NEUROSCIENCE

The Space Around Us

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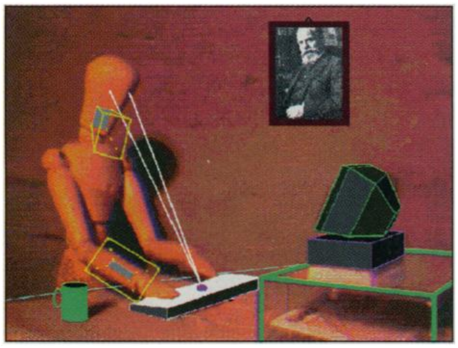
Space, although unitary when examined introspectively, is not represented in the brain as a single multipurpose map. On the contrary, in the brain there are numerous spatial maps (*1–3*). Of these, many are located in cortical areas that participate in the control of movement, such as eye movements, head movements, arm movements, and so on.



Spatial relativity: Visual receptive fields . . . The mannequin fixates a point (red spot) on a computer keyboard. The solids on the face and arm indicate two visual receptive fields coded in body-parts coordinates. The gray areas inside the solids represent tactile receptive fields.

The map located in the ventral premotor cortex (area F4) is paradigmatic among the spatial maps related to skeletal movements. In this area, most neurons discharge in association with movements of the head or the arm (*4*). Furthermore, a large proportion of them are bimodal, responding both to visual three-dimensional stimuli and to tactile stimuli, mostly applied to the face or arm. A surprising property of F4 neurons is that their visual receptive fields (RFs) are circumscribed to the space around the tactile RFs, as if the cutaneous space extended into the visual space adjacent to it (peripersonal space) (*4–9*). Another surprising property is that visual RFs of F4 neurons remain anchored to the body regardless of the position of the eyes and of the body parts on which the tactile RF is located (*7–11*) (see figure).

Until recently it appeared that moving stimuli were required to trigger F4 visual responses. But now Graziano, Hu, and Gross report on page 239 of this issue (*12*) that many F4 neurons fire tonically at the presentation of stationary three-dimensional objects within monkey peripersonal space. The most intriguing finding, however, of this very interesting report is that some of these tonically discharging neurons continue to fire when, unknown to the monkey, the stimulus previously presented has been withdrawn, and the monkey "believes" that it is still near its body. Space representation in the premotor cortex can be generated, therefore, not only as a consequence of an external stimulation but also internally on the basis of previous experience.

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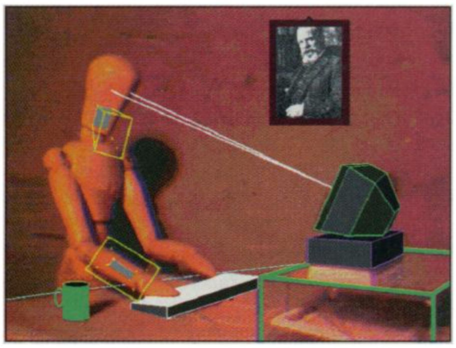
What is the nature of this representation? There are two main possibilities. The first is that the premotor neurons code space visually; that is, given a reference point (for example, the body parts on which the visual receptive field is anchored), the neurons signal the location of objects by using a Cartesian or some other geometrical coordinate system (visual space). The alternative possibility is that the discharge of neurons reflects a potential action, a motor schema (*13, 14*), directed toward a particular spatial location (motor space). The presentation of a visual stimulus or the memory of its location, as in the new study (*12*), would evoke automatically one of these schemata, which, regardless of whether it is executed, maps the stimulus position in motor terms.

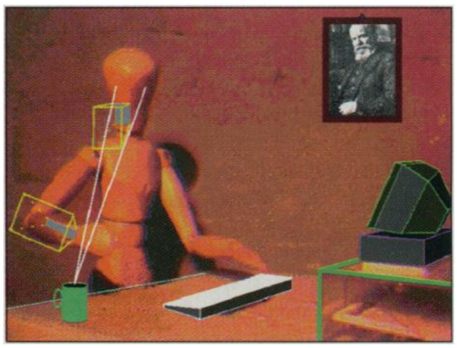


. . . coded in body-part coordinates . . . The mannequin fixates the computer screen. In spite of a change of gaze, the location of the two visual receptive fields remains in the same position as in the first panel. A visual receptive field, if coded in retinal coordinates, would move with the gaze.

Arguments in favor of a strictly "visual" hypothesis are the tight temporal link between stimulus presentation and the onset of neuron discharge, the response constancy, and the presence of what appears to be a visual receptive field (*4–9*). On the other hand, F4 is a premotor area directly connected to the primary motor cortex (*15*). It sends projections to the spinal cord (*16*), and its intracortical microstimulation evokes body part movements (*4*). These elements appear to favor the notion that F4 contains a store of motor schemata for bringing the head or the arm toward specific spatial locations. Although an answer to the "visual" versus "motor" representation issue cannot be given at present, it seems to us most likely that the neurons are coding a motor scheme.

Why? First, a Euclidean space, as assumed by the visual hypothesis, excludes time. Each set of neurons, when activated, specifies the object location in space regardless of stimulation temporal dimension. The prediction is, therefore, that the spatial map as expressed by receptive field organization is basically static. In contrast, in the case of motor space, because time is inherent to movement, the spatial map may have dynamic properties and may vary according to the change in time of the object's spatial location. Fogassi *et al.* (*11*) provide evidence that this is the case: The receptive field extension of F4 neurons increases in depth when the speed of an approaching stimulus increases.

Second, in the ventral premotor cortex there is another functional area (area F5) related to object-to-hand movements transformation (*14, 17*) rather than to space-to-head or arm movements transformation. Experiments in which object shape (visual hypothesis) and object graspability (motor hypothesis) were compared showed that the responses evoked by object presentation better correlated with the way in which objects



. . . move only when the body moves. The mannequin moves its head, directing its gaze toward the mug. The arm is also moved toward it. The spatial location of the receptive fields moves with the body parts, remaining anchored to the tactile receptive fields. The portrait on the wall is that of the philosopher Edmund Husserl, founder of phenomenology.

had to be grasped rather than with object pictorial aspects (*18*). Therefore, objects appear to be described in F5 more in motor than in visual terms. Admitting that the basic transformation process is analogous in the various ventral premotor cortex sectors, the fact that in F5 objects are coded in motor terms suggests a similar motor interpetation for space coding in F4.

Finally, the motor interpretation offers a better or at least a more economical explanation for the location of spatial receptive fields around the body. If the visual interpretation were correct, one would have to postulate an ad hoc, complex visual mechanism able to eliminate visual information coming from points outside the peripersonal space. In contrast, the three-dimensional properties of premotor receptive fields are easily accommodated by a motor interpretation. According to this view, movements progressively carve out a working space from undifferentiated visual information. The anatomical basis underlying this process may be represented by the fronto-parietal connections. These connections would constrain motorically the visual parietal neurons, through a visuomotor coupling between visual stimuli and movements directed toward them. The functional properties of bimodal parietal neurons of areas VIP (*19*) and PF (*6*, *20*), both strictly linked to F4 (*21*, *22*), are consistent with this interpretation. The movement-based space (which may be subserved also by other fronto-parietal circuits) becomes then our experiential peripersonal visual space.

The data reviewed above and the hypotheses we discuss are at odds with the traditional view of cognitive sciences that percepts are built from elementary sensory information via a series of progressively more and more complex representations. In contrast, they stress the importance of motor areas and motor-to-sensory pathways for the construction of object and space perception, and the artificiality of constructing a rigid wall between sensory and motor representations. It is interesting to note the closeness of this view, emerging from single-neuron recordings, and the philosophical stance of phenomenological philosophers on space perception. Space is "not a sort of ether in which all things float.... The points in space mark, in our vicinity, the varying range of our aims and our gestures" (Merleau-Ponty) (*23*).

References and Notes

1. G. Rizzolatti, L. Riggio, B. M. Sheliga, in *Attention and Performance*, C. Umiltà and M. Moskovitch, Eds. (MIT Press, Cambridge, MA, and London, UK, 1994), vol. 15, pp. 231–265.
2. C. G. Gross and M. S. A. Graziano, *Neuroscientist* **1**, 43 (1995).
3. C. L. Colby and J.-R. Duhamel, *Brain Res. Cogn. Brain Res.* **5**, 105 (1996).
4. M. Gentilucci *et al.*, *Exp. Brain Res.* **71**, 475 (1988).
5. G. Rizzolatti, C. Scandolara, M. Matelli, M. Gentilucci, *Behav. Brain Res.* **2**, 147 (1981).
6. M. S. A. Graziano and C. G. Gross, in *The Cognitive Neurosciences*, M. S. Gazzaniga, Ed. (MIT Press, Cambridge, MA, 1994), pp. 1021–1034.
7. M. S. A. Graziano, G. S. Yap, C. G. Gross, *Science* **266**, 1054 (1994).
8. M. S. A. Graziano, X. T. Hu, C. G. Gross, *J. Neurophysiol.* **77**, 2268 (1997).
9. L. Fogassi, V. Gallese, L. Fadiga, G. Rizzolatti, in *Neural Bases of Motor Behaviour*, F. Lacquaniti and P. Viviani, Eds. (Kluwer Academic, Dordrecht, Netherlands, 1996), pp. 99–120.
10. M. Gentilucci, C. Scandolara, I. N. Pigarev, G. Rizzolatti, *Exp. Brain Res.* **50**, 464 (1983).
11. L. Fogassi *et al.*, *J. Neurophysiol.* **76**, 141 (1996).
12. M. S. A. Graziano, X. T. Hu, C. G. Gross, *Science* **277**, 239 (1997).
13. M. A. Arbib, in *Handbook of Physiology, Section 1, Volume 2, Part 2*, V. B. Brooks, Ed. (American Physiological Society, Bethesda, MD, 1981), vol. 2, pp. 1449–1480.
14. M. Jeannerod, M. A. Arbib, G. Rizzolatti, H. Sakata, *Trends Neurosci.* **18**, 314 (1995).
15. M. Matelli, R. Camarda, M. Glickstein, G. Rizzolatti, *J. Comp. Neurol.* **251**, 281 (1986).
16. S. Q. He, R. P. Dum, P. L. Strick, *J. Neurosci.* **13**, 952 (1993).
17. G. Rizzolatti *et al.*, *Exp. Brain Res.* **71**, 491 (1988).
18. A. Murata *et al.*, *J. Neurophysiol.*, in press.
19. C. L. Colby, J.-R. Duhamel, M. E. Goldberg, *ibid.* **69**, 902 (1993).
20. L. Leinonen, J. Hyvärinen, G. Nyman, I. Linnankoski, *Exp. Brain Res.* **34**, 299 (1979).
21. M. Petrides and D. N. Pandya, *J. Comp. Neurol.* **228**, 105 (1984).
22. M. Matelli, G. Luppino, A. Murata, H. Sakata, *Soc. Neurosci. Abstr.* **20**, 404 (1994).
23. M. Merleau-Ponty, *Phenomenology of Perception*, C. Smith, Transl. (Routledge and Kegan Paul, London, UK, 1962).
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OPTOELECTRONICS

Stacked Organic Light-Emitting Diodes in Full Color

James R. Sheats

The proliferation of portable electronic devices such as pagers, cellular telephones, personal digital assistants, and hand-held computers has driven designers to search for a new generation of display technology. These portable tools demand something more sophisticated than the simple alphanumeric displays of kitchen appliances yet must be smaller than a full-fledged laptop computer. Although a monochromatic display is adequate for some applications, full color is necessary for many and desirable for most; yet it is not easy to achieve in inexpensive, battery-powered devices. Recently, Shen *et al.* (*1*, page *2009*) described a novel approach to full-color organic electroluminescent (EL) displays that could satisfy this need and demonstrates dramatically the versatility of thin-film organic optoelectronics.

Portable display technology is constrained by the need for low-cost battery-compatible drive voltage, high efficiency, reasonable lifetime, and resistance to the temperature extremes of outdoor or automobile use. Most approaches, such as plasma displays, vacuum fluorescence, and inorganic thin-film electroluminescence, face some combination of these obstacles. Inorganic light-emitting diodes (LEDs) are simply too expensive. As a result, the market has been largely left to liquid crystals (generally without backlighting), which leave much to be desired in the way of viewability.

Organic electroluminescence, a subject with roots in the 1960s, has now reached the point where commercialization of small, pixel-addressed displays seems close to reality (*2*). Device lifetime, a major concern only a few years ago, is now several thousand hours for many systems, and in the tens of thousands for the best; it remains acceptable for temperatures up to at least 60°C or more. Efficiencies are superior to most of the other competitors. A bias of 10 V or less is sufficient to drive a passive matrix-addressed 64 × 256 pixel display, and the voltage drop along the metal and indium-tin-oxide (ITO) lines is acceptable for a display of this size. Drivers with adequate current capacity are available at reasonable (though significant) cost. Thus, despite the difficulties involved in the introduction of such a new technology,

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