

and physical characteristics of the speaker⁶. Indeed, there is a 'voice' area in the anterior superior temporal sulcus of the human brain that processes human voices with priority over other animal vocalizations and natural sounds⁷. This voice area may be unique to humans because of the importance of speech in mediating language. To test this idea, Petkov *et al.*⁴ carried out an elegant functional imaging study on macaques, comparing auditory responses to their own species-specific calls with responses to control sounds that had the same spectral profile and duration, as well as to other animal vocalizations and natural sounds. What they found was surprising; macaques do have a voice area that is especially sensitive to conspecific vocalizations in the same manner as the human voice region, but the anatomical location is entirely different. The macaque voice area is located in the anterior superior temporal plane that lies in the lateral sulcus. By contrast, the human voice area lies in the superior temporal sulcus, well below the lateral sulcus (Fig. 1b). This again suggests that the neural circuitry related to voice processing in humans is modified from an ancestral voice area that was present in the common ancestor of macaques and humans.

That both humans and macaque monkeys have a voice area that is sensitive to conspecific voices begs the question of what is so special about conspecific voices. One possibility is

that there is nothing special about conspecific voices, but that the neurons in this area are sensitive to formants. Formants are acoustic signatures related to the shape and length of the vocal tract (the oral and nasal cavities above the larynx). As sound travels from the larynx through the vocal tract, it gets filtered, so that some frequency bands are enhanced (the formants), whereas others are suppressed. As an individual's vocal tract is uniquely shaped and has a length dependent on body size, formants are acoustic cues to both individual identity and other physical characteristics^{8,9}. Petkov *et al.*⁴ indirectly tested this idea by showing that the response of the voice area, in essence, habituates to different calls (for example, a grunt and a coo call) from the same individual (and thus similar formant signatures), but does not habituate when two calls of the same category (a coo and a coo), but from different individuals (and thus, different formant signatures), are presented. These data suggest sensitivity to formants more generally, regardless of the species producing the vocalization. This idea is ripe for testing.

Debate on how language came to be involves many branches of knowledge—philosophy, artificial intelligence, anthropology and now neuroscience—but this discussion is often very speculative, and there are few hard data. In contrast, the studies by Rilling *et al.*³ and Petkov *et al.*⁴, capitalizing on the power of both

imaging and comparative functional anatomy, provide a much-needed empirical foundation for our understanding of the origins of human communication. Together, their results suggest that the neural circuitry in humans evolved gradually from primate precursors, which parallels findings from ethology that indicate a gradual emergence of vocal sophistication in the primate lineage^{10,11}. The human language circuits did not appear *de novo* through a chance mutation or as a 'spandrel' of increased brain size, as some have argued, but instead have their basis in modified versions of neural structures shared by related species.

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What's in your mind?

Brian A Wandell

Previous 'mind-reading' studies have differentiated patterns of brain activity without understanding the underlying processes. A new study in *Nature* uses a model of neural encoding mechanisms to identify brain activity patterns.

There is a provocative claim that functional magnetic resonance imaging (fMRI) of the human brain can provide an objective measure of a person's sensory experience and thoughts. The possibility of such mind reading has led to various applications and engaged broad public interest. Some propose to use fMRI to reveal whether a person is telling the truth¹. Others use the method to measure "unconscious evaluation of Black and White social groups"². Economists and marketing experts want to measure the brain to determine how much a person values a product³. Clinicians seek to use biofeedback to help patients control their

thoughts and feelings⁴. The research and applications have triggered discussions about privacy, ethics and free will⁵.

Now comes a paper by Kay *et al.*⁶, who used fMRI brain measurements to estimate what a subject was seeing. The authors made this estimate in two steps. They first measured primary visual cortex (V1) signals while a subject viewed a large set of gray-scale natural images (Fig. 1a). From these measurements, the authors derived a model of the populations of neurons in the subject's V1–V3; the model is based on fundamental principles of receptive fields derived from physiology and psychophysics⁷. They used the model to predict the responses to a large set of new images and estimate which image the subject is viewing by finding the best match between the model predictions and

the observed fMRI response (Fig. 1b). Their work is the most advanced result in the mind-reading literature.

Such experiments before Kay *et al.*⁶ provoked a wide range of reactions in the scientific community. For some, the possibility of using sensory and motor signals to infer what a subject is seeing, hearing or doing seems to be nothing more than a parlor trick. For example, we can classify whether a signal is seen or heard simply by noting whether the response is in auditory or visual cortex; in visual cortex, we can classify the location of a signal in the visual field from its position in the visual field map in V1 (ref. 8). Furthermore, we can determine whether the stimulus is likely to be moving or still, colored or achromatic, or a face or a texture from the relative amplitudes in other portions of visual cortex. The ability

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to perform such classifications is based on long-standing neurological and physiological measurements of the brain, often called functional specialization⁹.

The most recent versions of the mind-reading experiments use multivariate statistical methods that go beyond simple functional specialization. Conventional analyses examine brain responses one region at a time. Multivariate methods find spatial patterns of brain response, identifying correlations between these spatially distributed brain regions and perception, thought and action. These methods created considerable interest because they appeared to be too good to be true at first; multivariate classifiers can discern image features, such as the orientation of a pattern, that are represented in the brain at a spatial resolution that should be too small to be detected by fMRI¹⁰. Yet it seems that the statistical classifiers are simply very good at picking up patterns that arise for incidental reasons. For example, there seems to be a random and uneven distribution of orientation-selective responses in different V1 voxels. The uneven weighting of the orientation signals provides clues that can be detected by the statistical classifiers¹¹. These clues do not, however, reflect a basic organization of neural responses.

The new work by Kay *et al.*⁶ resembles the prior work on mind reading in certain ways, but it is profoundly different in an important respect. Other mind-reading analyses do not integrate information about the neurons giving rise to the fMRI signal; rather, they treat the fMRI data as an arbitrary signal and use statistical signal-processing methods. These methods apply equally well to scalp potentials or any other multivariate signal. The work by Kay *et al.*⁶ stands apart because they use fMRI signals to derive a model of the V1 neuronal responses and then use the model to perform the mind reading. The ability to fit a model that predicts the cortical responses to a wide class of images is an impressive step.

A central goal of visual neuroscience is to develop models that predict the neuronal responses to any visual stimulus. The receptive field models used by Kay *et al.*⁶ were developed using simple, controlled stimuli, such as lines, bars and harmonic functions. That models derived using these stimuli succeed at identifying the natural image confirms that the traditional approach generalizes¹²; the success of the image classifier validates this classic approach to understanding neural response properties. There are, however, some quantitative discrepancies, and additional information may be derived by studying both simple, controlled stimuli and natural images.

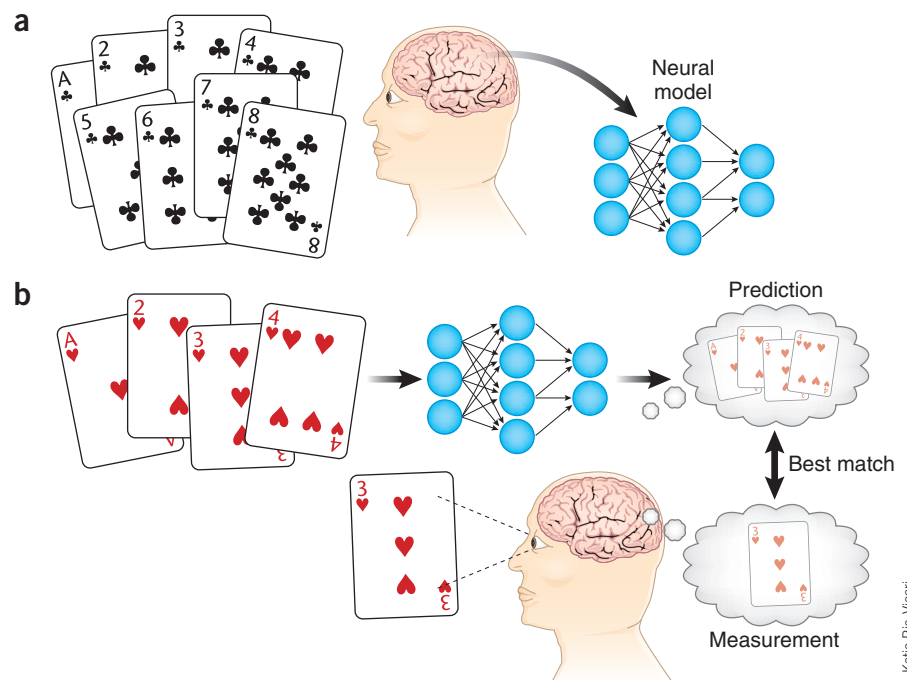


Figure 1 Kay *et al.*⁶ created a neural model that was based on visual receptive field properties to identify which image the subject was viewing from a large set of natural images. (a) The authors derived the parameters of the model from the visual cortex responses as the subject viewed a series of training images. (b) The authors then used the model to predict the responses to a novel array of images. To predict which image the subject was viewing, the authors measured the subject's response and found the best match between the measurement and the model predictions.

For example, using natural images, Kay *et al.*⁶ estimated that the receptive field diameter in the central fovea is roughly twice the size of fMRI estimates using simple contrast patterns¹³. It will be important to determine whether this difference arises because the stimuli evoke responses from different neural populations or whether the same neural populations behave differently in the presence of natural and artificial images.

Since its inception, fMRI has been used to discover a wide variety of insights about the human brain. But fMRI, the best spatially resolved method for studying the human brain, has been loosely connected to the response properties of neurons. There is now some progress on closing the gap between fMRI and neuronal responses. In one approach, investigators are combining the fMRI and single-neuron measures in animals¹⁴. This work is advancing steadily, and it further offers the hope of better understanding the relationship between blood oxygen level-dependent activation and neuronal signals¹⁵. A limitation of this approach is that human and monkey performance capacities differ significantly, as do their brains. Hence, we need other approaches that devise quantitative fMRI

methods that link blood oxygen level-dependent and neural response properties in the human brain. The work described by Kay *et al.*⁶ is an interesting and compelling advance that helps to integrate human fMRI and quantitative single-neuron models.

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