

# On Representation and Reproducibility

Alumit Ishai

Two papers were selected this year for their implementation of novel analytical approaches on archived data provided by the Dartmouth fMRI Data Center. Coincidentally, the two independent studies, conducted in different parts of the world, tested their models on the same data set, originally collected by Ishai, Ungerleider, Martin, Schouten, and Haxby (1999) and Ishai, Ungerleider, Martin, and Haxby (2000). Reanalyzing the same data set, however, was not the only common aspect of these two studies. Both have essentially replicated the original results, and more importantly, both have provided new and complementary tools that can be used in conjunction with the classical statistical parametric maps (SPM): a dynamic causal model (DCM) to estimate the connectivity between cortical regions (Mechelli, Price, Noppeney, & Friston, 2003), and an empirical Bayes method for estimating the reproducibility of activation within voxels (Liou, Su, Lee, & Cheng, 2003).

The representation of faces and objects in the human brain has been a topic of an ongoing debate. Functional MRI studies have identified category-selective patches, or “modules,” in the ventral occipito-temporal cortex that respond preferentially to faces (Kanwisher, McDermott, & Chun, 1997), places (Epstein & Kanwisher, 1998), and human body parts (Downing, Jiang, Shuman, & Kanwisher, 2001). However, other fMRI studies have shown that any given category, regardless of its biological significance (e.g., faces, houses, animals, tools, or even chairs, bottles, and shoes), evoked a widely distributed and overlapping pattern of activation, which included regions responding maximally to that category, as well as suboptimal responses in adjacent regions. Moreover, a variety of stimulus format (written words, photographs, line drawings) and cognitive tasks (passive viewing, naming, delayed matching, N-back, etc.) evoked virtually identical patterns of activation in the ventral stream (Haxby et al., 1999, 2001; Ishai et al., 1999, 2000; Chao, Haxby, & Martin, 1999). The functional architecture of the ventral pathway thus seems to consist of continuous, topologically arranged visual attributes, the nature of which is currently unknown.

The category-related activation in the ventral stream, however, is not the mere product of the hierarchical, bottom-up, “feature” analysis suggested by early fMRI studies (e.g., Malach et al., 1995). Selective attention

(e.g., O’Craven, Downing & Kanwisher, 1999) and mental imagery studies (Ishai, Ungerleider, & Haxby, 2000; Ishai, Haxby, & Ungerleider, 2002; O’Craven & Kanwisher, 2000) have indicated that face and object perception is also modulated by top-down effects, likely originating in the parietal and frontal cortex.

In their article “A Dynamic Causal Modelling Study on Category Effects: Bottom-Up or Top-Down Mediation?” Mechelli and colleagues investigated the extent to which category-related responses in the ventral occipito-temporal cortex are mediated by inputs from low-level visual areas and regions in the parietal cortex. To that end, they combined fMRI with a novel neural modeling technique. First, the original fMRI dataset was reanalyzed, using the classical SPM approach, to identify the visual response (i.e., regions that responded more to faces, houses, and chairs than to scrambled pictures), and the category-responsive regions (i.e., regions that responded maximally to one category relative to the other two). Then, for each individual subject, DCMs were constructed for the face-, house- and chair-responsive regions in the ventral stream, as well as two visually responsive, but not category-specific, dorsal regions, namely, V3<sup>1</sup> and the parietal cortex. DCM estimates the neuronal interactions between cortical regions within a Bayesian framework. In contrast with other models of cortical connectivity, the DCM uses designed perturbations with different inputs and assumes that the hemodynamic response is modulated by experimental parameters and not intrinsic noise (see Friston, Harrison, & Penny, 2003).

Interestingly, in all subjects, the category-related responses were mediated by input from V3, but not from the parietal cortex. For example, when subjects were viewing chairs, the intrinsic effective connectivity from V3 to the chair-responsive region in the occipital cortex was stronger than the connectivity to the face- or house-responsive regions. These findings are in support of bottom-up processing of visual attributes.

The lack of differential top-down effects from the parietal cortex is perhaps not surprising, as an imagery study has shown that the generation of mental images of faces, houses, and chairs evoked category-related responses in the extrastriate cortex, and nondifferential activation in the parietal (IPS and precuneus) and frontal regions (Ishai et al., 2000). Because the same network of parietal and frontal regions is activated in many attention, retrieval from memory, and visual imagery tasks, it is

likely that the top-down mechanism is more “general.” Additional empirical evidence is required, however, to rule out the existence of content-specific top-down effects.

These findings, together with studies of perceptual expertise (e.g., Gauthier, Skudlarski, Gore, & Anderson, 2000), indicate that functional specialization is not an inherent, hard-wired property of a cortical region. Rather, cortical specialization is modulated by the dynamics of forward and backward connections, and tuned by experience and training.

In their article “Bridging Functional MR Images and Scientific Inference: Reproducibility Maps,” Liou and colleagues have introduced the empirical Bayes method for assessing the reproducibility of activation within a given voxel, during the same experimental conditions. Given an optimal statistical threshold, a voxel was defined as “strongly reproducible” if its active or inactive status was consistent in at least 90% of the sessions. The reproducibility maps were constructed for visually responsive voxels (i.e., voxels that responded more to faces, houses, and chairs than to scrambled pictures).

Of particular interest is the comparison between the passive viewing and the delayed matching task. The density of the  $t$  values as a function of the reproducibility of voxels revealed a bimodal distribution. When the same comparison was performed on the same task/different stimulus format (i.e., delayed matching with grayscale photographs or black and white line drawings), a unimodal distribution was found. These results suggest that subjects used different strategies to perform the viewing and matching tasks. Interestingly, in the original study, Ishai and colleagues also reported task-related differences. The delayed match-to-sample, the more attention-demanding task, evoked significantly stronger activation than passive viewing of houses and chairs (but not faces). Moreover, the frequency and amplitude of eye movements made during performance of the delayed matching task were higher than those made during passive viewing (Ishai et al., 1999, 2000).<sup>2</sup>

As the ultimate goal of fMRI research is to understand behavior and correlate task performance with the underlying neural mechanism, the method suggested by Liou and colleagues has potential to reveal “hidden” differences in strategies used by subjects to perform a variety of cognitive tasks.

Taken together, both studies (see also Lloyd, 2002) have demonstrated that sharing data enables testing new predictions, as the voluminous, rich fMRI datasets deposited at the Dartmouth Center contain more information than any single study can ever report.

Reprint requests should be sent to Alumit Ishai, Laboratory of Brain and Cognition, National Institute of Mental Health, Building 10, Room 4C104, NIH, Bethesda, MD 20892, USA, or via e-mail: [alumit@n.nimh.nih.gov](mailto:alumit@n.nimh.nih.gov).

## Notes

1. The original study did not include retinotopic mapping. V3 was localized based on Tailarach coordinates.
2. No differential patterns of eye movements were found in response to the three object categories.

## REFERENCES

- Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in posterior temporal cortex for perceiving and knowing about objects. *Nature Neuroscience*, *2*, 913–919.
- Downing, P. E., Jiang, Y. H., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, *293*, 2470–2473.
- Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature*, *392*, 598–601.
- Friston, K. J., Harrison, L., & Penny, W. (2003). Dynamic causal modeling. *Neuroimage* (in press).
- Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience*, *3*, 191–197.
- Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*, *293*, 2425–2430.
- Haxby, J. V., Ungerleider, L. G., Clark, V. P., Schouten, J. L., Hoffman, E. A., & Martin, A. (1999). The effect of face inversion on activity in human neural systems for face and object perception. *Neuron*, *22*, 189–199.
- Ishai, A., Haxby, J. V., & Ungerleider, L. G. (2002). Visual imagery of famous faces: Effects of memory and attention revealed by fMRI. *Neuroimage*, *17*, 1729–1741.
- Ishai, A., Ungerleider, L. G., & Haxby, J. V. (2000). Distributed neural systems for the generation of visual images. *Neuron*, *28*, 979–990.
- Ishai, A., Ungerleider, L. G., Martin, A., & Haxby, J. V. (2000). The representation of objects in the human occipital and temporal cortex. *Journal of Cognitive Neuroscience*, *12*, 35–51.
- Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences, U.S.A.*, *96*, 9379–9384.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311.
- Liou, M., Su, H.-R., Lee, J.-D., & Cheng, P. E. (2003). Bridging functional MR images and scientific inference: reproducibility maps. *Journal of Cognitive Neuroscience*, *15*, 935–945.
- Lloyd, D. (2002). Functional MRI and the study of human consciousness. *Journal of Cognitive Neuroscience*, *14*, 818–831.
- Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Kennedy, W. A., Ledden, P. J., Brady, T. J., Rosen, B. R., & Tootell, R. B. H. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *92*, 8135–8139.
- Mechelli, A., Price, C. J., Noppeney, U., & Friston, K. J. (2003). A dynamic causal modelling study on category effects: Bottom-up or top-down mediation? *Journal of Cognitive Neuroscience*, *15*, 925–934.
- O’Craven, K. M., Downing, P. E., & Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature*, *401*, 584–587.
- O’Craven, K. M., & Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *Journal of Cognitive Neuroscience*, *12*, 1013–1023.