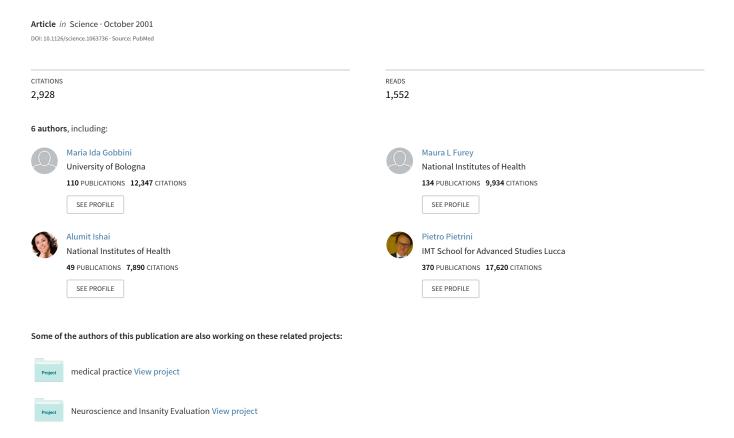
Distributed and Overlapping Representations of Faces and Objects in Ventral Temporal Cortex



Distributed and Overlapping Representations of Faces and Objects in Ventral Temporal Cortex

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The functional architecture of the object vision pathway in the human brain was investigated using functional magnetic resonance imaging to measure patterns of response in ventral temporal cortex while subjects viewed faces, cats, five categories of man-made objects, and nonsense pictures. A distinct pattern of response was found for each stimulus category. The distinctiveness of the response to a given category was not due simply to the regions that responded maximally to that category, because the category being viewed also could be identified on the basis of the pattern of response when those regions were excluded from the analysis. Patterns of response that discriminated among all categories were found even within cortical regions that responded maximally to only one category. These results indicate that the representations of faces and objects in ventral temporal cortex are widely distributed and overlapping.

The ventral object vision pathway in the human brain has the capacity to generate distinct representations for a virtually unlimited variety of individual faces and objects, but the functional architecture that embodies this capacity is a matter of intense debate. Singlecell recording studies in the nonhuman primate have demonstrated differential tuning of individual neurons in temporal cortex to faces, whole objects, and complex object form features (1-3). Although columns containing cells that respond selectively to faces or similar features tend to cluster together, these studies have not revealed any consistent larger scale organization for object representation. Numerous computational models for object recognition have been developed (4), but the correspondence between these models and the neural architecture of the ventral object vision pathway is uncertain.

Unlike single-cell studies, functional brain imaging has revealed a large-scale spatial organization for specialization within the ventral object vision pathway, as demonstrated by differential patterns of response, i.e., increases in neural activity indicated by localized increases in blood oxygenation, to faces and other categories of objects in ventral temporal cortex (5–17). Models for this functional architecture fall into three classes.

One model proposes that ventral temporal cortex contains a limited number of areas that are specialized for representing specific categories of stimuli (5-8). Thus far, two specialized areas have been described: the fusiform face area (FFA) and the parahippocampal place area (PPA) (Fig. 1). A second model proposes that different areas in ventral temporal cortex are specialized for different types of perceptual processes (9-11). In particular, this model proposes that the FFA is specialized for expert visual recognition of individual exemplars from any object category, not just faces. The third model proposes that the representations of faces and different categories of objects are widely distributed and overlapping (12-15). According to this model, which we have named "object form topography," ventral temporal cortex has a topographically organized representation of attributes of form that underlie face and object recognition. The representation of a face or object is reflected by a distinct pattern of response across a wide expanse of cortex in which both large- and small-amplitude responses carry information about object appearance. Unlike the other models, object form topography predicts how all categories might evoke distinct patterns of response in ventral temporal cortex and, thereby, provides an explicit account for how this cortex can produce unique representations for a virtually unlimited number of categories.

We tested our model by investigating the patterns of response evoked in ventral temporal cortex by faces and multiple categories of objects. Our model predicts that each category elicits a distinct pattern of response in ventral temporal cortex that is also evident in the cortex that responds maximally to other categories.

Analysis of patterns of neural response to object categories. Patterns of response were measured with functional magnetic resonance imaging (fMRI) in six subjects while they viewed pictures of faces, cats, five categories of man-made objects (houses, chairs, scissors, shoes, and bottles), and control, nonsense images (18) (Fig. 2). The data were analyzed to determine whether each stimulus category evoked a pattern of response in the ventral object vision pathway that could be distinguished from the patterns of response evoked by all other individual categories. Patterns of response were examined in ventral temporal object-selective cortex, defined as those voxels with responses that differed significantly by category. The data for each subject were split into two sets, namely even and odd runs. We then determined whether the stimulus category that a subject was viewing could be identified by examining the similarity between the patterns of response evoked by each category on even and odd runs (19).

Correlations between patterns of response served as indices of similarity (Fig. 3). For example, to determine whether the pattern of response to one category, such as chairs, could be distinguished from the pattern of response to a different category, such as shoes, the correlation between the pattern of response to chairs on even runs and the response to chairs on odd runs (within-category correlation) was compared with the correlation between the response to chairs on even runs and the response to shoes on odd runs (between-category correlation).

Distinct patterns of neural response for multiple categories of objects. The pattern of response in object-selective ventral temporal cortex correctly identified the category being viewed in 96% of pairwise comparisons (20). The pattern of response indicated when subjects were viewing faces, houses, and scrambled pictures with no errors (Table 1). Identification accuracy for the small man-made objects (bottles, scissors, shoes, and chairs) was significantly better than chance for each category (21).

Category identification based on patterns of nonmaximal responses. Although these results suggest that category-specific patterns of response are distributed and overlapping, higher within-category correlations could be due simply to the regions that reliably respond maximally to each category, with no information about a specific category carried by the pattern of response in cortex that responded maximally to other categories. To test whether the patterns of nonmaximal responses carry category-related information, we analyzed whether each stimu-

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lus category evoked a distinct pattern of response in cortex that responded maximally to other categories. For each comparison between patterns of response evoked by two categories, all of the voxels that responded maximally to either category in either half of the data were excluded from the calculation of correlations (22). The specificity of the pattern of response to each category was barely diminished by thus restricting the analysis (Fig. 4), with a mean accuracy of 94% for identifying the category being viewed (Table 1) (23).

Patterns of response within cortical regions that respond maximally to one category. These results indicate that the category specificity of responses in ventral temporal cortex is not restricted solely to regions that respond maximally to certain stimuli, thus raising the question of whether the representation of faces and objects in this cortex has a topographic organization that exists with a finer spatial resolution than that defined by such regions. To investigate whether the category specificity of response exists at this finer spatial resolution, we examined the patterns of response within regions that responded maximally to a single category or a small set of categories (22) (Table 1). Within only the cortex that responded maximally to houses, the pattern of response correctly identified the category being viewed with 93% accuracy. Within only the cortex that responded maximally to small, man-made objects, the pattern of response identified the category being viewed with 94% accuracy. Even within the much smaller region that responded maximally to faces, the pattern of response identified the category being viewed with 83% accuracy, and accuracies were significantly better than chance for all categories except shoes. Similarly, the pattern of response within the region that responded maximally to cats identified the category being viewed with 85% accuracy, with accuracies that were better than chance for all categories except bottles.

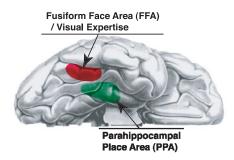


Fig. 1. Schematic diagram illustrating the locations of the fusiform face area (FFA), which also has been implicated in expert visual recognition, and the parahippocampal place area (PPA) on the ventral surface of the right temporal lobe. In most brains, these areas are bilateral.

These results demonstrate that the pattern of response in ventral temporal cortex carries information about the type of object being viewed, even in cortex that responds maximally to other categories, but the nature of this information is unknown. To examine whether this information concerns only lowlevel features of gray-scale photographs that are shared by a category, such as mean luminance, mean contrast, and spatial frequencies, we reanalyzed data from a previous study in which subjects viewed photographs and line drawings of three categories (faces, house, and chairs) (13). We examined whether the pattern of response to a category of line drawings can be identified on the basis of its similarity to responses to photographs of the same and different categories and, conversely, whether the pattern of response to a category of photographs can be identified on the

basis of its similarity to responses to line drawings. The results of this reanalysis showed that similarities between patterns of response to photographs and line drawings of the same category correctly identified the category being viewed, even when the analysis was restricted to cortex that did not respond maximally to either of the categories being discriminated (96% correct pairwise discriminations) [for detailed results, see supplemental material (24)]. This result shows that patterns of nonmaximal responses do not represent low-level features that are specific to the type of stimuli, such as photographs, but, rather, appear to reflect information that is more definitive of object category.

Discussion. These findings demonstrate distinct patterns of response in ventral temporal cortex for multiple categories of objects, including different types of small man-

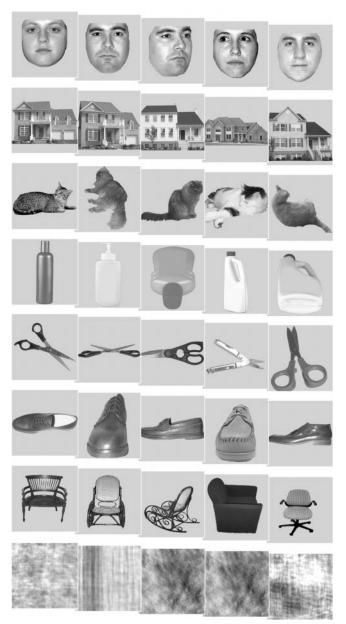


Fig. 2. Examples of stimuli. Subjects performed a one-back repetition detection task in which repetitions of meaningful pictures were different views of the same face or object.

made objects. This specificity is not restricted to categories for which dedicated systems might have evolved because of their biological significance. The specificity of the pattern of response for each category was a property of a much greater extent of objectselective cortex in the ventral temporal lobe than the sector that responded maximally to that category. The category being viewed still could be identified when the cortex that responded maximally to that category was excluded from the analysis. This result indicates that the representations of faces and objects in ventral temporal cortex are widely distributed and overlapping and that small or submaximal responses are an integral part of these representations. When the analysis was further restricted to regions that responded maximally to a single category (houses, faces, or cats) or a small number of categories (i.e., man-made objects-bottles, scissors, shoes, and chairs), the patterns of response to other categories within these regions were still significantly distinct. This result suggests that regions such as the "parahippocampal place area" or the "fusiform face area" are not dedicated to representing only spatial arrangements or human faces but, rather, are part of a more extended representation for all objects (25).

Object form topography. We have shown in previous studies that the maximally responsive regions for several of these categories-faces, houses, chairs, animals, and tools—have a consistent topography across individuals (12-14). Here, we show that the topographic arrangement of the full pattern of response is consistent within subjects, but we are not able to perform a similar correlational analysis across subjects because current methods for warping individual brains to a common shape are inadequate at this level of detail. The spatial resolution of this topography is smaller than that defined by categoryselective areas (>1 cm), because categoryrelated patterns can be discerned within these areas, and greater than that of randomly arranged single columns or small clusters of columns (<1 mm), because of the spatial resolution of the fMRI images in this study (>3.5 mm). Single-unit recording studies in the monkey have suggested the existence of a columnar organization for representations of complex features of form but have not revealed any larger scale topographic arrangement (2).

We have proposed the term object form topography for the topographic organization of the distributed representation of faces and objects in ventral temporal cortex. Our results demonstrate a spatially organized functional architecture within subregions of ventral temporal cortex that are defined by a maximal response to a single object category. This architecture may be analogous to that found

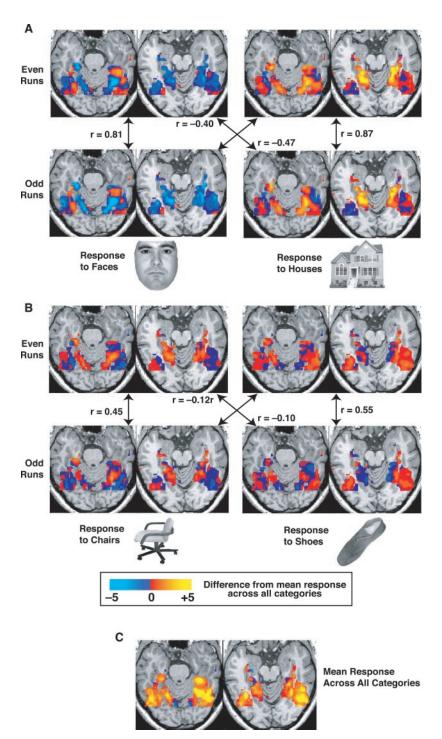


Fig. 3. The category specificity of patterns of response was analyzed with pairwise contrasts between within-category and between-category correlations. The pattern of response to each category was measured separately from data obtained on even-numbered and odd-numbered runs in each individual subject. These patterns were normalized to a mean of zero in each voxel across categories by subtracting the mean response across all categories. Brain images shown here are the normalized patterns of response in two axial slices in a single subject. The left side of the brain is on the left side of each image. Responses in all object-selective voxels in ventral temporal cortex are shown. For each pairwise comparison, the within-category correlation is compared with one between-category correlation. (A) Comparisons between the patterns of response to faces and houses in one subject. The within-category correlations for faces (r = 0.81) and houses (r = 0.87) are both markedly larger than the between-category correlations, yielding correct identifications of the category being viewed. (B) Comparisons between the patterns of response to chairs and shoes in the same subject. The category being viewed was identified correctly for all comparisons. (C) Mean response across all categories relative to a resting baseline.

within early visual areas, such as V1, which contain spatially organized maps of simpler visual features, such as retinotopic location, edge orientation, and color. Object form topography presumably reflects how the more complex attributes of visual appearance that underlie object and face recognition are related visually, structurally, or semantically.

Population encoding of visual appearance. The representation of a face or object involves the concerted neural activity in a widely distributed cortical space. Our analysis shows that the pattern of large and small responses, not just the location of large responses, carries category-related information, suggesting that small responses are an integral part of the representation. Population responses in simpler systems, such as color vision, similarly rely on both large and small responses to determine the quality of the integrated percept. In color vision, the perceptual quality of a hue that evokes a maximal red response in red-green neurons is also dependent on small responses in yellow-blue neurons that determine whether that hue is perceived as being more orange or violet (26-28).

What attributes of visual appearance could underlie a population encoding of objects and faces in which both large and small responses determine the quality of the integrated percept? Others have suggested that these attributes may be two-dimensional, view-dependent (2) or three-dimensional, structural (29) primitives that make up an alphabet for shape recognition. In a representation based on primitive features, however, a face or object would be specified by the strong responses that indicate the features that are present in the stimulus, not by a combination of large and small responses. Another possibility is suggested by models of face appearance and perception that describe a face on the basis of a small number of dimensions—operationalized as principal or independent components—that capture how configurations of features typically covary across faces (30-32). In a representation based on continuous dimensions, small and intermediate responses would be as important as large responses for specifying the location of a vector in feature space that best describes the appearance of a perceived face. Psychophysical evidence (33, 34) supports the proposal that the neural representation of faces may be based on such dimensions, represented as opponent processes referenced to the population mean. This opponent process model demonstrates how a limited number of channels can represent complex variations of form, such as those that distinguish one face from another, and suggests, further, how a limited cortical space could represent an unlimited variety of faces.

Our analysis did not reveal any sectors of

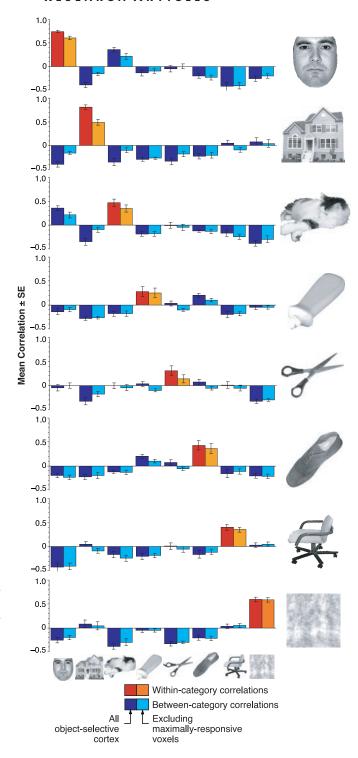


Fig. 4. Mean withincategory and tween-category correlations (±SE) between patterns of response across all subjects for all ventral temporal object-selective tex (red and dark blue) and for ventral temporal cortex excluding the cortex that responded maximally to either of two categories being compared (orange and blue). The SE of within-category correlations after excluding maximally responsive cortex was based on the mean correlation pairwise

across 14

subject.

comparisons for each

ventral temporal cortex that did not convey information about discriminations among several stimulus categories, which leaves open the question of how lesions can cause selective impairments for recognizing individual faces (prosopagnosia) or discriminating between members of a single category of objects (35-37). Our results do not address the distribution or spatial scale of patterns of response that discriminate between exemplars within a category. Moreover, it is unclear whether any of these syndromes can be caused by a restricted lesion in a ventral temporal region that responds maximally to one category (38).

A population encoding based on the pattern of large and small responses in a wide expanse of cortex has the capacity to produce unique representations of a virtually unlimited number of object categories. Models of the functional architecture of ventral extrastriate cortex that analyze only mean responses in

Table 1. Accuracy of identification of the category being viewed based on the patterns of response evoked in ventral temporal cortex. Accuracies are the percentage of comparisons between two categories that correctly identified which category was being viewed.

Region	Volume (cm³ ± SE)	Identification accuracy (%)							
		Faces	Houses	Cats	Bottles	Scissors	Shoes	Chairs	Scrambled
All ventral temporal object-selective cortex	22.9 ± 2.8	100***	100***	98 ± 2***	90 ± 6***	92 ± 6***	92 ± 7***	96 ± 2***	100***
Minus regions that were maximally responsive to categories being compared Regions maximally responsive to:	15.4 ± 1.8	100***	100***	95 ± 2***	89 ± 6***	85 ± 9**	90 ± 8**	98 ± 1***	100***
Faces Houses Cats Small objects	3.1 ± 0.9 9.6 ± 1.8 2.6 ± 0.4 6.9 ± 1.1	94 ± 7*** 100*** 96 ± 4*** 100***	99 ± 1*** 100*** 96 ± 2*** 100***	76 ± 13* 88 ± 5*** 82 ± 8** 95 ± 3***	81 ± 14* 85 ± 10** 65 ± 11 83 ± 7**	77 ± 9* 81 ± 6** 69 ± 5** 92 ± 8**	70 ± 16 96 ± 2*** 76 ± 9* 94 ± 6***	77 ± 11* 94 ± 3*** 95 ± 4*** 90 ± 6***	92 ± 7*** 100*** 100*** 96 ± 4***

Differs from chance (50%): *, P < 0.05; **, P < 0.01; ***, P < 0.001.

regions that are putatively specialized for restricted categories of stimuli (faces and places) (5, 7) or specific perceptual processes (visual expertise) (9-11) provide no explicit account for how neural representations of all object categories differ (39). By contrast, our results indicate how ventral extrastriate cortex can produce unique representations for all object categories. Fortuitously, these representations have a consistent topographic arrangement that may provide a key for decoding the information that underlies face and object recognition.

References and Notes

- C. G. Gross, C. E. Rocha-Miranda, D. B. Bender, J. Neurophysiol. 35, 96 (1972).
- 2. K. Tanaka, Annu. Rev. Neurosci. 19, 109 (1996).
- N. K. Logothetis, D. L. Scheinberg, Annu. Rev. Neurosci. 19, 577 (1996).
- 4. S. Edelman, Trends Cogn. Sci. 1, 296 (1997).
- N. Kanwisher, J. McDermott, M. Chun, J. Neurosci. 17, 4302 (1997).
- G. McCarthy, A. Puce, J. C. Gore, T. Allison, J. Cognit. Neurosci. 9, 605 (1997).
- 7. R. Epstein, N. Kanwisher, Nature 392, 598 (1999).
- G. K. Aguirre, E. Zarahn, M. D'Esposito, Neuron 21, 373 (1998).
- I. Gauthier, M. J. Tarr, A. W. Anderson, P. Skudlarski, J. C. Gore, Nature Neurosci. 2, 568 (1999).
- 10. I. Gauthier, *Trends Cognit. Sci.* **4**, 1 (2000).
- P. Skudlarski, J. C. Gore, A. W. Anderson, Nature Neurosci. 3, 191 (2000).
- 12. J. V. Haxby et al., Neuron 22, 189 (1999).
- A. Ishai, L. G. Ungerleider, A. Martin, J. L. Schouten, J. V. Haxby, *Proc. Natl. Acad. Sci. U.S.A.* **96**, 9379 (1999).
- L. L. Chao, J. V. Haxby, A. Martin, *Nature Neurosci.* 2, 913 (1999).
- J. V. Haxby, A. Ishai, L. L. Chao, L. G. Ungerleider, A. Martin, Trends Cognit. Sci. 4, 3 (2000).
- S. Edelman, K. Grill-Spector, T. Kushnir, R. Malach, Psychobiology 26, 309 (1998).
- 17. K. Grill-Spector *et al.*, *Neuron* **24**, 187 (1999).
- 18. Neural responses, as reflected in hemodynamic changes, were measured in six subjects (five female and one male) with gradient echo echoplanar imaging on a GE 3T scanner (General Electric, Milwaukee, WI) [repetition time (TR) = 2500 ms, 40 3.5-mm-thick sagittal images, field of view (FOV) = 24 cm, echo time (TE) = 30 ms, flip angle = 90] while they performed a one-back repetition detection task. High-resolution T1-weighted spoiled gradient recall (SPGR) images were obtained for each subject to provide detailed anatomy (124 1.2-mm-thick sagittal images, FOV = 24 cm). Stimuli were gray-scale images of faces, houses, cats, bottles, scissors, shoes,

chairs, and nonsense patterns. The categories were chosen so that all stimuli from a given category would have the same base level name. The specific categories were selected to allow comparison with our previous studies (faces, houses, chairs, animals, and tools) or ongoing studies (shoes and bottles). Control nonsense patterns were phase-scrambled images of the intact objects. Twelve time series were obtained in each subject. Each time series began and ended with 12 s of rest and contained eight stimulus blocks of 24-s duration, one for each category, separated by 12-s intervals of rest. Stimuli were presented for 500 ms with an interstimulus interval of 1500 ms. Repetitions of meaningful stimuli were pictures of the same face or object photographed from different angles. Stimuli for each meaningful category were four images each of 12 different exemplars. Image data were analyzed with multiple regression with no spatial smoothing (40). To identify objectselective cortex, we used an eight-regressor model. The first regressor was the contrast between stimulus blocks and rest. The remaining seven regressors modeled the response to each meaningful category. The omnibus effect of these seven regressors was used as a test of the significance of differences among the responses to stimulus categories. To determine the patterns of response to each category on even-numbered and odd-numbered runs, we used a 16-regressor model—eight regressors to model the response to each category relative to rest on even runs and eight regressors to model the response to each category on odd runs with no regressor that contrasted all stimulus blocks to rest. The β weight for each regressor was used as an estimate of the strength of response relative to rest. Volumes of interest (VOI) were drawn on the high-resolution structural images to identify ventral temporal, lateral temporal, and ventrolateral occipital cortex. The VOI for ventral temporal cortex extended from 70 to 20 mm posterior to the anterior commissure in Talairach brain atlas coordinates (41) and consisted of the lingual, parahippocampal, fusiform, and inferior temporal gyri. The VOI for lateral temporal cortex also extended from 70 to 20 mm posterior to the anterior commissure and consisted of the middle temporal gyrus and both banks of the superior temporal sulcus. The VOI for ventrolateral occipital cortex extended from the occipital pole to 70 mm posterior to the anterior commissure and consisted of the lingual, fusiform, inferior occipital, and middle occipital gyri. Voxels within these VOIs that were significantly object-selective ($P < 10^{-6}$, uncorrected) were used for the analysis of within-category and between-category correlations.

19. Analysis of the accuracy with which the category being viewed could be identified focused on comparisons between patterns of response for pairs of categories, as illustrated in Fig. 3. Mean response in each voxel across categories was subtracted from the response to each individual category in each half of the data before calculating correlations. If the within-category correlation (for example, response to category A on even and odd runs) was larger than the betweencategory correlation (correlation of the response to category A on even runs with the response to category B on odd runs), that comparison was counted as a correct identification. For each pair of categories, therefore, there were four such comparisons (within-category A versus category A on odd runs with category B on even runs, within-category A versus category A on even runs with category B on odd runs, and similar comparisons involving the within-category correlation for category B). The probability that the accuracy of identifying each individual category exceeded chance was determined with a simple test: The accuracy of identifying that category was determined for each subject as the proportion of pairwise comparisons that yielded correct identifications, and a t test (df = 5) was used to test whether the mean accuracy across subjects exceeded chance (50%).

- 20. The category being viewed was correctly identified against all other categories in 83% of cases (within-category correlation for a given category was the greatest of all correlations between the response to that category in one half of the data and the responses to that and other categories in the other half of the data; chance accuracy would be 12.5%). Accuracies for identifying patterns for individual categories as compared with all other categories ranged from 100% (faces, houses, and scrambled pictures) to 67% (bottles and scissors). Detailed results are published as supplemental material (24).
- 21. Identification of the category being viewed when that category was one of the four, small, man-made categories (bottles, scissors, shoes, and chairs) was significantly better than chance even when only the comparisons among these categories were considered, both for all object-selective ventral temporal cortex (bottles: mean accuracy across subjects was 83% for pairwise comparisons among small manmade objects, differs from 50%, P < 0.02; scissors: 86%, P < 0.01; shoes: 86%, P < 0.02; chairs: 97%, P < 0.001) and for only cortex that responded maximally to other categories (bottles: 86%, $\it P < 0.01$; scissors: 83%, P < 0.01; shoes: 86%, P < 0.02; chairs: 100%). The analysis concentrated on patterns of response in ventral temporal cortex, where the category being viewed could be identified with greatest accuracy, but identification accuracies were nearly as great for lateral temporal (94%) and ventrolateral occipital cortices (92%). The ability to identify the category being viewed on the basis of the patterns of response within several subregions of ventral temporal cortex as well as in ventral occipital and lateral temporal cortex suggests the existence of multiple representations that encode different types of information about categories, such as visual form, typical patterns of motion, and internal spatial arrangements. We have suggested, for example, that the lateral temporal cortex represents different patterns of motion that are associated with faces and different categories of objects (42, 43).

- 22. For correlation analyses of subsets of object-selective cortex, the category that elicited the maximal response in each voxel was determined for even runs, odd runs, and all runs. To examine whether the pattern of response to a category could be discerned in cortex that responded maximally to other categories, we restricted comparisons of responses to pairs of categories to voxels that did not respond maximally to either category on either even or odd runs. This was the most exacting test of this prediction that we could devise. To examine the response in regions that responded maximally to only a single category (faces, houses, or cats) or to only small man-made objects, we included only those voxels that had maximal responses averaged across all runs. Thus, there was no overlap between these regions.
- 23. The image data were not smoothed before analysis; nonetheless, it is possible that voxels outside of the regions showing maximal responses to a given category could still be influenced by the maximally responsive region because of spatial smoothness due to imaging techniques and partial volume effects. To address this issue, we also analyzed our data after excluding all voxels that responded maximally to the two categories being compared as well as all voxels that were adjacent to these regions. On average, this analysis excluded 58% of voxels from the calculation of correlations. Nonetheless, overall accuracy for identifying the category being viewed was 92%, demonstrating that the results are not attributable to the effect of maximally responsive regions on adjacent voxels.
- Supplemental data are available on Science Online at www.sciencemag.org/cgi/content/full/293/5539/ 2425/DC1.
- 25. Within the region that responds maximally to faces, sites may exist that respond exclusively to faces that are interdigitated with sites that respond maximally, but not exclusively, to faces, as suggested by studies of evoked potentials recorded with electrodes on the

- cortical surface (44). It is important to note, however, that most face-selective recording sites in these studies do show some response to other objects and even the sites that demonstrate an N200 response exclusively to faces appear to respond to other objects also but with different latencies.
- E. Hering, Outlines of a Theory of the Light Sense (Harvard Univ. Press, Cambridge, MA, 1964).
- L. M. Hurvich, D. Jameson, Psychol. Rev. 64, 384 (1957).
- R. L. De Valois, Cold Spring Harbor Symp. Quant. Biol. 30, 567 (1965).
- 29. I. Biederman, Psychol. Bull. 94, 115 (1987).
- A. J. O'Toole, H. Abdi, K. A. Deffenbacher, D. Valentin, J. Opt. Soc. Am. A 10, 405 (1993).
- 31. P. J. B. Hancock, A. M. Burton, V. Bruce, *Mem. Cognit.* **24**, 26 (1996).
- 32. A. Lanitis, C. J. Taylor, T. F. Cootes, *IEEE Trans. Pattern Anal. Mach. Int.* 19, 743 (1997).
- V. Blanz, A. J. O'Toole, T. Vetter, H. A. Wild, Perception 29, 885 (2000).
- 34. D. A. Leopold, A. J. O'Toole, T. Vetter, V. Blanz, *Nature Neurosci.* 4, 89 (2001).
- 35. H. Hecaen, R. Angelergues, Arch. Neurol. 7, 24 (1962)
- 36. A. Damasio et al., Neurology 32, 331 (1982).
- 37. E. K. Warrington, T. Shallice, Brain 107, 829 (1984).
- St. C. Walmigoth, I. Saintice, Jan. 107, 26 (1904).

 St. Of the category-selective agnosias, only prosopagnosia is a purely visual agnosia, and controversy still exists over whether a pure prosopagnosia exists that has no effect on other aspects of visual object perception (45). Other category-selective agnosias also involve loss of nonvisual knowledge about the affected category and are associated with lesions in cortices other than those of the ventral temporal lobe (37). The literature on lesions that cause prosopagnosia is uninformative about what part of ventral temporal cortex is critical for face recognition. The lesions that cause prosopagnosia tend to be large (37). It has never been demonstrated that the critical

- part of lesions that cause prosopagnosia involves damage to the small region that responds maximally to faces. For a lesion to cause prosopagnosia, it may require damage in regions that show the most modulation of response to different individual faces, which may not be coextensive with the region that responds maximally to faces, or damaged connections to cortices in other parts of the brain that are critical for face recognition, such as the superior temporal sulcus or the anterior temporal cortex.
- 39. Models of the functional architecture of ventral extrastriate cortex that focus analysis on mean responses in regions that are putatively specialized for stimulus category (5, 7) or perceptual process (9-11) are not inconsistent with a coexisting functional architecture that embodies the distinct representations for all categories. Unlike the object form topography model proposed here, however, these specialized region models do not provide an explicit account for how such a coexisting functional architecture is organized or how the representations for an unlimited variety of categories could differ from each other within this architecture.
- 40. J. V. Haxby, J. M. Maisog, S. M. Courtney, in *Mapping* and *Modeling the Human Brain*, P. Fox, J. Lancaster, K. Friston, Eds. (Wiley, New York, in press).
- J. Talairach, P. Tournoux, Co-Planar Stereotoxic Atlas of the Human Brain (Thieme, New York, 1988).
- J. V. Haxby, E. A. Hoffman, M. I. Gobbini, *Trends Cognit. Sci.* 4, 223 (2000).
- A. Martin, L. G. Ungerleider, J. V. Haxby, in *The New Cognitive Neurosciences*, M. S. Gazzaniga, Ed. (MIT Press, Cambridge, MA, 1999), pp. 1023–1036.
- 44. T. Allison, A. Puce, D. D. Spencer, G. McCarthy, Cereb. Cortex 9, 415 (1999).
- 45. I. Gauthier et al., J. Cogn. Neurosci. **12**, 495 (2000).
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REPORTS

Field-Induced Superconductivity in a Spin-Ladder Cuprate

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We report on the modulation of the transport properties of thin films, grown by molecular beam epitaxy, of the spin-ladder compound $[CaCu_2O_3]_4$, using the field effect in a gated structure. At high hole-doping levels, superconductivity is induced in the nominally insulating ladder material without the use of high-pressure or chemical substitution. The observation of superconductivity is in agreement with the theoretical prediction that holes doped into spin ladders could pair and possibly superconduct.

Because of the prediction of the presence of spin-gap and possible appearance of d-wave superconductivity, much attention has been paid

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to the so-called spin-ladder systems (I–4). Ladder systems are considerably easier to study theoretically than two-dimensional models, because they are basically quasi–one-dimensional and they can provide a playground for studies of high-critical temperature (high- $T_{\rm c}$) superconductors (4). Spin-ladder systems, especially two-leg ladders (Fig. 1), are interesting model materials to investigate low-dimensional quantum systems. Two-leg ladders are essentially one-dimensional (1D), and doped ladders are a fascinating mixture of a dilute Fermi gas with strong attractions and a concentrated Fermi system with a large Fermi surface (3). In addition, the similarities between doped ladders and

doped CuO₂ planes make for interesting comparison. However, a difficulty that arises in the preparation of undoped and doped materials is that structural changes due to chemical doping may mask the effect of the change of the doping level and that doping-induced disorder might suppress the observation of superconductivity. It has been shown that the modulation of the carrier concentration leading, for example, to gate-induced superconductivity is a powerful tool to study the electronic properties of various materials as a function of the doping level (5–9), which circumvents the issue of doping-induced disorder.

So far, only Sr-rich $Sr_{1-x}Ca_xCu_2O_3$ and $(Sr_{1-x}Ca_y)_{14}Cu_{24}O_{41}$ materials, prepared under

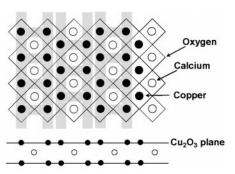


Fig. 1. Schematic structure of the two-leg ladder compound [CaCu₂O₃]₄.