Dispatches

Visual Cortex: How Are Faces and Objects Represented?

The way in which information about complex objects and faces is represented in visual cortex is controversial. One model posits that information is processed in modules, highly specialized for different categories of objects; an opposing model appeals to a distributed representation across a large network of visual areas. A recent paper uses a novel imaging technique to address this controversy.

Timothy J. Andrews

Visual areas of the brain involved in object recognition form a processing stream that projects toward the temporal lobe [1]. Lesions to this region of the brain often result in difficulties in recognizing, identifying and naming different categories of objects. For example, damage to the inferior temporal lobe often impairs the ability to identify individuals by their facial characteristics [2]. Nonetheless, these lesions often leave the ability to recognize other objects largely preserved. In contrast, lesions to other areas of the temporal lobe leave face recognition intact, but impair an individual's ability to identify other objects [3].

The notion that discrete areas of the temporal lobe are specialized for different categories of objects receives mixed support from studies using different physiological methods. For example, functional imaging studies show that some regions in the temporal lobe are more responsive to faces than to other complex objects [4]. Other imaging studies have found similar category-specific visual responses for inanimate objects [5], buildings [6] and human body parts [7]. In contrast, single cell recordings in the temporal lobe of non-human primates are more consistent with a distributed representation underlying object perception [8]. For example, although these neurons have response properties that are important for object recognition, such as selectivity for form, texture, color and even faces, there does not appear to be any consistent larger scale organization for particular categories of objects.

So, why have studies using these different methods come to such different conclusions about the way that information is represented in the temporal lobe? One possibility is that there is a fundamental difference in the organization of visual cortex in humans and monkeys. Imaging studies suggest that this is not the case, demonstrating that monkeys have discrete face- and object-selective regions that are similar in size and distribution to those found in the human temporal lobe [9]. Another

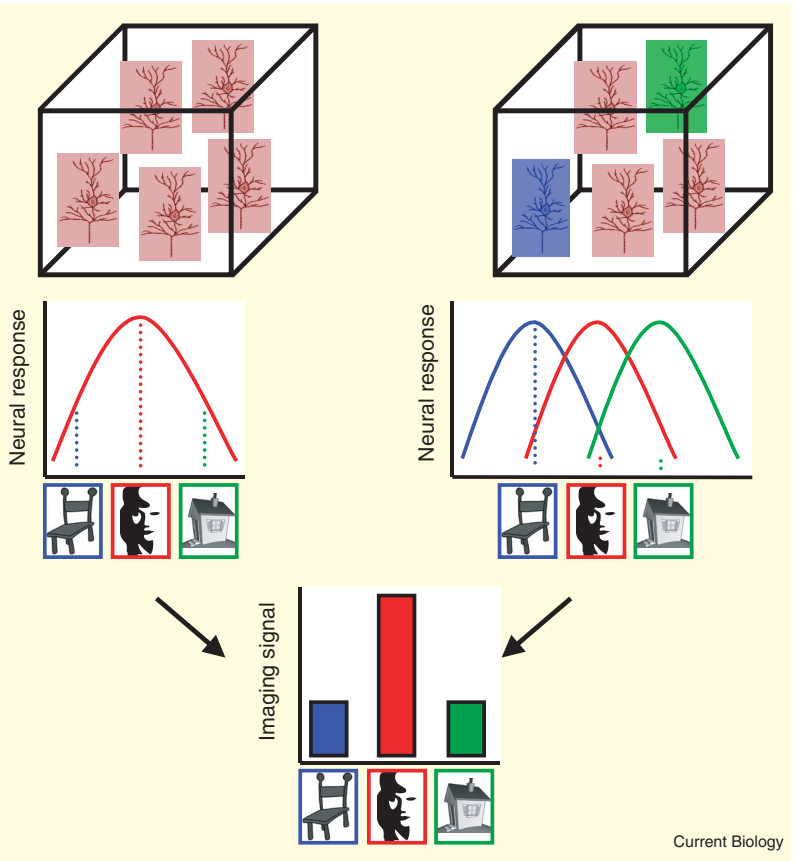

Figure 1. Two possible neuronal ensembles in a 'face-selective' region of visual cortex.

Because of the spatial limitations of functional imaging, the measured signal is determined by the summed activity of many thousands of neurons. Regions defined as 'face-selective' could either contain a homogeneous population of face-selective neurons (left) or a heterogeneous population of neurons with the majority being selective for face images (right). Responses to non-face objects (chairs or houses, for example) could therefore arise from a sub-optimal activation of face-selective neurons or from the activation of a sub-population of neurons that are selective for these non-face objects. Both scenarios would lead to a similar functional imaging signal. (Adapted from [11].)

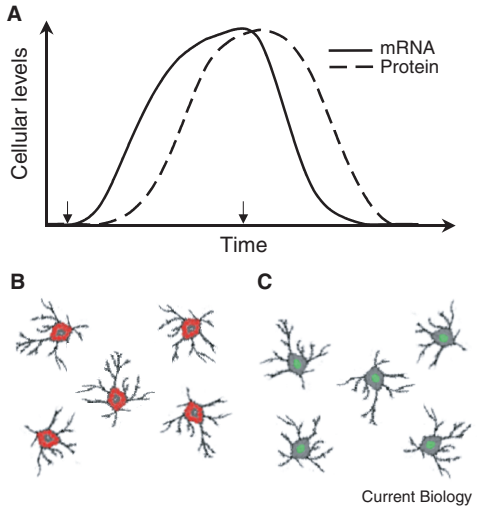

Figure 2. The differential induction and decay of the mRNA and protein of immediate early genes following neuronal activity.

(A) When neurons become active, immediate early genes such as *c-fos* or *zif268* are upregulated, resulting in an increased accumulation of mRNA in the cytoplasm, followed by increased levels of the encoded protein in the nucleus. When the neurons return to a resting state, levels of immediate early gene mRNA protein show a differential decline toward basal levels. Arrows indicate the beginning and end of neural activity. Using a double labeling approach, levels of mRNA (B) and protein (C) can be detected with *in situ* hybridisation and immunohistochemistry, respectively. By exploiting the differential appearance and disappearance of immediate early gene RNA and protein levels, it is possible to determine activity maps for two different behavioral conditions [12].

possibility could lie in the type of information the different techniques provide. The spatial limitations of functional imaging means that it monitors the average activity across hundreds of thousands of neurons. So if a specific region shows a selective response to a particular category of object, such as a face, this does not mean that all the neurons in this region are face-selective – only that the majority of neurons show this preference (Figure 1). Indeed, functional imaging studies have shown that the response to any category of object is not restricted to the area that responds maximally to that particular category; many brain regions show significant responses to a number of different stimuli [10]. Thus, an unresolved question remains: what is the functional significance of responses to 'non-preferred' stimuli? Do they result from the activation of a subset of highly selective neurons? Or do they just reflect a non-specific activation of a homogeneous population of neurons that are selectively tuned for a specific category of visual information [11]?

To answer this question, a study published recently in *Current Biology* [12] has used a novel imaging technique that is able to visualize individual neurons and determine their selectivity for different sensory experiences. The technique exploits the differential time course of the appearance and disappearance of the mRNA and protein from an immediate-early gene (*zif268*) following neuronal activity.

Zangenehpour *et al.* [12] have developed a double-labeling technique that allows them to distinguish between neurons that are activated by two different sensory events (Figure 2), and have now used this technique to ask how information about objects and faces is represented in the temporal lobe. In the first experiment, monkeys viewed images of complex inanimate objects followed by images of faces. The presentation times were chosen so that the presence of *zif268* mRNA in neurons would reflect face-selective activity, while expression of Zif268 protein would indicate object-selective activity. Using this approach, the authors were able to determine if individual neurons are face-selective, object-selective or were active during both stimulus blocks. In the next experiment, images of faces were shown followed by images of objects. In this case, levels of *zif268* mRNA and protein should correspond to object- and face-selective neurons, respectively.

The results clearly demonstrate that homogenous patches of face-selective neurons are evident in the temporal lobe. Moreover, these are of a similar size and distribution to those observed by functional brain imaging. Although some neurons responded to both objects and faces, there appeared to be a clear segregation between face-selective and (non-face) object-selective regions. Zangenehpour *et al.* [12] also report that face-selective clusters are larger and more prevalent in the right-hemisphere — a result consistent with functional imaging and brain lesion studies in humans [2,4]. These findings would suggest that single neuron studies may not be optimal for understanding the larger scale organization of neurons in this region of the visual system.

The demonstration of homogeneous regions of face-selective neurons in the temporal lobe is consistent with a number of functional imaging studies that suggest face-selective regions are specialized for processing face images [13–16]. For example, the activity in face-selective regions of visual cortex does not appear to provide useful information for discriminating between non-face objects [13]. A similar specialization for face processing is apparent in adaptation studies, where a reduction in signal following repeated presentations of identical face images is only apparent in face-selective regions of visual cortex [16].

Although these findings suggest that face perception is carried out by modules specialized for processing faces, it is not clear whether this process is selective for face images (domain-specific) or whether it can also operate on non-face stimuli that require expert discrimination (domain-general). For example, responses in face-selective regions to images of unfamiliar objects have been shown to increase when subjects learnt to recognize these objects; similarly, responses to images of

birds and cars are greater in face-selective regions of bird and car experts, respectively, than in non-experts [17].

Behavioral evidence also supports a domain-general model of processing. For example, dog experts show a comparable inversion effect — the impaired recognition of upside-down images — for inverted dogs and inverted faces; control subjects only show an inversion effect for faces [18]. But more recent behavioral and neuroimaging studies [19,20] have challenged these studies and provide compelling evidence for a domain-specific view of face processing. In conclusion, it would appear that information about faces is represented in specialized regions of visual cortex, but it is not yet clear how other categories of objects are represented.

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Department of Psychology, University of York, York YO10 5DD, UK.
E-mail: t.andrews@psych.york.ac.uk

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Candida albicans Biofilms: More Than Filamentation

Candida albicans **is the fungal species most commonly associated with biofilm formation in immunosuppressed patients. Recent work offers a fresh new look at the role of filamentation in *C. albicans* biofilm formation, and describes the application of a powerful tool for the molecular dissection of these important developmental processes.**

José L. López-Ribot

The majority of microbes in their natural habitats are found in biofilm ecosystems attached to surfaces and not as free-living (planktonic) organisms [1]. Formation of biofilms is involved in a significant proportion of human infections [2], including those caused by *Candida albicans*. *Candida* species are frequently found in the normal microbiota of humans and do not normally cause disease in immunocompetent hosts. However, immunodepressed patients are susceptible to candidiasis, which is now the fourth most common nosocomial infection worldwide with high morbidity and mortality rates [3,4]. Formation of *Candida* biofilms carries important clinical repercussions because of the increased antifungal drug resistance of these biofilms, their ability to resist host immune defenses and their potential for causing failure of implanted devices [5,6].

Ultrastructural Characteristics of *C. albicans* Biofilms

C. albicans biofilm structure has been studied mainly *in vitro* using a variety of model systems, in work pioneered by the Douglas group [7]. Results indicate that *C. albicans* biofilm formation occurs through different developmental phases that include initial attachment and colonization, followed by cell division, proliferation, and biofilm maturation [8,9]. Mature *C. albicans* biofilms show a complex three-dimensional architecture and display extensive spatial heterogeneity, consisting of a dense network of yeasts, hyphae and pseudohyphae encased within a matrix of exopolymeric material (Figure 1). This structural complexity represents the optimal spatial arrangement to facilitate the influx of nutrients, disposal of