

Decoding the neural correlates of consciousness

Rimona S. Weil^{a,b} and Geraint Rees^{a,b}

^aWellcome Trust Centre for Neuroimaging at UCL, Institute of Neurology, University College London and ^bUCL Institute of Cognitive Neuroscience, University College London, London, UK

Correspondence to Dr Rimona Weil, Wellcome Trust Centre for Neuroimaging at UCL, 12 Queen Square, London WC1N 3BG, UK
Tel: +44 20 7833 7472; fax: +44 20 7813 1420;
e-mail: r.weil@fil.ion.ucl.ac.uk

Current Opinion in Neurology 2010, 23:649–655

Purpose of review

Multivariate pattern analysis (MVPA) is an emerging technique for analysing functional imaging data that is capable of a much closer approximation of neuronal activity than conventional methods. This review will outline the advantages, applications and limitations of MVPA in understanding the neural correlates of consciousness.

Recent findings

MVPA has provided important insights into the processing of perceptual information by revealing content-specific information at early stages of perceptual processing. It has also shed light on the processing of memories and decisions. In combination with techniques to reconstruct viewed images, MVPA can also be used to reveal the contents of consciousness.

Summary

The development of multivariate pattern analysis techniques allows content-specific and detailed information to be extracted from functional MRI data. This may lead to new therapeutic applications but also raises important ethical considerations.

Keywords

consciousness, decoding, fMRI, multivariate pattern analysis

Curr Opin Neurol 23:649–655
© 2010 Wolters Kluwer Health | Lippincott Williams & Wilkins
1350-7540

Introduction

Consciousness is the rich, constantly changing internal experience which makes us who we are. At its most basic level, it is the degree of wakefulness, necessary for any conscious experience [1]. But when we are awake (and sometimes when we are asleep and dreaming) we can have experiences with particular phenomenal content [2]. Phenomenal consciousness is the content of our perceptions, such as the experience of the colour red, and access to those contents is achieved when we report those contents to others, or reflect upon them. This latter process may rely upon a fronto-parietal network [1], requiring the phenomenal content to be broadcast to areas of the brain responsible for reasoning and planning [3]. Here we focus on the extent to which the phenomenological contents of consciousness can be decoded from activity patterns in functionally specialized brain regions.

Consciousness can be fundamentally changed by diseases damaging the brain. As well as affecting level of consciousness, disease can alter both phenomenal contents and access to consciousness, both globally as in dementia, psychosis and seizures, and focally as in spatial neglect, the agnosias and functional disorders. Much of medical practice involves eliciting the content of phenomenal states (the contents of consciousness) through communication. Yet probing the contents of consciousness in this

way is not always possible when communication or insight is limited. Therefore techniques allowing direct determination of mental content through measuring brain activity may provide important insights into these diseases, and in future may enable communication in altered states of consciousness [4].

Neuroimaging, neurophysiological and behavioural studies provide insight into the location and processing of conscious experiences. Functional MRI (fMRI) can also demonstrate residual cognitive function in minimally conscious patients [5–7] and in deeply anaesthetized volunteers [8]. However, conventional fMRI can be limited in its ability to represent the content of conscious states. Multivariate pattern analysis (MVPA) is an emerging technique for analysing neuroimaging data that appears to permit reconstruction of a greater variety of cognitive states from noninvasive measurements of brain activity in humans. This makes it possible to use this new technique to explore how the contents of conscious experiences are encoded in the brain. The mechanisms underlying access to consciousness have not yet been studied using MVPA, but have been recently explored using other methods [9–11].

Here we review the use of MVPA in the neuroimaging of consciousness. First we outline important differences between conventional neuroimaging and MVPA. We then review recent applications of MVPA in studies of

the neural correlates of consciousness, in the domains of perception, thought and intention. Finally, we consider limitations of MVPA and potential applications in understanding neurological and psychiatric disease.

What is multivariate pattern analysis?

Conventional fMRI measures the blood oxygen level-dependent (BOLD) signal at each location (voxel) in a brain image. The BOLD signal arising during different cognitive tasks can then be compared to determine whether a brain location is involved in a particular function [12]. In contrast, MVPA examines the pattern of responses across many voxels simultaneously. This is achieved by viewing the voxel activity pattern (rather than overall level of activity) as points in multidimensional space, with as many dimensions as there are voxels, and defining a boundary separating the patterns belonging to each condition. This technique affords MVPA several potentially important advantages over conventional fMRI analysis.

Conventional fMRI analysis typically considers activity at a single point in space (voxel) or averaged across a set of voxels (a 'region-of-interest' analysis). Both these approaches lead to loss of information about the spatial pattern of activity local to a voxel. In contrast, MVPA retains this fine-grained spatial information lost during conventional analysis; it is now apparent that these patterns can encode information about mental states. Pattern analysis can also detect changes in spatial patterns of activity associated with different mental states that occur without any overall change in activation. Thus, MVPA provides potentially increased sensitivity to content-specific information, providing a deeper understanding of the neuronal activity underlying a person's cognitive state.

How is multivariate pattern analysis carried out?

Multivariate pattern analysis requires a series of stages of analysis [13,14]:

- (1) Data splitting: The fMRI time series is divided into 'training' and 'test' data for use in steps 5 and 6 below. This division is arbitrary and often based on scanner runs, for example even runs for training, odd runs for testing to ensure the two sets are independent from each other.
- (2) Preprocessing: The data are preprocessed (as in conventional fMRI analysis) by co-registering the images into the same anatomical space and correcting for participant movements.
- (3) Activity estimation: A time course of activity for every voxel in each individual participant is gener-

ated, either using the raw BOLD signal or by using parameter estimates [12] that represent closeness to a fit to an expected model (see [15] for alternative methods).

- (4) Voxel selection: Some voxels are likely to be more informative for MVPA than others. An initial step is usually to decide which voxels to include in the analysis. This selection must use criteria that are orthogonal to the classification being tested in the MVPA analysis. Typically there is restriction to a region of interest obtained from independent anatomical or functional data (see also [16,17]). More recently 'searchlight' approaches which sequentially examine cliques of voxels throughout the cortex like a searchlight scanning over cortex have become popular.
- (5) Training the classifier: A classifier is trained on the training data. This typically involves determination of a plane in multidimensional space that best separates the patterns arising from the multivariate voxel time series associated with the different experimental conditions. There are a variety of ways of making this determination (see [15] for a comparison between different classifiers).
- (6) Testing the classifier: The classifier is then applied to the independent test set. For each voxel pattern in the test set, the classifier predicts which condition it best belongs to, based on the separation between patterns established in the training phase. Better than chance performance at this blind classification (compared to the known experimental condition labels) suggests the BOLD response in that set of voxels contains information sufficient to discriminate the experimental condition.

Decoding perceptual experience

A fundamental aspect of consciousness is perception of the external world. One serious limitation of conventional fMRI analysis for the study of perception is its spatial resolution of 1.5–3 mm³ voxels. Many aspects of neuronal processing are organized at a finer spatial scale than this. For example, the orientation of edges in the visual environment is encoded in neuronal activity associated with orientation columns in visual cortex that measure only a few hundred micrometers across [18,19]. Conventional fMRI analyses cannot detect information at this spatial scale as multiple orientation columns fall within each voxel. Nevertheless, two recent studies [20,21] showed how MVPA could be used to recover this information and determine which of two differently oriented stimuli a participant was viewing. The authors realized that slightly different proportions of cells with different orientation properties are sampled by each voxel. This produces small biases in the response of each voxel to each orientation. Thus, when viewing images with different orientations, each orientation evokes a slightly

different response pattern. When the overall response pattern is analysed, the orientation of lines being perceived can be reliably determined (see also [22,23]). Similar pattern-based analysis can decode the direction of movement being viewed in regions of visual cortex not previously thought to contain direction sensitive information [24]. Importantly, this study could identify which of two overlapping motion directions was the current focus of the participant's attention. Thus, correlates of attention can be detected early in the visual processing pathway. More recently several studies have used MVPA to decode the experience of colour [25,26] and the binding of colour and form [27] from early visual areas. These studies thus enable fMRI to be used to study signals associated with information about very early perceptual processing, and their relationship to the contents of consciousness.

Decoding object categories

One of the first uses of MVPA was to decode the category of object (e.g. face, house or household object) that a person was viewing from patterns of BOLD signals in occipito-temporal cortex [28] (see also [29,30]). Since this landmark study, further work has used MVPA to identify increasingly detailed information associated with these higher levels of visual processing. For example, Eger and colleagues [31] could decode different types of chairs presented to participants by examining patterns of activity within lateral occipital complex (an object-sensitive region in human occipito-temporal cortex). They could achieve this even when using different viewing angles for the training and test sessions, thus showing object invariance of the fMRI signals to object orientation at this later stage of perceptual processing. Several other studies have decoded various forms of category information not previously possible using conventional fMRI analyses, such as the identity of individual faces [32,33], distinguishing between numbers [34] and natural scenes [35] and identifying pairs of objects using data collected from viewing objects individually [36].

Intriguingly, category information can be extracted from object-responsive voxels in ventral-temporal cortex even without perception of the object itself [37,38,39] (see also [40]). Similarly, Haynes and Rees [41] decoded changes in conscious experience during binocular rivalry. They presented dissimilar images to each eye inducing competition for perceptual dominance, generating frequent changes in conscious experience despite the stimulus remaining constant. By examining the pattern of responses to each feature they tracked the dynamic time course of subjective experience.

Decoding other sensory modalities

Although initial MVPA studies primarily explored visual perception, recent work has used similar approaches in

other sensory modalities. For example, touches applied to different fingers of the same hand can be distinguished by examining patterns of activation in primary somatosensory areas [42] and the speech content and identity of speaker can be decoded from patterns of auditory cortical activations [43]. Moreover, content-specific activity in auditory cortices is associated with the subjective experience of sound in the absence of auditory stimulation induced by muted films implying particular sounds [44].

Decoding natural images

Initially, MVPA was only used to decode simple figures that had previously been viewed by the participant. A greater challenge is to discriminate between patterns of brain activity evoked by viewing natural images, which are more complex than line drawings but more closely reflect actual perceptual experience and to be able to identify novel images not previously viewed by the participant. Kay and colleagues [45] recorded fMRI data while participants viewed hundreds of natural images. They then generated a model for every voxel in visual cortex, based on fundamental principles of receptive fields, such as information on the orientation of edges in the images. Next, they showed the participants new images. They used the model estimated from the first set of images to predict the pattern of activity each new image would generate in visual cortex. This predicted pattern could then be matched to the actual pattern of brain signals. Using this technique, the authors could reliably detect which novel image was being viewed by the participant (see also [46]).

The approach has been taken a step further by recent studies that reconstructed the image a person was viewing by decoding their brain signals. Miyawaki and colleagues [47] showed participants flickering checkerboard patterns whilst recording fMRI signals; they used these brain signals to reconstruct the patterns the participants had seen. Naselaris and colleagues [48] reconstructed realistic images using pattern analysis combined with a Bayesian approach which takes into account prior information about the structure and content of natural scenes. Nishimoto and colleagues [49] could identify continuous natural movies from brain activity measurements and, intriguingly, they could reconstruct this continuous visual experience directly, by creating a reproduction of a film a person was watching by monitoring their brain activity. These results have potentially extraordinary future implications for understanding first-hand the experiences of patients in the vegetative state and for direct visualization of hallucinations and dreams (see also [50]).

Decoding other influences on sensory processing

As MVPA is increasingly used to study the neural correlates of consciousness, studies are emerging that begin to challenge notions of how primary sensory cortices process

information. Indeed, it is becoming apparent that primary sensory cortex contains information beyond simple sensory processing. For example, orientations of line gratings held in working memory can be decoded from activity patterns in human visual cortex, suggesting that early visual areas are not restricted to sensory processing but may also be involved in maintaining visual features in memory [51•] (see also [52,53]). Similarly, vocal emotions can be decoded from pattern analysis of voice-sensitive regions, suggesting that emotional information is represented by distinct spatial patterns in sensory cortex [54] (see also [55]).

Decoding other mental states

The contents of consciousness are not only determined by perception: internal memories and thoughts are a significant constituent of mental life. Specific memory traces can be detected in the hippocampus using MVPA [56•]. Volunteers were shown films of everyday events and then asked to vividly recall each of the episodes during fMRI scanning. The specific memory being recalled could be predicted by analysing the pattern of activity in the hippocampus. MVPA can also provide insight into the way memories are retrieved [57,58]. Using a slightly different computational model, Mitchell *et al.* [59] examined patterns of activity throughout the brain to determine the noun a participant was thinking about, even for nouns not previously encountered by their algorithm.

Decoding covert mental states

The studies discussed above involved cooperation on the part of the individual, but thoughts and memories are often private, and may on occasion be deliberately concealed from others. Conventional neuroimaging studies of deception have demonstrated that deceit involves more effort than truth-telling and is associated with activity in prefrontal cortices [60–62]. As MVPA has higher sensitivity for classifying answers to specific questions in individuals, it has received interest as a potential lie-detection technology. Davatzikos and co-workers [63] used pattern analysis to accurately discriminate truthful and deceitful responses regarding possession of a playing card. Importantly, they could also classify patterns from new participants not previously used for training the algorithm, suggesting this form of lie detection might have an application outside controlled laboratory conditions.

An alternative approach to lie detection is examining brain activity related to the concealed information rather than the act of deception *per se*. Nose *et al.* [64], using conventional fMRI analysis, found activation in prefrontal and parietal areas during processing of concealed stimuli (similar to [60,65]). More recently, MVPA was

used to detect whether an individual has previously encountered a particular piece of information [66•]. Participants were scanned while making recognition judgements for studied and novel faces. Although MVPA could reliably decode which face participants perceived as old and which new, it could not reliably detect whether a particular face was actually old or new. These results suggest important limitations in the power of such analyses to objectively detect an individual's past experiences.

These studies raise important ethical considerations [67–70]. One concern is that if pattern analyses were allowed as evidence in the judicial system, they might have potential for harm if results were inaccurate or over-interpreted. It remains unclear whether use of fMRI as a legal tool is valid in more complex situations and when an individual may have a strong incentive not to cooperate [71]. Moreover, the possibility of reading another person's mind raises important issues of mental privacy, particularly if done against a person's will. Even with a person's consent, there is a risk of incorrectly reading brain signals and arriving at inaccurate conclusions, highlighting the importance of ethical guidelines for acquisition and storage of these data.

Decoding intention

Deciphering the neural processes underlying intention is a particular challenge in the study of consciousness. Haynes and colleagues [72] addressed this question by showing volunteers two numbers and allowing them free choice of either addition or subtraction. Using MVPA, they decoded whether volunteers were planning to add or subtract from the pattern of signals in prefrontal cortex. Hampton and O'Doherty [73] measured brain activity while individuals performed a reward-based decision-making task. Using MVPA, they decoded the subsequent behavioural choice of participants from brain activity in the previous trial and found that their decisions could be discriminated even before they made their choice. Intriguingly, Soon *et al.* [74] found regions in the prefrontal and parietal cortex that showed activity patterns predicting the outcome of a decision up to 10 s before that decision had been consciously made. These studies pose an interesting challenge to the understanding of consciousness and autonomy, suggesting that some of our seemingly conscious decisions might be formed before entering awareness.

Limitations

Although the use of MVPA to decode the content of what a person is thinking can be impressive, it also suffers from several limitations. MVPA studies typically classify the brain activity patterns associated with a limited number

of categories (see [45,59] for exceptions). Yet, in real life, a person can have a potentially limitless number of thoughts and people often have two or more thoughts concurrently. It is not at all clear whether pattern analysis can generalize over all such potential thoughts or whether it could cope with multiple simultaneous thoughts. Generalization across individuals is also problematic: one person's representation of a stimulus feature might elicit a completely different voxel pattern to another person's representation. Furthermore, MVPA is a form of pattern recognition. It requires an extensive training dataset to learn to differentiate between mental states and depends on the experimenter knowing the mental state associated with each pattern. Thus mind reading with no preliminary training period remains a hypothetical scenario.

At present, most multivariate pattern analyses are performed after data collection. In future, these methods may converge with developments in near-real-time analysis of fMRI data, raising the possibility of online decoding a person's thoughts in near-real-time and potentially using biofeedback to change the environment in association with these thoughts [75–77].

Another important limitation of fMRI MVPA is its relatively poor temporal resolution. This is because blood-flow changes lag several seconds behind electrical activity of neurons. But MVPA approaches can also be used to analyse magnetoencephalography (MEG) and EEG datasets that have millisecond temporal resolution but poor spatial resolution. In future these methods might be used in combination to provide the temporal and spatial resolution required to access the rich and changing contents of consciousness.

Finally, current neuroimaging technology suffers from practical issues if it is to be used in real-world environments, particularly in the context of usable brain-machine interfaces. MRI technology requires large, fixed installations and positioning of participants in an enclosed space. Future and emerging technologies may circumvent this problem, but at present transportable fMRI-based devices able to decode another person's thought processes remain a future development.

Future clinical applications

Until now, MVPA has been used to probe the contents of consciousness in the healthy brain. However, it may have potential applications in neurological disease. In addition to enabling communication with patients in minimally conscious states, which is already being explored [4], MVPA might be used to assess patients with limited communication, such as expressive aphasia. It may also have a role in directly probing the contents of hallucina-

tions or psychoses or in the assessment of patients with functional disorders. Work is also emerging on the use of biofeedback in the control of chronic pain [78] and the increased sensitivity of MVPA may prove powerful in similar applications.

Multivariate pattern analysis is increasingly being applied to anatomical MRI data as a diagnostic tool to separate patients with Alzheimer's disease from healthy aging individuals [79] and patients with autism spectrum disorder from healthy controls [80]. These techniques can also identify individuals currently without symptoms who are likely to develop Huntington disease later in life [81] and predict which patients with mild cognitive impairment are more likely to go on to develop Alzheimer's disease [82,83].

Conclusion

Multivariate pattern analysis provides a powerful framework for examining the neural correlates of phenomenal consciousness. It has revealed information at stages of processing not previously thought to be present and changed our understanding of the organization of perceptual processing, as well as allowing reconstruction of the contents of consciousness. It has potential clinical applications in assessment of patients with expressive aphasia and management of chronic pain. However, to understand the neural correlates of consciousness requires convergent use of MVPA alongside complementary methodologies that include conventional fMRI, MEG, EEG and behavioural studies, and investigation of patients with disorders of consciousness.

Acknowledgements

We thank S.M. Fleming, D.S. Schwarzkopf and J. Winston for helpful discussions on the manuscript. G.R. is supported by the Wellcome Trust.

References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- of special interest
- of outstanding interest

Additional references related to this topic can also be found in the Current World Literature section in this issue (p. 709).

- 1 Rees G, Kreiman G, Koch C. Neural correlates of consciousness in humans. *Nat Rev Neurosci* 2002; 3:261–270.
- 2 Block N. Two neural correlates of consciousness. *Trends Cogn Sci* 2005; 9:46–52.
- 3 Dehaene S, Changeux JP, Naccache L, *et al.* Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends Cogn Sci* 2006; 10:204–211.
- 4 Monti MM, Vanhaudenhuyse A, Coleman MR, *et al.* Willful modulation of brain activity in disorders of consciousness. *N Engl J Med* 2010; 362:579–589.
- 5 Owen AM, Coleman MR, Boly M, *et al.* Detecting awareness in the vegetative state. *Science* 2006; 313:1402.
- 6 Boly M, Coleman MR, Davis MH, *et al.* When thoughts become action: an fMRI paradigm to study volitional brain activity in noncommunicative brain injured patients. *Neuroimage* 2007; 36:979–992.

- 7 Coleman MR, Rodd JM, Davis MH, *et al.* Do vegetative patients retain aspects of language comprehension? Evidence from fMRI. *Brain* 2007; 130:2494–2507.
- 8 Davis MH, Coleman MR, Absalom AR, *et al.* Dissociating speech perception and comprehension at reduced levels of awareness. *Proc Natl Acad Sci U S A* 2007; 104:16032–16037.
- 9 Lau HC, Passingham RE. Relative blindsight in normal observers and the neural correlate of visual consciousness. *Proc Natl Acad Sci U S A* 2006; 103:18763–18768.
- 10 Fleming SM, Weil RS, Nagy Z, *et al.* Relating introspective accuracy to individual differences in brain structure. *Science* 2010; 329:1541–1543.
- 11 Del Cul A, Dehaene S, Reyes P, *et al.* Causal role of prefrontal cortex in the threshold for access to consciousness. *Brain* 2009; 132:2531–2540.
- 12 Friston KJ, Holmes AP, Worsley KJ, *et al.* Statistical parametric maps in functional imaging: a general linear approach [abstract]. *Hum Brain Mapp* 1995; 2:189–210.
- 13 Mur M, Bandettini PA, Kriegeskorte N. Revealing representational content with pattern-information fMRI—an introductory guide. *Soc Cogn Affect Neurosci* 2009; 4:101–109.
- In an easily accessible manner, this review explains the underlying concepts of pattern analysis and provides a step-by-step guide to performing MVPA.
- 14 Pereira F, Mitchell T, Botvinick M. Machine learning classifiers and fMRI: a tutorial overview. *Neuroimage* 2009; 45:S199–S209.
- 15 Misaki M, Kim Y, Bandettini PA, Kriegeskorte N. Comparison of multivariate classifiers and response normalizations for pattern-information fMRI. *Neuroimage* 2010; 53:103–118.
- 16 Etzel JA, Gazzola V, Keysers C. An introduction to anatomical ROI-based fMRI classification analysis. *Brain Res* 2009; 1282:114–125.
- 17 Kriegeskorte N, Simmons WK, Bellgowan PS, Baker CI. Circular analysis in systems neuroscience: the dangers of double dipping. *Nat Neurosci* 2009; 12:535–540.
- 18 Hubel DH, Wiesel TN, Stryker MP. Anatomical demonstration of orientation columns in macaque monkey. *J Comp Neurol* 1978; 177:361–380.
- 19 Obermayer K, Blasdel GG. Geometry of orientation and ocular dominance columns in monkey striate cortex. *J Neurosci* 1993; 13:4114–4129.
- 20 Kamitani Y, Tong F. Decoding the visual and subjective contents of the human brain. *Nat Neurosci* 2005; 8:679–685.
- 21 Haynes JD, Rees G. Predicting the orientation of invisible stimuli from activity in human primary visual cortex. *Nat Neurosci* 2005; 8:686–691.
- 22 Swisher JD, Gatenby JC, Gore JC, *et al.* Multiscale pattern analysis of orientation-selective activity in the primary visual cortex. *J Neurosci* 2010; 30:325–330.
- 23 Sapountzis P, Schluppeck D, Bowtell R, Peirce JW. A comparison of fMRI adaptation and multivariate pattern classification analysis in visual cortex. *Neuroimage* 2010; 49:1632–1640.
- 24 Kamitani Y, Tong F. Decoding seen and attended motion directions from activity in the human visual cortex. *Curr Biol* 2006; 16:1096–1102.
- 25 Brouwer GJ, Heeger DJ. Decoding and reconstructing color from responses in human visual cortex. *J Neurosci* 2009; 29:13992–14003.
- 26 Parkes LM, Marsman JB, Oxley DC, *et al.* Multivoxel fMRI analysis of color tuning in human primary visual cortex. *J Vis* 2009; 9:1–13.
- 27 Seymour K, Clifford CW, Logothetis NK, Bartels A. Coding and binding of color and form in visual cortex. *Cereb Cortex* 2010; 20:1946–1954.
- 28 Haxby JV, Gobbini MI, Furey ML, *et al.* Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science* 2001; 293:2425–2430.
- 29 Carlson TA, Schrater P, He S. Patterns of activity in the categorical representations of objects. *J Cogn Neurosci* 2003; 15:704–717.
- 30 Cox DD, Savoy RL. Functional magnetic resonance imaging (fMRI) ‘brain reading’: detecting and classifying distributed patterns of fMRI activity in human visual cortex. *Neuroimage* 2003; 19:261–270.
- 31 Eger E, Ashburner J, Haynes JD, *et al.* fMRI activity patterns in human LOC carry information about object exemplars within category. *J Cogn Neurosci* 2008; 20:356–370.
- 32 Kriegeskorte N, Formisano E, Sorger B, Goebel R. Individual faces elicit distinct response patterns in human anterior temporal cortex. *Proc Natl Acad Sci U S A* 2007; 104:20600–20605.
- 33 Natu VS, Jiang F, Narvekar A, *et al.* Dissociable neural patterns of facial identity across changes in viewpoint. *J Cogn Neurosci* 2010; 22:1570–1582.
- 34 Eger E, Michel V, Thirion B, *et al.* Deciphering cortical number coding from human brain activity patterns. *Curr Biol* 2009; 19:1608–1615.
- 35 Walther DB, Caddigan E, Fei-Fei L, Beck DM. Natural scene categories revealed in distributed patterns of activity in the human brain. *J Neurosci* 2009; 29:10573–10581.
- 36 Macevoy SP, Epstein RA. Decoding the representation of multiple simultaneous objects in human occipitotemporal cortex. *Curr Biol* 2009; 19:943–947.
- 37 Reddy L, Tsuchiya N, Serre T. Reading the mind’s eye: decoding category information during mental imagery. *Neuroimage* 2010; 50:818–825.
- This study shows, using MVPA, that feedback signals in the absence of bottom-up input can be sufficient to evoke category-specific representation in ventral-temporal cortex.
- 38 Stokes M, Thompson R, Cusack R, Duncan J. Top-down activation of shape-specific population codes in visual cortex during mental imagery. *J Neurosci* 2009; 29:1565–1572.
- 39 Sterzer P, Haynes JD, Rees G. Fine-scale activity patterns in high-level visual areas encode the category of invisible objects. *J Vis* 2008; 8:10–12.
- 40 Schurger A, Pereira F, Treisman A, Cohen JD. Reproducibility distinguishes conscious from nonconscious neural representations. *Science* 2010; 327:97–99.
- 41 Haynes JD, Rees G. Predicting the stream of consciousness from activity in human visual cortex. *Curr Biol* 2005; 15:1301–1307.
- 42 Beauchamp MS, Laconte S, Yasar N. Distributed representation of single touches in somatosensory and visual cortex. *Hum Brain Mapp* 2009; 30:3163–3171.
- 43 Formisano E, De Martino F, Bonte M, Goebel R. ‘Who’ is saying ‘what’? Brain-based decoding of human voice and speech. *Science* 2008; 322:970–973.
- 44 Meyer K, Kaplan JT, Essex R, *et al.* Predicting visual stimuli on the basis of activity in auditory cortices. *Nat Neurosci* 2010; 13:667–668.
- 45 Kay KN, Naselaris T, Prenger RJ, Gallant JL. Identifying natural images from human brain activity. *Nature* 2008; 452:352–355.
- 46 Thirion B, Duchesnay E, Hubbard E, *et al.* Inverse retinotopy: inferring the visual content of images from brain activation patterns. *Neuroimage* 2006; 33:1104–1116.
- 47 Miyawaki Y, Uchida H, Yamashita O, *et al.* Visual image reconstruction from human brain activity using a combination of multiscale local image decoders. *Neuron* 2008; 60:915–929.
- 48 Naselaris T, Prenger RJ, Kay KN, *et al.* Bayesian reconstruction of natural images from human brain activity. *Neuron* 2009; 63:902–915.
- This study combines MVPA of fMRI signals with models containing information about the structure and content of natural images to generate a reconstruction reflecting the spatial structure and semantic information of the observed image.
- 49 Nishimoto S, Vu A, Gallant J. Decoding human visual cortical activity evoked by continuous time-varying movies [abstract]. *J Vis* 2009; 9:667.
- 50 Naselaris T, Kay KN, Nishimoto S, Gallant JL. Encoding and decoding in fMRI. *Neuroimage* 2010 [Epub ahead of print].
- 51 Harrison SA, Tong F. Decoding reveals the contents of visual working memory in early visual areas. *Nature* 2009; 458:632–635.
- By showing that early visual areas can retain specific information about visual features held in working memory, this study challenges understanding of the role of early cortical sensory regions.
- 52 Serences JT, Ester EF, Vogel EK, Awh E. Stimulus-specific delay activity in human primary visual cortex. *Psychol Sci* 2009; 20:207–214.
- 53 Ester EF, Serences JT, Awh E. Spatially global representations in human primary visual cortex during working memory maintenance. *J Neurosci* 2009; 29:15258–15265.
- 54 Ethofer T, Van DV, Scherer K, Vuilleumier P. Decoding of emotional information in voice-sensitive cortices. *Curr Biol* 2009; 19:1028–1033.
- 55 Peelen MV, Atkinson AP, Vuilleumier P. Supramodal representations of perceived emotions in the human brain. *J Neurosci* 2010; 30:10127–10134.
- 56 Chadwick MJ, Hassabis D, Weiskopf N, Maguire EA. Decoding individual episodic memory traces in the human hippocampus. *Curr Biol* 2010; 20:544–547.
- This study uses MVPA to document that traces of episodic memories can be detected and distinguished in the human hippocampus.
- 57 Johnson JD, McDuff SG, Rugg MD, Norman KA. Recollection, familiarity, and cortical reinstatement: a multivoxel pattern analysis. *Neuron* 2009; 63:697–708.
- 58 McDuff SG, Frankel HC, Norman KA. Multivoxel pattern analysis reveals increased memory targeting and reduced use of retrieved details during single-agenda source monitoring. *J Neurosci* 2009; 29:508–516.

- 59 Mitchell TM, Shinkareva SV, Carlson A, *et al.* Predicting human brain activity associated with the meanings of nouns. *Science* 2008; 320: 1191–1195.
- 60 Spence SA, Farrow TF, Herford AE, *et al.* Behavioural and functional anatomical correlates of deception in humans. *Neuroreport* 2001; 12:2849–2853.
- 61 Ganis G, Kosslyn SM, Stose S, *et al.* Neural correlates of different types of deception: an fMRI investigation. *Cereb Cortex* 2003; 13:830–836.
- 62 Abe N, Suzuki M, Tsukiura T, *et al.* Dissociable roles of prefrontal and anterior cingulate cortices in deception. *Cereb Cortex* 2006; 16:192–199.
- 63 Davatzikos C, Ruparel K, Fan Y, *et al.* Classifying spatial patterns of brain activity with machine learning methods: application to lie detection. *Neuroimage* 2005; 28:663–668.
- 64 Nose I, Murai J, Taira M. Disclosing concealed information on the basis of cortical activations. *Neuroimage* 2009; 44:1380–1386.
- 65 Gamer M, Bauermann T, Stoeter P, Vossel G. Covariations among fMRI, skin conductance, and behavioral data during processing of concealed information. *Hum Brain Mapp* 2007; 28:1287–1301.
- 66 Rissman J, Greely HT, Wagner AD. Detecting individual memories through the neural decoding of memory states and past experience. *Proc Natl Acad Sci U S A* 2010; 107:9849–9854.
- This is an important study to show the limitations of MVPA in detecting objective past experience. Although MVPA could reliably determine whether a person believed they had seen an image, it was unable to reveal whether or not that image had actually been experienced.
- 67 Sip KE, Roepstorff A, McGregor W, Frith CD. Detecting deception: the scope and limits. *Trends Cogn Sci* 2008; 12:48–53.
- 68 Meegan DV. Neuroimaging techniques for memory detection: scientific, ethical, and legal issues. *Am J Bioeth* 2008; 8:9–20.
- 69 Schauer F. Neuroscience, lie-detection, and the law: contrary to the prevailing view, the suitability of brain-based lie-detection for courtroom or forensic use should be determined according to legal and not scientific standards. *Trends Cogn Sci* 2010; 14:101–103.
- 70 Gazzaniga MS. The law and neuroscience. *Neuron* 2008; 60:412–415.
- 71 Miller G. Science and the law. fMRI lie detection fails a legal test. *Science* 2010; 328:1336–1337.
- 72 Haynes JD, Sakai K, Rees G, *et al.* Reading hidden intentions in the human brain. *Curr Biol* 2007; 17:323–328.
- 73 Hampton AN, O'Doherty JP. Decoding the neural substrates of reward-related decision making with functional MRI. *Proc Natl Acad Sci U S A* 2007; 104:1377–1382.
- 74 Soon CS, Brass M, Heinze HJ, Haynes JD. Unconscious determinants of free decisions in the human brain. *Nat Neurosci* 2008; 11:543–545.
- 75 Weiskopf N, Sitaram R, Josephs O, *et al.* Real-time functional magnetic resonance imaging: methods and applications. *Magn Reson Imaging* 2007; 25:989–1003.
- 76 deCharms RC. Applications of real-time fMRI. *Nat Rev Neurosci* 2008; 9:720–729.
- 77 Laconte SM. Decoding fMRI brain states in real-time. *Neuroimage* 2010 [Epub ahead of print].
- 78 deCharms RC, Christoff K, Glover GH, *et al.* Learned regulation of spatially localized brain activation using real-time fMRI. *Neuroimage* 2004; 21:436–443.
- 79 Kloppel S, Stonnington CM, Chu C, *et al.* Automatic classification of MR scans in Alzheimer's disease. *Brain* 2008; 131:681–689.
- 80 Ecker C, Marquand A, Mourao-Miranda J, *et al.* Describing the brain in autism in five dimensions—magnetic resonance imaging-assisted diagnosis of autism spectrum disorder using a multiparameter classification approach. *J Neurosci* 2010; 30:10612–10623.
- 81 Kloppel S, Chu C, Tan GC, *et al.* Automatic detection of preclinical neurodegeneration: presymptomatic Huntington disease. *Neurology* 2009; 72:426–431.
- 82 Davatzikos C, Xu F, An Y, *et al.* Longitudinal progression of Alzheimer's-like patterns of atrophy in normal older adults: the SPARE-AD index. *Brain* 2009; 132:2026–2035.
- 83 Misra C, Fan Y, Davatzikos C. Baseline and longitudinal patterns of brain atrophy in MCI patients, and their use in prediction of short-term conversion to AD: results from ADNI. *Neuroimage* 2009; 44:1415–1422.