EPPENDORF 2006 WINNER

A Dedicated System for Processing Faces

In the regions of the brain that are most highly activated by faces, single cells make different measurements that are pooled together to characterize the face.

Doris Tsao

If you're planning to rob a bank, there's one thing you must not forget: to cover your face. Otherwise, just a brief glance will allow all the other social animals around you to identify you. What is the neural basis of the extraordinary ability of humans to recognize faces? Localized strokes can selectively destroy face recognition abilities while preserving the ability to recognize other objects ("prosopagnosia") (*1*). Furthermore, functional magnetic resonance imaging (fMRI), a technique that measures blood flow changes induced by brain activation, consistently reveals several discrete brain regions that respond more to faces than to other objects (*2*). One of these regions, the fusiform face area, shows increased blood flow even when subjects merely imagine faces (*3*). These findings suggest that face processing is mediated by specialized modules inside the human brain. Such specialization is surprising since, from introspection, it seems that our recognition of faces flows seamlessly into that of all the other objects in the world.

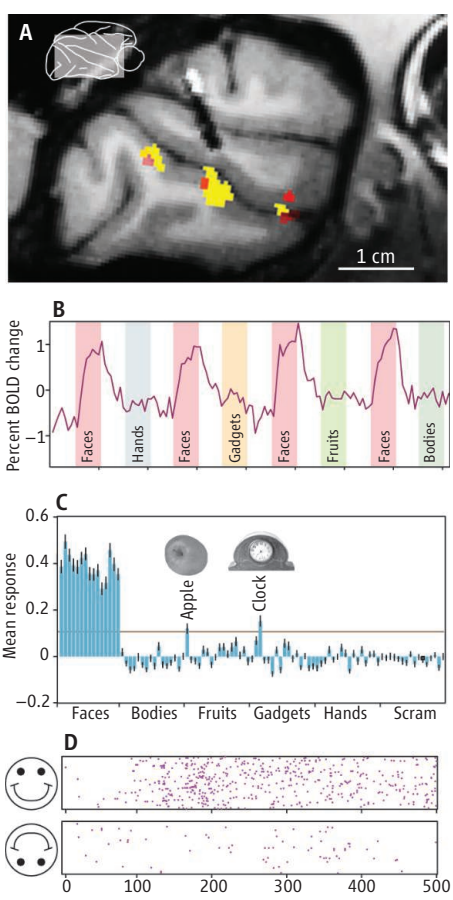
Are face-selective regions unique to humans? Charles Gross and co-workers studied a large region in the macaque brain known as the temporal lobe and reported in 1981 that this region contains some cells that respond exclusively to faces and not to other visual forms (*4*). This was a remarkable finding: How can a single cell be wired to detect something so complex as a face? The discovery immediately turned fuzzy questions about holistic integration and gnostic units into a concrete research goal: What are face cells detecting, and how are they wired?

One problem, however, stood in the way of understanding these cells: It was difficult to find them. In single-unit recording experiments, one can see only as far as the tip of one's electrode (≤100 μm wide). Several groups that studied face cells reported that they were scattered throughout the temporal lobe, with at most 10 to 20% of the cells in any one region being face-selective (*5*–*7*). Meanwhile, the discovery by fMRI of face-selective regions in humans generated great interest in understanding what is being coded by these regions. One might guess that the fMRI-identified face-selective regions contain lots of face cells. Alternatively, they could contain cells activated by any animate object, or by symmetrical objects, or by the behavioral process of fine scrutiny. Indeed, fMRI evidence was marshaled for several competing theories about face-selective activation.

In order to clarify the link between face cells and fMRI face areas, I performed fMRI experiments in alert monkeys to look for face-selective regions (*8*). Comparing activation to faces versus five other object categories (fruits, bodies, gadgets, hands, and scrambled patterns) across the entire macaque brain, I identified face-selective activation in three discrete regions of the temporal lobe (see the figure, left, panel A). These regions showed a blood oxygen level–dependent (BOLD) response to faces that was stronger than the response to any of the nonface categories by a factor of 7 (see figure, panel B). This suggests that face processing in monkeys is performed by specialized regions, possibly homologous to those found in humans. Furthermore, the arrangement of the face regions along an anterior-posterior axis suggests a hierarchy, given that we know from other studies that complexity in shape selectivity increases from the back to the front of the visual system.

Having found these fMRI face regions in monkeys, I then asked: What is the selectivity of single neurons within an fMRI-identified face patch? I started by recording from single neurons—almost 500 of them—in the middle face patch of two monkeys, and found 97% of the visually responsive neurons to be face-selective (*9*) (see figure, panel C). These cells responded almost 20 times as strongly to faces as to other objects, and many were even suppressed by nonface objects. Up to now, one major difficulty with understanding object recognition has been the problem of determining which object, among an infinite number of possible objects, a single cell in the temporal lobe might be coding. The existence of a region in which all the cells are coding faces goes a long way toward overcoming this difficulty.

What is it about a face that these cells like? Surprisingly, most cells responded to human, monkey, and even highly simplified



Recognizing faces: (**A**) Three patches of face-selective fMRI activation (yellow regions) in the macaque temporal lobe. (**B**) Time course from the face patches. Blood flows to these regions only when the monkey views faces. (**C**) Average response across 182 cells from the middle face patch of one monkey to 96 different images. The first 16 images are faces. (**D**) Responses of a face cell to repeated presentations of an upright and an inverted cartoon face. Each dot represents an action potential.

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cartoon faces (see figure, panel D). In fact, many of the cells showed a weak but significant response to a few particular nonface objects; all of these objects turned out to be round (see figure, panel C). The weak but significant responses to round clocks and fruits in this area, as well as its relatively posterior position within the temporal lobe, indicate that it constitutes an early stage in the form-processing hierarchy. Recording from this area is a bit like peeking into a carpenter's shop and seeing the rough frame before fine chiseling—exactly what one wants for piecing together the basic mechanisms underlying face selectivity.

How do face cells encode specific faces? Early recordings in the middle face patch suggested that face cells distinguish faces on the basis of visual shape (e.g., the cells responded weakly to the round outline in a clock and an apple). To explore shape tuning of these cells quantitatively, I took advantage of their robust response to cartoon faces, which can be easily parameterized. I probed face cells with a cartoon face space consisting of 19 different feature dimensions, each sampled at 11 values; the space thus contained 11^{19} possible different faces. The cartoon dimensions included ones describing the overall facial shape, the shape of individual features (e.g., iris size), and the relationship between features (e.g., intereye distance). Across the population, a vast majority of cells showed strong tuning to at least one cartoon dimension, and no cell was tuned to more than eight dimensions. The two most popular dimensions were face aspect ratio (i.e., Bert versus Ernie) and iris size. Most cells responded best to extreme features such as large irises, Ernie's or Bert's face, etc. These results show that we can understand face cells: Each cell acts as a set of face-specific rulers, measuring faces along multiple distinct dimensions. By combining the measurements of all these little rulers, it should be possible to reconstruct any face (including a bandit's, if not covered well).

My experiments show that the neural machinery for face processing in macaque monkeys consists of a set of discrete brain regions packed with highly dedicated components. This system offers a unique opportunity for exploring high-level form perception. By recording from several large, homogeneous populations of face cells identified through monkey fMRI, we can now understand the process by which the brain synthesizes the percept of a face in terms of underlying single-cell components.

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10. All the experiments here were performed together with Winrich Freiwald. I owe deepest thanks to my adviser Margaret Livingstone and to my father Thomas Tsao.

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2006 Grand Prize Winner

The author of the prize-winning essay, Doris Tsao, was born in Changzhou, China, and grew up in College Park, Maryland. Dr. Tsao studied biology and mathematics at Caltech, receiving her B.S. in 1996. She moved on to do graduate work in the laboratory of Dr. Margaret Livingstone at Harvard Medical School, where she studied binocular depth perception.

While a graduate student, she became interested in monkey fMRI as a way to chart unexplored regions of the brain, and worked together with Roger Tootell to image macaque brain regions involved in depth and face perception. She received her Ph.D. in 2002 but remained as a postdoctoral fellow in Dr. Livingstone's laboratory in order to continue her experiments on face perception. In 2004, she received a Sofia Kovalevskaya Award from the Humboldt Foundation. This award allowed her to set up her own lab at the University of Bremen, Germany. Dr. Tsao's goal is to understand how a sheet of cells 2 mm thick can construct a three-dimensional world and effortlessly recognize the multitude of objects within it. Her laboratory uses a combination of electrophysiology, imaging, psychophysics, and anatomical techniques. Outside the laboratory, she likes to swim, cook, and play the violin.

Finalists

Bernardo Sabatini for his essay, "Establishing synaptic independence: How neurons create diffusional barriers." Dr. Sabatini was born and raised in New York. He received his undergraduate degree in biomedical engineering from Harvard College in 1991. He received his M.D. and Ph.D. degrees in 1999 from Harvard Medical School, having completed his thesis work in the laboratory of Dr. Wade Regehr. After graduation, he joined the lab of Dr. Karel Svoboda at Cold Spring Harbor Laboratory as a postdoctoral fellow. In 2001, Dr. Sabatini started his own laboratory in the Department of Neurobiology at Harvard Medical School, which is focused on understanding the processes that regulate the structure and function of synapses and how these processes are perturbed in neurological diseases. His life outside of science is mostly spent trying to keep up with his three sons.

Gábor Tamás for his essay, "Lighting the fire in cortical microcircuits: Exciting role for chandelier cells." Dr. Tamás was born in Dunaújváros, Hungary, and completed undergraduate studies in biology at the University of Szeged, Hungary. As a graduate student he was trained in neuroanatomy and physiology in the group of Peter Somogyi at the University of Oxford, where he investigated the function, number, and location of synapses between neocortical neurons. In 1998, Dr. Tamás returned to Szeged to establish his own laboratory and identified the first intercellular mechanism capable of synchronizing cortical neurons at gamma frequency. His group discovered that the so-called neurogliaform interneuron is capable of eliciting slow, $GABA_B$ receptor–mediated inhibition in the cerebral cortex. Dr. Tamás was a gymnast for 15 years but now gets his exercise from whitewater rafting, skiing, and hiking in the mountains.

For the full text of essays by the finalists and for information about applying for next year's awards, see *Science* Online at www.sciencemag.org/feature/data/prizes/eppendorf/eppenprize.shtml.

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