Areas of the Brain: Movements and Memories

The report "An area specialized for spatial working memory in human frontal cortex" by S. M. Courtney *et al.* (27 Feb., p. 1347) does not follow the convention of referring to the area under study as premotor cortex (PM). Researchers investigating spatial working memory (SWM) in humans have had difficulty attributing a cognitive function to brain areas, such as the cerebellum and the basal ganglia, that historically have been associated with motor functions. In these cases, the cognitive function is thought to be related to the known motor function.

PM is involved in the planning of movements, and spatial memory is an integral part of this function. There are at least three pieces of evidence pointing to the possibility that spatial mnemonic mechanisms for motor planning are also used for cognitive tasks. First, human PM activity during SWM tasks remains high, even in the absence of the activity associated with the motor components of the tasks. Second, spatial mnemonic activity of monkey PM neurons can occur in the absence of movement, or can be associated with relevant sensory events rather than movements (*1*). Third, SWM performance is impaired when humans are required to make movements that are spatially incompatible with the information to be remembered (*2*).

The idea that spatial cognition is related to spatiomotor processing is not new. Almost a century ago, the mathematician Poincaré suggested, "When it is said...that we 'localise' such an object in such a point in space, what does it mean? It simply means that we represent to ourselves the movements that must take place to reach that object. And it does not mean that to represent to ourselves these movements they must be projected into space" (*3*). Mounting evidence suggests similarly that when we are keeping the location of an object in mind, we are maintaining neural representations of the movements that would have to take place to reach that object.

I presume that part of the reluctance to follow convention in this case stems from the functional connotation of the root "motor" in PM. However, the word "premotor" is often used to define PM's anatomical position relative to motor cortex, rather than its function. Even if a functional definition is used, it is unnecessary to avoid calling PM by its conventional name, considering that its role in SWM may be related to its role in motor planning.

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References

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2. R. H. Logie, *Visuo-spatial Working Memory* (Erlbaum, Hove, UK, 1995).
3. H. Poincaré, *Science and Hypothesis* (Scott, London, 1901/1905).

Response: Meegan apparently reasons that the area in the superior frontal sulcus that we identified as important for spatial working memory should have been labeled as "premotor" cortex. In our report, we referred to this area as being located in "frontal" cortex, specifically avoiding a designation of either "premotor" or "prefrontal" because we simply do not know what the designation should be. We agree with Meegan that this area has traditionally been referred to as premotor cortex. However, as stated in our report, there are reasons to question this common assumption that the superior frontal sulcus is homologous to the region of monkey cortex that has been defined as "premotor."

There are insufficient cytoarchitectonic data in humans with regard to the cortex deep within the superior frontal sulcus for one to know whether this is agranular

(premotor) or granular (prefrontal) cortex (*1*). Many classic cytoarchitectural maps have nevertheless labeled this region as premotor area 6. We are not the only ones to question the designation of this region as area 6. Luna *et al.* (*2*), who describe the location of the human frontal eye field (FEF), point out that "If FEF were still to demarcate the border zone of areas 6 and 8 in human, as it does on macaque monkey, it would imply that human prefrontal cortex proceeds far more posteriorly than is traditionally appreciated." The alternative to this conclusion is that the human FEF would be "in area 6, and if so, [the field] would be comprised of agranular cortex...[representing] a significant lack of homology in the cytoarchitecture of saccade-related FEF in human and non-human primates." Another reason to question the traditional premotor designation is that the spatial working memory area in the superior frontal sulcus lies anterior to the frontal eye fields in humans, while the premotor cortex in monkeys lies posterior to the frontal eye field. It would be unexpected if the topological relationship between these areas had changed over the course of evolution.

In sum, while we are willing to remain "agnostic" about whether the superior frontal sulcus is in agranular or granular cortex, keeping the traditional premotor designation and assigning a cognitive function to it, as Meegan suggests, would create more puzzles than it would solve. As indicated in our report, it seems more likely that the human spatial working memory area in the superior frontal sulcus is homologous to the monkey spatial working memory area in the principal sulcus, which lies anterior to the monkey frontal eye field. We agree with Meegan that spatial cognition and spatiomotor behavior must be intimately related. Complex motor behavior must require spatial attention and, often, spatial working memory, but it is not clear that spatial cognition and spatiomotor behavior are identical functions, or that they are performed by identical neural substrates.

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1. M. B. Carpenter, *Core Text of Neuroanatomy.* (Williams & Wilkins, Baltimore, MD, 1985).
2. B. Luna *et al.*, *Cereb. Cortex* **8**, 40 (1998).

Corrections and Clarifications

■ In the letter "Coral disease" by James M. Cervino *et al.* (24 Apr., p. 499), the e-mail address for James M. Cervino was incorrect. It should have been "cnidaria@earthlink.net."

■ The affiliation of Frederick Prete, the second author of the report "Visual input to the efferent control system of a fly's 'gyroscope'" by Wai Pang Chan *et al.* (10 Apr., p. 289) was given incorrectly. He is in the Department of Biological Sciences (not "Psychology") at DePaul University in Chicago, Illinois.

Letters to the Editor

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