsilesional (ipsi) hand in two conditions: movement execution (filled triangles and solid lines) and motor imagery (open circles and dashed lines). (C) Same format as B, showing lesion site and data for one parietal-lesioned patient. Figure courtesy of J.-R. Duhamel. Modified, with permission, from Refs 9,10.

and basal ganglia, are not necessary for generating mental images of motor acts, *per se*. However, these structures might contribute to motor imagery indirectly. Motor imagery seems to involve activation of the same movement representation employed by the executive motor system, that is, a single representation of movements as they must occur, in compliance with the physical laws of motor control and incorporating all physiological and pathophysiological constraints. In a sense, then, these patients have no deficit in motor imagery, which reflects faithfully their deteriorated motor abilities. By contrast, parietal-cortex lesions do appear to produce a frank motor-imagery deficit, causing the breakdown of the correspondence of timing between imaged and real movements, and of Fitts' law for imaged movements.

Importance of the parietal cortex

Data from cognate disciplines also point to parietal cortex as an important partici-

pant in motor imagery. Using positron emission tomography (PET), Stephan *et al.*¹⁵ recorded extensive activation of superior and inferior parietal cortex (Fig. 2, upper) during motor imagery. In their study, regional cerebral blood flow for motor imagery was contrasted with reference scans recorded when subjects prepared but did not execute the same movements. The same areas were also more active during task execution, when compared with motor imagery, with the additional activation of rostral parts of parietal cortex (Fig. 2, lower), as well as the dorsal premotor cortex and cingulate cortex.

Physiological recordings in monkey posterior parietal cortex (area 5) also have some relevance to motor imagery. Although studies comparable to those of Sirigu *et al.* are difficult to imagine in non-human primates, Kalaska and Crammond¹⁶ studied parietal-cortex activity when motor responses were instructed, then either executed or suppressed intentionally. There were two kinds of trials, termed 'GO' and 'NOGO' trials. In both

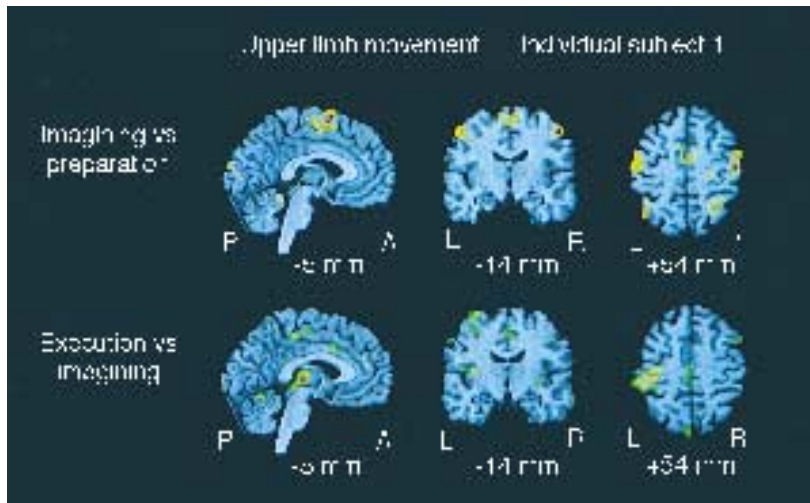


Fig. 2. Changes in blood flow during mental and executed tasks. Sagittal (left), coronal (middle) and transverse (right) slices of positron emission topography (PET) comparisons of two conditions: (Upper) Mental imaging versus movement preparation; and (Lower) movement execution versus movement preparation, superimposed on magnetic resonance image (MRI) of one subject for a joy-stick motor task involving the right hand. The colors represent different ranges of z-values that constitute statistical parametric maps which identify the site of areas of statistically significant ($P < 0.05$ threshold) blood-flow changes occurring as a result of the differences in relative perfusion between task conditions: green, $z \geq 2.8$ and $z < 3$; yellow, $z \geq 3$ and $z < 4$; and red $z \geq 4$. Figure courtesy of R.S.J. Frackowiak. Reproduced, with permission, from Ref. 15.

trial types, monkeys were presented with an instruction cue that designated a location that could be a movement target on that trial. After a variable delay period, a non-spatial signal was presented, which was the same in all trials. In 'GO' trials this signal served to trigger the movement. However, in addition to conveying spatial information, the instruction cue, by its color, also informed the monkey to execute movement in 'GO' trials and to withhold movement in 'NOGO' trials. In 'GO' trials (Fig. 3), the activity that followed the target instruction cue reflected the intended movement direction. In 'NOGO' trials, this same pattern of parietal activity was recorded, virtually unchanged (Fig. 3A), although no movement was to be ex-

ecuted on that trial. These results show that posterior parietal cells synthesize a neuronal representation of intended movements, regardless of whether the movement is executed. This finding was contrasted to recordings in the dorsal premotor cortex (area 6) of the same monkeys. In this frontal motor area, as with area 5, spatially tuned patterns of neuronal discharge were recorded during the preparation of movement in 'GO' trials. However, in the 'NOGO' trials, premotor cells emitted spatially tuned activity for only the first 500 ms of the preparatory period, after which activity returned to baseline levels (Fig. 3B). It seems, then, that activity in premotor cortex reflects the monkey's intended action, whether

that involves movement or postural stability. By contrast, parietal areas reflect possible motor behaviors even when overt movement is not intended and does not occur, a situation not unlike the human act of motor imagery.

Imagery: a distributed cortical network

One should not be left with the impression that the parietal cortex is the sole domain of motor imagery. Structures outside parietal cortex also contribute. For example, in the PET studies of Stephan *et al.*, mentioned above, medial and lateral premotor cortex, anterior cingulate areas, along with ventral opercular premotor areas, were also activated during motor imagery (Fig. 2). Other studies using brain-imaging methods^{8,15,17,18} and topographic EEG mapping¹⁹ find a similar broad network of cerebral activation when comparing activity recorded during execution and imagery of motor tasks. These areas include the primary motor and premotor cortex where blood flow during motor imagery^{8,17} is less than that recorded during motor execution (Fig. 4), but is nevertheless increased significantly. Also, DC potentials localized to the primary sensorimotor cortex have similar topography but reduced amplitudes in motor imagery compared with those recorded with motor performance¹⁹. It is tempting to postulate that the nominal activation of primary motor areas in motor imagery (Fig. 4) is the neuronal correlate of the motor efference copy. In another PET study²⁰, the topography of brain structures activated during motor imagery of grasping an object was compared with that obtained during visual imagery, or observation, of the same motor task. The cortical and subcortical areas activated with motor imagery did not overlap with the

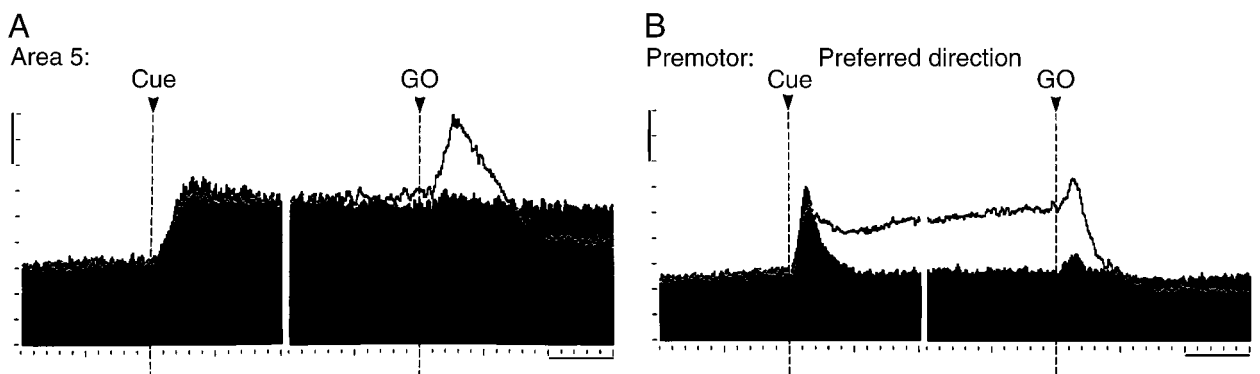


Fig. 3. Population histograms of the mean response of the posterior parietal cortex (area 5) and the premotor cortex during mental and executed tasks. Single-cell activity recorded in monkeys performing a reaching movement and plotted at each individual cell's preferred direction for maximal movement-related activity. Mean responses in (A) the posterior parietal cortex (area 5) and (B) the premotor cortex are shown during 'GO' (outlined histograms) and 'NOGO' (solid histograms) trials. Monkeys held a pointer at a central location (1 s) during which a visual instruction cue was illuminated at one of eight potential movement-target locations. Illumination of a green LED was the cue signaling that movement was to be executed; illumination of green, red and yellow LEDs was the cue signaling that movement was to be withheld, in response to the subsequent non-spatial, visual signal. After a variable delay period all red LEDs were illuminated in all trials as this visual signal, labeled the 'GO' signal. Scale bars: 500 ms, 10 spikes s^{-1} . Figure modified, with permission, from Ref. 16.

mainly visual (extrastriate and medial occipital) cortical areas activated during visual imagery of the same motor act. Thus, motor imagery is a distinct mental process, one not dependent on imaging the limb movement in a visual sense.

In the context of these other data, the behavioral studies reported by Sirigu *et al.* lead to three major conclusions. First, the parietal cortex plays a crucial, though non-exclusive, role in motor imagery. Second, motor imagery activates and employs nearly the same set of brain structures as does overt movement, at least to the point at which executive brain structures are ordinarily recruited to generate efferent motor commands. And third, imaging movement results from the utilization of stored representations of action, which are subject to the same constraints as real movements. This means that motor imagery is something quite separate from the creative imagination, which is not so easily shackled: it seems that we can only mentally rehearse doing something that we have done before, and only as we experience it in practice.

Insight: parietal-lobe function

The results from brain-lesioned patients might also contribute to our understanding of the function of the posterior parietal lobe. These new data suggest that the parietal cortex is a structure where the evaluation of motor performance, real and imaged, can occur based upon a comparison of corollary discharge and multimodal reafferent sensory signals with a stored internal representation of the motor plan as it normally unfolds. In line with this idea, it has been reported^{21,22} that parietal-lesioned patients cannot complete the second of two, sequenced, saccadic eye movements without visual feedback of eye and target locations, which could be interpreted as a failure to use corollary discharge to evaluate movement. By contrast, the parietal-lesioned patients studied by Sirigu *et al.*⁹ are able to execute properly but not image movement sequences, a finding that might indicate a dependence upon evaluating reafferent signals. It is possible that these different forms of motor-evaluation deficits result from lesions that disrupt separate subregions of the posterior parietal lobe and, consequently, separate components of the posterior parietal network for evaluating ongoing motor behavior. That the superior parietal lobe (SPL) contributes to decision-making processes by evaluating visuospatial information has been demonstrated recently in a magnetic resonance imaging (MRI) study of mental rotation²³. The level of SPL activation was proportional to the number of errors made by subjects, who had to mentally rotate one of two visual images and

decide whether the images were the same or mirror reflections of each other.

Parallel data from physiological studies in monkeys also indicate that posterior parietal neurons, long known to have visuomotor activity unrelated to simple sensory or motor signals, might be organized into functional groups according to how each contributes to the process of movement evaluation. Within area 5, one population of cells, which discharges only following the onset of voluntary limb movement, becomes silent after peripheral deafferentation of the performing limb, while a second population, which discharged well in advance of the same limb movement, was unaffected by limb deafferentation²⁴. In addition, neuronal activity recorded from a visuomotor intraparietal cortical area prior to eye-movement onset, reflects the sensory signals that would be expected were the eyes already at the final target position²⁵; activity that could result only from a corollary discharge. Therefore, posterior parietal activity appears to reflect both reafferent signals and corollary discharge. Taken in conjunction with the finding of neuronal activity representing intended movements¹⁶ (Fig. 3), the posterior parietal network has all the necessary components to transform visuospatial information^{26,27} into the signals that are required to evaluate movements²⁸ as they occur.

Patients with parietal lesions can, despite their problems, mentally image movements and perform them. Thus, they do not have a failure of imagination, rather, unlike controls, the internal mental 'movements' of patients with parietal lesions do not appear to obey physical laws or to be tied to physiological constraints. Perhaps this is because rather than imaging movements, they are free to imagine moving however they want to, as in a dream.

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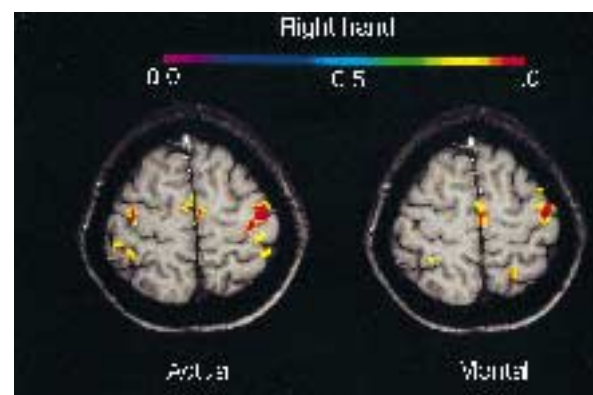


Fig. 4. Magnetic resonance images during actual and mental tasks. Activation map of functional magnetic resonance imaging (fMRI) from one subject obtained in response to actual performance (left image) and to mental simulation (right image) of a manual motor task. The fingertips of the right hand were opposed to the thumb in a back and forth sequence tuned at a frequency of 1.3 Hz by means of a flashing red light transmitted through eye glasses. Image plane (5 mm thick) was located 55 mm above and parallel with the anterior–posterior commissural plane. Color scale represents the cross-correlation coefficient between the power spectra of the functional responses and the paradigm. Left hemisphere is on the right. Figure courtesy of J. Decety. Reproduced, with permission, from Ref. 8.

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