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### Object representations in the human brain: a functional MRI survey

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# **Object Representations in the Human Brain:**

# **A Functional MRI Survey**

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This thesis is submitted in part fulfillment of the degree of Doctor of Philosophy, completed at the Centre for Cognitive Neuroscience, School of Psychology, University of Wales, Bangor.



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#### Abstract

In this fMRI survey, a series of investigations examined the prevalence and specificity of category-selective regions in the human visual cortex. Participants were scanned while viewing scenes and 19 different object categories. There were significant category preferences in the fusiform face area (FFA), parahippocampal place area (PPA), and extrastriate body area (EBA). Apart from these regions, other category-selective regions were not observed in the visual cortex. However, a facebias activation was found in the right prefrontal cortex. This activation is consistent with the findings that face-selective cells were identified in monkeys' prefrontal cortex. Several categories produced significant activation overlapping the FFA, PPA, or EBA. However, in each of these regions, faces, scenes, or bodies remained the most-effective categories, even when tested at the individual-subject level. Further, there was a crude division of activation between animate and inanimate objects, along the lateral and medial ventral cortex. This survey represents the broadest survey to date of category selectivity in the visual cortex. The results demonstrate both the strong selectivity of a small number of regions, and the scarcity of such regions. The face-bias activation in the right prefrontal cortex was further investigated; this region was later labelled as the right inferior prefrontal junction (rIFJ). Initial results showed the response patterns of the rIFJ mirrored that of the right FFA in the non-working memory task, 1-back working memory task, and in whole/part processing of objects. Later investigation showed the rIFJ, but not the rFFA, was sensitive to the presence of pairs of eyes. It is speculated here that the rIFJ extracts object-based and behaviourally relevant information. The results suggest overlapping but distinct roles in face representation between the rIFJ and rFFA, which may reflect top-down control from the prefrontal region to the ventral cortex.

# **Chapter 1**

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# Introduction

# **Object Representations in the Human Ventral**

Stream

We humans are capable of identifying objects at lightning speed. Extracting relevant object information from a complex scene involves the processing of both spatial location and identity of objects. Therefore, efficient processing of object information requires a sophisticated neural organization to represent various types of object properties. A general organizational principle in the visual cortex has been proposed by Mishkin, Ungerleider and Macko (1983) based on their research on macaque monkeys. The dorsal stream, also known as the "where" pathway, projects from area V1 to the posterior parietal cortex, it is involved in the processing of spatial location of objects. The ventral stream, also known as the "what" pathway, projects from V1 to the inferotemporal cortex, and plays a crucial role in the identification and recognition of objects. It is widely accepted that there is a similar division of dorsal and ventral streams in the human visual cortex (Culham & Kanwisher, 2001; Culham, Danckert, DeSouza, Gati, Menon, & Goodale, 2003; Tootell, Tsao and Vanduffel, 2003).

To date, in the ventral stream, researchers have identified several regions or modules that are dedicated to processing an object category: the fusiform face area (FFA; Kanwisher, McDermott, & Chun, 1997a; Haxby, Horwitz, Ungerleider, Maisog, Pietrini, 1994), the parahippocampal place area (PPA; Epstein & Kanwisher, 1998; Epstein, Harris, Stanley, & Kanwisher, 1999), and the extrastriate body area (EBA; Downing, Jiang, Shuman, & Kanwisher, 2001b). To what extent is our visual system organized in such a modular manner? Alternatively, what other possible principle(s) can govern the organization of

visual representation? To increase our understanding of the functional organization of the visual cortex is the central theme of this thesis.

Currently, there are four major accounts for visual object representation in the human ventral stream. **1)** Modular account-domain specific (Kanwisher et al., 1997a; Kanwisher, Stanley, & Harris, 1999), **2)** Processing account-domain general (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Gauthier, Skudlarski, Gore, & Anderson, 2000), **3)** Distributed account (Haxby, Gobbini, Furey, Ishai, Schouten, & Pietrini, 2001), and **4)** Eccentricity account (Hasson, Levy, Behrmann, Hendler, & Malach, 2002; Hasson, Harel, Levy, & Malach, 2003; Levy, Hasson, Avidan, Hendler, & Malach, 2001; Malach, Levy, & Hasson, 2002). Each account will be reviewed in this chapter, along with neuropsychological evidence, fMRI studies of healthy human subjects and neurological patients, and recent relevant work in object recognition in monkeys.

### 1) Modular account

In computer science, a module is a component of a program that performs a specific function. A module can function by itself or can function along with other modules of the same program. In human cognition, according to Fodor (1983), higher-level psychological processes are also self-contained (modular), and each module is domain specific. Specifically, a module is specialized for and unique to a certain function. The assumption of modularity is also closely associated with the view that information is being encapsulated (Fodor, 1983). According to this view, it is assumed that each module carries its specialized information and has no information about other modules. Thus, a modular assumption indicates that the damage of one module will not affect the normal

### Chapter 1-Introduction

functioning of another one (Bischof, 1997), and therefore will only lead to selective impairment of a particular cognitive function.

In human cognition, the terms locality and modularity are often interchangeable. This is based on Tsotsos' (1990) assumption that, in order for efficient processing of information, and to perform similar functions effectively, neurons with similar properties should be located adjacent to each other. This in turn suggests that if the organizational structure of a function is modular, the organization should also be local (Bischof, 1997). It should be noted that the above assumptions of cognitive structure are open to interpretations. Indeed, many cognitive neuropsychologists agree that informational encapsulation and/or the locality of the effects of brain lesions are assumptions only, the actual effects of brain lesions could vary along a continuum, reflecting a strong version of the assumption at one end and a weak version of the assumption at the other end (Bischof, 1997; Farah, 1994).

In the neuroimaging literature on visual object processing, some researchers proposed that the visual system could be organized into modules. Throughout this thesis, a module is defined as a dedicated group of neurons within a restricted part of the cortex in the ventral stream, which represents a particular class of object with a strong selective <sup>1</sup> response. In this sense, in the ventral stream, a category-specific region is a module. It is hypothesized that the

<sup>&</sup>lt;sup>1</sup> Selective: In their single-unit study Tovee, Rolls, Treves, and Bellis (1993) defined selective responses for a stimulus when the responses of a neuron were at least twice as strong as to the preferred (most-effective) stimuli category relative to those to the non-preferred (less effective) stimuli category. Here, this term has been generalised to a situation where the activation for the most effective/most preferred category is significantly stronger than the less effective/non-preferred categories (Downing et al., 2006; Kanwisher, 2006).

ventral stream contains several modules for the visual processing of a few classes of object categories (Kanwisher et al., 1997a; Kanwisher, 2000). Even before the discovery of those category-specific regions (FFA, PPA, and EBA), earlier fMRI studies had already shown that the Lateral Occipital Complex (LOC; Malach, Reppas, Benson, Kwong, Jiang, Kennedy, et al., 1995; Grill-Spector, Kourtzi, & Kanwisher, 2001; Kourtzi & Kanwisher, 2001), a region that extends from the occipital lobe to anterior regions of the temporal cortex, is involve in object shape analysis relative to lower level visual features (scrambled images of objects). However, because the LOC is not responsive to any particular object category, this thesis will mainly focus on the category-specific object areas— FFA, PPA, and EBA.

In fMRI, the response in a category-specific region for the preferred category (most effective category) must be significantly stronger than those for the non-preferred categories (less effective categories). It is also hypothesized that the category-specific region should at least be responsible for the perception, detection, or identification of members of the most effective category (Grill-Spector, Knouf, & Kanwisher, 2004; Cohen & Tong 2001). Hence, lesions to a category-specific region should elicit a selective deficit in processing members of the most effective category. Evidence supporting this modular account initially comes from neuropsychological studies of brain-damaged patients, where a lesion to an anatomical region has led to a certain cognitive deficit. Specifically, it has been reported that some patients with brain lesions lose the ability to recognize one class of object category but not the others.

### Deficit in face recognition

Supporting evidence for the modular account comes from patients who have lost their ability to recognize a particular class or category of objects. For example the selective deficit in face recognition in prosopagnosic patients (Bodamer, 1947; Toghi Watanabe, Takahashi, Yonezawa, Hatano, & Sasaki, 1994) has motivated interest in understanding the mechanisms underlying face processing. De Renzi (1986) reported patients with a selective impairment in face recognition, but these patients had an intact ability to recognize many other objects, such as wallets, neckties, and photographs of cats. In many cases, these prosopagnosic patients had lesions in the occipital temporal lobe overlapped with the fusiform gyrus (De Renzi, Perani, Carlesimon, Silveri & Fazio, 1994; Farah, Rabinowitz, Quinn, & Liu, 2000). This dissociation in abilities to recognize faces and objects has been demonstrated by other studies on patients.

For example, Sergent & Signonet (1992) reported a prosopagnosic patient who demonstrated normal ability to discriminate between different models of the same make of car, but who was unable to discriminate between faces. A study on patient CK (Moscovitch, Winocur, & Behrmann, 1997), who had a profound deficit in recognising common objects (object agnoisa) demonstrated a normal ability to recognize faces. This double dissociation in performance for face and object identification suggests that there may be independent neural mechanisms for processing faces and objects. Due to the above evidence, some researchers believe that faces constitute a special class or category, and that faces may be processed by a highly specialised face module.

On the other hand some researchers have argued (Damasio, Rizzo, Varney, & Gersh, 1982; Damasio, 1989; Damasio, Tranel, & Damasio, 1990) that a deficit in recognizing faces relative to other object categories, could be due to the fact that face recognition is difficult, and therefore the disorder is not face specific and should be generalised to other object categories. On the contrary, Farah, Levinson, & Klein, (1995) provided neuropsychological evidence to show that the deficits in at least some prosopagnosic patients were unrelated to task difficulties, and hence their deficits were face specific. One of their patients LH suffered from lesions to the anterior temporal lobe, temporal occipital regions, and right inferior frontal lobe. LH showed the expected recognition deficit in faces compared to objects. However, when comparing his performance with control subjects between faces and eyeglasses, in which successful recognition of both categories required within-category discrimination, he showed normal recognition to eveglasses but impaired performance to faces. Thus, the above suggests that even when task demand was controlled, the deficit in recognizing faces remained. This in turn suggested that LH's deficit in face recognition was not due to his inability to carry out within-category discrimination.

Interestingly, the experimenters noticed that LH, similar to many prosopagnosic patients, had some difficulties in recognizing living categories. However, patients' deficits were not strictly confined to the living categories, and sometimes patients showed deficits in recognizing non-living objects, for example clothes or musical instruments. Other studies on LH showed that apart from animals or plants, he could identify members of other visually similar object categories. Further analysis conducted by Farah, McMullen, & Meyer,

(1991) examined the ability to LH in recognize many living categories and nonliving categories in line drawing. They then performed a regression analysis of the factors accounting for patients' mistakes. Farah et al., (1991) found that living and non-living division could explain a major portion of the variance in patients' error, however, the requirement for within-category naming instead of more general category level naming could not. Thus, LH's deficits in face recognition seemed to overlap with the deficits in recognizing living categories.

However, caution is required when interpreting evidence from patients with brain lesions as evidence for the loss of a particular cognitive function. It is therefore useful to consider the following.

First, lesion sites are usually extensive; they can be distributed all over the cortex even within a well-defined patient group where patients display the same deficit. Seemingly similar deficits could be a result of several lesion sites. Second, due to the fact that multiple lesion site(s) could be found at once, pure cases for a cognitive deficit are rare. Indeed, Tohgi et al., (1994) claimed that there seemed to be a fair amount of variation in the level of cognitive deficits and/or the anatomical location of lesions among patients. Hence, because lesions do not reliably produce a certain deficit, therefore when comparing task performances across patients with dissociable deficits, the dissociations are rarely clear-cut. On the other hand, studying a group of patients with the same isolated lesion and identical cognitive deficit could be useful for researchers to define a cognitive function of a given brain region; however, such cases are rare. Due to the reasons above, a non-invasive neuroimaging technique such as fMRI is a

particularly useful tool for exploring the function of a brain region. In the following section, research in object recognition in patients with brain lesion and in fMRI studies in humans will be reviewed in parallel.

### fMRI evidence for a face specific region

Neuroimaging studies using fMRI on healthy subjects have provided supporting evidence for the view that face processing relies on a modular representation of faces. Kanwisher et al., (1997a) identified a region in the mid fusiform gyrus that is selective to faces. They later named the region the fusiform face area (FFA). Further experiments conducted by Kanwisher and colleagues (1997a, 1999) showed that the FFA responded selectively to faces relative to houses, animals, common objects and human hands. In addition, FFA's activation for face stimuli (including human faces, faces from different angles, cartoon faces, and animal faces) was significantly stronger than the activation for non-face stimuli, such as houses, tools, and other common objects (Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000).

Others have reported that activation in the FFA was tightly correlated with conscious awareness of faces. This indicates that activation in the FFA is necessary for the conscious perception for faces, but not for other categories. Tong, Nakayama, Vaughan, and Kanwisher, (1998) conducted a binocular rivalry experiment in the fMRI scanner, in which subjects viewed a face stimulus overlapping with a house stimulus; however, by wearing a pair of red and green filter glasses, subject could only see a face through one eye and a house through the other eye. This procedure led to binocular rivalry, as subjects reported a

switching between a face-dominant percept and house-dominant percept. An increase in FFA activation was found when subjects reported a face-dominant percept and, at the same time, a weak activation was found in the PPA during a face-dominant percept. A reverse pattern was found during a house-dominant percept. In addition, using Rubin's vase-face as stimulus (Andrews, Schluppeck, Homfray, Matthews, & Blakemore, 2002), an increase in FFA activation was found when subjects perceived a face, relative to a vase. Again this indicates that responses in the FFA are driven by the perception of faces. Similarly, an increased activation was also found in the FFA when subjects viewed ambiguous black and white mooney faces relative to images of black and white patches (Andrews & Schluppeck, 2004). As mentioned, it is assumed that a module, as a dedicated region for the processing of a specific category, should also be involved in the correct perception and identification of that specific object category. Grill-Spector et al., (2004) directly tested this assumption and demonstrated that the activation in the FFA was correlated strongly with the successful detection or identification of faces rather than other non-face categories e.g. guitar, cars, house, flowers, and textures (except for birds, see the debate for detailed discussion on Grill-Spector et al's (2004) findings p. 41). Importantly, activation in the FFA was not correlated with the correct detection or identification of non-face categories. The above evidence supports the view that the mid fusiform region (the FFA) is a module for face processing, and it plays an active role in detecting and identifying face stimuli instead of other nonface stimuli.

### Deficit in landmark and scene recognition

Neuropsychological evidence also suggests that there is a categoryspecific brain region for the representation of topographic information, namely deficits in recognizing landmarks and scenes. Evidence comes from patients who suffered from a deficit of topographic disorientation, after lesions to the occipital lobe. In particular, a group of these patients showed deficits in recognizing places and landmarks (landmark agnoisa). Some of the patients from the above group had suffered from damage to the medial occipital cortex (Aguirre & D'Esposito 1997; Aguirre & D'Esposito, 1999; Hecaen, 1979; Landis, Cummings, Benson, & Palmer, 1986; Levin, Warach, Farah, 1985; Whiteley & Warrington, 1978). These lesions often overlapped with the parahippocampal cortex (Epstein, DeYoe, Press, Rosen, & Kanwisher, 2001; Habib and Sirigu, 1987).

There has been a study on landmark agnosic patients with lesions confined to the parahippocampal region after surgical resections (Marguire, Burke, Phillips, & Staunton, 1996). This study showed that these patients had an intact ability to represent spatial information of the local environment, such as route learning; however, they were unable to recognize landmarks or specific buildings. Many of those landmark agnosic patients demonstrated an intact ability for object recognition, but they failed to recognize scenes and landmarks. To compensate their deficits, they relied on non-landmark details for orientation, such as the mailbox in front of their house or house number. However, they were able to draw maps and describe routes, which suggested that they had intact lower level vision (Landis et al., 1986; McCarthy, Evans, & Hodges, 1996; Whiteley & Warrington, 1978).

In addition, Bohbot, Kalina, Stepankova, Spackova, Petrides, and Nadel (1998) tested patients with a dry version of the Morris water maze task, which was designed to measure spatial memory and learning. In this task, patients entered a room through one door, and were asked to find a hidden sensor beneath the carpet of a furnished room. 30 seconds later the patients had to re-enter the room through another door to find the sensor in the same location again. Another trial was performed 30 mins later, and the patients had to find the same sensor hidden in the same location. Successful completion of this task required memory for orientation and landmarks. Bohbot et al., (1998) reported that patients with lesions confined to the parahippocampal cortex were impaired in the 30 mins delay trial only. Those patients with lesions of the right or left hippocampus and epileptic controls were unimpaired in the same task regardless of trial types. This report has shown a dissociating functional role between the parahippocampal and hippocampus in representing topographic information. The above finding indicated that the parahippocampal region could be involved in representing spatial relationships between landmarks over time.

### fMRI evidence for a place-selective region

fMRI studies have provided strong evidence supporting the role of the parahippocampal cortex in representing landmarks and scenes. Epstein et al., (1998) reported selective responses from the parahippocampal cortex to scenes relative to faces, houses, objects and scrambled versions of the above categories. In addition, this region also responded strongly to landmarks, landscapes, outdoor scenes, furnished rooms, and previously furnished rooms without the

furniture (empty rooms). Interestingly, this region responded weakly to faces, objects, and pictures of objects that were cut out from the furnished room. The experimenters also found that this region was sensitive to the coherent representation of space, where high responses were found to photos of a "fractured room" (images of an empty room but the walls and floor were torn apart and revealed gaps of space) and an intact room (image of a room). However, a lower response was found to images of a "fractured room" with the parts re-arranged randomly (coherency was disrupted). With the above evidence, Epstein et al., (1998) concluded that the parahippocampal area was specialized in processing scenes, landmarks, and spatial layout, and therefore labelled this region as the parahippocampal place area (PPA).

Aguirre, Zarahn, & D'Esposito, (1998a, 1998b) also reported similar findings; they reported that the parahippocampal cortex was sensitive to buildings compared to inanimate objects such as cars, faces, general objects, and texture. In addition, faces and buildings elicited activation in two separate regions, the posterior fusiform region and the parahippocampal region respectively. This neuroimaging double dissociation supported the view that independent mechanisms or modules exist for faces and scenes (Kanwisher, 2000; Cohen & Tong, 2001).

Furthermore, a series of investigations conducted by Epstein and colleagues had explored the role of the PPA in the long-term and short-term representation of scenes and in navigation. First, Epstein et al., (1999) investigated the effect of familiarity to scene representation in the PPA. They

presented subjects with familiar and non-familiar scenes, and found that the PPA responded robustly regardless of familiarity. From these results, Epstein et al., (1999) concluded that PPA was not involved in matching perceptual information that was stored in the memory. Second, in order to explore if navigation would elicit a strong response in the PPA, they compared the response to scenes that were presented as a "movie" of scenes depicting forward motion similar to exploring and navigating in an environment, with the response to a series of snapshots of places. They found that the response for the latter condition was greater, but strong activation was observed in both conditions. From the above results, it is thought that the primary role of PPA is to represent environment and spatial layout, and that the PPA does not play a direct role in navigation.

Further experiment has also investigated whether representation of scenes in the PPA was viewpoint specific or viewpoint invariant. In one investigation, Epstein et al., (2003) presented subjects with five conditions of scenes: a viewpoint change of the same place condition, a place change condition, central object change condition, and peripheral object change condition, and a no change condition as baseline. Relative to the no change condition, the PPA responded strongest to both place change and viewpoint change of the same place, and significantly lower to central object change of the same place, and peripheral object change of the same place. Their results demonstrated that the PPA was viewpoint specific because it treated different views of the same place like two distinct scenes. In addition, the lower responses to the central and peripheral object change conditions suggest that the PPA is concerned with changes in the

spatial relationship between the observers and scenes rather than changes of objects in a scene.

A more recent study explored the above further by investigating if the effect of viewpoint in the PPA was associated with experience with the scenes. Epstein, Higgins, and Thompson-Schill (2005) used an fMRI adaptation paradigm to demonstrate that scene representations were initially viewpoint specific but become more viewpoint invariant over time. fMRI adaptation is defined as a reduction in responses to repeated information compared to novel information. A reduction in activation in a given region indicates that the given region is processing the repeated information (Grill-Spector and Malach, 2001; Henson, Shallice, & Dolan, 2000).

Epstein et al., (2005) presented subjects with three conditions of scenes (scans 1-3, see figure 1 below for Epstein et al's experimental design): no change condition (identical scenes), viewpoint change of the same place condition, and place change condition. In scan 4, subjects were presented with old views of previous scenes (those scenes had been presented in scan 1-3 already), new views of the previous scenes, and new places. Activation in the PPA was compared within trial and across scan session in order to access the short-term and long-term adaptation effect. Their results showed that there was more viewpoint specific effect in the PPA than the viewpoint invariant effect in the within trial comparison. At the same time, there was a developing and increasing viewpoint invariant effect which began from scan 1 to 3. Therefore, when comparing scans 1-3 with 4 to assess for long-term repetition effect, the

viewpoint specific effect was not significantly different to the viewpoint invariant effect. This suggested that when subjects gained more experience with a scene, scene representation became more viewpoint invariant. The above results also led Epstein et al., (2005) to claim that both viewpoint specific and viewpoint invariant effect could occur in the PPA at the same time. Epstein et al., (2005) thus concluded that scene representation is neither completely viewpoint specific nor viewpoint invariant.



Figure 1: Experiment design in Epstein et al's experiment, this image was reproduced from Epstein et al., (2005).

To further investigate if experience with scenes is associated with activation in the PPA, in the same study Esptein et al., (2005) correlated the adaptation effect with the scores on the Santa Barbara Sense of Direction Scales (SBSOD; Hergarty, Richson, Montello, Lovelace, & Ilavanil, 2002). The SBSOD is a self-reported test to assess the ability to acquire and update spatial knowledge through direct experience in an environment. That is the knowledge of a place gained from self-motion and exploration of the environment rather than the knowledge gained from drawing maps or estimating distances between locations. Esptein et al., (2005) found stronger adaptation effects for good navigators who gained high scores in SBSOD, relative to bad navigators who gained low scores in SBSOD. Specifically, it was believed that good navigators might have used more efficient encoding tactics for familiar views and places, which led to a reduction in PPA's responses to old views (when compared to new views) and to new views of old places (when compared to new places).

The above findings demonstrated that the PPA responded strongly to different types of scenes relative to other objects, view representation in the PPA interacted with experience of scenes, and PPA's responses were correlated strongly with navigation performance. The above evidence seems to be consistent with the idea that the PPA is a module for representing topographical information. The strong correlation between activation and ability in scene encoding in the PPA suggested that the region is necessary for the processing of topographical information.

#### Deficits in human body recognition

Previous studies have reported a deficit related to body representation known as autotopagnosia. These autotopagnosic patients were unable to localize their own or others' body parts whether the instructions were presented verbally

or it was a demonstration on a model by another person (Pick, 1922). Buxbaum and Coslett (2001) reported an autotopagnosic patient (GL) who had lesions involving the inferior frontal, lateral occipital, and temporal lobe of the left hemisphere. Due to these lesions, GL could not point to his own or others' body parts when he was instructed verbally, and he was also unable to match real or pictures of human body parts with changes in visual angles. His deficits seemed to be specific to the human body as he could perform well in similar tasks with animal and manmade objects. He was able to reach and grasp objects correctly with his body parts, correctly matched items of clothing to body parts, and could locate parts of animals and man-made objects correctly; hence indicating that GL's deficits were not related to difficulties in accessing semantic knowledge of the body. Interestingly, Felician, Ceccaldi, Didic, Thinus-Blanc, and Poncet (2003) reported a double dissociation between two patients, both with lesions in the parietal lobes. JR displayed a deficit in pointing to his own body but an intact ability to point to others, whilst AP had a deficit in pointing to the body parts of others but not her own. Both patients had intact performances in naming body parts, pointing to pictures of animal parts, object parts and body parts relative to control subjects.

Some studies in patients have proposed several possible neural mechanisms for body representations (Schwoebel & Coslett, 2005), for example lesions in the left temporal lobe were associated with impaired performance on tasks in which patients had to assess knowledge of the shape or semantic information about the body, and names of body parts. In addition, lesions in the dorsolateral frontal and parietal regions were often associated with deficits in

tasks related to body schema e.g. patients had to imagine hand movement and performed finger pointing (Sirigu, Duhamel, Cohen, Pillon, Dubois, & Agid, 1996; Schwoebel & Coslett, 2005). However, there is a lack of evidence for lesions in the visual cortex associated with a deficit in recognizing human bodies.

The above studies are consistent with Sirigu, Grafman, Bressler, and Sunderland's (2001) claim, in which they suggested that there are three types of body representations, each represents a specific aspect of body knowledge: 1) semantic information about the human body parts, for example the ability to match clothing and accessories with specific parts of the body, 2) information about the position of one's body in space, and 3) the visuospatial structural representation of one's body, and others' bodies. However, it seems that there is a lack of direct neuropsychological evidence for the visual recognition of body.

### fMRI evidence for a body-selective region

Recently, Downing et al., (2001b) reported an area in the lateral occipito-temporal region that responded strongly to visually presented body stimuli of different formats. They found robust activation from the region to photos of human bodies, human body parts, stick figures, human silhouettes, and line drawings of human bodies, compared to human faces, tools, scrambled stick figures, and other common objects. This region was later labelled as the extrastriate body area (EBA). More recent evidence demonstrated that this region was functionally and anatomically distinctive to nearby areas such as the motion selective area MT+ /V5 (Peelen, Wiggett, & Downing, 2006). Furthermore, Peelen et al., (2006) have also shown that this area could extract body form from

biological motion when subjects viewed point-light stimuli. Others have found that the EBA is selective to the body of self as well as others (Chan, Peelen, & Downing, 2004; Saxe, Jamal, & Powell, 2006). Specifically, Chan et al., (2004) tested their subjects with photos of the subjects' own bodies and of familiar others' bodies, in an egocentric or allocentric view. This study found that the EBA slightly preferred the view of any bodies in allocentric view relative to the egocentric view.

Surprisingly, there are no reports of specific deficits in the visual recognition of body parts resulting from a focal lesion to the extrastriate cortex. More direct evidence for a disturbance in visual recognition of body comes from a recent TMS study on the EBA (Urgesi, Berlucchi, Aglioti, 2004). In this study, the experimenters used event-related repetitive transcranial magnetic stimulation (rTMS) to create transient inactivation of cortical areas in healthy participants. By applying rTMS to the EBA, Urgesi et al., (2004) aimed to see whether interruption to the EBA would lead to a temporary deficit in the visual discrimination of body parts.

Subjects performed a within category match-to-sample task on body parts, face parts, and motorcycle parts. These researchers found that applying rTMS to the right EBA 150 msec after the presentation of sample had led to a significant increase in reaction time for matching body parts, but not for face parts or motorcycle parts. This significantly longer reaction time for matching body parts happened only when stimulations were applied to the EBA rather to V1 or sham stimulations. Furthermore, the finding that applying rTMS to the EBA did not affect subjects' performance in matching face parts suggests that there are separate cortical representations for faces, and body parts, at least in the lateral surface of the occipital temporal cortex. Thus, these series of experiments reinforced the role of EBA in processing body stimuli. Urgesi et al's (2004) findings suggest that neural activity in the EBA does not only correlate with the perception of bodies, but the activity is necessary for visual processing of body stimuli.

In summary, the findings that responses in the FFA, PPA, and EBA could be driven by the visual perception of faces, scenes, and bodies respectively, have been interpreted as offering strong supporting evidence for the modular account.

### 2) Processing Account

However, the modular account is not universally accepted. As mentioned earlier, assumptions of cognitive architecture are open to interpretations. The modularity assumption is one of many ways to interpret category-specific deficits and category-specific activations. The processing account gives an alternative view in object representation in the ventral stream. This account argues that cortical representation of object is organized by processing demand, and that object categories that require the same processing will recruit the same mechanism (domain-general). This account disagrees with the category-specific hypothesis (domain-specific), which argues that representation of objects is organised in terms of object category.

Observations of prosopagnosic patients led some researchers to argue that the deficit was not specific to faces, but to a more general discrimination of

visually similar members of the same categories (Damasio et al., 1982, 1989, 1990). This is supported by the observation that some patients could detect faces, recognize their gender, age and facial expression, but could not recognize faces at individual levels (Tranel, Damasio, & Damasio, 1988). In addition, some prosopagnosic patients have deficits in discriminating among members within another specific category; for example a bird watcher cannot identify birds (Boernstein, 1963), and car experts were unable to recognize car makes (Lhermitte, Chain, Escouroole, Ducarne, & Pillon, 1972). The above evidence subsequently led some researchers to propose that the FFA's activation might not reflect face processing per se, but instead reflected a fine grain discrimination mechanism when identifying faces. The processing account proposes that the underlying function of the FFA is for expert discrimination between visuallysimilar exemplars of the same category. Hence, the mechanism of the FFA is a domain general one; any kinds of objects that require subordinate processing should also activate the FFA. It is therefore argued by some researchers that the strong activation from the FFA is a result of humans' expertise in identifying faces at individual levels (Gauthier et al., 1999).

Neuroimaging evidence supporting this account comes from the findings that activation in the mid fusiform gyrus increases with expertise in recognizing novel objects (Gauthier et al., 1999). In their study, subjects were trained to recognize a set of computer-generated stimuli called Greebles (see samples in Appendix, Figure A3, p. 242), and each Greeble was given gender, and a family. To gain expertise in recognizing Greebles, training for subjects involved identifying Greebles in terms of their family or individual names. While subjects

were in the fMRI scanner they were required to perform a sequential matching identity task for blocks of Greebles and blocks of faces, and there were upright or inverted conditions for both stimuli types. The results showed that the activation in the mid fusiform area increased when subjects discriminated Greebles, and discrimination between faces also recruited strong responses in the FFA. Furthermore, these researchers reported a stronger activation in the mid fusiform area in subjects who had been trained to discriminate Greebles (Greebles experts), relative to the activation in subjects who had no previous experience with Greebles (Greebles novices).

In addition, an inversion effect (indicated by a lower FFA response) was found for both inverted faces and inverted Greebles relative to these upright ones. It is believed by many that an inversion effect is specific for faces relative to other object categories. Many behavioural experiments have pointed out that the inversion effect is specific for face rather than to other objects, and in particular, recognition for faces was disrupted when faces were inverted (Yin, 1969). The inversion effect reflects the configural processing and fine grain identification for faces. Hence, the fact that an inversion effect is also found in Greebles indicates that training to initially novel objects can induce configural processing, a processing which is much needed for processing faces. Similar behavioural and neural mechanisms for processing expert stimuli (Greebles in this context) and faces have subsequently been used as evidence to support the processing account and that the function of the FFA is a domain-general one. With the above evidence, these experimenters concluded that the FFA primarily was not a face

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area, but the activation for faces might be a "product" of our extensive experience with them.

In summary, Gauthier et al's (1999) findings have several implications on the possible roles of the FFA. They showed that the fusiform face region responded strongly to non-face stimuli after training, and thus argued that the function of the FFA was a domain general one. The inversion effect for Greebles has suggested that increased experience with the novel stimuli (Greebles) will induce a processing demand similar to that for faces. Importantly, an increased activation in the FFA to Greebles as a function of training and familiarities has indicated that object category is not the only factor that determines specialization of the middle fusiform gyrus. Processing demand could be one of the factors as well.

As illustrated by Gauthier et al.'s (1999) study, the level of categorization could influence activation in the mid fusiform gyrus; in particular when our expertise in extracting diagnostic features from objects is required. Humans recognize faces at an individual level (Bob vs Bill), and we mostly recognize common objects at a basic level (a dog vs a cat); thus we have less experience in discriminating between exemplars within other categories. Further evidence supporting this processing account comes from car and bird experts in Gauthier et al's (2000) experiment. Subjects in their experiment were people who had long-term experience with cars or birds. In the fMRI scanner, subjects performed a 1-back matching task in which they responded to an immediate repetition of location or identity of either a car or a bird. These researchers then examined the

activation in the centre of the right FFA. In both groups of experts, greater activation was found for faces than for cars or for birds. In the same region, bird experts produced significantly stronger activation to birds than to car experts, however, both car and bird experts produced similar activation to cars.

In a behavioural task aimed to measure the level of expertise, subjects were required to perform a matching task with four categories, namely upright and inverted images of cars, and upright and inverted images of birds. In each of the car trials, subjects were asked to decide whether the first stimulus and the second stimulus was the same model but of different years. In each of the bird trials, they had to decide if the first stimulus and the second stimulus were from the same species. Gauthier et al., (2000) found a strong correlation between behaviour (expertise level) and activation in the right FFA when subjects attended to the location of the cars and birds (1-back matching task). Interestingly, no such correlation was found when both groups of subjects were required to perform a subordinate categorization in the identity task with both categories.

The experimenters concluded that subordinate level of processing was automatic (Gauthier et al., 2000), and that the strong activation in the FFA for expertise items suggested that the neurons in the ventral cortex might not be organized according to the visual features but by the processing demand required for an object category.

The processing account provides an alternative explanation for categoryspecific activation in the FFA. It is possible that this account can be applied to other category-specific regions. One possible candidate is the PPA. Recent findings by Bar and Aminoff (2003) can be interpreted as evidence supporting the processing account. Specifically, Bar and Aminoff (2003) argued that the primary role of the PPA was to process stimuli that contained strong contextual information (stimuli associated with a specific place, e.g. a microscope was found only in a laboratory) rather than to process scenes or spatial layout per se. Indeed, their view is consistent with Lynch's (1960), who claimed that buildings had a "high landmark value". In other words, houses are objects with a strong relationship to the environment. Thus, strong activation in the PPA could well reflect an object-place relationship, a context associated with a particular environment. In Bar and Aminoff 's (2003) fMRI experiment they found that the posterior part of the PPA responded strongly to highly contextual stimuli (objects that are strongly related to a specific context, e.g. a microscope is usually found in a laboratory), compared to low contextual stimuli (objects that can be found in many circumstances e.g. plants). Their results also showed that the activation for highly contextual stimuli was similar to that for indoor scenes and outdoor scenes. Therefore, the experimenters concluded that the PPA was not specific for processing spatial layout, but instead the PPA was primarily involved in processing any stimuli that were strongly related to a specific context.

In summary, both domain-specific and domain-general accounts agree that the neural substrates for object processing are organized in a modular manner, but each account proposes a different underlying function of a module. The domain-specific account proposes that only a particular class of categories will strongly activate a specific region, whereas the domain general account proposes that any object which shares similar processing properties will activate the same region. Alternatively, the object form topography account proposes that object representation is distributed.

#### 3) Object form topography

Ishai, Ungerleider, Martin, Schouten, & Haxby (1999) proposed that object representation in the visual cortex could be organized in terms of visual features, that is "featurotopic". According to this idea, the visual ventral cortex contains a map in which similar visual features are found adjacent to one another; hence, visually similar objects should activate overlapping regions in the visual cortex. Specifically, Ishai et al., (1999) replicated the findings that faces produced the strongest activation in the lateral fusiform gyrus, which overlaps with the FFA, and houses and chairs evoked the strongest activation in the medial fusiform gyrus, which overlaps with the PPA. However, the responses in each of the above regions for the less effective categories were strong too. Thus, the above evidence has led Ishai et al., (1999) to conclude that each category produces a distributed response pattern across the ventral stream, this pattern includes both high and low responses. Hence, it is possible that categories sharing similar features will elicit responses around the same region and elsewhere, rather than an exclusive focal activation in a specific region.

Further evidence supporting the above idea has been provided by Haxby et al., (2001). They proposed that visual object representation is distributed and

overlapping. Haxby et al., (2001) claimed that all classes of objects evoke distributed activation in the ventral cortex, and that the weaker activation for a class of stimuli was equally as important as the strong activation. Thus, categoryspecific areas could not be thought of as modules because these areas responded to less effective categories. The above hypothesis predicted that weaker activation in the FFA for houses might contribute to the successful recognition of houses.

Specifically, Haxby et al., (2001) asked their subjects to view faces, cats, houses, chairs, scissors, shoes, bottles, and textures. They then used a correlation technique to analyze their fMRI results. For each category, the experimenters correlated the activation map from the odd runs of the scan session with the map from the even runs. Results showed that each category produced a distinct response pattern, and there was a strong positive correlation for within-categories comparison (e.g. the pattern for houses in the odd scan session was correlated with the pattern for houses in the even scan session). They also found weak correlations across categories e.g. faces in odd run versus houses in the even run. More importantly, houses or faces did not exclusively activate the PPA and FFA, as they also elicited strong activation in the other visual areas. Even when the strong responses of the PPA and FFA were excluded from the correlation analysis correlation between scans for a category remained strong. These results led Haxby et al., (2001) to conclude that weak responses carry as much information as strong responses.

In summary, the evidence supporting the object form topography account posed challenges for both the modular and processing account. Haxby et al., (2001) used statistical methods to demonstrate that neural representation for objects might be distributed; however, they did not provide further insight into the nature of such distributed neural activities. In particular, they did not address the following issues: why strong activation was found for a certain category in a specific region (Cohen and Tong, 2001), why lesions to parts of the ventral cortex produced selective deficit in recognizing a particular object category, and whether the response patterns are distributed randomly or systematically with some kind of organization principles. The eccentricity account could perhaps provide us with some insight the nature of object representation and organization in the ventral stream.

### 4) Eccentricity account

Malach and colleagues (Hasson et al., 2002; Hasson et al., 2003; Levy et al., 2001; Malach et al., 2002) recently proposed that object representation in the ventral stream could be organized in terms of retinotopic mapping. Much of their research was based on the well-established findings that the early visual area could be mapped by two orthogonal axes (see Figures 2 & 3 below): namely by polar angle, and eccentricity (Engel, Glover, & Wandell, 1997; DeYeo, Carman, Bandettini, Glickman, Wieser, Cox, et al., 1996; Tootell, Mendola, Hadjikhani, Ledden, Liu, Reppas, et al., 1997;).
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Figure 2: Polar angle axis and its corresponding cortical areas, this image was reproduced from Jody Culham (n.d.).

The axis of the polar angle represents the visual field that lies on a specific radius that is originated from the centre of the retina (see Figure 2 above). Each sector of the visual field corresponds to a strip of cortex, for example the upper visual field is represented by areas below the calcarine sulcus, whilst the lower visual field is represented by areas above the calcarine sulcus. The left visual field corresponds to the right hemisphere, and the right visual field corresponds to the left hemisphere.



Figure 3: Eccentricity axis and the corresponding cortical areas, this image was reproduced from Levy et al., (2001). Extreme left, eccentricity maps superimposed on an inflated brain. Extreme right, an eccentricity map superimposed on an unfolded cortical surface from both hemispheres. The areas surrounded by the red line represent regions activated by common objects. Regions in yellow indicate the centre of the retina, and the central visual field representation in the cortex. Regions in purple indicate the middle region of the retina and the middle visual field representation in the cortex. Regions in green indicate the periphery region of the retina, and peripheral visual field in the cortex.

The axis of eccentricity (see Figure 3, above) organization can also be found in the early visual area. Regions in this axis are represented by each of these rings, and each ring extends from the centre of the retina. Each of these rings corresponds to a specific location in the visual cortex, specifically, the centre of the retina corresponds to the lateral regions of the cortex, and the periphery region of the retina corresponds to the medial regions. It has been reported that (DeYeo et al., 1996, Engel, et al., 1997; Malach et al., 2002) eccentricity is associated with the cortical surface devoted to the representation of a unit distance on the retina - the magnification factor. Specifically, the centre of the retina (the fovea) has an enormously large cortical magnification, and the magnification factor reduces as the distance from the fovea increases. Hence, the central visual representation is finely mapped onto the cortical surface, where each point on the central visual field cortex represents a small retinal and visual field distance. The centre of the retina is thus specialized for detail, fine, and high-resolution visual analysis. In contrast, peripheral regions of the retina are coarsely mapped onto the cortical surface, where each point on the peripheral visual field cortex represents a larger retinal and visual field distance. The peripheral regions of the retina are thus responsible for coarser visual analysis.

To date, several research teams such as DeYeo et al., (1996), Engel, et al., (1997) and Tootell et al., (1997) have found cortical organization by polar angle,

and eccentricity in the retinotopic areas in both humans and primates. In general, eccentricity mapping can be clearly demonstrated in the higher-level visual area, whilst polar angle mapping is rather blurry in the higher-level visual area (Levy et al., 2001). However, few researchers have applied the principle of eccentricity (i.e. centre-peripheral organization) to the brain region involved in higher-level object recognition beyond the retinotopic region.

Levy et al., (2001) therefore further explored the relationship of eccentricity bias regions and object selective regions further (see Figure 4, below). Their rationale was based on the finding that faces elicited robust activation in the lateral fusiform gyrus (FFA); and place and scenes elicited robust activation in the medial fusiform gyrus, which overlaps with the parahippocampal area/ anterior collateral sulcus (PPA). These researchers localized the subjects' FFA and PPA. They then measured these areas' responses to common objects that were presented in the centre, middle and peripheral regions of the retina (eccentricity). Their main finding was that FFA responded most strongly when objects were presented in the centre of the retina, as compared to the middle and periphery of the retina. On the other hand, the PPA showed bias activation to objects presented in the periphery regions of the retina. Subsequently, they superimposed the eccentricity map of their subjects onto the activation map of the place and face conditions. As predicted, the face specific region (FFA) overlapped with the cortex that was associated with the central visual field representation, whilst the place specific region (PPA) overlapped largely with the cortex that corresponded to the peripheral visual field

representation and also to some cortex corresponding to the middle visual field representation.



Figure 4: Eccentricity axis overlapping the face- and place- selective responses, this image was reproduced from Levy et al., (2001). a) Ventral, axial, and coronal views of a brain, showing face-selective activation in the lateral fusiform gyrus and place-selective activation in the medial fusiform gyrus or along the anterior collateral sulcus. (b) The face and place regions are shown on the unfolded cortical surface of the right hemisphere. White dotted lines marked the borders of retinotopic visual areas. The white circle indicates the location of face selectivity region reported by previous studies (e.g. Kanwisher et al., 1997a). In addition, the location of the lateral occipital region (LO), posterior fusiform gyrus (pFs), and anterior collateral sulcus (Ant. CoS) were labelled. (c) The red border marks the face-selective regions and the blue border represents the building-selective regions, this map is then overlaid on the central (yellow), mid (purple) and peripheral (green) visual field representations obtained by Levy et al., (2001). The central visual field representation

overlaps with the face-selective activation, and the mid and peripheral visual field representations overlap with the place-selective activation.

One immediate question is whether or not this eccentricity bias mapping reflected by the activation for face and place stimuli is due to some kind of lower level visual properties, such as the size of the image. In another word, an image of a scene occupies larger area in the visual field, and thus leads to a peripheral bias representation, whilst an image of a face occupies a smaller area in the visual field, and thus leads to a centre bias representation. To investigate this Levy et al., (2001) carried out another experiment where they used both regular and large face, and regular and small building stimuli (regular faces =  $12^{\circ} \times 12^{\circ}$ , large faces and regular buildings =  $17.5^{\circ} \times 17.5^{\circ}$ ; small building =  $5.8^{\circ} \times 5.8^{\circ}$ ). Their results showed that manipulation of size affected the early retinotopic region; larger pictures activated regions overlapped with more peripheral visual field representation, whilst smaller pictures activated a more central visual field representation. In particular, large faces activated the medial brain region, and small buildings elicited activation in the lateral region. Interestingly, a reverse pattern was found in the higher-level visual area, which is outside the retinotopic area. Responses to both large and regular face stimuli overlapping with the central field visual representation, along the lateral fusiform gyrus, whilst responses to regular and small building stimuli overlapped with the peripheral visual field representation, along the medial fusiform gyrus.

With these results, the authors proposed a general principle for object representation, a centre-periphery organization (Hasson et al., 2002; Hasson, et al., 2003; Levy et al., 2001; Malach et al., 2002), and suggested that the origin of

this organization might be related to the resolution needed to process an object. For example, object categories that require detailed analysis or fine discrimination (Gauthier et al., 1999) of the visual features will tend to receive more input from the centre of the retina. Thus, activation for categories such as faces, which require fine discrimination, will overlap the lateral area of fusiform gyrus (a central visual field representation). On the other hand, object categories that are usually processed at a coarse level will be represented by the medial brain regions (a peripheral visual field representation).

A more recent study by Hasson et al., (2003) extended the above findings and demonstrated that a map of eccentricity could exist in the ventral and dorsal streams of the occipital temporal lobe (VOT and DOT respectively). In their study, the ventral stream refers to the ventral inferior occipital cortex that extends from the posterior fusiform gyrus to the medial region of the collateral sulcus. The dorsal stream refers to the region from transverse occipital sulcus that extends to the inferior temporal sulcus. Face related response in the lateral fusiform gyrus, object related response in middle posterior fusiform gyrus, scene related responses in the collateral sulcus were found in the VOT, in addition a mirror-symmetry pattern of the above responses were also found in the DOT. This again demonstrated that the category-specific regions, especially for faces and scenes, overlapped with the map of visual eccentricity. With the support of these results, Hasson et al., (2003) therefore claimed that the whole occipital temporal cortex could be mapped by visual eccentricity, and their results also suggested that object representation might be associated with a single eccentricity map.

In summary, the above evidence demonstrates that eccentricity bias account may provide one of the explanations for the origin of some of the category-specific regions (FFA, and PPA). These findings also suggest the possibility that eccentricity bias representation, modular account, and processing account (only apply to Gauthier's interpretation of the responses in the FFA) can all account for object representation in the visual cortex (Kanwisher, 2001). However, it remains an open question whether this organizational scheme is genetic-specified or experience-dependent. Kanwisher (2001) speculated that eccentricity bias could be genetically specified, and that face and place-selective regions developed because they were abundant in our environment. In addition, perhaps top down influence from the frontal region could be one of many factors in determining such cortical organization for higher-level object recognition.

The following section will review the debate between the above three major accounts. Highlighting some of the contradictory evidence found in recent fMRI work will provide a grounding for the first experiment in this thesis.

#### The debate on specificity of category-specific regions

The intense debate regarding the specificity of category-selective region has emphasized the strong activation for faces in the mid fusiform region (or the FFA), in particular, whether the activation from the FFA reflects a domainspecific mechanism or a domain-general mechanism. The debate regarding the underlying function of FFA can also be interpreted as a debate of whether cortical specialization is determined by object category or by processing demand.

Therefore, discussing the nature of FFA responses in face and object perception will subsequently help us to address a broader question of how object categories are represented in the visual cortex.

The domain-specificity account argues that some object categories are important to the survival of humans, and thus lead to an emergence of a specialized neural mechanism for processing certain kinds of objects. Faces therefore are one of the special categories, and thus lead to many researchers proposing that perception of faces is handled by a dedicated neural mechanism (Kanwisher 1997a, 2000; Cohen and Tong, 2001). On the other hand, Gauthier and colleagues argue that activation in the FFA can be driven by fine-grained discrimination between visually similar exemplar within an object category, not primarily driven by face processing. Thus, the FFA should also produce a strong response to non-face stimuli during a within-category discrimination task. Following this line of reasoning, Gauthier et al., (1999) argue that the strong activation from the FFA is a result of subjects' increased experience with an object category during within-category discrimination; thus FFA's activation reflects an expertise effect. Findings from both camps are compared here, and the behavioural and neural signatures for face processing are reviewed here, which can certainly provide a better picture of the underlying functional architecture in one of the category-specific regions.

#### Activation for non-face categories in the FFA

One major criticism against the domain-specific account is the finding of intermediate activation to non-face objects. Direct evidence comes from the

finding that increased activation in the FFA was found after subjects received training in recognizing novel objects (Greebles). Recently, several researchers have investigated the effect of training in the FFA (Duchaine, Dingle, Butterworth, & Nakayama, 2004; Op de Beeck, Baker, DiCarlo, & Kanwisher, 2006; Xu, Liu, & Kanwisher, 2005b). In particular, Op de Beeck et al., (2006) trained subjects to discriminate between a set of computer-generated objects to examine responses in the FFA. They scanned subjects before and after training, and found that the FFA showed little effect of training. The only subject who had shown training effects in the FFA was the one who saw the stimuli as human-like (as women wearing hats). The above led to some researchers (Kanwisher & Yovel, in press; Op de Beech et al., 2006) arguing that the increased activation for Greebles in the FFA might be due to the fact that Greebles look like people.

Another debatable issue is the finding of the training effect found for Greebles. Kanwisher and Yovel (in press) argued that Gauthier et al., (1999) failed to provide direct evidence for the training effect for non-face objects (greebles). Instead of reporting the differences in percent signal change for upright greebles before and after training, Gauthier et al., (1999) reported the percent signal change of the differences between upright greebles minus inverted greebles. Thus, the training effect was not directly measured.

In addition, due to the fact that names and families were assigned to greebles, this might have encouraged subjects to encode greebles as people with faces and bodies. Therefore, strong activation when discriminating greebles in the FFA could have been confounded by the similarities between greebles, faces, and bodies. Thus, "body-look-alike" stimuli may also have elicited strong activation in the FFA. Support for this comes from the recent report that the human body activated an area near the FFA, which was later named as the fusiform body area (FBA; Peelen & Downing 2005; Schwarzlose, Baker, & Kanwisher, 2005). In addition, it has been shown that that activation in the FFA switched with the perception of faces when subjects viewed Rubin's vase-face and "mooney" faces (Andrews et al., 2002, 2004). If the subjects perceive the stimuli as faces, the stimuli will evoke strong activation in the FFA. Hence, the above evidence suggests that strong activation in the FFA for discriminating between greebles may not be a direct result of within-category discrimination.

#### Activation for expertise categories in the FFA

The debate over the function of the FFA continues with the finding of an expertise effect in car and bird experts in the FFA (Gauthier et al., 2000). According to the processing account, if the activation in the FFA is reflecting fine grain discrimination within a category, then bird and car experts, who are good at discriminating between birds or between cars, should also produce strong activation in the FFA (an expertise effect). These researchers subsequently showed that, in the centre of the right FFA, and whole right FFA, bird experts elicited significantly stronger activation to faces and birds than to cars. The evidence seems to support the prediction that experts of a certain category, who are good at within-discrimination between members of the expertise category, should also show strong activation in FFA when viewing both the members of the expert category and faces. Therefore Gauthier et al's (2000) findings seem to support the domain-general account. However, it should be noted that car experts

produced similar activation in the FFA for both cars and birds, and the activation for the expert category (cars) and non-expert category (birds) were much lower than the activation for faces. Therefore, it seemed that the expertise effect was only found in bird experts, in which the activation for birds and faces was stronger than for cars. One possible reason is that birds contain faces and bodies, which elicited intermediate activation in the FFA. Indeed, it has been reported that animal faces, whole animals, and animals' bodies without heads elicited some responses in the FFA even though the responses were not as robust as human faces (Kanwisher et al., 1999; Tong et al., 2000).

In addition, Gauthier et al., (2000) found a strong correlation between the level of expertise and activation in the right FFA when subjects attended to the location of the cars and birds. However, no such correlation was found when both groups of subjects were required to perform a subordinate categorization in the identity task in both categories. This result seems to be inconsistent with the assumption of the expertise account, which hypothesized that the level of categorization should positively correlate with FFA's activation.

#### The role of FFA in within-object categorization

The role of the FFA in discriminating within-category identification was further investigated by Grill-Spector et al., (2004). These researchers examined the responses in the FFA and PPA during identification and detection of object categories. In one of their experiments they compared the activation for faces, birds, cars, flowers, houses, and guitars in two tasks. A detection task, in which subjects had to decide whether the image was an object or a texture, and an identification task in which subjects had to report the specific names of each stimulus (subordinate member of a category e.g. pigeon, Harrison Ford etc). The time courses of the voxels in the PPA and FFA were then extracted to reveal the activation for faces, birds, and guitars. The data showed that the activation in both the bilateral FFA was significant stronger for successful detection of faces (detection hits) than failure in face detection (detection misses), and for successful identification of faces (identification hits) than failure in face identification (identification misses). In addition, there was also a higher activation for identification hits compared to detection hits. Higher activation was also found for detection hits of paces than detection hits of faces, and the activation was weakest for detection misses of faces. Grill-Spector et al's (2004) findings showed that perception of faces was tightly linked to responses in the FFA.

Furthermore, in the FFA there was a strong correlation between FFA response and correct detection, and identification of faces. In addition, the activation in the PPA was not correlated to correct detection or identification of faces and other non-scene categories. This indicated that, during face detection and identification, the activation in other non-face selective regions did not correlate with behavioural performance.

The next question is whether the activation in the FFA is correlated with the identification and detection of non-face categories. Grill-Spector et al's (2004)

results showed that the activation from the FFA was not strongly correlated with successful identification and detection for most non-face objects (house, flowers, cars, and guitars). Interestingly, activation in the FFA was positively correlated with correct identification and detection of birds. In three subjects the FFA response was also weakly correlated with the perceptual performance for car stimuli. Across all of the five subjects, and only in the right FFA, there was a higher activation for the correct identification of cars compared to the correct detection of cars. However, the FFA responses to car detection hits and misses were very low.

To investigate the above effect for cars further, in the same study Grill-Spector et al., (2004) scanned five car experts using the same paradigm but with just car and face conditions. Their data showed that there was no correlation between the response of the right FFA and success in car identification or detection in car experts. Importantly, when the data sets of car novices and car experts were collapsed together, the significantly higher response in the right FFA for car identification hits than detection hits disappeared. Furthermore, using the same behavioural task as Gauthier et al., (2000), Grill-Spector et al., (2004) examined the correlation of the level of expertise in cars and responses in the FFA. Across experts and novice subjects they found no correlation between the level of expertise for cars and the response for correct identification for cars. Grill-Spector's evidence seems to argue against the role of the right FFA in within category identification of objects of expertise.

Interestingly, Xu (2005a) used an event-related design, and found expertise effects in cars and birds experts. The author hence argued that Grill-Spector et al's (2004) expertise experiment did not provide evidence against the expertise effect; and the lack of expertise effect in cars experts was due to the fact that their car identification task was not specific enough. Specifically, car experts were asked to identify a Harrison Ford's face among other faces in the face task, but they were only asked to identify jeeps from cars in the car task. Thus, the level of identification was not equivalent between the face and car tasks. However, it should be noted that the expertise effect found in cars experts (Xu, 2005a) was similar to Gauthier et al's (2000) findings that in car experts, the right FFA responded strongest to faces, birds, followed by cars, and objects. In bird experts, the right FFA responded strongest to faces, and birds, and weakest to cars, and objects. This again showed that the FFA in car experts showed strong activation to non-expertise items (birds) as well as cars. The consistent strong FFA activation for birds in both expert groups found by Gauthier et al., (2000) and Xu's (2005a), and the positive correlation of FFA activation with the correct identification and detection of birds found by Grill-Spector et al., (2004), have thus suggested that the FFA may reflect visual processing of birds, animals, or bodies.

Taken together, the research reviewed above demonstrates that activation in the FFA is mainly driven by perception of faces, and such activation correlates with the correct identification and detection of faces. However, it also leads to further questions about how objects are presented in the ventral cortex. First, it is worth noting that the positive correlation between the FFA response and bird

identification reported by Grill-Spector et al., (2004) and the "expertise" effect reported by Gauthier et al., (2000) have indicated a possibility that processing body-like or animal stimuli (namely birds) can influence activation near to or overlapping with the FFA (also see Grill-Spector, Sayres, & Ress, 2006, which will be discussed in detail in Chapter 2 p. 55 and General Discussion p. 189). Hence, it will be interesting to investigate the response profile of FFA to animals (see fMRI survey). Second, although the above research has provided us with some explanation for the FFA's intermediate activation to certain non-preferred categories (greebles, cars, and birds), such intermediate activation has led some researchers to propose that category-specific regions might not be strictly modular. Non-preferred activation in a category-specific region may represent information about other objects. In particular, Haxby et al., (2001) have proposed that the organization of the visual cortex is topographically distributed, and that both strong and weak activation convey useful information about an object. This leads us to the debate on neural specialization in object representation.

## The debate on neural specialization in object representations

As mentioned earlier, the modular "domain-specific" account is insufficient to explain the activation to non-preferred stimuli in category-specific areas. Although many experimenters have demonstrated strong activation of the FFA to face stimuli relative to other object categories, this activation does not occur in an all-or-nothing fashion, and the magnitude of activation between face stimuli and non-face stimuli varies and depends on categories tested. Indeed, different non-face categories produce different levels of activation relative to faces. For example, Kanwisher and colleagues (1999, 2001) showed a decrement

in the percent signal change (PSC; the mean signal for a given condition minus the mean signal for the fixation-only epoch, divided by that value across all subjects) in the FFA. Specifically, strongest PSC was found for faces relative to other categories (PSC for faces > human eyes > human bodies > objects > buildings > human hands), it is possible that this response pattern may reflect some underlying functions of the FFA.

On the other hand, the processing account attempts to explain some of the non-preferred activation in the category-specific areas. For example, Gauthier et al., (2000) demonstrated that expert items activated the FFA more than non-expert items. However, the activation for faces remained the strongest among those items, and the non-expert items still evoked some activation in the FFA (e.g. an intermediate activation in the FFA was found when cars experts viewed birds). In theory, if a given category-specific region is truly responsible for a specific type of processing (e.g. subordinate processing), then the strong activation in that region should only be evoked by the processing of a category that requires that specific type of processing demand, but not by other categories that do not require that specific type of processing demand. Thus, the processing demand account cannot fully explain the strong and weak activations in a category-selective region either.

Given that neither the domain-general account nor the domain-specific account alone is sufficient to explain the above, Haxby et al., (2001) proposed that the neural representation of objects is not modular; rather it is a network in which a specific category evokes different levels of responses, from weak to

strong. Recognition of an object requires a combination of both non-maximal and maximal responses. Thus, their assumption disagrees with a modular representation of objects, whether it is a module for domain-specific processing or domain-general processing. Furthermore, unlike the above two accounts, the object form topography account provides some explanations for the activation elicited by non-preferred categories. However, the main problems of this theory are: first, it cannot explain the results from prosopagnosic patients (Sergent & Signonet, 1992) and topographic agnosic patients (Aguirre & D'Esposito, 1999). Specifically, it cannot explain the fact that a category-specific deficit was found after a lesion to a specific brain region, and there are dissociable deficits for different categories. Further, it cannot explain the fact that in some prosopagnosic patients there is a lack of activation and selectivity for faces in the FFA, as well as a lack of face-selective activation anywhere along the ventral cortex, namely patients GA and RP reported by Behrmann and Avidan (2005). The object topography account cannot explain why the above prosopagnosic cases occur if the weaker activation could contribute to the successful identification of faces. The fact that weaker activation from other regions is unable to take over the processing of the damaged cortex in turn implies that robust activation in the FFA is required for face recognition. Due to the above reasons, the object topography account may have over-estimated the role of weaker activation in object recognition.

As mentioned, Grill-Spector et al. (2004) demonstrated that weaker activation in a category-specific region does not strongly correlate with the correct identification of an object. On the other hand, Spiridon & Kanwisher (2002) attempted to explore the origin of the weaker responses from two of the category-specific regions, the FFA and the PPA. In Spiridon and Kanwisher's fMRI experiment, they used a correlation method similar to Haxby et al. (2001), but within each scanning session their subjects viewed different exemplars and image formats (photos and line drawings) of each category from various view-points.

Before discussing their findings, it is important to explain the term "mean percentage correct discrimination". For a given region of interest (ROI), its activation to one object category is compared with the activation to other category/categories. If these activations are similar to each other then the correlation between them will be strong. A strong correlation indicates that the ROI cannot distinguish the two categories (a low mean percentage correct discrimination). On the other hand, if these activations yield a weak correlation, then it will suggest that the activation to one category is significantly different to the other category, indicating this given ROI is able to distinguish between the two categories (a high mean percentage correct discrimination), and thereby suggesting the selectivity of this given ROI to a specific object category.

As an index of the different activation between categories in a given brain region, the mean percentage correct discrimination of activation maps between faces and objects, between houses and objects, and between objects and objects were calculated for FFA, PPA, and V1.



Figure 5: Mean percentage of correct discrimination and standard deviation in FFA, PPA, and V1, this graph was reproduced from Spiridon and Kanwisher (2002)

Spiridon and Kanwisher found that in the FFA (see Figure 5, above) there was a high mean percentage correct discrimination for faces versus objects, and a low mean for houses versus objects, and objects versus objects. In the PPA the mean percentage correct discrimination was high for houses versus objects, low for faces versus objects, and low for objects versus objects. In V1, all comparisons had low mean percentage correct discrimination, suggesting that V1 has no preference for any of the above object categories.

The above results demonstrate that the FFA and PPA contain more information about their preferred categories than the other categories. The low mean percentage correct discrimination scores between non-preferred categories (houses > objects, objects > objects) in the FFA and the PPA were similar to the low mean percentage correct discrimination scores in V1. This led Spiridon and Kanwisher (2002) to conclude that the activation for the non-preferred categories in the PPA and the FFA only reflected the low level feature-based information that had already been extracted in the retinotopic cortex (V1). Therefore, they concluded that the FFA (for example) was a face processor that also detected when a stimulus is not a face, and so the activation for the non-preferred object could be a product of filtering out the non-preferred stimuli. Hence, Spiridon and Kanwisher (2002) argued against the idea that weak activation contributed to higher-level object processing.

In summary, there is no doubt that cortical specialization for some object categories do exist in the ventral cortex. In some cases, many researchers mainly disagree with the use of the term "category-specific" and "category-selective" to describe the FFA, PPA, and EBA, because of the regions' intermediate responses to non-preferred categories. Nevertheless, activation in each of the above regions was strongly biased to one object category, and perhaps the term "category-bias" would be more acceptable. Throughout this thesis, I have used the terms "category-specific" and "category-selective" interchangeably, referring to a ROI that produced significantly stronger activation to the most effective categories, relative to other less effective categories.

Furthermore, it is likely that neither the domain-specific account nor the domain-general account alone is sufficient to provide a wider picture of how the visual cortex is organized. This is mainly because research from both camps has focused on faces and activation in the FFA. Other researchers such as Haxby et al., (2001), have used statistical methods to demonstrate that neural representation for objects might be distributed. However, they did not provide

further insight into the nature of the distributed neural activities. In particular, their results did not address whether the neural activities are distributed randomly or systematically with some organization.

Taken together with the findings from Malach and colleagues, it is therefore reasonable to suggest that the ventral stream consists of strong category-selective regions (FFA, EBA, PPA), and these regions overlap with the eccentricity visual field representation (Kanwisher, 2001; Malach et al., 2002). On the other hand, it is also possible that there are more than one general organizational principles in the same surface of cortex in the ventral stream. All the above subsequently brings us back to the central aims of the present survey: 1) To investigate the extent of specificity of FFA, PPA, and EBA, and to examine the response profile for non-preferred categories, which could also be useful when interpreting underlying functions of these regions. 2) To investigate the prevalence of category-selective regions, which aims to examine if there are other category-selective regions in the ventral cortex. 3) To examine if there is another general division of object representation in the brain by scanning subjects with a broader spectrum of object categories than previous studies.

Chapter 1-Introduction

## **Outline of the thesis**

The research reviewed above has provided fruitful knowledge regarding the organization of the human ventral cortex. The first three theories offer seemingly conflicting views about the functional organization for object representations, whilst Malach's eccentricity-bias account gives a new angle about the principle of visual object representations. Nonetheless, the neural organization of the category-specific areas remains debatable; in particular the non-preferred responses elicited by the category-specific regions require further investigation.

In order to extend our understanding to the functional organization of object presentation in the ventral stream, using Functional Magnetic Resonance Imaging (fMRI), I first present an fMRI survey on object representations in the ventral stream in Chapter 2. This fMRI survey consisted of 20 object categories <sup>2</sup>, which were visually presented in the scanner, and it aimed to achieve three goals. First, it aimed to examine the specificity of the category-specific regions (FFA, PPA, and EBA). Investigation 1 was conducted and the response profiles (responses for the most-effective category to the least-effective category) in each of the above regions were revealed. It also investigated whether the FFA, PPA and EBA responded strongest to their most-effective categories (faces, scenes, bodies) relative to the other categories.

<sup>&</sup>lt;sup>2</sup> 20 object categories were tested: human faces, human bodies (without heads), outdoor scenes, handheld tools, mammals, fish, fruit and vegetables, reptiles, spiders, rocks and crystals, musical instruments, cars, insects, microbes, birds, weapons, flowers, prepared foods, clothes, and chairs.

In addition to the FFA, PPA, and EBA, recent work indicated a biased activation to handheld tools compared to animals in the middle temporal gyrus (middle temporal gyrus tool area or MTG-TA; Chao, Haxby, & Martin, 1999; Chao & Martin, 2000). There was a stronger activation for tools compared to animals, houses, and faces during a variety of semantic tasks, e.g. word reading/semantic retrieval task and the picture-naming task. In general, the authors concluded that the MTG was a category-related activation (not a category-specific region), and responses from the MTG mainly reflected the retrieval of semantic knowledge about tools. The activation profile in the MTG-TA was examined here, however, unlike the FFA, PPA, and EBA, the MTG-TA is not a category-selective region for visually presented stimuli; and thus it will not be discussed in detail here.

Second, this survey aimed to examine the prevalence of a categoryspecific region in a whole brain group average analysis (Investigation 2). This is an attempt to investigate whether or not other category-specific regions exist in the ventral stream. Finally, since a wider range of categories was used here, which included many animate and inanimate objects compared to previous experiments (Kanwisher, 1997a, 1999), this survey also aimed to examine if there is a general bias in activation to animate and inanimate objects (Investigation 3). The findings in the fMRI survey were published in *Cerebral Cortex* (Downing, Chan, Peelen, Dodds, & Kanwisher, 2006).

Interestingly, from Investigation 2, a region in the right lateral prefrontal cortex was found to elicit biased activation to faces, and this region was

investigated further in Chapter 3. Chapter 3 aimed to explore this strong facerelated prefrontal region, which was then labelled in this thesis as the right inferior frontal junction (rIFJ). This face-related activation is consistent with the findings from single unit studies. Specifically, O'Scalaidhe, Wilson, & Goldman-Rakic, (1997, 1999) had identified face-selective cells in monkeys' prefrontal cortex, during a non-working memory task and a working memory task. In line with their studies, Chapter 3 presents three investigations (Investigations 4-6) to examine the response properties of the rIFJ in parallel with the rFFA. Investigation 4 aimed to compare the activation in the rIFJ and rFFA in both free-viewing (non-working memory) and 1-back working memory tasks. Investigation 5, like many other imaging studies in object recognition, aimed to explore whether there was a part/whole difference for faces and other objects in the rIFJ. Investigation 6 aimed to investigate if the rIFJ could be driven by the presence of eyes, the most relevant part of faces, as they convey the emotions and intentions of others.

Finally, Chapter 4 discusses the findings of the thesis along with recent neuroimaging evidence then presents the limitations of these investigations, and suggestions for future studies.

# Chapter 2

## An fMRI Survey on Object Representations

#### **Overview**

This fMRI survey consisted of three goals, all aimed to extend our understanding of the organization of the human visual cortex and to address a broader question of how object categories are represented in the brain. First, this survey aimed to examine the specificity of the fusiform face area (FFA), parahippocampal place area (PPA), extrastriate body area (EBA), and middle temporal gyrus- the "tool area" (MTG-TA). The response profiles were examined in each of the above regions for 20 object categories, in order to determine whether each of the above ROI remains strongly biased to their most preferred categories (faces, scenes, bodies, or tools) in the presence of many nonpreferred categories. In addition, the response profile of the non-preferred categories in each of these areas could also be characterized. Similarly, Itier and Taylor (2004) used ERP to determine the gradient of sensitivity of N170 to faces compared to other objects. In their experiment, they used a wider range of object categories, namely upright and inverted faces, house, lions, tools, mushrooms, road signs, and textures, and they demonstrated the specificity of the N170 amplitude and shorter latency to faces.

By examining whether the category-selective regions responded robustly to only one category, this thesis should be able to shed light on the debate between the domain-specific and domain-general accounts. Second, the survey aimed to investigate the prevalence of such category-specific regions by testing whether there were category-specific regions other than the FFA, PPA, and EBA. This could increase our insight into the debate on cortical specialization in the

visual cortex; in particular, whether or not reliable focal activation can be found for other object categories on an individual subject level. Finally, by using a wider spectrum of object categories relative to previous studies (Kanwisher et al., 1997a, 1999; Tong et al., 2000), this survey also aimed to investigate if there was other general organizational principle in the ventral cortex, in particular if there is a general bias of activation for animate vs inanimate objects.

## The selection of twenty object categories in the fMRI survey

There is considerable accumulated evidence for neural specialization for object categories. The evidence ranges from neuropsychological studies in patients to fMRI studies in healthy subjects and patients. Apart from the selective visual impairment in the recognition of faces, landmarks, and scenes which have been reviewed earlier, there are frequent reports of dissociable impairment in visual recognizing and in naming of animate vs inanimate objects, such as impairment in recognizing animals relative to manufactured artefact categories (Carammazza & Shelton, 1998, Damasio et al., 1996; Tyler & Moss, 2001; Warrington & McCarthy, 1983; Warrington & Shallice 1984). Since these deficits are expressed as visual, semantic, and lexical in nature, and due to the fact that the present fMRI survey only examined the visual object representations of 20 object categories, thereby this survey only aimed to investigate the neural representation of animate vs inanimate categories in the visual domain.

The 20 object categories tested here were (see Figure 6, p. 61): human faces, human bodies (without heads), indoor and outdoor scenes, handheld tools, mammals, fish, fruit and vegetables, reptiles, spiders, rocks and crystals, musical

instruments, cars, insects, microbes, birds, weapons, flowers, prepared foods, clothes, and chairs. These categories were also chosen because of the reported category deficits associated with faces, scenes, tools, mammals, fruit and vegetables, gemstones/rocks, and musical instruments. It is also believed that gemstones/rocks, and musical instruments are usually impaired along with living things (McRae & Cree, 2002). Others categories were selected because of neuroimaging findings of category-specific activation, namely faces, scenes, and bodies. In addition, tools were included because it had been reported the MTG-TA elicited strong activation during tasks when subjects were required to retrieve semantic knowledge for tools (Chao et al., 1999, 2000). Some categories were selected because they were used in a picture naming task used in neuropsychological testing in which familiarity and visual complexity within each category were similar, e.g. animals, insects, birds, fruit, vegetables, foods, body parts, cars, household tools, clothing, musical instruments, and chairs (furniture) were the categories used and developed by Bunn, Tyler and Moss (1998).

In this fMRI survey, twelve healthy subjects were scanned and 20 object categories were presented visually. There were three types of analyses to explore the data set in the fMRI survey. These analyses aimed to achieve three goals, which have been mentioned earlier. Specifically, Investigation 1 was conducted to examine the specificity of the FFA, PPA, EBA, and MTG-TA. In this investigation the FFA, PPA, EBA, and MTG-TA were localized in each subject and the activation profiles were examined. Investigation 2 was conducted to examine the prevalence of category-specific regions. In this investigation a group

average whole brain analysis was performed which aimed to identify other category-selective regions. Investigation 3 was conducted to explore if there is a general division across animate and inanimate objects. Here, a group average whole brain analysis was carried out.

#### **General methods**

#### fMRI survey

## **Participants**

Twelve healthy adult volunteers were recruited from the University of Wales, Bangor community. All participants had normal to corrected-to-normal vision. Participants satisfied all requirements for volunteer screening, completed a consent form provided by Ysbyty Gwynedd, and gave informed consent approved by the School of Psychology at the University of Wales, Bangor, and the North West Wales Health Trust. The purpose of the investigation, procedures, and potential risks were explained. They were allowed to withdraw or refuse participation without penalty at any time of the scan session. The experimenter debriefed the participants after the scan session, and participants were compensated at £20 per session for their participation.

#### Stimuli

20 object categories were presented (see Figure 6, below, and Appendix Figure A1 for more samples, p. 239), which were divided into three sets. Set 1 included faces, human bodies without heads, scenes, and tools. Set 2 included

images of mammals, fish, fruit and vegetables, reptiles, spiders, rocks and crystals, musical instruments, and cars. Set 3 included insects, microbes, birds, weapons, flowers, prepared food, clothes, and chairs. Forty full colour images (400 x 400 pixels) were used for each category, which were divided into two stimuli versions. One version was presented in half of the scans, and another one for the other half.

All stimuli were presented on a white background by an Apple Macintosh iBook laptop, running Psychophysics Toolbox package (Brainard, 1997) in Matlab (The Mathworks, Inc.). Images were projected onto a screen positioned either near to the feet of the participants or behind the scanner. Participants viewed stimuli through an angled mirror that was attached to the head coil.

Chapter 2- fMRI Survey



Figure 6: Sample stimuli from the twenty object categories fMRI survey. From the top row, from left to right: birds, bodies, cars, microbes, and chairs. Second row from top: clothes, faces, fish, and flowers, prepared food (food). Third row from top: insects, mammals, musical instruments (instruments), reptiles, and rocks and crystals (crystals). Bottom row: scenes, spiders, tools, fruit and vegetables (fruit & veg), and weapons (see Figure A1 for more sample stimuli, Appendix p. 237).

## **Design and procedure**



Figure 7: Design and presentation order of blocks of condition for set 1. Conditions are represented in different colours and dots represent blocks of fixation (for similar figures of sets 2 & 3, see Figures A2 & A3, p. 240-241).

The fMRI survey was a blocked-design experiment. There were twelve runs for eight participants. Each set was tested four times, and scans for the three sets were interleaved to reduce adaptation effect to stimuli. Within each run there were twenty-one 15-sec blocks. Blocks 1, 6, 11, 16, 21 were a fixation only baseline condition. Each of the remaining blocks comprised presentation of 20 exemplars from a single category. There were two order versions. The first half and second half of one version were swapped to create the second version. The order of blocks was symmetrically counterbalanced within each version, so that the first half of each version was the mirror order of the second half. The result is that the mean serial position of each condition was equated. Within a block, each image was presented for 300 msec, with an ISI of 450 msec between images, thus each run lasted for 5 minutes and 15 second. The stimuli in each block (20 images) were randomly selected. Participants were instructed to view the stimuli passively while remain fixated to the centre of the screen.

Four participants, due to fatigue or technical problems, were tested without completing all the scans (these subjects had performed 7-10 runs), but they all had at least two runs for each set.

## **Image acquisition**

Functional images were acquired using a 1.5T Philips scanner, and a birdcage head coil was used in the fMRI survey. Functional images were acquired using an EPI sequence (T2 weighted, TR=3000msec, TE=50msec, flip angle =  $90^{\circ}$ ). 30 slices, FOV = 240, inplane = 240/64 = 3.75, 64 x 64 in-plane matrix, 4 or 5mm thickness/slice, and no gap, which covered the whole brain and most of the cerebellum. A high resolution T1 anatomical scan (1mm x 1mm x 1.3mm) was acquired.

#### Data preprocessing and analysis

Pre-processing of data and statistical analyses were performed using Brain Voyager 4.9 (Brain Innovation, Maastricht, The Netherlands). Three dummy volumes were acquired before each scan in order to reduce the effect of T1 saturation.

Pre-processing of functional images included: 3D-motion correction of functional data using trilinear interpolation, temporal high pass filtering (0.006Hz cutoff), and spatial smoothing with a Gaussian kernel (full width, half maximum 6mm). Functional data were manually co-registered with threedimensional T1 scans (1mm x 1mm x 1.3 mm resolution), and subsequently resampled to isometric 1mm x 1mm x 1mm voxels with trilinear interpolation. The 3D-scans were transformed into Talairach space, and the parameters for this transformation were then applied to the co-registered function data.

For multiple-regression analyses in Brain Voyager, predictors were generated for each condition. The event time series for each condition were convolved with a model of hemodynamic response. Voxel time series were znormalized for each run.

#### Methods

#### **Investigation 1**

## **Region of interest analysis**

The aim of this investigation was to test the level of specificity of the FFA, PPA, EBA, and MTG-TA to their most effective categories, and the profiles of response to the non-preferred categories in each of these areas were also revealed.

## Split-half method

A split-half method was used to define the regions of interest. The data of each individual participant, according to the order version, was divided into two sets. Runs with order version 1 were used to define the ROIs and runs with order version 2 to estimate the responses of the ROIs across conditions, and vice versa. This procedure ensured that all data contributed to the analysis, and that the data was independent from that used for ROIs definition. This method also prevented an overestimation of responses for the positively weighted category. When a robust ROI could not be identified with both halves of the data, the ROI was defined by the one half analysis. The average of both halves was computed, and all data were submitted to a paired-samples t-test, and the responses between the most-effective category and the second most-effective category were compared.

#### **ROI** definition

The ROIs were defined by the following contrasts: A subtraction of faces minus all other categories was used to define the right FFA, bodies minus all

other categories was used to define the bilateral EBA, scenes minus all other categories was used to define the bilateral PPA, and tools minus all other categories was used to define the left MTG-TA. The most activated voxel in each region was identified within a restricted part of the cortex (based on previously reported anatomical locations). The ROIs were defined as the set of contiguous voxels that were significantly activated within 9 mm in the direction of anterior/ posterior, superior/inferior, and medial/lateral direction of the most activated voxel. This procedure was used to ensure that the ROIs defined were segregated from nearby selective activations, and to ensure that each ROI contained a similar number of voxels. In addition, due to the fact that only half of the data were used to define a ROI in a split-half analysis, each ROI was therefore defined at a lenient threshold of uncorrected p < .05.

#### Details of statistical analysis

As mentioned above, betas were extracted from the FFA, PPA, and EBA, and were submitted to paired-samples t-tests. Beta (beta weights) is the value of the parameter estimated of an effect for a given condition (predictor in the design matrix), thus there are betas for each predictor in the design matrix. In fMRI data analysis using the general linear model (GLM), which is similar to a multiple regression analysis, the beta weight is the slope of the regression line for an effect. In other words, betas are estimated to fit the pre-specified model or design matrix as well as possible. In addition to the paired-samples t-tests, the responses to the non-preferred categories in each ROI were tested with a one-way ANOVA. This was done to identify whether there were differences in responses among the non-preferred categories
#### Methods

#### **Investigation 2**

# Whole brain analysis

The aim of this whole-brain analysis was to identify a possible new category-specific region. 20 separate contrasts using the group average model (n = 12) were constructed e.g. faces minus all the other 19 object categories. In order to increase the sensitivity of detecting a potentially category-specific region, a lenient threshold (random effect, uncorrected p < .001) was used. Unless specified, all contrasts were tested at the above threshold.

#### Criteria for selecting regions to report and further examination

The group average contrasts of each category against all 19 other categories produced activation across various regions of the brain. However, it is impractical to discuss and carry out further statistical analyses on all the clusters of activation. Therefore, the following criteria were established to select regions of interest:

Regions of interest were investigated further if they satisfied the following:

i) The size of the activation (uncorrected threshold of p < .001) was over 100 mm<sup>3</sup>.

ii) The ROIs demonstrated a strongest activation to the defining category in the contrast. This category-selectivity had to be true at both the group level and at the individual subject level. For example, in the contrast of prepared food-all, there was activation in the left superior frontal sulcus; prepared food was the defining category and elicited the strongest activation (most-effective category) in this region. This ROI was then analysed further. In some cases the defining category did not elicit the strongest activation, for example in the contrast of flowers-all there was activation in the right posterior occipital region but instead of flowers, prepared food elicited the strongest activation. This ROI was not analysed further.

Once a ROI met the above criteria of biased activation at the group level, betas for each participant were extracted from the group average model, and then the betas were analysed in a paired-sample t-test. The activation from the most-effective category had to be significantly stronger than the second most-effective category when tested with a paired-samples t-test. Note that this one category minus all the other categories comparison produced responses (betas) biased or maximum to the positively weighted category, thus the strong response for the defining category would not represent a genuine specialization for that category (type I error). Therefore, further examinations into the region's responses would be required. Nonetheless, this procedure was a quick and practical way to identify the location of potentially category-specific voxels.

**iii)** Those ROIs (potentially category-specific regions) which met the above criteria (i and ii) were tested with further analyses. A group split-half analysis would be performed to identify each of those ROIs with the contrasts of

"potential category" (the most-effective category of the potentially categoryspecific region) against all other categories (random effect, uncorrected p < .05).

In a group split-half analysis, the region's betas for each subject were extracted from the group average model. This group split-half analysis was performed with the data from the eight subjects who had performed all 12 runs in the scan session (a complete scan session). This is due to the fact that each of these subjects had equal runs for each order version, that is six runs of order version 1 and six runs for order version 2. Thus, the region could be easily defined by order version 1 and data extracted from order version 2. The region was defined by the same ROI definition approach as that in Investigation 1. If a ROI was genuinely category-selective, the defining category should give the strongest response and should be significantly different to the second most-effective category when tested with a pairedsamples t-test. If any ROIs remained selective to a certain category after the group-spilt half analysis then, those ROIs would be examined further by the split-half analysis within each individual subject (see methods of Investigation 1, p. 65). If any of those ROIs remained selective to a certain category after the group-spilt half analysis (see details in B), then those ROIs would be examined further by step iv or v.

iv) For those potentially category-selective regions that were located within the visual ventral stream, in the inferior-temporal cortex, split-half analyses within individual subjects were conducted with the contrast of the "potential category" against all other categories. Here, the same split-half analysis and

ROI definition methods were used as in Investigation 1 (p. 65-66). A pairedsamples t-test was conducted to determine whether the response to a "potential category" was strongest relative to all other categories. In many cases, the response to the most-effective category was compared with the response to the second most-effective category in the paired-samples t-test.

v) For some of those potentially category-selective regions located outside the visual ventral stream, follow-up experiments were conducted using stimuli that targeted the properties of those regions. This is due to the fact that the main focus of this investigation was to identify a new categoryspecific region in the visual ventral stream using visual stimuli, the use of the present testing approach (passive viewing/free-viewing) and the present visual stimuli might not be appropriate to test the response properties of those ROIs.

Further analyses were conducted on regions of interest that were found adjacent to or overlapping with those category-selective regions (FFA, PPA, and EBA). Details for further analyses are as follow:

Regions of interest adjacent to or overlapping with those categoryspecific regions FFA, PPA, and EBA were re-defined by a series of split-half analyses within each subject at the threshold of uncorrected p < .05 (for details of split-half analysis see p. 65). These activations could be the results of intersubject variability in the location of category-selective activations. That is, it is possible that at the group level, e.g. the activation to mammals coincides with the

EBA, but at the individual level, there may be a separate region that responds maximally to mammals.

#### Methods

#### **Investigation 3**

# Animate vs inanimate objects

The aim of this analysis was to identify a general division of activation for animate vs inanimate objects, thus a group contrast was performed. Animate objects (bodies, faces, mammals, birds, fish, insects, spiders, and reptiles) were contrasted with inanimate objects (tools, crystals, musical instruments, cars, weapons, prepared foods, clothes, chairs, and fruit & vegetables), at the uncorrected threshold of p < .001.

Specifically, the contrasts of animate-objects minus inanimate objects, and inanimate-objects minus animate objects were performed. A series of group split-half analyses were carried out to examine the response patterns in each of the ROIs (uncorrected p < .001). A lower threshold was used because only half of the data was used to define the ROIs here. Betas were extracted across all subjects from the ROI from this whole brain group average analysis. This group split-half analysis was performed with the data from the eight subjects who had performed all 12 runs in the scan session (a complete scan session), this group split-half analysis was the same as that in Investigation 2.

#### Results

#### **Investigation 1**

#### **Region of interest analysis**

#### FFA, PPA, EBA, and MTG-TA

The FFA, PPA, EBA, and MTG-TA were localized within each individual participant. The average spatial coordinates (in Talairach [x, y, z]) of the peak activated voxel of the ROIs across all participants and standard deviation (SD x, y, z) were reported here. Note that these response magnitudes were calculated from data that were independent of those used to functionally define each region, and therefore they provided an unbiased estimate of the magnitude of each region's response to each of the 20 stimulus categories. To investigate if each of the above ROIs is selective to the most effective category (faces, bodies, scenes, tools), paired-samples t-tests were conducted to test the difference between the most-effective category and the second effective category (see Tables 1 & 2, p. 76 & 77). The response profiles for the ROIs are shown in Figures 8-13.

The right FFA [37, -46, -16] (SD: 4, 7 5) was defined in 12/12 individual participants. There was a significant difference between the faces and bodies t (1,11) = 2.41, p = .034. From the same contrast (face minus all), the right occipital faces area (OFA) was also found in 10/12 participants. The OFA is not the focus of the present study, but the activation can be potentially interesting, thus its activation profile is presented in the Figure A5 (Appendix, p. 243).

The PPA was defined bilaterally [-22, -47, -4] (SD: 11, 3, 3), [23, -45, -5], (SD: 4, 6, 2) in 12/12 participants. In both left and right hemisphere, the differences between scenes and chair was significant in the left, t (1,11) = 8.969. p < .0001; and in the right hemispheres t (1,11) = 4.90, p < .0005.

The left and right EBA [-46, -69, 5] (SD: 5, 7, 5), [45 -67 5] (SD: 5, 7, 5) were defined in 12/12 participants. In the right EBA, the differences between bodies and mammals were significant t (1,11) = 2.439, p = 0.032. In the left EBA, the difference between bodies and mammals was non-significant t (1,11) = .169, p = 0.868, even the difference between bodies and birds (third most-effective category) did not reach significance, t (1, 11) = 1.15, p = .27. A significant difference emerged when bodies were compared with insects (sixth most-effective category), t (1,11) = 2.622, p = .024. The above results were consistent with previous evidence that body selectivity was stronger in the right EBA than the left (Downing et al., 2001).

The left MTG-TA [-49, -59, -4] (SD: 7, 8, 4) from the contrast of tools minus all other categories was defined in 12/12 participants. The difference between tools and instruments was non-significant t (1,11) = .506, p = .62. In a different analysis, the MTG-TA [-49 -59 -1] (SD: 6, 6, 5) (see Figure 14) was identified by the contrast tools, weapons, and musical instruments minus mammals, birds, and reptiles in 11/12 subjects. In this contrast, all of the positively weighted items were manipulable, inanimate objects, and all of the negatively weighted items were animals (Chao et al., 1999). In this comparison, there were no significant differences between fruit and vegetable (most-effective

category) and each of the next three preferred categories, namely musical instruments (t (1,10) = .327, p = .75), weapons (t (1,10) = .354, p = .73), and tools (t (1,10) = .62, p = .55).

The response pattern to non-preferred stimuli in each ROI was also tested with a one-way ANOVA. For example, the FFA was tested for significant differences among the responses to non-face stimuli. This analysis aimed to examine if the intermediate responses elicited by the less effective categories were uniform. Significant differences were found among non-preferred categories in all ROIs: right FFA, F(18,180) = 3.5, p < 0.001, left PPA, F(18,198) = 3.2, p < 0.001, right PPA, F(18,198) = 7.1, p < 0.001, left EBA, F(18, 198) = 10.0, p < 0.001, right EBA, F(18, 198) = 10.7, p < 0.001, and left MTG-TA, F(18,198) = 1.8, p < 0.05. These results suggested that there were diverse responses between the less effective categories in each ROI.

# Summary

This investigation demonstrated that faces, bodies, and scenes are the most-effective categories of those tested here for the right FFA, right EBA, and bilateral PPA respectively. Each of the above regions remained selective to their most preferred categories, even when the responses of those categories were compared with 19 other categories. The left MTG-TA, as defined by two different contrasts, elicited weak activation to tools and all 19 other categories, this suggests that this region is not specific to tools.

Table 1: Paired-samples t-tests results and mean Talairach coordinates of the FFA, PPA, EBA, and activation overlapping with them (right hemisphere).

			(*) significant results	Mean Coords		
Right hemisphere	N (out of 12)	Most-effective cate. > 2nd most-effective cate	t-test results	X	Y	Z
FFA						
Faces-[all others]	12	faces> bodies	t(1,11) = 2.41, p = .034*	37	-46	-16
near FFA						
Mammals-[all others]	12	faces> bodies	t(1,11) = 2.23, p = .046*	37	-48	-14
Bodies-[all others]	11	clothes > bodies	t(1,10) = .037, p = .97	39	-47	-14
PPA	E			(B)		
Scenes-[all others]	12	scenes > chairs	$t(1,11) = 4.90, p < .0005^{**}$	23	-45	-5
near PPA						
Chairs-[all others]	12	scenes > food	$t(1,11) = 7.14, p = .0001^{**}$	24	-45	-7
Prepared Food-[all others]	11	scenes> food	t(1.10) = .139, p = .89	27	-50	-10
		ana				
EBA						
Bodies-[all others]	12	bodies>mammals	t(1,11) = 2.439 p = .032*	45	-67	5
near EBA						
Mammals-[all others]	10	bodies>mammals	t(1,9) = 1.99, p = .07	43	-67	4
Clothes-[all others]	10	bodies>spiders	t(1,9) = 1.43, p = .185	49	-64	0
Birds-[all others]	11	bodies>mammals	t(1,10) = 3.94, p = .003**	44	-66	2
Right OFA						
Faces-[all others]	10	mammals>cars	t(1,9) = 0.302, p = 0.769	34	-76	-15

Table 2: Paired-samples t-tests results and mean	Talairach coordinates of the FFA, PPA, EBA, and activation overlapping with them (left hemisphere).

				Mean Coords		
I fo have law have	N (out of 17)	Mart offertive entry 2 and most offertive entry	(*) significant results	v	v	7
	N (OUL OF 12)	Most-effective cate. > 2nd most-effective cate.	t-test results	^	1	2
Fra Escas-[all others]	_	_	_	_	-	
near FEA						
Mammals_[all others]	-	-	-	-	-	-
Rodies-[all others]		_		-	-	
PPA						
Scenes-[all others]	12	scenes> chairs	$t(1,11) = 8.969, p < .0001^{**}$	-22	-47	-4
near PPA		2				
Chairs-[all others]	11	scenes> chairs	$t(1,10) = 4.84, p < .001^{**}$	-25	-50	-7
Prepared Food-[all others]	11	scenes> food	t(1,10) = 1.43, p = .182	-28	-54	-11
FRA						
Bodies-[all others]	12	bodies>mammals	t(1.11) = .169, p = .868	-46	-69	5
boules [all others]		bodies>insects (6th most-effective cate.)	$t(1.11) = 2.62, p = .024^*$	10000		
near FBA			~~ · · ·			
Mammals-[all others]	11	bodies>birds	t(1,10) = 1.561, p = .149	-46	-72	2
Clothes-[all others]	3 <b></b> 0	-		-	-	-
Birds-[all others]	11	bodies>mammals	t(1,10) = 1.298, p = .223	-43	-72	1
Left MIG-IA	10	tools>instruments	$t(1 \ 11) = 506 \ n = 622$	_49	_50	-4
100IS-[all others]	11	fruit > instruments	t(1,11) = .500, p = .022 t(1,10) = .327, p = .75	-49	-59	-1
[100IS + weapons + instruments] -[mammais + birds + reptiles]			(1,10) = .527, p = .75		55	-

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Figure 8. Mean betas of the response to each category in the fusiform face area (FFA). Each ROI was identified individually in each subject. The data sets used to define the ROIs were independent from those used to produce the values in this figure and in Figures 8-14 (splithalf analysis). Error bars reflect the standard error of the mean. Asterisks (\*) mark significant paired-samples t-tests results.

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Figure 9. Mean betas of the response to each category in the left parahippocampal place area (PPA). Each ROI was identified individually in each subject.

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Figure 10. Mean betas of the response to each category in the parahippocampal place area (PPA). Each ROI was identified individually in each subject.

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Figure 11. Mean betas of the response to each category in the left extrastriate body area (EBA). Each ROI was identified individually in each subject.

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Figure 12. Mean betas of the response to each category in the right extrastriate body area (EBA). Each ROI was identified individually in each subject.



Figure 13. Mean betas of the response to each category in the left middle temporal gyrus tool area (MTG-TA). Each ROI was identified individually in each subject.



Figure 14: Mean betas of the response to each category in the left middle temporal gyrus tool area (MTG-TA), defined by a contrast of [weapons+tools+musical instruments] – [mammals+birds+reptiles]. ROIs were identified individually in each subject. The data sets used to define the ROIs were independent from those used to produce the values in these figures.

#### Results

#### **Investigation 2**

#### Whole brain analysis

The aim of this whole-brain analysis was to identify possible new category-specific regions. Using the group average model (n = 12) twenty separate contrasts were performed e.g. faces vs all the other 19 object categories. All clusters of activation in the whole brain analysis were reported along with their responses to all 20 object categories in Supplementary Tables 1-4 (Appendix p. 244-248). In these tables, each row gives the volume of the cluster, the location of the centre of that cluster in Talairach coordinates, the maximum and mean T value for the region, the associated *p* value for the region as a whole, and the approximate anatomical location of that cluster. For each activated cluster, the last columns contain the responses to all 20 object categories, as measured by the regression analysis (beta weights).

This whole analysis did not identify any new category-specific regions in the ventral visual cortex, interestingly, a face-related activation was found in the prefrontal cortex in which there has been no previous direct evidence reported by fMRI literature in humans. This face related activation was further investigated in Chapter 3. The FFA, PPA, and EBA were strongly activated by faces, scenes and bodies respectively. These clusters of activation were expected, and because they have been examined thoroughly in Investigation 1, they would not be discussed in detail here. Interestingly, consistent with Investigation 1, tools minus all did not elicit robust activation in the left MTG-TA in this whole brain

analysis. Other activations for faces, bodies, scenes, and tools across the whole brain were reported here. In addition, some of the contrasts revealed activation near to or overlapping with the FFA, PPA, and EBA, and subsequently, a series of split-half analyses were conducted to examine the response profiles of those clusters of activation. These subsequent analyses aimed to examine if other object categories could also activate regions overlapped with the FFA, PPA, and EBA reliably and strongly within each individual subject. In addition, a number of frequently reported activations within and outside the visual cortex had also been identified by the whole brain analysis, and their response profiles will be discussed here.

#### Activations near to and overlapping with the FFA, PPA, or EBA

In the whole brain group analysis (see figures 15-28), mammals elicited activation overlapping with the right FFA. Bodies also produced activation overlapping with the right FFA. Chairs, and prepared food elicited activations overlapping with the bilateral PPA. Birds, and clothes produced activations overlapping with the right EBA, and mammals elicited activation overlapping with bilateral EBA.

To examine the above regions, a series of split-half analyses were conducted to examine the response profiles of these regions (Tables 1 & 2, p. 76 & 77). Each region was defined within each subject, and betas from individual subjects were extracted, and the average across all subjects was calculated. In each region paired-samples t-test was performed to compare the responses between the most-effective category and the second most-effective category.

Apart from the contrast of bodies-all, in which the activation nearby the FFA also responded strongly to clothes, bodies, and faces, in all the other comparisons, the most-preferred category was always the most-effective category: faces was the most-effective category in the region overlapping the right FFA, scenes was the most-effective category in the regions overlapping bilateral PPA, and bodies was the most-effective category in the regions overlapping bilateral EBA. The above results demonstrated that even when the regions were defined with the less effective categories, faces, scenes, and bodies remained the most-effective categories in the regions nearby and overlapping with the FFA, PPA, and EBA.

#### Split-half analysis for activation near to and overlapping with the right

**FFA:** From the contrast of mammals-all, the right cluster was identified in 12/12 participants. The average coordinate of the peak voxel was [37, -48, -14] (SD: 4, 6, 5). The difference between faces (most-effective category) and bodies (second most-effective category) was significant t (1, 11) = 2.23, p = .046. From the contrast of bodies-all, the right cluster was identified in 11/12 participants, average peak coordinate was [39, -47, -14] (SD: 4, 7, 5). The difference in between the most-effective category (clothes) and second most-effective category (bodies) was non-significant, t (1, 10) = 0.037, p = .97, between clothes and faces (third most-effective category) was non-significant t (1, 10) = .36, p = .72, and between bodies and faces was also non-significant t (1, 10) = .37, p = .72.

# Split-half analysis for activations near to and overlapping with the bilateral **PPA:** From the contrast of chairs-all, a bilateral cluster was identified. The right

cluster was found in 12/12 participants, average peak coordinate was [24, -45, -7] (SD: 4, 7, 3). The left cluster was found in 11/12 participants, the average peak coordinate was [-25 -50 -7] (SD: 4, 5, 4). In the right, scenes elicited activation significantly stronger than food, t (1,11) = 7.14, p = .0001. In the left, scenes also elicited activation significantly stronger than chairs, t (1, 10) = 4.84, p < .001. From the contrast of food-all, the right clusters were found in 11/12 participants, the average peak activation was [27, -50, -10] (SD: 3, 9, 4). 11/12 participants had activation in the left, the average peak activation was [-28, -54, -11] (SD: 5, 6, 4). In the right, the difference between the most-effective category (scenes) and the second most-effective category (food) was non-significant, t (1,10) = 1.93, p = .89. In the left, scenes was the most-effective category, and food was the second most-effective category, but the difference between them

#### Split-half analysis for activation near to and overlapping with the EBA:

From the contrast of mammals-all, bilateral clusters were found. The right cluster was found in 10/12 participants [43, -67, 4] (SD: 5, 6, 6), and the left cluster was found in 11/12 participants [-46, -72, 2] (SD: 5, 7, 4). In the right, bodies was the most-effective category, but the difference between bodies and mammals (the second most-effective category) was non-significant, t (1, 9) = 1.99, p = .07. In the left, the difference between the most-effective category (bodies) and the second most-effective category (birds) was non-significant, t (1,10) = 1.56, p = .149. From the contrast of birds-all, bilateral clusters were found in all 11/12 participants, the average peak coordinate in the right was [44, -66, 2] (SD: 3, 4, 3), and in the left was [-43, -72, 1] (SD: 6, 4, 6). In the right, the response from

the most-effective category bodies was significantly different to the response from the second most-effective category mammals, t(1,11) = 3.94, p = .003. In the left, the difference between the most-effective bodies and the most-effective category mammals was also non-significant, t(1,11) = 1.30, p = .22. From the contrast of clothes-all, the right cluster was identified in 10/12 participants [49, -64, 0] (SD: 5, 9, 4), again bodies was the most-effective category, and the difference between bodies and the second most-effective category spiders was non-significant, t(1,9) = 1.43, p = .185.

# Figures 15-28: Regions of interests near to and overlapping with the FFA, PPA, or EBA



Figure 15: Activation for faces, bodies, and mammals, all activated regions overlapping the fusiform region. An uncorrected threshold was used to define the above contrasts: facesall, p < .001, and for mammals-all and bodies-all, p < .0001.

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Figure 16. Mean betas of the response to each category near to and overlapping with the fusiform face area (FFA), the region was defined by the contrast of mammals-all. Each ROI was identified individually in each subject. The data sets used to define the ROIs were independent from those used to produce the values in this figure (split-half analysis). In figures 16-27, error bars reflect the standard error of the mean. Asterisks (\*) mark significant paired-samples t-tests results.



Figure 17. Mean betas of the response to each category near to and overlapping with the fusiform face area (FFA), the region was defined by the contrast of bodies-all. Each ROI was identified individually in each subject. The data sets used to define the ROIs were independent from those used to produce the values in this figure (split-half analysis).

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[23 -48 -10]



Figure 18: Activation for scenes, chairs and food, all activated regions overlapping the parahippocampal region. An uncorrected threshold was used to define the above contrasts: Scenes-all, p < .0001, and for Chairs-all and Food-all, p < .001.



Figure 19: Mean betas of the response to each category near to and overlapping with the left parahippocampal place area (PPA), the region was defined by the contrast of bodies-all. Each ROI was identified individually in each subject. The data sets used to define the ROIs were independent from those used to produce the values in this figure (split-half analysis).



Figure 20: Mean betas of the response to each category near to and overlapping with the right parahippocampal place area (PPA), the region was defined by the contrast of chairsall. Each ROI was identified individually in each subject. The data sets used to define the ROIs were independent from those used to produce the values in this figure (split-half analysis).



Figure 21: Mean betas of the response to each category near to and overlapping with the left parahippocampal place area (PPA), the region was defined by the contrast of prepared food-all. Each ROI was identified individually in each subject. The data sets used to define the ROIs were independent from those used to produce the values in this figure (split-half analysis).

Betas



Figure 22: Mean betas of the response to each category near to and overlapping with the right parahippocampal place area (PPA), the region was defined by the contrast of prepared food-all. Each ROI was identified individually in each subject. The data sets used to define the ROIs were independent from those used to produce the values in this figure (split-half analysis).



[39 -71 -1]



Figure 23: Activation for bodies, birds, clothes, and mammals, all activated regions overlapping the extrastriate body area (EBA). An uncorrected threshold was used to define the above contrasts: Bodies-all, p < .0001, and for Birds-all, Clothes-all, and Mammals-all, p < .001.

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Figure 24: Mean betas of the response to each category near to and overlapping with the left extrastriate body area (EBA), the region was defined by the contrast of mammals-all. Each ROI was identified individually in each subject. The data sets used to define the ROIs were independent from those used to produce the values in this figure (split-half analysis).



Figure 25: Mean betas of the response to each category near to and overlapping with the right extrastriate body area (EBA), the region was defined by the contrast of mammals-all. Each ROI was identified individually in each subject. The data sets used to define the ROIs were independent from those used to produce the values in this figure (split-half analysis).



Figure 26: Mean betas of the response to each category near to and overlapping with the right extrastriate body area (EBA), the region was defined by the contrast of clothes-all. Each ROI was identified individually in each subject. The data sets used to define the ROIs were independent from those used to produce the values in this figure (split-half analysis).

Betas

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Figure 27: Mean betas of the response to each category near to and overlapping with the left extrastriate body area (EBA), the region was defined by the contrast of birds-all. Each ROI was identified individually in each subject. The data sets used to define the ROIs were independent from those used to produce the values in this figure (split-half analysis).
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Figure 28: Mean betas of the response to each category near to and overlapping with the right extrastriate body area (EBA), the region was defined by the contrast of birds-all. Each ROI was identified individually in each subject. The data sets used to define the ROIs were independent from those used to produce the values in this figure (split-half analysis).

#### Activations for faces, bodies, scenes, and tools

Apart from the FFA, PPA, and EBA, faces, scenes, and bodies also elicited strong activation in other regions of the brain. Faces-all elicited activation in the right anterior insula, dorsal precentral gyrus, inferior frontal sulcus/gyrus, posterior superior temporal sulcus (STS, e.g. Puce & Perrett, 2003; Allison et al., 2000; Perrett & Emery, 1994; Perrett et al., 1992), and the precentral sulcus. Bodies-all elicited activation in the right medial fusiform gyrus. Scenes-all activated the left cuneus, regions in the left medial occipital lobe, right calcarine sulcus, and the bilateral region along the posterior intraparietal sulcus/transverse occipital suclus (TOS). Tools activated a small cluster of activation along the left post central gyrus, and right splenuim. Some of these will be further discussed below.

#### Other activations in the occipital ventral cortex

Scenes- all elicited activations in the bilateral posterior intra-parietal sulcus, which also known as the trans-occipital sulcus (TOS) this activation has previously been reported by Epstein et al., 2005; Grill-Spector, 2003; Levy et al., 2004; Spiridon et al., 2006. The coordinate of the centre of this activation was [25 -76 10; -25 -86 16]. The most-effective category for the right TOS was chairs. This region is not examined further as the most-effective category was not the defining category (see methods of Investigation 2, (B)). In the left TOS, scenes was the most-effective category, however, a paired-samples t-test showed that the response was not significantly different to that from the second most-effective category (food), t (1,11) = 2.02, p = .07.

In addition, scenes-all produced activation in the left cuneus [-11 -92 2], the response to the most-effective category scenes was significantly different to the response to the second most-effective category, crystals, t(1,11) = 2.21, p =.05. However, in the group split-half contrast of scenes-all, this region [-9 -88 -1] show a non-significant difference between scenes and the second most-effective category (crystal) t(1,11) = 1.69, p = .12. (Table 3, p. 109)

In the right hemisphere, prepared food-all elicited strong activation in the right posterior occipital lobe [24 -81 -8], the difference in response between the most-effective category (food) and the second most-effective category (scenes) was significant, t (1,11) = 3.27, p = .01. However, further group split-half contrast of food-all revealed that this region [28 -85 -4] responded strongest to spider, and that the difference between spider and the second most-effective category food did not reach a significant level, t (1,11) = .76, p = .47.

#### Other activations outside the ventral stream

The activation in the posterior superior temporal sulcus (STS; Puce and Perrett, 2003; Allison et al., 2000; Perrett & Emery, 1994; Perrett et al., 1992) was revealed by the group average whole brain contrast of faces-all [41, -46 15]. There was a significant difference between faces (most-effective category) and the second most-effective category bodies, t(1,11) = 3.47, p = .01. The group split-half contrast of faces-all [38, -45, 18] showed that, in the STS, faces produced the strongest activation, followed by bodies, and the difference between faces and bodies was significant, t(1,11) = 2.86, p = .02. In addition, there was a region at the junction where the inferior frontal gyrus meets the precentral sulcus [37 -1 35] this was also activated by the contrast faces-all. Interestingly, in single unit studies, O'Scalaidhe et al., (1997, 1999) had identified some faces selective cells in monkeys' prefrontal cortex when the monkeys were performing a working memory task or a non-working memory task. To pursue this finding, a series of investigations were conducted, and the findings were reported in Chapter 3, Investigations 4-6.

From the contrast of musical instruments-all, activation near Heschl's gyrus was found [-48, -32, 8]. The Heschl's gyrus is also known as the primary auditory area (Penhune, Zatorre, MacDonald, & Evans, 1996; Rademacher, Caviness, Steinmetz, & Galaburda, 1993; Zatorre, Belin, & Penhune, 2002). This may reflect activation of sound-processing regions by visual objects that are associated with musical instruments (Kraemer, Macrae, Green, & Kelley, 2005; Maeder, Meuli, Adriani, Bellmann, Fornari, Thiran, et al., 2001). Four subjects who did not participate in the present experiment were tested in an auxillary <sup>3</sup> experiment. To localize the temporal region's sensitivity to auditory stimulation, comparison was made between blocks of music with blocks where no music was played. However, the activation localized by the auxillary experiment was anterior to the activation produced by musical instruments-all, and the two activations did not overlap. The above finding suggests that visual presentation of musical instruments do not engage primary sound-driven cortical areas.

<sup>&</sup>lt;sup>3</sup> Localizer for the auditory cortex: Participants: Four other subjects who had not participated in the fMRI survey participated. Stimuli, design and procedures: This was a blocked design scan session, each block lasted for 30 seconds. Music (Bach S. Allegro 5: 26) played on and off alternately, the experiment started with music presentation. Image acquisition and data preprocessing: The same as those in the general method section of the fMRI survey (p. 63). Data Analysis: The group Heschl's gyrus was defined by contrasting music on condition and music off condition. The region were defined at the corrected threshold of p < .0001.

Weapons activated the superior parietal region [-23 -62 61], and consistent with its location in the dorsal visual stream, the activation could be associated with motor co-ordination (Milner & Goodale, 1993). In addition, tools produced two clusters of activation in the left post-central gyrus [-31 -43 41; -40 -33 41], the clusters fell near to the left motor-sensory activation [-33 -29 55] localized by the hand-wiggling task <sup>4</sup>. These findings appeared to be reflecting the association between the manipulability of the objects and the information associated with fine motor control. (Chao, et al, 2000; Handy, Grafton, Shroff, Ketay, & Gazzaniga, 2003; Grafton, Fadiga, Arbib, & Rizzolatti 1997).

# Potential category-selective regions

In this whole brain group average analysis, there were a few regions that initially appeared to be selective to the defining categories, however, group splithalf and paired-samples t-tests revealed that in most cases, the responses for the most-effective categories were not significantly stronger than the second mosteffective categories. The anatomical location of the ROIs, peak coordinates of the activations, paired-samples t-tests results, the most-effective and the secondmost effective categories of the ROIs are discussed below and summarized in Table 3, p. 109.

<sup>&</sup>lt;sup>4</sup> Hand-wiggling task: Participants: Within the same scan session, four of the twelve subjects in Investigation 1 had also participated in this localizer scan. Stimuli: Subjects were required to wiggle their left and right hands alternately. Design and procedures: In this blocked design scan session, each block lasted for 30 seconds. Participants performed left and right wiggling alternately, started with left hand wiggle. Image Acquisition, and data preprocessing: See general methods (p.63). Data Analysis: The group left motor sensory area was defined by the contrast right-hand-wiggle minus left-hand-wiggle, and the reverse contrast was used to define the right hand sensory area, both regions were defined at the corrected threshold of p < 0.0001(fixed effect). Activation from bilateral central sulcus was found.

From the whole brain contrast of clothes-all, activation was found in the left frontal pole [peak activation: -12, 66, 15]. Paired-samples t-test revealed that activation for the most-effective category (clothes) was significantly stronger than for the second most-effective category, insects, t(1,11) = 2.80, p = .017. However, in the group split-half analysis of clothes-all [-19, 66, 18], this region showed a non-significant difference between clothes and the second most-effective category birds, t(1,11) = .442, p = .667.

From the whole brain contrast of prepared food-all, it revealed several activations that initially appeared to be selective. In the left anterior hippocampus [-31, -16, -10], the difference between the most-effective category (prepared food) and the second most-effective category (insects) was initially significant, t (1,11) = 3.05, p = .011. The group split-half analysis revealed that the difference between food and insects in this region [-29, -16, -10] was non-significant, t (1,11) = 2.01, p = .07. In the left superior frontal sulcus [-18, 31, 54], the difference between prepared food (most-effective category) and the second most-effective category clothes was initially significant, t (1,11) = 2.27, p = .04. However, the group split-half contrast of prepared food-all revealed that the difference between prepared food and crystals in this region [-18, 32, 58] was non-significant, t (1,11) = 1.34, p = .21. In the right lateral central sulcus [41, - 30, -62], the difference between prepared food (most-effective category) and the second most-effective category fruit and vegetables was initially significant, t (1,11) = 2.179, p = .05. The group split-half analysis [45, -30, -61] showed that

the differences between prepared food and insects was non-significant, t(1,11) = .031, p = .77.

# Summary

The results from the whole brain analysis (Investigation 2) reported that there were no other category-selective regions in the ventral cortex. In addition, there were some activations elicited by non-faces, non-scenes, and non-bodies overlapping with the FFA, PPA, and EBA. Individual split-half analyses on the above activations had demonstrated that faces, bodies, and scenes were still the most-effective categories in these regions. Interestingly, in the whole brain analysis, there were some regions in the ventral stream initially showed selective responses to the defining categories, but a series of group split-half analyses showed that, apart from the right posterior STS, none of those regions showed genuine selectivity to the defining categories (see Table 3, below). Thus, this whole brain analysis has shown that category-specific regions are rare.

Table 3: Table shows the peak coordinates and paired-samples t-tests results of those potential category-specific ROIs from the group split-half analysis. Asterisk (\*) marks statistically significant results.

ROIs		X	Y	Z	t-tests results	Most > second most- effective category
L. frontal pole	Clothes - all	-19	66	18	t(1,11) = .442, p = .667	Clothes > Birds
R. post. STS	Faces -all	38	-45	18	$t(1,11) = 2.862, p = .015^*$	Faces > Bodies
L. ant. hippocampus	Food - all	-29	-16	-10	t (1,11) = 2.009, p = .07	Food > Insects
L. post. occipital	Food - all	-24	-82	6	t (1,11) = .582, p = .57	Food > Chairs
L. sup. frontal sulcus	Food - all	-18	-32	58	t (1,11) = 1.34, p = .207	Food > Crystals
R. lateral central sulcus	Food - all	45	-30	-61	t (1,11) = .301, p = .769	Food > Insects
R. post. occipital lobe	Food - all	28	-85	-4	t (1,11) = .754, p = .467	Spiders > Food
L. cuneus	Scenes-all	-9	-88	-1	t (1,11) = 1.693, <i>p</i> = .119	Scenes > Crystals

#### Results

#### **Investigation 3**

# Animate vs inanimate objects

A group average contrast (uncorrected t = 4.43, p < .001) was performed to test for a general "animate vs inanimate" division in visual cortical representations. As mentioned earlier two contrasts were performed, animateobjects minus inanimate-objects, and inanimate-objects minus animate-objects. The ROIs from the above contrasts were then defined by a series of group splithalf analyses. This section presented the response patterns, and the peak coordinates of the activations of the ROIs (Figures 29-37, p. 111-119).

There were several regions showing more activation to animate (bodies, faces, mammals, birds, fish, insects, spiders, and reptiles) than inanimate objects (tools, crystals, musical instruments, cars, weapons, prepared foods, clothes, chairs, and fruit/vegetables). Specifically, the bilateral mid fusiform gyrus [peak coordinates: -45, -48, -23; 35, -56, -15] and bilateral lateral temporal region [-51, -73. 0; 47 -64, 3], these regions partially coincided with the EBA and FFA in both hemispheres (Figure 29, upper panel). The activations elicited by the animate kinds appeared to be limited to areas already known to respond strongly to images of the bodies and faces of humans and, to a lesser extent, to other biological categories. On the other hand, weaker activations for the inanimate objects were also observed, which was consistent with the idea that representation of inanimate objects could be found in the FFA. For example,

Ewbank, Schluppeck, and Andrews (2005) reported fMRI-adaptation to repeated inanimate objects in the FFA, and their findings indicated that inanimate objects could contribute the activation in the FFA.

There were regions that elicited more activation to inanimate than animate objects (Figure 29, lower panel); they included the lingual/parahippocampal gyrus [-24, -58, -11; 20 -46, -8] (overlapping with the PPA) and the transverse occipital sulcus [-24, -85, 21; 26, -79, 6] (TOS), which also gave strong activation in the whole brain contrast of scenes-all. The activations generally elicited by inanimate kinds appeared to overlap with those activations generated by scenes, even when scenes were excluded from the inanimate minus animate contrast. Previous studies of the PPA have also shown that it responds very weakly to faces (Epstein & Kanwisher, 1998), and here the data showed that the PPA responded weakly to other biological stimuli as well. In sum, the data demonstrated a general bias of activation for animate categories in the FFA and EBA, and for inanimate categories in the PPA.

# Summary

This investigation revealed that there were general biases of responses to animate objects in the fusiform and lateral temporal region; however, inanimate objects also elicited weaker responses. There was a general bias of activation to inanimate objects in the parahippocampal and TOS regions, but animate objects also elicited weaker activation. These data are consistent with the findings that non-preferred categories are represented in those category-specific regions

(Ewbank et al., 2005; Haxby et al., 2001; Grill-Spector, 2006;). In summary, this investigation revealed a crude division of activation between animate and inanimate categories in the ventral cortex.





Left Hem.

Animate objects > inanimate objects



Inanimate objects > animate objects

Figure 29: Upper panel, activations in the bilateral mid fusiform gyrus (left), and bilateral lateral temporal region. Lower panel, activations in the bilateral parahippocampal gyrus (left), and bilateral transverse occipital sulcus (TOS). The contrasts were defined at the uncorrected threshold of t = 4.43, p < .001.



Figure 30: Mean betas of the response to each category in the left lateral temporal cortex, revealed by the contrast of animate-inanimate objects. The data sets used to define the ROIs were independent from those used to produce the values in this figure (group splithalf analysis). Error bars reflect the standard error of the mean.

Betas



Figure 31: Mean betas of the response to each category in the right lateral temporal cortex, revealed by the contrast of animate-inanimate objects. The data sets used to define the ROIs were independent from those used to produce the values in this figure (group splithalf analysis). Error bars reflect the standard error of the mean.



Figure 32: Mean betas of the response to each category in the left mid fusiform gyrus, revealed by the contrast of animate-inanimate objects. The data sets used to define the ROIs were independent from those used to produce the values in this figure (group splithalf analysis). Error bars reflect the standard error of the mean.



Figure 33: Mean betas of the response to each category in the right mid fusiform gyrus, revealed by the contrast of animate-inanimate objects. The data sets used to define the ROIs were independent from those used to produce the values in this figure (group splithalf analysis). Error bars reflect the standard error of the mean.



Figure 34: Mean betas of the response to each category in the left parahippocampal gyrus, revealed by the contrast of inanimate-animate objects. The data sets used to define the ROIs were independent from those used to produce the values in this figure (group split-half analysis). Error bars reflect the standard error of the mean.



Figure 35: Mean betas of the response to each category in the right parahippocampal gyrus, revealed by the contrast of inanimate-animate objects. The data sets used to define the ROIs were independent from those used to produce the values in this figure (group splithalf analysis). Error bars reflect the standard error of the mean.



Figure 36: Mean betas of the response to each category in the left TOS, revealed by the contrast of inanimate-animate objects. The data sets used to define the ROIs were independent from those used to produce the values in this figure (group split-half analysis). Error bars reflect the standard error of the mean.



Figure 37: Mean betas of the response to each category in the right TOS, revealed by the contrast of inanimate-animate objects. The data sets used to define the ROIs were independent from those used to produce the values in this figure (group split-half analysis). Error bars reflect the standard error of the mean.

#### **Chapter discussion**

This fMRI survey achieved three goals: First, responses in the categoryspecific regions (FFA, PPA, EBA) remain specific to the most-preferred category, each has elicited significantly stronger response to the most-effective category (faces, scenes, bodies respectively) than to the second most-effective category. However, instead of revealing an all-or-nothing response to the mosteffective category, there was a systematic gradation in responses from the mosteffective categories to the least effective categories in each region. It is therefore possible that non-preferred object categories that contain the same or similar features as the preferred category produce intermediate activation. In addition, the left MTG-TA responded weakly across all categories, this was expected, as the left MTG-TA is a tool-related area involved in storing semantic knowledge of tools and other manipulable objects (Chao et al., 1999, 2000), rather than a region highly responsive to the visual presentation of tools.

Second, no other strong category-specific regions were identified in the ventral stream. By testing the neural response to 20 different stimulus categories, this study has presented the broadest survey to date of category selectivity in the visual cortex. It demonstrates both the strong selectivity of a small number of category-specific regions and the scarcity of such regions in the visual stream.

Third, there was a general bias of activation for animate objects in the lateral region of the ventral cortex, and for inanimate objects in the medial

ventral cortex. All the above findings with respect to each of these goals will be discussed in turn below.

#### Selectivity in FFA, PPA, and EBA

In the right FFA, bilateral PPA, and right EBA, the responses to faces, scenes, and bodies respectively, were significantly greater than to their second most-effective categories. Thus, even when tested against a wide range of control categories, the FFA, PPA, and EBA exhibit strong biased responses to faces, scenes, and bodies. There were strong biased responses to the preferred categories even when some of categories were visually or semantically quite similar to these regions' most-effective categories. Furthermore, there was a systematic gradation in responses from the most-effective to the least-effective categories in each region. The findings suggest that substantial populations of neurons within these category-specific regions are tuned to respond specifically to one or more features present in images of faces, bodies, and scenes respectively.

The findings here are complementary to the research using other neuroimaging techniques in humans and non-human primates. fMRI and PET studies in humans revealed face-selective activation in the lateral posterior fusiform gyrus (or fusiform face area, FFA; Haxby et al., 1994; Kanwisher et al., 1997a; McCarthy et al., 1997; Schwarzlose et al., 2005). This region responded selectively to faces relative to hands, scenes and other common objects. Intracranial electrode recordings in epileptic patients also showed patches of neurons in the medial temporal lobe that fired selectively to faces and to landmarks (Quiroga, Reddy, Kreiman, Koch, & Fried, 2005). Intracranial ERP studies in humans also revealed face-specific potentials N200 (Allison, Puce, Spencer, & McCarthy, 1999; McCarthy, Puce, Belger, & Allison 1999; Puce, Allison, & McCarthy, 1999). The face-specific N200 signals were mainly found in the lateral region of the fusiform gyrus, and on the lateral surface of the temporal cortex near to the middle temporal gyri (Allison et al., 1999). Evidence from ERP studies also showed N170 responses for faces (Bentin et al., 1996; McCarthy et al., 1999). Itier and Taylor (2004), using an ERP paradigm, demonstrated the specificity of the N170 amplitude and shorter latency to faces with a wider range of object categories. Face-specific MEG response, the "M170" component, was also identified (Liu, Harris, & Kanwisher, 2002; Xu et al., 2005b), it is believed that this component corresponds to the N170 component in the ERP studies, and the N200 components in the intracranial ERP studies.

In non-human primates, fMRI and single unit studies also showed regional specialization for faces in the temporal lobe of macaque monkey (Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003; Tsao, Freiwald, Tootell, & Livingstone, 2006). In addition, Zangenehpour & Chaudhuri (2005) measured gene expression (*zif*268), and identified spatially distinct patches of faceselective neurons and object-selective neurons in monkey's inferotemporal cortex. Other researchers also reported face selectivity in monkey's superior temporal sulcus (Desimone, Albright, Gross, & Bruce, 1984; Perrett, Rolls, &

Caan, 1982; Perrett, Smith, Potter, Mistlin, Head, Milner, et al., 1985; Perrett, Oram, Harries, Bevan, Hietanen, Benson, et al., 1991; Pinsk, Desimone, Moore, Gross, & Kastner, 2005). Interestingly, Pinsk et al., (2005) reported that the region contiguous to the face-selective patch in the STS also responded strongly to body parts.

On the contrary, the category-related region MTG-TA did not exhibit selective activation for tools. In each of the two different contrasts used to localize the MTG-TA, activation for tools was weak and similar to the activation for other categories. Specifically, in many subjects, this posterior occipitotemporal region responded strongly to tools as well as other manipulable inanimate objects (musical instruments, and weapons). This is consistent with the idea that the MTG-TA is more responsive to semantic knowledge about the functions of tools and other manipulable objects (Chao et al., 1999, 2000).

# Intermediate responses to non-preferred categories in the FFA, PPA, and EBA

Within the FFA, PPA, and EBA, the responses to the non-preferred categories varied significantly. These regions did not respond in an all-or-none fashion to their preferred category, instead there was a systematic gradation in responses from the most-effective category to the least effective category. Thus, it is likely that non-preferred object categories that contain the same features as or similar features (visually and/or semantically) to the preferred category are likely to produce intermediate responses. Interestingly, the intermediate

responses elicited by some categories were strong enough to activate region overlapping with or near to the FFA, PPA, or the EBA in the group average whole brain analysis.

Specifically, results from Investigation 1 (split-half analysis) showed that the right EBA had responded strongly to human bodies, however, mammals, birds, reptiles, insects, spiders, and clothes, which were "body-like categories" also produced some intermediate activation in the right EBA. Thus, the response pattern in the EBA is consistent with the idea that neural populations in a category-specific region are specialized to the processing of a single feature or property (Tsao et al., 2006). This indicates that neurons in a category-selective region may also be tuned to other stimuli that are similar to the most-effective category.

Within each of those category-specific regions, neurons may represent detailed parametric information of the most preferred category, and when other categories also carry similar information; they also elicit intermediate activation (but the activation will still be weaker relative to the preferred category). Hence, featural similarity (it may be visual, semantic, or other factors) between the mosteffective category and the less effective category could contribute to the systematic gradation in responses. This idea is again most consistent findings in Investigation 2 (whole brain analysis) where non-human-body categories elicited activation near to and overlapping with the EBA. Specifically, birds,

clothes and mammals, which were visually similar to human bodies, had elicited responses near to and overlapping with the EBA.

However, it is also possible that other information other than visual features could also contribute to such graded responses. Bar and Aminoff (2003) proposed that activation in the PPA was correlated with the level of context associated with the stimuli. They claimed that the higher contextual level of an object, the higher response from the PPA. Thus, the activation in the PPA elicited by the contrasts of chairs-all and food-all could be related to a particular context associated with these stimuli. A speculation will be that a chair is associated with a place to sit, and prepared food is often associated with places to eat e.g. restaurants, leading to the intermediate responses in the PPA elicited by nonscenes categories.

In the FFA, contextual information (Cox, Meyers, & Sinha, 2004) associated with faces might have also contributed to the intermediate responses elicited by non-face categories. In particular, the strong activation evoked by bodies in the FFA found in Investigation 1, and the activation near to and overlapping with the FFA found in Investigation 2 could be related to the contextual association between faces and human bodies. The contextual link between faces and bodies is probably aroused because they both give important information about other people's identities, emotions, as well as intentions. However, it is unclear why faces did not elicit comparable strong activation in the EBA. Furthermore, mammals also produced strong activation overlapping

with the FFA, which could be due to the fact that mammals have bodies and faces.

The intermediate responses to the non-preferred categories in the FFA, PPA, and EBA, as well as the responses overlapping with those regions are consistent with several alternative organizing principles within the ventral cortex: i) There may be a systematically graded representation of category in terms of similarity in visual features. For example, biological object categories activated the FFA and the EBA. Body-like stimuli (e.g. birds, clothes, mammals) activated the right EBA strongly. This could reflect fine-tuning of neurons to visually similar categories (Saigal & Logothetis, 2002, Tsao et al., 2006). ii) It is likely that there are neurons that are selective to the "non-preferred categories", and these neurons are "buried" within the category-specific regions (Avidan, Hasson, Hendler, Zohary, & Malach, 2002; Grill-Spector, et al., 2006). iii) Another possibility is that some of the selective neurons have multiple representations of objects (Grill-Spector et al., 2006).

Due to the relatively poor spatial resolution in standard-solution fMRI, more direct evidence for a fine-scale object representation in the visual cortex could only come from other neuroimaging techniques with higher spatial resolution. For example, from intracranial electrode recordings in humans (Quiroga et al., 2005), from high-resolution fMRI scanning (1mm x 1mm x 1mm voxel size) (Grill-Spector et al., 2006) and from single unit recording in Monkeys (Tsao et al., 2006).

Recent work has attempted to disentangle the above possibilities in the FFA. The present survey and earlier studies found strong FFA activation (and adjacent cortex) to animals (Chao, et al., 1999; Kanwisher et al., 1999), birds (Gauthier et al., 2000; Grill-Spector et al., 2004; Xu 2005a), and to human bodies (Peelen & Downing, 2005b; Spiridon et al., 2005). Peelen and Downing (2005b) argued for overlapping but functionally separate selective representations of the human body and face in the posterior fusiform gyrus. This claim is further supported by high-resolution fMRI (Schwarzlose, Baker, & Kanwisher, 2005), specifically, this study showed very small, distinct, adjoining patches of cortex that are selective for either faces or human bodies in the mid fusiform region. The implication is that using typical voxel resolutions, the small clusters of body-selective activation was "buried" within a larger cluster of face-selective activation in the FFA.

Most recently, Grill-Spector et al., (2006) demonstrated that intermediate responses for non-preferred categories reflect a fine-scale functional organization of the FFA. Specifically, using high-resolution fMRI, they aimed: First, to identify the source or the origin of intermediate responses in the FFA. Second, to test if all the neurons in the FFA respond strongly and selectively to faces, that is, to examine whether the FFA is a "homogeneous" region for faces. Third, they aimed to examine the spatial distribution of the non-preferred activation in the FFA. Their results showed a heterogeneous structure within the FFA where pockets of highly selective face neurons were intermingled with patches of highly selective non-face neurons (animals, car, and sculptures). Nonetheless, the population of face-selective neurons was higher than that of non-face selective neurons. Interestingly, some face-selective neurons were also animal-selective, which is consistent with the finding that the FFA also responded strongly to human bodies and mammals (Investigations 1 & 2). However, Grill-Spector et al's findings have recently been challenged by Baker, Hutchison, and Kanwisher (2007), and Simmons, Bellgowan, and Martin (2007). These two groups of researchers have identified flaws in Grill-Spector et al's analyses. Due to these challenges, Grill-Spector, Sayres, Ress (2007) later re-analyzed their original data to address their errors. Based on their new analyses, Grill-Spector et al., (2007) stated that the FFA was a heterogeneous region but the selectivity for the non-face objects was lower than originally reported. Details of Baker et al, (2007) Simmons et al., (2007), and Grill-Spector et al., (2007) will be discussed in the General Discussion (see Corrigenda, Chapter 4, p. 197).

Another way to examine the functional significance of activation in the visual cortex is to establish the causal relationship between neural activity and behavioural performance. In line with this idea, recent studies have correlated activity in the FFA with the detection and identification of faces on a trial-by-trial basis (Grill-Spector et al., 2004). Others have used TMS to measure the behavioural performance after disrupting the neural activity in the category-specific region (Urgesi et al., 2004). Most recently, instead of interrupting the process of object recognition in the visual cortex, Afraz, Kiani, & Esteky (2006) applied microstimulation to the face-selective clusters in monkeys' inferior temporal cortex in order to examine the causal relationship between neural

activity and behavioural performance. In their experiment, microstimulation was applied when monkeys were performing a face categorization task. In this task, the monkeys viewed degraded faces and degraded non-face objects, and they had to respond by making an eye movement to the left or right when they believed the degraded stimulus was a face. Afraz et al., (2006) found that microstimulation to the face-selective clusters had strongly biased monkeys' choices to identify degraded the objects as faces, whereas microstimulation to the non-face clusters did not. The above findings support the view that responses in faces-selective regions in the ventral region are tightly linked to the perception of faces.

# Do other category-selective regions exist?

Apart from the FFA, PPA, and EBA, the survey did not identify any other category-selective regions in the visual cortex. There are several possibilities why category selectivity might have been missed with the present techniques. One possibility is that other category-selective regions may exist at a grain that is below the voxel resolution used here (Grill-Spector et al., 2006; Schwarzlose et al., 2005). The second possibility is that diffuse networks of neurons could in principle work coherently to represent a particular class of visual stimulus (Haxby et al., 2001). Finally, the selection of categories in this survey could influence the sensitivity of identifying new category-selective regions. It is also possible that functional and anatomical specialization in the ventral cortex could be revealed by different ways of grouping object categories, or by different task demand. Nonetheless, given these limitations, the present fMRI survey represents

the most comprehensive search for such regions to date, as most previous work has only compared a small handful of stimulus types within subjects.

# Animate vs inanimate objects

According to the eccentricity account (Levy et al., 2001), stimuli that required fine grain visual processing (e.g. faces) tend to activate the lateral region of the visual cortex strongly (central bias representation), whereas stimuli that required coarse visual processing (e.g. scenes) tend to activate the medial region (peripheral bias representation). This pattern of activation coincides and overlaps with the activation patterns elicited by animate vs inanimate objects, where animate categories strongly activated the lateral region of the ventral cortex, overlapping with the fusiform region, and inanimate categories strongly activated the medial region of the ventral cortex, overlapping with the parahippocampal region. It is possible that the crude animate vs inanimate division of activation could be associated with the eccentricity mapping, which in turn could indicate that this general division may be linked to acuity demand in visual processing (Hasson et al., 2002; Levy et al., 2001; Malach et al., 2002).

One speculation is that animate objects such as faces and bodies contain important and relevant information, which required detail visual processing. Subtle changes on faces, and movements by body (gait) can convey a lot of information. For example, local intrinsic information such as eyes, nose, and mouth on a face, direction and posture of bodies, could all indicate identities, emotions, and intentions of others, and hence require more accurate and high

resolution processing and lead to a central bias representation. On the other hand, inanimate objects like chairs and prepared food require coarser visual processing relative to faces and bodies, and thus lead to a peripheral bias representation. It had been shown that letter strings and words, which required high resolution visual analysis, also elicited stronger activation in the lateral region of the ventral cortex (Hasson et al., 2002). Therefore, the strong responses in the lateral and ventral regions evoked by animate and inanimate objects respectively, is more likely to be associated with the acuity demand, rather than the level of mobility of an object category per se.

The hypothesis of acuity demand in eccentricity mapping is also compatible with the idea that visual object categorization involves "basic" and "subordinate" levels of categorization (Gauthier et al., 1997; Malach et al., 2002). It is believed that basic level (e.g. a bird vs a dog) required a coarserresolution representation of objects, whereas subordinate level (e.g. a sparrow vs a pigeon) required a fine-resolution representation (Tyler, Stamatakis, Bright, Acres, Abdallah, Rodd, et al., 2004). Hence, Gauthier et al's (2000) findings of stronger FFA activation in bird experts to birds than to cars could also be contributed by the central bias visual representation in the lateral/mid fusiform region.

#### Conclusions

The present fMRI survey investigated the prevalence and specificity of category-selective regions in the human visual cortex. First, there was significant category-bias of responses in the FFA, PPA, and EBA, for faces, scenes, and bodies relative to the remaining 19 categories. In MTG-TA, a weaker bias was found for inanimate manipulable objects (e.g. tools) relative to animals. Furthermore, the FFA, PPA, and EBA showed significant and systematic variations in their responses to the non-preferred object categories.

Second, apart from the FFA, PPA and EBA, there were no other strong category-selective regions in the visual cortex. Several categories produced significant activations near to and overlapping with the FFA, PPA, or EBA. However, in each of these regions, the most preferred categories (faces, scenes, and bodies) were also the most-effective categories even when tested at the individual-subject level. Hence, intermediate responses are likely to reflect interleaving but dissociable set of neurons' responses to visually or semantically similar categories (Avidan et al., 2002; Grill-Spector et al., 2006).

Third, there was a general bias of responses to animate vs inanimate categories in the lateral fusiform gyrus and parahippocampal gyrus respectively, and such a crude division in activation could possibly be associated with the eccentricity mapping. In summary, this study represents the broadest survey to

date of category selectivity in the visual cortex. The results demonstrate both the strong selectivity of a small number of regions, and the scarcity of such regions.

# Chapter 3

# Face Selectivity in the Human Prefrontal Cortex

# Chapter 3-Face Selectivity in the Prefrontal Cortex

In the fMRI survey in Chapter 2, faces elicited activations in the mid fusiform gyrus, occipital fusiform gyrus, superior temporal sulcus, and interestingly the lateral region of the prefrontal cortex (PFC). Specifically, this prefrontal face-related activation is located at the junction where the pre-central sulcus meets the inferior frontal sulcus; it has therefore been labelled the right inferior frontal junction (rIFJ) [group-averaged peak voxel from Investigation 4 (free-viewing task): 41, 4, 36, Figure 38 below] throughout this thesis. Intriguingly, to date there has been no direct evidence in the literature for a face-selective region in the human PFC. The motivation for conducting a series of follow-up studies on the PFC mainly comes from single unit recording studies in non-human primates (O'Scalaidhe et al. 1997, 1999). Their research identified clusters of face-selective cells in the prefrontal region of monkeys that had been trained with a working memory (WM) task and in monkeys trained with a non-WM task. This chapter aimed to further investigate the response properties of this prefrontal region in humans. Three investigations were conducted in order to explore the response properties of the human PFC to faces and other objects. Apart from O'Scalaidhe et al's (1997, 1999) studies, recent neuroimaging work reporting the lateral prefrontal cortex's involvement in face WM and non-WM tasks will be reviewed below.

#### Face-selective cells in monkeys' prefrontal cortex

In macaques, O'Scalaidhe et al., (1997, 1999) reported a small percentage of highly face-selective neurons in the PFC. These neurons were found in a localized and restricted part of the frontal cortex, specifically, the inferior convexity of the prefrontal cortex (IFC). The IFC had the highest percentage (~5%) of face-selective neurons relative to other frontal regions. Fewer face-selective neurons were found in

the lateral orbital sulcus, and none were found in the principal sulcus or the superior frontal convexity (see below, Figure 38 B for the recording site in O'Scalaidhe et al's studies (1997, 1999)).



Figure 38: (A) IFJ activation from the free-viewing task (green, t = 3.91, uncorrected p < .0001) overlapping with IFJ's responses from the 1-back task (orange, t = 3.91, uncorrected p < .0001). The activation was defined by the contrast of faces-tools. Activation from an eye movement experiment activated the Frontal Eye Field (FEF) (light blue, t = 15.60, uncorrected p < .00001), which occupied a distinctively different region to the IFJ. (B) The circled region indicates where face-selective cells were found in a single unit study of monkeys' prefrontal cortex. The image was reproduced from O'Scalaidhe et al., (1997).

Using a wider range of stimulus types, O'Scalaidhe et al., (1997, 1999) had subsequently tested the response properties of these face-selective cells in the IFC.

First, these cells were tested with local features of faces. They found that responses to pictures of faces were robustly stronger than to scrambled faces. These face-selective neurons remained selective to faces relative to other familiar objects and items with emotional or motivational significance. These stimuli included pictures of food, leather gloves, snacks etc. Furthermore, cells in the IFC also responded robustly to monkey faces with different facial expressions and different identities. They tested monkeys with pictures of two different monkeys (different identity), and with various facial expressions such as neutral, threatening, and yawning. Eight faces-selective neurons showed strong responses for the above conditions. Specifically, seven of these neurons demonstrated an effect of identity, and five showed an effect of expression, and five other neurons showed an effect of both identity and expression. In summary, O'Scalaidhe et al. (1997, 1999) revealed that there was a distinctive population of neurons which produced selective firing to face stimuli, but elicited very weak or even no response to non-face items.

Face-selective cells in the IFC were then tested with a WM task and a non-WM task (O'Scalaidhe et al.,1997). In the WM task, monkeys had to first fixate on the fixation cross, then the cue (face or object) appeared, followed by a delay period with a fixation cross at the centre. The fixation disappeared, and monkeys had to perform a memory guided saccade based on the identity of the cue (the cue was assigned to either a leftward or rightward saccade). Monkeys were also tested with two colour stimuli (blue and yellow), two colour pattern stimuli, two peripherally presented spatial cues, and one monkey was also presented with two faces. In the non-WM task, monkeys had to maintain fixation throughout the trial. First, a pre-stimuli fixation cross appeared, then a visual stimulus (face or object) appeared, followed by
a post stimulus fixation cross. Face-selective activity was observed during the delay period when monkeys performed the WM task, as well as during the post-stimulus fixation period when monkeys performed the non-WM task. This result suggested that face-selective cells in the IFC were insensitive to WM manipulation.

Interestingly, similar to the receptive field organization in the ventral visual cortex, where neurons in the ventral regions are most responsive to foveal stimulation (Desimone & Gross, 1979; Gross, Rochamir, & Bender, 1972; Rodman, Scalaidhe, & Gross, 1993), O'Scalaidhe et al., (1997, 1999) also found a receptive field organization in the PFC. Specifically, some face-selective cells in the IFC were tested with their optimal stimuli at nine locations. Each stimulus was presented centrally, and also at eight other locations, 13 degrees away from the central fixation. The face-selective neurons responded strongest to stimuli presented in the fovea, and weakly to stimuli presented in the peripheral, and weakest responses were found to peripheral presentations of 0.5 degree spots of light. In addition, peripherally presented faces did elicit some weak responses, but their responses were still stronger than the responses to peripherally presented spots of light.

One notable difference between the PFC and the ventral region inferior temporal cortex (ITC) is that there was a lower proportion of face-selective cells in the monkeys' PFC, relative to that in the ITC (Baylis, Rolls, & Leonard 1987; Perrett Rolls, & Caan, 1982). Indeed, it had been demonstrated that 30-40% of neurons in the PFC were selective to complex visual stimuli, compared to the 60-80% of neurons in the ITC (Rodman et al., 1993). In addition, a human ERP recordings study showed that face-specific potentials were located in the inferior PFC; however, the magnitude

was smaller than those seen in the fusiform gyrus (Allison et al., 1999). Recent evidence showed that the PFC and ITC play distinctive roles in visual recognition and category-based behaviour. Freedman et al., (2002, 2003) trained monkeys to perform a category-matching task using cats and dogs that were parametrically morphed from cats to dogs. They found that the PFC was more category sensitive than the ITC, but the ITC was more stimulus sensitive than the PFC. Specifically, they found that signals in the ITC peaked sharply around the time when stimuli were presented but, on the other hand, the PFC showed strong prolonged signals during the delay maintenance period. With these results, Freedman et al., (2003) concluded that the ITC was prominently involved in the processing of visual shape, whereas neurons in the PFC were more involved in representing and maintaining information that was task (and behaviourally) relevant.

The above findings demonstrated overlapping but distinct roles of visual processing of the PFC and ITC (Freedman et al., 2003). These findings also suggest that the PFC could be part of a trans-cortical network specific for face processing, and that it exchanges information with the visual ventral cortex. Indeed, connectivity between the PFC and the ITC has been illustrated by the injection of wheat germ agglutinin-horseradish peroxidase or fluorescent dyes to monkeys (O'Scalaidhe et al., 1997). Subsequently, O'Scalaidhe et al., (1997) found that all of the face-selective neurons that were located in the inferior convexity, received more than 95% of input from the temporal visual cortex. Specifically, these neurons received inputs from the ventral bank of the STS, as well as the neighbouring inferior temporal gyrus. These ventral regions have been frequently reported to contain face-selective neurons

(Desimone et al., 1984; Perrett, Smith, Potter, Mistlin, Head, Milner, et al., 1985; Perrett, et al., 1982, 1991; Pinsk et al., 2005).

The connection between the IFC and the ITC has been well documented by many other researchers, for example Bullier, Schall, and Morel (1996), Jones and Powell (1970), Kuypers, Szwarcbart, Mishkin, and Rosvald (1965), Ungerleider, Gaffan, and Pelak (1989). In particular, Levy and Goldman-Rakic, (2000) argued the fact that the IFC receives input from the ventral region, an area that is specialized in visual processing, strongly suggesting that there is comparable domain-specific organization between the prefrontal region and ITC. Goldman-Rakic and colleagues (1996, 2000) therefore proposed that the PFC is functionally associated with and is an extension of the ventral cortex, and that there is selective connectivity between the two cortical regions. To date, it is a common knowledge that the PFC and the ITC are two interconnected regions involved in visual recognition in monkeys (Freedman et al., 2001, 2002, 2003; Rao, Rainer, & Miller, 1997)

With the above evidence, it is therefore speculated here that face-selective response in the human PFC could be similar to the face-selective responses in the monkey PFC. However, in many neuroimaging studies in humans, prefrontal responses have been interpreted as a result of applying WM processes to object stimuli. Thus, some of the relevant WM findings will be reviewed in the following section.

#### The role of the human prefrontal cortex in face/object working memory

In humans, prefrontal activation has been widely reported in the WM literature. WM refers to the ability to represent a limited amount of information online. It also refers to a short-term storage capacity for maintaining mental representation in an active state in order to guide appropriate behaviour (Baddeley, 1986, 1992). It has been proposed that performing a visual WM task involved a collection of complex cognitive processes, such as encoding, maintaining, resisting interference, manipulating, updating visual information within a short space of time, saccade generation to locate target stimuli, motor planning, etc. (Baddeley, 1992; Haxby et al., 2000; Druzgal & D'Esposito, 2000; Levy and Goldman-Rakic, 2000; Sakai, Rowe, & Passingham, 2002; Linden, Bittner, Muckli, Waltz, Kriegeskorte, Goebel, et al., 2003; Roth, Serences, & Courtney, 2005). The above processes have elicited activations in various prefrontal regions, such as the dorsal lateral prefrontal cortex (DLPFC), the frontal eye field (FEF), and the supplementary frontal eye field (SFEF; Berman, Colby, Genovese, Voyvodic, Luna, Thulborn, et al., 1999; Halger & Sereno, 2006).

Much current work has been aimed at dissociating the neural substrates underlying spatial and object working memories in the DLPFC using face stimuli (Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998; Haxby, Petit, Ungerleider, & Courtney, 2000; Owen et al., 2000). Typically, in a set of object WM trials (Courtney et al., 1998; Druzgal & D'Eposito 2003; Haxby et al. 2000; Sayala, Sala, & Courtney, 2006), subjects were asked to encode several faces, and then maintained those faces in the WM during a delay period. During this period subjects were instructed to fixate on the centre of the screen. The delay period was followed by a retrieval period where a probe face was presented, and subjects had to give a motor response to indicate

whether the probe face matched one of the faces seen during the encoding period. The spatial WM trials were similar to the object WM trials but subjects would encode, maintain, and respond to the location of lower-level stimuli (e.g. texture pattern or scrambled face pattern) instead. By contrasting the activation for object WM and spatial WM tasks, many reported an increased activation in the DLPFC (which overlapped with the IFJ). Other experiments, which aimed to examine the neural activities during a face WM task (Courtney et al., 1998; Druzgal and D'Esposito, 2003), have also reported strong activity in the DLPFC for maintaining face identity relative to the identity of lower-level control stimuli (scrambled faces). Specifically, Druzgal and D'Esposito (2003) reported robust face-WM responses in the DLPFC during the encoding period, and slightly reduced but strong prolonged responses during the maintenance/delay period, and the responses peaked again in the retrieval period. This strong prolonged activity for a stimulus during the delay period is known as the maintenance effect. Interestingly, the FFA produced strong activation during the encoding, and the retrieval periods, but weaker responses during the maintenance period.

In the context of O'Scalaidhe et al.'s (1997, 1999) findings, the evidence reviewed above, and the face-related activation found in the fMRI survey (Chapter 2; Downing et al., 2006), evidence has strongly suggested that this strong WM activation in the DLPFC could at least partly reflect a category preference for faces in the DLPFC. Taken together, the increased activation in the PFC for faces in a face WM task could be a result of applying greater WM and attentional resources to face stimuli (Downing, Liu, & Kanwisher, 2001; O'Craven, Downing, & Kanwisher, 1999; Wojciulik, Kanwisher, & Driver, 2000), relative to non-face control stimuli. Thus, the

role of the PFC in object WM could have been over-estimated by some previous studies. Conversely, in some WM studies, face stimuli were used in both spatial WM task and object WM task (Courtney, Ungerleider, Keil, & Haxby, 1996; Druzgal & D'Eposito 2003; Halger & Sereno, 2006; Haxby et al. 2000). In such cases, it is possible that the strong DLPFC response for the spatial WM task could be confounded by the presence of faces. This in turn suggests the possibility that the effect of spatial WM in the DLPFC in those studies could have been under-estimated. In summary, it remains possible that the DLPFC plays a dual role in the WM process and representing face-related information.

As mentioned in the above section, the human PFC, especially DLPFC, has been defined as a region involved in WM. In particular, there is evidence to demonstrate that a specific part of the DLPFC, the left inferior frontal junction (IFJ), is involved in cognitive control (Derrfuss, Brass, & von Cramon, 2004). Supportive evidence also showed that the left IFJ and nearby region were involved in more specific cognitive functions such as updating contents in object WM (Roth et al., 2005). Others also proposed that the IFJ might be involved in resisting irrelevant information during maintenance, for example when maintaining the locations of stimuli in the WM in the presence of distracting stimuli (Sakai et al., 2003), as well as resisting highly familiar stimuli (words) in a Stroop task, and a stream of interfering stimuli during an n-back WM task (Derrfuss et al., 2004).

Face related responses in the PFC have been neglected by research in object recognition. Researchers in the field of object recognition have concentrated on category-selective regions in the ventral visual cortex, and have not explored the

possibility of a category-bias region in the PFC. Indeed, substantial research using functional imaging to investigate face selectivity in the human visual cortex has often missed the face-selective activation in the PFC. For example, Kanwisher et al., (1997a, 1999) scanned subjects with twelve coronal slices covering only the occipital lobe and the posterior part of the temporal lobe. Gauthier et al. (1999) scanned subjects with six axial slices covering the longitudinal extent of the middle fusiform gyrus, and most of the temporal lobe only. Therefore, in many cases, face bias activation in the PFC has not been widely reported in many fMRI studies. Even when a strong face related activity was found in the frontal regions, the experimenters usually attributed the activation to WM. For example, Behrmann and Avidan (2005) recently reported face-selective activation in the PFC using a 1-back task paradigm, but without conducting a non-WM passive viewing experiment to compare, the authors concluded that the activation was a result of WM.

One exception to the above is that Ishai, Schmidt, & Boesiger (2005) reported bilateral activation in the anterior PFC [coordinates of activation peaks: 51, 23, 22; -47, 19, 22] for faces compared to scrambled faces. They further reported that the left prefrontal region responded most strongly to familiar faces, with weaker responses to emotional, unfamiliar, and line drawn faces. The right region responded strongest to emotional faces, and intermediate responses to familiar unfamiliar, and line drawn faces. In addition, a PET study conducted by Nakamura, Kawashima, Ito, Sugiura, Kato, Nakamura, et al., (1999) also reported activation in the anterior PFC when subjects had to judge facial emotions. In their experiment Nakamura et al., (1999) asked subjects to perform a face emotion test where they had to categorise happy, calm, sad or angry faces into three categories, positive (happy), neutral (calm), and

negative (sad or angry). In the control test subjects were required to judge the faces as attractive, neutral or unattractive. By comparing the face emotion test with the control test, they found a strong activation in the anterior PFC, and the authors concluded that the region was involved in identification of facial emotion. Both Ishai et al. (2005) and Nakamura et al., (1999) attributed their findings to emotional analysis of faces, instead of considering the possibility that the PFC may be involved in visual representation of faces.

Intriguingly, in a case study on an epileptic patient during surgery, Vignal, Chauvel, and Halgren (2000) reported that a direct electrical stimulation to the right anterior frontal gyrus had led to hallucinations of faces. Specifically, during the stimulation to the anterior inferior prefrontal gyrus, the patient hallucinated a series of faces when viewing a blank background, and a distorted face when the patient was looking at a face. Importantly, stimulation of other prefrontal regions (e.g. the left anterior prefrontal gyrus) did not evoke face-related hallucinations. An ERP study on the same patient conducted by Marinkovic, Trebon, Chauvle, and Halgren (2000) showed face-selective ERPs for images of faces, relative to distorted faces (unrecognizable pattern), an oval frame with coloured and grey contours, and an oval filled in colour. These face-selective ERPs were observed along the right inferior frontal gyrus, but not in the left, and the responses occurred about 150 msec after face onset. The above studies provide supportive evidence to the inferior frontal region's involvement in face related processing.

On the strength of the evidence reviewed above, and the weaknesses in some previous experiments, one immediate question is, to what extent does the rIFJ process

faces like the FFA? Subsequently, three fMRI experiments were conducted to investigate the role of the rIFJ in face representation and to compare the rIFJ's responses with the responses in the right FFA (rFFA). Investigation 4, in line with O'Scalaidhe et al's (1997, 1999) approach in monkey studies, examined the response patterns in the rIFJ and rFFA in a free-viewing task (passive viewing, non-WM task) and a 1-back WM task for faces, bodies, tools, and scenes. Investigation 5 examined the activities in the rIFJ and rFFA in processing face parts, body parts, and object parts, and whole faces, bodies, and objects. Finally, Investigation 6 explored the response profiles of the two regions in representing internal face features.

#### **Investigation 4**

# Response properties of the rIFJ and the rFFA in a non-WM task and a 1-back WM task

#### Overview

Following a similar approach to O'Scalaidhe et al., (1997, 1999), Investigation 4 aimed to compare the activation in the rIFJ between a non-WM task and a 1-back WM task. Specifically, the response profiles to faces, bodies, tools, and scenes across the two tasks were examined here. These object categories were selected in order to assess the extent of category preference in the rIFJ in the presence of task demands, and its responses in relation to the face-selective rFFA.

#### Methods

#### **Participants**

Twenty healthy adult volunteers were recruited from the University of Wales, Bangor community. Ten participated in the free-viewing session and ten performed a 1-back (WM) task. Participants satisfied all requirements in volunteer screening, in which they had to complete a consent form provided by Ysbyty Gwynedd (North Wales Hospital). They had also been given informed consent that was approved by the School of Psychology at the University of Wales, Bangor, and the North West Wales Health Trust. Participants were compensated at £20 per session.

#### **Design and procedures**

This blocked-design experiment consisted of four runs, and within each run there were twenty-one 15-sec blocks. Blocks 1, 6, 11, 16, 21 were a fixation only baseline condition. Each of the remaining blocks comprised presentation of 20 exemplars from a single category. There were two order versions. The first half and second half of one version were swapped to create the second version. The order of blocks was symmetrically counterbalanced within each version, so that the first half of each version was the mirror order of the second half, resulting in an equivalent mean serial position of each condition. Within a block, each image was presented for 300 msec, with an ISI of 450 msec between images, which made each run 5 mins 15 sec long.

The same design and procedures were used across twenty participants. Ten were instructed to view the stimuli passively (a free-viewing task) during the scan session. The other ten were required to perform a 1-back WM task, where they had to press a button whenever an image occurred twice in immediate succession. Two image-repetition trials occurred at randomly selected time points in each block in the 1-back task. With a presentation rate of 300 msec for each stimulus, and an ISI of 450 msec between images, subjects had to keep each stimulus in WM for a short period of time in order to perform the task successfully.

All stimuli were presented on a white background by a Macintosh iBook laptop, running the Psychophysics Toolbox package (Brainard, 1997) in Matlab (The Mathworks, Inc.). Images were projected onto a screen positioned behind the scanner. Participants viewed stimuli through an angled mirror that was attached to the head coil.

#### Stimuli

Images of faces, bodies without heads, tools, and scenes were presented (400 x 400 pixels). Forty full colour images were used for each category, which were divided into two stimuli versions. One version was presented in half of the scans, and another one in the other half. These were the same stimuli used in the fMRI survey.

#### Image acquisition

Images were acquired using a 1.5T Philips scanner with a SENSE parallel coil. Functional images were acquired using an EPI sequence (T2\* weighted, TR=3000ms, TE=50ms, flip angle =  $90^{\circ}$ ). Thirty slices were acquired, FOV = 240, inplane = 240/64 = 3.75,  $64 \times 64$  in-plane matrix, 5mm thickness/slice, and no gap, which covered the whole brain and most of the cerebellum. A high resolution T1 anatomical scan (1mm x 1mm x 1.3mm) was acquired.

#### Data preprocessing and analysis

Pre-processing of data and statistical analyses were performed using Brain Voyager 4.9 (Brain Innovation, Maastricht, The Netherlands). Three dummy volumes were acquired before each scan in order to reduce the effect of T1 saturation. Pre-processing of functional images included: 3D-motion correction of functional data using trilinear interpolation, temporal high pass filtering (0.006Hz cutoff), and no spatial smoothing was applied. Functional data were manually co-registered with three-dimensional T1 scans (1mm x 1mm x 1.3 mm-resolution), and subsequently resampled to isometric 1mm x 1mm x 1mm voxels with trilinear interpolation. The 3D-scans were transformed into Talairach space, and the parameters for this transformation were then applied to the co-registered functional data.

For multiple-regression analyses, predictors were generated for each condition. The event time series for each condition were convolved with a model of hemodynamic response. Voxel time series were z-normalized for each run, and additional predictors accounting for baseline differences between runs were included in the design matrix.

#### **Region of interest analysis**

Using a split-half method, the data of each participant, according to the order version, was divided into two sets. Runs with order version 1 were used to define the ROIs and runs with order version 2 to estimate the responses of the ROIs across

conditions, and vice versa. This procedure ensured that all data contributed to the analysis, and that the data was independent from that used for ROI definition (see the section of region analysis, above). This method prevented an overestimation of responses. Where a robust ROI could not be identified with both halves of the data, the results from the ROIs defined by one half were analysed. Subsequently, data from set 1 and 2 were submitted to a repeated measures within-subject ANOVA for statistical analysis.

The rIFJ and rFFA were defined by the contrast of faces minus tools in each participant. The most activated voxel in each region was identified within a restricted part of the cortex based on previously reported anatomical locations. In the case of the rIFJ, the anatomical location was reported by the fMRI survey (Chapter 2). ROIs were defined as the set of contiguous voxels that were significantly activated within 9 mm in the direction of anterior/ posterior, superior/inferior, and medial/lateral direction of the most activated voxel (p < .05 uncorrected; because only half of the data was used, the strength of any activation was weaker, therefore such a lenient threshold was used in this split half analysis). This procedure ensured that the ROIs defined were segregated from nearby selective activation, and ensured that each ROI contained a similar number of voxels.

#### Behavioural data

Behavioural data from the 1-back task were submitted to a repeated-measures  $2 \times 4$  ANOVA. With subjects' performance, that is the percentage of correct detection (hit) and percentage of failure to detect (miss), as one factor, and object categories,

faces, bodies, tools, and scenes, as the other factor. In each subject, and within each run, the percentages of hit and miss for each category were calculated. Behavioural data from six out of eight subjects (eight subjects with significant activation in both rIFJ and rFFA, see results & discussion below) were submitted to the ANOVA analysis. Behavioural data of two subjects were not able to be recorded due to technical problem (the response box was out of order). However, in order to control for subjects' attention, they were asked to perform a 1-back task regardless, without the knowledge that the response box was out of order.

#### Results

In the free-viewing task, ten out of ten subjects showed significant activation in the rIFJ, but only eight of them showed significant activation in the rFFA. Thus, only eight subjects showed significant activation in both regions. In the 1-back WM task, all subjects showed significant activation in both the rIFJ and rFFA. Thus, altogether, ROI and statistical analyses were performed on those eight subjects who showed significant activation in both regions in the free-viewing task, and another eight out of ten subjects were randomly selected from the 1-back WM task.

The peak Talairach coordinates for rIFJ in the whole brain analysis for the free-viewing task were [41, 4, 36] and the 1-back task were [45, 6, 35] (see Figure 39, p.152). The Talairach coordinates of the average peak voxels, and their standard deviation (SD): x, y, z) across all subjects for each region and task are as follows: 1-back task, rIFJ: [48, 8, 33]; (SD: 6, 7, 5), and rFFA [38, -45, -17]; (SD: 3, 7, 4), free-

viewing task, rIFJ [43, 11, 35]; (SD; 7, 9, 6), and rFFA [38, -48, -14]; (SD: 3, 8, 4). Using a split-half method within each subject, betas of the ROIs were extracted for each object category, and were submitted to a repeat-measures ANOVA. ROI, and category were within factors, and task was a between factor (see Figures 40 and 41, p. 155-156).

In a separate experiment, the cortical regions for eye movements were localized in four other subjects. These four subjects were tested in a blocked-design experiment. They were required to perform alternating blocks of repeated eye movement and fixation. In the eye movement condition, subjects were required to look at the central fixation cross first, then look to the left, back to the centre and then right and back to the centre and so on for 30 seconds. In the fixation condition, subjects were required to fixate at the fixation cross for 30 seconds. Each blocked lasted for 30 seconds. A whole brain fixed effect analysis was conducted at the uncorrected threshold of t > 10, p < 0.00001. The bilateral FEF and the SFEF were defined by the contrast of eye movement minus fixation. In the whole brain analysis, the group average activation of FEF (peak voxel of the right FEF, 50, -1, 42; of the left FEF, -48, -4, 45) and SFEF (0, -10, 66) did not overlap with the activation in the rIFJ. This suggested that this face related activation in the PFC was not a result of eye movement when subjects viewed faces with direct gaze, or as a result of subjects scanning through different parts of faces (Berman et al., 1999; Fox, Fox, Raichle, & Burde, 1985; Anderson, Jenkins, Brooks, Hawken, Frackowiak, & Kennard, 1994).

As for the behavioural data from the 1-back task, ANOVA analysis revealed that there was no significant main effect for categories, F(1, 5) = 1.009, p = .36. There was a significant main effect for performance (hit vs miss), F(1, 5) = 13.30, p = .015, mean percentage for hit (77%) was greater than the mean percentage for miss (22%), and there was less than 1% of false-alarm rate. In addition, there was no significant interaction between performance and categories, F(1, 5) = 2.84, p = .21. The results suggest that subjects allocated attention equally to all categories.



[X = 45]

Figure 39: Whole brain analysis showed the group average activation. The above showed the face-selective right inferior frontal junction activation in the 1-back task (orange) [peak activation 45, 6, 35] and in free viewing task (green) [peak activation 41, 4, 36], and the right fusiform face activation [peak activation 39, -48, -19], t = 3.91, uncorrected p < .0001. All the above regions were defined by faces minus tools.

As for statistical results for the main investigation, a significant main effect of ROIs was found, F(1,7) = 74.88, p < .001. In general the rFFA produced stronger responses than the rIFJ across all conditions. This significant main effect was confirmed by a paired-samples t-test, t(1,63) = 7.81, p < .0001. A significant main effect of task, F(1,7) = 25.91, p < .001 was also found; in general the 1-back task elicited stronger responses than the free-viewing task, t(1,63) = 5.14, p < .0001. A

significant main effect of category was found, F(3,5) = 25.38, p < .005, faces elicited the strongest responses compared to other object categories in both the rFFA and rIFJ. In addition, a significant ROI x category interaction was found, F(1,7) = 12.65, p< .001, indicating that faces elicited the strongest responses relative to bodies, scenes, and tools in the rFFA in both tasks. There was also a significant task x category interaction F(1, 7) = 6.39, p = .04, indicating that faces elicited the strongest responses in the 1-back task. There was a lack of significant ROI x task x category interaction, F(3, 21) = .34, p = .79, this indicates that both regions elicited similar response patterns across both 1-back and free-viewing tasks.

As indicated by the non-significant three-way interaction, both the rFFA and rIFJ elicited similar response patterns across tasks and object categories. Face bias activation was in fact found in both regions and for both tasks. Indeed, follow-up paired-samples t-tests showed that in the free-viewing task, faces produced significantly stronger activation than bodies in the rFFA (bodies elicited the second strongest response), t(1,7) = 3.64, p < .005. In the 1-back task, faces elicited significantly stronger responses than bodies, t(1,7) = 2.70, p = .03. In the rIFJ, in the free-viewing task, faces and bodies both produced the stronger responses, and the difference between them was non-significant, t(1,7) = .79, p = .45. However, faces produced significantly stronger response than scenes (the third best category), t(1,7) = 3.49, p = .01. In the 1-back task, faces again produced a strongest activation than bodies in the rIFJ, t(1,7) = 3.41, p = .01. These statistics also confirmed the main effect of category which was mentioned earlier, that faces released the strongest responses in both regions. They also confirmed the significant ROI x category, in

which faces elicited the strongest responses relative to other categories in the rFFA, in both tasks.

The above statistics indicated the similarity in response pattern between the two regions. In order to examine their level of similarity in activation across object categories, correlation tests between the regions were performed. In addition, given that "task" was a between subject factor, thus the correlation analysis comparing the response pattern between the rFFA and rIFJ was performed within each task separately. In each subject, a correlation coefficient was obtained by correlating subjects' responses (betas) across all conditions in the rFFA, with those in the rIFJ, and then an average correlation coefficient was calculated across all subjects, in each region. To reach the level of significance for a two-tailed test of .05, *r* must be greater than or equal to the critical value of .754. This correlation analysis revealed a significant correlation between rFFA and rIFJ in the free-viewing task (average r = .80), and a significant correlation between the two regions in the 1-back task (average r = .84).

# **Right FFA activation**



Figure 40: Graph showing betas for free viewing task and one-back tasks in rFFA for faces, bodies, scenes, and tools. Error bars reflect the standard error of the mean (n = 8). The asterisks (\*) mark the statistically significant difference between conditions.

#### **Right IFJ activation**



Figure 41: Graph showing betas for free viewing task and one-back tasks in rIFJ for faces, bodies, scenes, and tools. Error bars reflect the standard error of the mean (n = 8). The asterisks (\*) mark the statistically significant difference between conditions. *ns* marks the non-significant difference between conditions.

#### Discussion

In summary, these findings were consistent with previous findings of the FFA. The FFA is selective to faces in both a free-viewing task and a 1-back task, relative to common objects and bodies (Kanwisher et al., 1999). As expected, the rFFA as a ventral region elicited much stronger activity for faces, which contributed to the significant interaction of region and categories. Interestingly, in the free-viewing task, the rIFJ produced the highest activation to faces, and bodies, relative to tools and scenes. Face selectivity was stronger in the 1-back task in both regions, and in general,

the rIFJ's responses to all categories in the 1-back task were higher than those in the free-viewing task. The present investigation on human's PFC showed comparable results to O'Scalaidhe et al's (1997, 1999) findings of face-selective responses in monkeys' PFC. Here, faces-selective activation was found in human rIFJ, and its selectivity to faces was similar to that of the rFFA. Faces elicited robust activation in the rIFJ in both WM and non-WM tasks, indicating that category preference was strong regardless of task. In addition, the similar response patterns between rIFJ and rFFA suggested that the two regions could be functionally associated, which also suggested a possible role of the rIFJ in object recognition.

#### **Investigation 5**

# Response properties of the rIFJ and rFFA when processing whole objects and object parts

#### Overview

The present investigation used whole faces, whole bodies, whole objects, face parts, body parts, and object parts to examine the response properties of the rIFJ in parallel with the rFFA. It is thought that upright faces are processed as wholes, and that the perception of a face relies on integrating facial features instead of the processing of independent parts of faces. On the other hand, processing of other nonface objects depends on parts or features (McKone, Martini, & Nakayama, 2001; Tanaka & Farah, 1993, 2003). This holistic hypothesis for face perception (Tanaka & Farah, 1993) was supported by the findings that subjects performed better when the discrimination between two face parts (e.g. two eyes) were tested in the context of the whole face, compared to when face parts were tested in isolation (a whole-part effect).

Holistic representation for faces can also be demonstrated by the composite face effect (Young, Hellawell, & Hay, 1987). This effect occurs when subjects are required to make a same-or-different judgment on two separate faces. Specifically, when the two identical top halves of faces are aligned with two different bottom halves; subjects tend to perceive two top halves as different too. However, when the two bottom halves are misaligned (laterally offset), the effect disappeared. Recently, this composite effect has been reflected by activation in the mid fusiform gyrus (or the FFA). Schiltz and Rossion (2006) compared the activation in the FFA when subjects

made a same-or-different judgment between two aligned identical faces, and between two aligned faces with different bottom halves. The FFA responded stronger to the latter condition. They then examined the FFA's activation when subjects judged between two misaligned identical faces, and between two misaligned faces with different bottom halves. They found no difference in activation between these two conditions. These authors therefore concluded that the FFA was involved in combining facial information from parts into whole, and their findings further support the hypothesis that face representation is holistic. Single unit studies in monkeys also showed that some cells in the inferior temporal cortex were selective to whole faces, and elicited low responses to scrambled parts of faces e.g. anterior portion of face profile, and one half frontal-view of a face (Desimone, Albright, Gross, & Bruce, 1984). The above evidence suggests that faces are processed as wholes instead of each element of faces being processed separately. In line with the above experiments, the present investigation aimed to test if the activation in the rIFJ would reflect a wholepart difference as the rFFA does.

In addition, instead of using a blocked fMRI design as in Investigation 4, an event-related design was adopted here. This aimed to investigate whether face selectivity would still be observed when subjects could not predict which object categories they were going to view.

#### Methods

#### **Participants**

Fourteen healthy adult volunteers were recruited from the University of Wales, Bangor community. Participants satisfied all requirements in volunteer screening, in which they had to complete a consent form provided by Ysbyty Gwynedd (North Wales Hospital). They had also been given informed consent that was approved by the School of Psychology at the University of Wales, Bangor, and the North West Wales Health Trust. Participants were compensated at £20 per session.

#### Stimuli

Images of whole-faces, whole bodies, and whole common objects (such as tools), and non-symmetrical parts of faces, bodies, and common objects were presented in grey-scale in the centre of the screen with a fixation dot in the centre. There were 20 images (400 x 400 pixels) for each condition in total (see sample stimuli Figure 42, below).



Figure 42: Samples stimuli in Investigation 5. Whole objects, bodies, faces, and object parts, body parts and face parts were presented in this investigation.

#### **Design and procedure**

An event-related paradigm was used; subjects viewed a rapid succession of stimuli trials that was generated by an "in-house" program in Matlab (The Mathworks, Inc.). There were 360 condition trials and 16 fixation only trials (8 trials were presented in the beginning and 8 trials were presented at the end of the presentation). Each trial lasted for 2 seconds (750 msec on, 1250 msec blank). There were 60 presentation of each stimulus type, and thus each run lasted for 12.5 minutes. There were six versions of the presentation sequence, and within each version trial histories were counterbalanced, that is the order of each trial for each condition were preceded and followed equally often by trials from each of the other conditions for two trials back and two trials forwards. Stimuli presentation order was also counterbalanced across the six versions. Each of the six versions was assigned to each participant, and each participant only needed to perform one run. For example, participant 1 was assigned to version 1, then the next subject in line was presented with the second version, and so on. All participants were required to perform a free-viewing task.

All stimuli were presented on a white background by a Macintosh iBook laptop, running Psychophysics Toolbox package (Brainard, 1997) in Matlab. Images were projected onto a screen positioned behind the scanner. Participants viewed stimuli through an angled mirror that was attached to the head coil.

#### Image acquisition

Images were acquired using a 1.5T Philips scanner with a SENSE parallel coil. Functional images were acquired using an EPI sequence (T2\* weighted, TR=3000ms, TE=50ms, flip angle =  $90^{\circ}$ ). Fifteen slices were acquired, FOV = 240, 64 x 64 in-

plane matrix, 5mm thickness/slice, and no gap, which covered the whole brain and most of the cerebellum. Voxel dimension = 3.75mm x 3.75mm x 5mm. A high resolution T1 anatomical scan (1mm x 1mm x 1.3mm) was acquired.

#### Data preprocessing and analysis

Same as those in Investigation 4.

**Region of interest analysis:** The ROIs were defined with the two runs of localizer, where subjects performed a 1-back task (same as the 1-back task in Investigation 4) on faces, bodies, tools, and scenes (see stimuli session in Investigation 4). Within each participant, the rIFJ and rFFA were defined by the contrast of faces minus tools in each participant at the threshold of p < 0.001 (uncorrected). The most activated voxel (the peak voxel) in each region was identified within a restricted part of cortex based on previously reported anatomical locations. ROIs were defined as the set of contiguous voxels that were significantly activated, within 9 mm in the direction of anterior/ posterior, superior/inferior, and medial/lateral direction of the peak voxel. This procedure was to ensure that the ROIs defined were segregated from nearby selective activation, and to ensure that each ROI contained a similar number of voxels.

#### Results

In this experiment, 14 out of 15 subjects showed robust activations in both rFFA and rIFJ, which were defined by the contrast of faces minus tools from the localizer scans (uncorrected p < .0001). Thus, ROI and statistical analyses were

performed on those 14 subjects. The average peak Talairach coordinates for the rFFA were [41, -49, -20], SD [5, 7, 5], and for the rIFJ were [48, 7, 35], SD [6, 8, 8]. Betas were extracted from the defined ROIs and then submitted to a complete within subject repeated-measures ANOVA with ROI, whole/parts, and category as factors. (See Figures 43 and 44 below)

A three-way factorial ANOVA revealed a significant main effect of region, F (1,13) = 38.06, p < .0001; in general all responses from the rFFA were much stronger than those from the rIFJ, t (1,83) = 13.54, p < .0001. A significant main effect of category was also found, F (2,12) = 9.50, p < .005, where faces and bodies elicited the strongest activation on average, this will be further confirmed by the follow-up pair-samples t-tests for the whole/part and category interaction. There was a significant interaction between ROI and category, F (2,12) = 15.18, p < .0005, where responses to faces were stronger in the FFA (faces > bodies, t (1,27) = 2.16, p = .03; faces > objects, t (1,27) = 7.30, p < .0001). This was expected, as the rFFA is a face-selective region (Haxby, et al., 1994; Kanwisher et al., 1997). There was also a significant interaction between whole/part and category, F (2,12) = 8.70, p = .005.

This significant interaction between whole/part and category could have resulted from the strong activation for faces, or for bodies in the whole condition relative to objects. A series of pair-samples t-tests were performed to examine this interaction. It is possible that the interaction could be a result of a stronger activation for whole faces relative to whole objects. In the rFFA, whole face > whole bodies, t(1,13) = 2.38, p = .03, whole faces > whole objects t (1, 13) = 8.51, p < .0001, face parts = body parts t (1,13) = .32, p = .75, and faces parts > objects parts, t (1,13) = 2.47, p = .03. In the rIFJ, whole faces = whole bodies, t(1,13) = .75, p = .46, whole faces > whole objects, t(1,13) = 3.70, p = .003, faces parts = body parts, t(1,13) =1.75, p = .101, and face parts = object parts, t(1,13) = .49, p = .64. Alternatively, it could be a result of a stronger activation for whole bodies relative to whole objects. In the rFFA, whole bodies > whole objects t(1, 13) = 5.49, p = .0001, and body parts > object parts, t(1,13) = 2.38, p = .03; in the rIFJ, whole bodies marginally > whole objects, t(1,13) = 3.70, p = .056, and body parts = object parts, t(1,13), p = .48.

The lack of significant three-way interaction was also observed F(2, 12) = .51, p = .61. The lack of three-way interaction and a significant interaction between whole/part and category suggested that there was a similar response pattern across the rFFA and rIFJ, which could be mainly contributed by the similar activation across whole categories. Subsequently, a correlation test was performed between the two regions. In each subject, a correlation coefficient was obtained by correlating subject's responses (betas) in the rFFA across all conditions with those in the rIFJ, and an average correlation coefficient was then calculated across all subjects for each region. To reach the level of significance for a two-tailed test of .05, r must be greater than or equal to the critical value of .532. The result showed a significant correlation between ROIs across the whole conditions only, r = .68, and a non-significant correlation between the regions across the part conditions, r = .20. These results were consistent with the findings in Investigation 4, as both rFFA and rIFJ responded strongly to whole faces and whole bodies.

## **Right FFA activation**



Figure 43: Graph showing responses in the rFFA for whole and part faces, bodies, scenes, and tools. Error bars reflect the standard error of the mean (n = 14). The asterisks (\*) mark the statistically significant difference between conditions.

## **Right IFJ activation**



Figure 44: Graph showing responses in the rIFJ for whole and part faces, bodies, scenes, and tools. Error bars reflect the standard error of the mean (n = 14). The asterisks (\*) mark the statistically significant difference between conditions.

#### Discussion

The response pattern in the rIFJ mirrored that in the rFFA, especially in the whole conditions. Both regions responded significantly stronger to whole faces and whole bodies in this event-related paradigm, this is also similar to the response pattern reported in Investigation 4, with a blocked-design free-viewing paradigm. This finding is consistent with the report that bodies also showed strong activation in the region overlapping with the FFA (Peelen & Downing, 2005b; Schwarzlose et al., 2005). In addition, both regions showed non-bias responses to face parts and body parts compared to object parts. Thus the results again indicated that activation in the rIFJ was mainly driven by whole faces and to some extent by whole bodies in a free-viewing task.

Although this investigation tested the rIFJ responses to face parts, these stimuli were mainly asymmetrical elements of faces (part of the cheek, part of an ear, and chin etc), and thus these face parts did not capture the symmetrical features of faces, such as pairs of eyes. Therefore, Investigation 6 aimed to test whether the rIFJ was sensitive to the presence of eyes on faces. Pairs of eyes are particularly important stimuli. It is believed that establishing eye contact with a face would facilitate the efficiency of face processing, thus leading to better categorization and recognition (George et al., 2001). In addition, pairs of eyes are a particularly relevant cue in social situations. Indeed, perception of gaze is closely link to the development of theory of mind (ToM), because it allows one to interpret other people's intentions and behaviour. Specifically, eyes can convey one's emotional state; perception of gaze also facilitates regulation of turn taking in conversation, and hence joint attention

(Baron-Cohen, 1995). Many researchers believe that eye-gaze cues could override head and posture cues (Perrett et al., 1982; Langton, Watt, & Bruce, 2000) and suggest that eyes convey socially relevant information.

#### **Investigation 6**

#### rIFJ's and FFA's sensitivity to the presence of pairs of eyes

#### Overview

This investigation aimed to test whether the presence of eyes is necessary in producing strong responses in the rIFJ, and it also aimed to compare the responses in the rIFJ and rFFA. A similar experiment was conducted by Tong et al., (2000) has examined the role of gaze and eye perception of the FFA. Specifically, subjects viewed whole faces, whole faces with eyes masked, eyes alone, and houses as a control stimuli. They found strong FFA responses to the whole faces and eye masked conditions and intermediate responses to eyes alone, but very weak responses to houses. With these results they concluded that there was no selective region for gaze perception in the FFA, or in the ventral cortex. However, these authors admitted that they had only scanned subjects from the occipital pole to the posterior temporal region of the brain; thus, they speculated that gaze selective responses might be found in a more anterior region.

Indeed, this investigation aimed to explore the possibility of whether the rIFJ is sensitive to the presence of eyes. Participants in this present investigation viewed

whole faces, faces with eyes masked, pairs of eyes alone, and flowers (control stimuli, because, like faces, they are symmetrical, but they are not animate items), so as to investigate whether the activity in the rIFJ could be driven by pairs of eyes alone. Alternatively, the rIFJ may elicit similar response pattern to the rFFA, where whole faces and eyes masked elicited the strongest response relative to eyes alone and the control stimuli.

#### Methods

#### Participants

Nine healthy adult volunteers were recruited from the University of Wales, Bangor community. Participants satisfied all requirements in volunteer screening, in which they had to complete a consent form provided by Ysbyty Gwynedd (North Wales Hospital). They had also been given informed consent that was approved by the School of Psychology at the University of Wales, Bangor, and the North West Wales Health Trust. Participants were compensated at £20 per session.

#### Stimuli



Figure 45: Sample stimuli in Investigation 6: whole face, face masked, eyes alone, and flower.

Images of whole faces, faces with a grey rectangle covering the eyes (eyes masked, brightness of the grey rectangle was matched with the face in Adobe

Photoshop 8.0), images of just a pair of eyes (eyes alone), and flowers were presented in grey-scale. In total, there were 20 images (400 x 400 pixels) in each condition. Half of the stimuli for the whole-face, eyes-masked, and eyes-alone conditions were female, and half of them were male. Different faces were used in the whole faces condition and eyes masked condition. Stimuli in the eyes alone condition were "cut-outs" from the faces in the eyes masked condition.

#### **Design and procedure**

Same as those in Investigation 4.

#### **Image acquisition**

Images were acquired using a 1.5T Philips scanner with a SENSE parallel coil. Functional images were acquired using an EPI sequence (T2\* weighted, TR=3000ms, TE=50ms, flip angle = 90°). Fifteen slices were acquired, FOV = 240, 64 x 64 inplane matrix, 5mm thickness/slice, and no gap, which covered the whole brain and most of the cerebellum. Voxel dimension = 3.75mm x 3.75mm x 5mm. A high resolution T1 anatomical scan (1mm x 1mm x 1.3mm) was acquired.

#### Data preprocessing and analysis

Same as those in Investigation 4.

**Region of interest analysis:** The ROIs were defined from the four runs of localizer, where subjects performed a 1-back task (same as the 1-back task in Investigation 4). Subjects viewed faces, bodies, tools, and scenes, and faces used in the localizer were different from those in the main experiment (but same as those stimuli in Investigation

4). The rIFJ and rFFA were defined by the contrast of faces vs tools of each participant at the threshold of p < .0001 (uncorrected). The most activated voxel (the peak voxel) in each region was identified within a restricted part of cortex based on previously reported anatomical locations. ROIs were defined as the set of contiguous voxels that were significantly activated, within 9 mm in the direction of anterior/ posterior, superior/inferior, and medial/lateral direction of the peak voxel. This procedure was to ensure that the ROIs defined were segregated from nearby selective activation, and to ensure that each ROI contained a similar number of voxels.

#### Results

The ROIs were identified with a contrast of faces minus tools (uncorrected p < 0.0001) from the localizer scans. Significant rFFA activation was found in seven out of nine subjects, and robust rIFJ activation was found in eight out of nine subjects. ROI and statistical analyses were conducted on the seven subjects with robust activation in both rFFA and rIFJ. The average peak Talairach coordinates for the rIFJ were [43, 1, 41], SD [7, 7, 12]; and for the rFFA were [40, -47, -20], SD [3, 8, 9]. Betas of the ROIs were extracted for each condition. A complete within subjects repeated-measures ANOVA was performed with ROI (rIFJ and rFFA), and object category (whole faces, faces with eyes masked i.e. face masked, eyes-alone, and flowers) as factors (see figures 46 and 47 below).

The ANOVA revealed a significant main effect of ROI, F(1, 6) = 14.97, p = .008. As expected the rFFA as a visual object region responded much stronger than

the rIFJ in all conditions. There was a significant main effect of object category, F(3,18 = 8.67, p < .001. Since there was also a significant interaction of category and ROI (F(3,18) = 6.464, p < .001), a series of pair-samples t-tests was performed to examine the effect of category in each region. In the rFFA, whole faces seemed to be the strongest category; its activation was significantly stronger than that to eves alone (t(1,6) = 3.57, p = .011) and flowers (t(1, 6) = 3.85, p = .008), but similar to eyes masked (t(1, 6) = 1.48, p = .19). The non-significant difference between whole faces and eyes masked was probably due to the fact that the latter stimuli contained more face area. Whilst in the rIFJ eyes alone was the strongest category; its activation was significantly stronger than that for eyes masked (t(1, 6) = 2.89, p = .027) and flowers (t(1, 6) = 3.38, p = .015), but similar to whole faces, which also contained eyes (t(1, 6) = 0.015)= 1.44, p = 1.97). Hence, the main effect of category could be contributed by the strong activation for whole faces in rFFA, and the eyes alone in the rIFJ. In addition, since both regions responded strongly to whole faces, the interaction may lay in the conditions of eyes alone and eyes masked between the two ROIs. Indeed, a significant simple effect was found between eyes alone and eyes masked in the rIFJ, t(1,6) =2.89, p = .027, and there was a marginally significant difference between eyes alone and eyes masked in the rFFA, t(1,6) = 2.36, p = .055.

To explore the above significant category and ROI interaction, a post-hoc 2 x 2 factorial repeated-measures ANOVA was conducted, with eyes alone and eyes masked as one factor, and the two regions as another factor. The results confirmed the significant interaction reported above. The statistics revealed a significant main effect of ROI, F(1,6) = 5.93, p = 0.05. In general, the rFFA elicited stronger activation for all conditions than the rIFJ, t(1,13), p < .0001. A significant interaction between
category and ROI was found, F(1,6) = 16.64, p = 0.006. A significant simple effect was found in the rIFJ, where eyes alone elicited stronger responses than eyes masked, t(1,6) = 2.89, p = .028. A marginal significant simple effect was found in the rFFA, where eyes masked elicited slightly stronger responses than eyes alone, t(1,6) = 2.36, p = .056.

This significant interaction is consistent with the results in the FFA obtained by Tong et al., (2000), in which they demonstrated a gradation of responses from whole faces (the most effective category), faces with eyes masked, and eyes alone in the FFA compared to houses which elicited weak responses. Here, as expected, the rFFA elicited stronger activation for whole faces and eyes masked relative to the control stimuli flowers (whole faces > flowers t(1,6) = 3.85, p = .008). On the other hand, the rIFJ elicited stronger activation for eyes alone and whole faces, and its activation was significantly weaker to eyes masked and flowers. Unlike the rFFA, eyes masked elicited a weaker response in the rIFJ, and the response was similar to that for flowers (t(1,6) = .53, p = .612). Findings in the present investigation were consistent with previous studies (Kanwisher, et al., 1997a, 1999; Tong et al., 2000) and once again demonstrated that the FFA preferred face stimuli to eyes alone. Intriguingly, the rIFJ preferred eyes alone to whole faces, particularly when eyes within whole faces were masked (hence a significant simple effect). Thus, the whole face condition contained both faces and eyes, this led to a non-significant difference between whole faces and eyes masked in the rFFA (t(1,6) = 1.48, p = .188) and a marginal non-significant difference in the rIFJ (t(1,6) = 2.04, p = .08). Hence, the critical difference between the two regions could only clearly be revealed in the eyes

alone and eyes masked conditions, in which the two types of stimuli exclusively contained either eyes or faces.



**Right FFA activation** 

Figure 46: Mean betas of the response to each condition in rFFA. Error bars reflect the standard error of the mean (n = 7). The asterisk (\*) marks the statistically significant difference between conditions. *ns* marks the non-significant difference between conditions.





Figure 47: Mean betas of the response to each condition in rIFJ. Error bars reflect the standard error of the mean (n = 7). The asterisk (\*) marks the statistically significant difference between conditions.

### Discussion

In summary, the difference in response between the rFFA and rIFJ was demonstrated by the significant interaction between ROI and object category. Interestingly, the findings in the rIFJ resonate with Perrett et al's (1982) findings in which they identified some cells in the object responsive superior temporal sulcus (STS; Desimone et al., 1984; Perrett, et al., 1982, 1991; Perrett, Smith, Potter, Mistlin, Head, Milner, et al., 1985; Pinsk et al., 2005; Rolls, 2000; Tsao et al., 2006) which were sensitive to the presence of eyes and responded strongly to eyes alone and whole faces (containing eyes) rather than faces with eyes masked. Unlike Investigations 4 and 5, in which both regions showed a face bias response, Investigation 6 revealed a critical difference in response between the two regions. Specifically, the rIFJ was strongly biased to pairs of eyes alone rather than whole faces with eyes masked. This investigation demonstrates a novel finding that just the presence of eyes is necessary to elicit strong responses in the rIFJ.

### **Chapter discussion**

The series of investigations in this chapter aimed to compare the response patterns between the rIFJ and the rFFA, specifically their patterns across WM manipulation, whole and part representation of object categories, and the presence of pairs of eyes on faces. Investigations 4 and 5 demonstrated the similarity in response patterns between the regions. Intriguingly, Investigation 6 showed that the rIFJ preferred eyes alone than to whole faces with eyes masked, whereas the rFFA showed equivalent responses to these two conditions. Interpretation of the results from each investigation will be discussed in turn here.

The findings here, along with previous research in the PFC, have several important contributions to the current research literature. First, consistent with the findings from single unit studies on the PFC (O'Scalaidhe et al., 1997, 1999), Investigation 4 showed that the rIFJ in humans is biased to face stimuli. It is worth highlighting that the robust responses in human rIFJ for faces in both WM and non-WM tasks (Investigation 4) have not been reported in other fMRI literature. In the free-viewing task, the rIFJ was seemed to prioritize the processing of faces and bodies compared to tools and scenes, to some extent this could be due to the fact that the faces and bodies are salient categories and thus attention was allocated to them leading to the strong activation in the rIFJ. Intriguingly, the rIFJ remained strongly biased to faces relative to bodies, tools, and scenes, even when subjects were performing a 1-back task where they were instructed to pay attention equally across all object categories. Thus, the face bias responses are not simply due to a general attentional effect to one category.

The above findings have led to the speculation that the rIFJ prioritizes the processing of faces. This hypothesis is in line with the biased competition model for visual attention (Desimone & Duncan, 1995; Duncan, 1980; Roth et al., 2006), which proposed that because there is only a limited amount of information that can be processed in the environment, thus objects that are most relevant are given the highest priority, whereas objects that are less relevant or irrelevant are given lower priority. If this speculation about the role of the rIFJ is true, then previously reported strong responses in the PFC (overlapping with the rIFJ) during a face WM task (Courtney et al., 1996, 1997, 1998; Haxby et al., 2000a), might have resulted from making face stimuli task relevant. That is, by using faces as stimuli (the preferred category in the rIFJ), and by asking subjects to keep faces in WM, faces had become extra relevant; thus leading to an elevation in activation in the "already" face bias (as well as eyes bias) prefrontal region.

Investigation 5 demonstrated that the activation in rIFJ remained strongly biased to whole faces in a rapid event-related experiment, even when presentation of faces was brief and unpredictable, this suggested that the activation was not resulted from subjects processing the same kinds of stimuli for a longer period in a blockeddesign paradigm. In addition, responses from the rIFJ and rFFA were stronger for whole faces and whole bodies (free-viewing task) relative to common objects, and more importantly both regions did not have selective activation for asymmetrical parts of faces, bodies, or common objects. In addition, the similar response patterns between the rIFJ and rFFA indicated that the rIFJ like the rFFA was sensitive to the representation of the whole object instead of parts of the objects (Tong et al., 2000).

These results have suggested that activities in the rIFJ relied on the holistic presentation of faces rather than their parts. The results perhaps could be due to the fact that whole faces and bodies are more behaviourally relevant than parts of them.

Investigation 6 found that the rIFJ responded robustly to eyes alone more than to whole faces with eyes masked. This result suggest that the rIFJ does not simply represent object-based information but may also extract relevant information of objects, in this case pairs of eyes on faces. The robust activation by pairs of eyes here is likely to be associated with the fact that perception of gaze is closely associated with the perception of another person's intentions and emotions. One example is that effective monitoring of other's gaze can regulate turn taking in conversation, and correct perception of emotional information can regulate the content of conversations. These processes have been labelled as joint attention (Baron-Cohen, 1995). Indeed, Jellema et al., (2000) and Perrett et al., (1982) suggested that eyes-gaze could override directions indicated by head and body (Langton et al., 2000). Thus, pairs of eyes are important because they convey both socially and behaviourally relevant information.

In summary, the series of investigations presented here have shown that in the rIFJ, faces, bodies, and eyes elicited strong activation in the non-WM task, and faces elicited a sharper selectivity in the WM-task. The results suggest that both object category, and task demand could influence the level of activation in the rIFJ. To support this proposal, the following section will discuss recent work on the role of the IFJ in tasks requiring the processing of behaviourally relevant objects in humans.

### The role of IFJ in processing behaviourally and task relevant object information

Much of the research in humans' PFC has focused on its role in WM. In particular, whether the activation from the PFC simply reflects the maintenance of information in WM or whether the activation is based on the type of information involved (Haxby et al., 2000a; D'Esposito et al., 2000; Levy and Goldman-Rakic, 2000; Linden et al., 2003; Mohr, Goebel, & Linden, 2006; Owen, Lee, & Williams, 2000; Sala et al., 2003). In the light of evidence from the above single unit studies, and the biased responses from the rIFJ to faces and eyes reported here, it is therefore speculated here that the rIFJ as part of the PFC does not only involved in WM, it also extracts relevant object-based information (faces, and eyes). Hence, it is further reasoned that because the rIFJ was strongly biased to faces, bodies, and eyes in a freeviewing task (non-WM task), such bias in responses to faces stimuli were therefore "exaggerated" during a 1-back WM task. Thus, the results indicated that part of the robust activation in the PFC in object WM task reported by previous experiments could be contributed to by the use of faces as stimuli (Sala et al., 2003) and the already face bias properties of the rIFJ.

Indeed, in some cases, a stronger right lateral prefrontal activation (near the rIFJ) was found when the activation from a face WM task was compared to a spatial WM task of lower-level stimuli (Haxby et al. 2000a; Courtney et al., 1998), however, when other experimenters used non-face stimuli (computer-generated stimuli), they failed to dissociate objects WM with spatial WM in the PFC (Postle, Stern, Rosen, & Corkin, 2000). Interestingly, a recent study had compared activation in the PFC, when subjects manipulated colour information with just maintaining colour and spatial information during a WM task (Mohr et al., 2006). They demonstrated that when

lower-level category stimuli were used the responses near to or overlapping with the IFJ were sensitive to task demand.

Specifically, Mohr et al., (2006) presented subjects with colour or spatial manipulation tasks and colour or spatial maintenance tasks. In the colour manipulation task, subjects had to perform a colour-mixing WM task. In the sample period, two semi-circles of different colours were presented. During the delay period they had to remember the colours of two semi-circles in different colours that were presented, and then a semi-circle was presented in the test period, after that, they had to decide if the colour of the semi-circle in the test period was the intermediate colour of those semi-circles presented in the sample period. In the maintenance task, subjects only had to remember the colours of two semi-circles in the sample period, and had to decide if any of those matched with the colour of a semi-circle presented in the test period.

In the spatial manipulation task, subjects had to decide if the rotation angle of the two semi-circles in the sample period was the averaged rotation angle of the semicircle in the test period. In the spatial maintenance task, subjects had to decide if the rotation angle of semi-circles in the sample period matched with the rotation angle of a semi-circle in the test period. Thus, the manipulation tasks were more demanding than the maintenance tasks. By contrasting the manipulation and maintenance conditions, they reported a strong bilateral IFJ response for the manipulation task. In addition, there was no significant interaction in difficulty level (manipulation vs maintenance) and content level (colour vs spatial). This suggested that when lower level stimuli were used in a WM experiment the activation in the IFJ was sensitive to

task demand (manipulation > maintenance) rather than to the identities or spatial properties of the stimuli.

Taken together, the series of investigations have illustrated that activation in the rIFJ could be modulated by task demand and object category. In other words, the rIFJ activation in object WM is mainly because this region represents both behaviourally relevant information and object category information. The following section will discuss other non-WM fMRI experiments in order to highlight IFJ's role in extracting behaviourally relevant information.

One of the functions of the PFC is to maintain information online in a WM task (Haxby et al., 2000a; Levy and Goldman-Rakic, 2000; Owen et al., 2000; D'Esposito et al., 2000; Linden et al., 2003; Sala, Rama, & Courtney, et al., 2003), however, strong activation from the rIFJ to faces, bodies, and eyes in a non-WM task (free-viewing task) suggest that, extracting category information and behaviourally relevant information could also be a function of the rIFJ. This in turn suggests that the rIFJ as part of the PFC has a more specific role in tasks that required cognitive control Derrfuss, Forstmann, & von Cramon (2005); the ability to select relevant information. If this rationale is true, then the rIFJ should also respond strongly in other cognitive tasks (non-WM task and face stimuli were not used), which require the ability to select relevant information. Indeed, recent evidence from non-WM research supports the hypothesis that the rIFJ is involved in extracting behaviourally relevant information in order to achieve goal directed behaviour.

Brass, Derrfuss et al., (2005), Derrfuss et al., (2004), Derrfuss, Brass, Neumann, and von Cramon (2005) reported IFJ's involvement in tasks requiring cognitive control, namely in the Stroop task and in task-switching paradigm. In their meta-analysis study, Derrfuss et al., (2005) reported activation in the IFJ during a Stroop task where subjects had to extract colour information and ignore over-learnt stimuli i.e. reading the words. In addition, other tasks that required extracting behaviourally relevant information also activated the IFJ (Brass & von Cramon, 2004), such as in a task-switching paradigm (Mayr & Kliegl, 2000; Brass & von Cramon, 2002) where subjects had to alternate between different tasks using cues (e.g. simple shapes). Brass and von Cramon (2004) argued that this robust prefrontal response in task-switching reflected the process of updating task representations. It should be noted that the above findings of strong IFJ responses to non-object categories (e.g. colour and simple shapes) do not necessary contradict or undermine the hypothesis that the IFJ is biased to category-based relevant information (such as faces). Rather, by combining the above findings and results in this chapter, it again supports the idea that the activation in the rIFJ could be driven by the category of the test stimuli, and by task demand. In particular, when lower level stimuli are used, the effect of task demand on IFJ's activation becomes more prominent.

In summary, it has been demonstrated here that faces and eyes were very effective categories for the rIFJ, and when faces were also relevant to the task at the same time, they elicited a maximal activation in the rIFJ. The finding that pairs of eyes alone elicited stronger activation in the rIFJ than whole faces with eyes masked, suggested that the rIFJ "prioritizes" the processing of the most relevant information amongst objects. However, when lower level stimuli were used, it is revealed that

information relevant to task in hand can also elicit strong activation in the IFJ. In the light of the above findings, it is plausible to suggest that the IFJ could be involved in the processing of behaviourally relevant information of people, such as others' intentions and emotion.

### The role of the IFJ in extracting relevant cues of intention of others

Activation for faces and bodies in the ventral cortex has often been interpreted as a result of visual recognition and identity discrimination (Chan et al., 2004; Gauthier et al., 1999; Kanwisher et al., 1997a). However, in this chapter, the strong activation for faces, bodies, and eyes has suggested that the role of the rIFJ goes beyond representing object categories, and that the region could be involved in extracting information about the intentions of others, in particular emotions of others.

The possible role of the rIFJ in processing of emotion is supported by the findings of Marinkovic et al., (2000), as mentioned in the Introduction of this chapter. In their study, the patient was tested before and after the removal of tissues in the right inferior frontal gyrus; regions which had previously been shown to evoke face-selective responses. Specifically, the patient was tested on a face recognition test, a face emotion recognition test, and a general neuropsychological test in order to assess his ability in naming, verbal fluency, reading, writing, mathematics, verbal and non-verbal recent memory. The patient performed normally on face recognition and general neuropsychological tests before and 14 days after the surgery. However, in the face emotion recognition test, he showed a profound deficit in recognizing fear expressions (correct identification, 0%), and disgust expressions (50%), whilst his ability to recognize expressions of joy, sadness, surprise and anger was relatively

normal (similar to his normal performance before the surgery). Even three years after the surgery, his deficit in recognizing fearful expressions remained profound (57%), but his ability to recognize disgust expressions had recovered (100%). Hence, the above evidence suggests that it is likely that the rIFJ is sensitive to different expressions of emotions conveyed by eyes.

Indeed, eyes are particularly salient stimuli as well as behaviourally relevant to both humans and non-human primates. Some researchers argued that perceiving information from eyes may be innately specified, and humans are hypersensitive to information conveyed by the eyes (Adam & Kleck, 2003; Baron-Cohen 1995; Driver, Davis, Ricciardelli, Kidd, Maxwell, & Baron-Cohen, 1999; Emery, Lorincz, Perrett, Oram, & Baker, 1997; Hess & Petrovich, 1987; Hood et al., 1998; Macrae, Hood, Milne, Rowe & Mason, 2002). Perception of gaze is also important for social interaction (Baron-Cohen 1995, 2000; Bayliss & Tipper, 2006b; Perrett & Emery, 1994) because it is particularly crucial for social learning such as action through imitation, accessing mental states of others and hence joint attention (Baron-Cohen 1995; Calder, Lawrence, Keane, Scott, Owen, 2002), as well as social cueing for objects and space (Bayliss & Tipper, 2005a, 2005b; Driver et al., 1999; Emery et al., 1997). Hence, the above suggest that pairs of eyes alone are behaviourally relevant, and therefore they are over-learnt stimuli.

There is plenty of evidence revealing neural signals for eyes and gaze perception in human. For example, evidence from ERP studies showed N170 responses for both face (Bentin et al., 1996; McCarthy et al., 1999) and eyes stimuli (Allison et al., 2000; Bentin et al., 1996; Eimer, 1998; Puce, Smith, & Allison., 2000).

In particular, larger responses to averted gaze were found, and the responses remained strong even when eyes were presented alone (Puce et al., 2000), however, the source of the N170 to eye stimuli remained unclear. Subsequent imaging studies in primates and humans have focused on the role of STS in gaze observation (Allison et al., 2000; Haxby et al., 2000b; Hoffman & Haxby, 2000; Hooker, Paller, Gitelman, Parrish, Mesulam, & Reber, 2003; Pelphrey, Singerman, Allison, & McCarthy, 2003; Perrett et al., 1985; Puce, Allison, Bentin, Gore, & McCarthy, 1998; Wicker, Michel, Henaff, & Decety, 1998). It is therefore possible that the rIFJ receives input from the STS, and the ventral cortex, and thus plays an active role in monitoring the ongoing behaviour of another individual. Further investigations are needed to establish whether the rIFJ is sensitive to head direction, direction of eye-gaze, and emotion conveyed by eyes.

### Conclusions

In the light of the above evidence, the function of the rIFJ goes beyond simply discriminating object categories. Robust responses to faces, bodies, and eyes in WM and non-WM tasks suggested that the activation of the rIFJ depends on a combination of types of object categories and level of relevancy linked to the chosen stimuli (which could be manipulated by task instruction). Thus, maximal activation from the rIFJ could be caused by the use of effective stimuli (faces or eyes) and/or explicit instruction to make an object category more relevant to the task in hand. Present investigations showed that responses for eyes exceeded those for eyes masked, perhaps due to the fact that pairs of eyes could convey clearer information about another person's intention and emotion (Jellema et al., 2000; Marinkovic et al., 2000).

The take-home message is that the rIFJ plays a dual-role in representing behaviourally and task relevant information, as well as in representing some higherlevel object categories. It is speculated here that, because faces, bodies, and eyes can convey behaviourally relevant information of others, they thus elicited strong activation in the rIFJ. Hence, when object categories are presented in the absence of task demand, some object categories (faces, bodies, and eyes) produce strong activation in the rIFJ. When there is a task, that is when relevant behaviour is required, and responses are needed to select lower level stimuli (e.g. colours or simple shapes), "task" also produces strong activation. When a task is required, and responses are needed to select higher-level object stimuli such as faces, the rIFJ elicited a maximal activation.

In addition, future studies using high-resolution fMRI (Schwarzlose et al., 2005; Grill-Spector et a., 2006) may be able to investigate if there are pockets of neural populations within the rIFJ, which may respond differentially to the faces, body posture, and gaze in various directions, and emotions. Furthermore, it remains unclear whether the strong activation in the rIFJ for faces, bodies, and eyes reflects an experience-dependent mechanism to objects or is because these biological stimuli are innately relevant. To test this, further investigation could either examine the responses from the rIFJ for written words or examine if its response would change as a function of visual learning of novel stimuli.

## Chapter 4

### **General Discussion**

Chapter 2 of this thesis presented the broadest fMRI survey to date to investigate object representations in the visual ventral cortex. Specifically, the survey examined: First, the specificity of the category-selective regions (FFA, PPA, EBA) and the category-related region MTG-TA. Second, it examined the prevalence of the category-selective regions in the human visual cortex. Third, it examined a general division in processing animate and inanimate objects in the visual cortex. In addition, pursuing the intriguing strong activation for faces in the lateral prefrontal region found in the fMRI survey, Chapter 3 further investigated face and object representations in the right inferior frontal junction, and subsequently established had similarities and dissociations between the prefrontal face activation and the FFA. A short summary of major findings from each of the above investigations and the implications of those findings will be discussed here.

### Major findings from Chapter 2

In the FFA, PPA, EBA, and MTG-TA, the response patterns across 20 categories were arranged by the strength of activation, from the most-effective category, which elicited the strongest response, to the least preferred category, which elicited the weakest response. Since there were 20 object categories, which varied in visual features, and semantic functions, the response profiles across these categories might reflect the underlying function of each category-specific region, and might indicate the fine-tuning of neurons in each region. The specificity of the FFA, PPA, EBA, and MTG-TA were investigated by a series of split-half regions of interest analyses (Chapter 2, Investigation 1). In the right FFA, bilateral PPA, and right EBA, the responses to faces, scenes, and bodies respectively, were significantly greater than to their second most-effective categories. However, in the left EBA, bodies produced

similar activation as mammals, and the significant difference in activation only emerged between bodies and the sixth strongest category, insects. This is consistent with findings of previous study that, the left EBA is less selective relative to the right EBA (Downing et al., 2001). On the other hand, the category-related region MTG-TA did not exhibit selective activation for tools. In each of the two different contrasts used to localize the MTG-TA, activation for tools was weak and similar to the activation for other categories.

These results replicated previous findings of FFA, PPA, and EBA being strongly biased to faces, scenes and bodies respectively. It is believed that the strong responses or selectivity to the most-effective category correlated with the successful detection and identification of the preferred object categories in the FFA, and PPA (Grill-Spector et al., 2004). Thus, the strength of activation reflects (at least in FFA and PPA) the specific discrimination between the preferred category and nonpreferred categories, instead of a general mechanism for discriminating any different object categories (Spiridon and Kanwisher, 2002). On the other hand, the present fMRI survey showed a spectrum of activation in the FFA, PPA, and EBA, there were systematically graded responses from the strongest to the weakest. This indicates that a fine-scale functional structure could exist in the FFA, PPA, and EBA. Taken together, the nature and source of intermediate activation requires further explanation, which will be further discussed in relation to the latest findings by Gril-Spector et al., (2006).

The second aim of the fMRI survey was to identify new category-selective regions in the ventral cortex in the whole brain analysis (Chapter 2, Investigation 1,

see Supplementary Tables 1-4, p. 244-248). Here, apart from the FFA, PPA, and EBA, no other strongly category-specific regions were found in the visual cortex. Interestingly, some categories elicited strong activation overlapping with the FFA, PPA, and EBA. Mammals and bodies activate a region overlapping with the FFA, chair and prepared food activated a region overlapping with the PPA, and mammals, clothes, and birds activated region overlapping with the EBA. Further split-half analyses in individual subjects were conducted to examine the response profiles of these regions, and it was found that faces, scenes, bodies remained the most-effective categories, even when these regions were defined by the non-preferred categories. Outside the ventral cortex, the most intriguing finding was the strong face bias activation in the rIFJ. The finding was consistent with those in single unit studies, where face-selective cells were found in the prefrontal cortex of monkeys (O'Scalaidhe et al., 1997, 1999). A series of follow-up investigations (Chapter 3) were conducted to explore the role of the rIFJ in face and object perception.

Third, the fMRI survey also aimed to examine a general division of activation between animate and inanimate categories in the ventral cortex. A crude division of activation for animate vs inanimate object categories was found. Lateral regions of the ventral cortex, which overlapped the FFA, and EBA showed biased activation to animate kinds, whereas medial regions of the ventral cortex, which overlapped the PPA showed biased activation to inanimate kinds. It is speculated here that this division is associated with the eccentricity mapping in the ventral cortex (Hasson et al., 2002; Hasson et al., 2003a; Levy et al., 2001; Malach, et al., 2002). The lateral activation for animate objects overlapped with the centre bias region FFA, and the medial activation for inanimate objects was overlapped with the peripheral bias region

PPA. Because the eccentricity mapping is also thought to be associated with the visual resolution that is required for processing objects (i.e. fine vs coarse resolutions), this in turn suggests that the crude division in animate and inanimate objects also reflect the difference in levels of resolution required to process the two general kinds of object categories. Hence, it is speculated here that animate categories such as faces, bodies and animals are more behaviourally/biologically relevant, as each category contains internal features that require detailed visual analysis (fine resolution), and thus may lead to a centre-lateral representation. Conversely, inanimate objects are stationary and are less behaviourally/biologically relevant relative to animate objects, thus may require coarser resolution, and lead to a peripheral-medial representation.

# Implications for the specificity of category-specific regions and neural specialization in object representations

The issue of intermediate responses found in the category-specific regions has been the central issue in the debate of regional specialization in object representations. Recently, it has been proposed that intermediate responses in the category-specific region could reflect fine-tuning of neurons within the region to the non-preferred categories. This subsequently suggests that the spatial distribution of the intermediate responses can inform us about the cortical organization in the ventral stream (Andrews, 2005; Avidan et al., 2002; Grill-Spector et al., 2006). To this end, Grill-Spector et al., (2006) provided evidence that the category-specific region, namely the FFA, contained a heterogeneous structure. Specifically, by using high- resolution fMRI (voxel size: 1mm x 1mm x 1mm), their data showed that there were high concentrations of face-selective neurons interleaved with a small population of neurons that are highly selective to non-preferred categories (animals, car, and

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sculptures). Furthermore, they reported that animal-selective voxels had also responded strongly to faces relative to other categories. This subsequently led Grill-Spector et al., (2006) to suggest that those animal-selective voxels could also be faceselective voxels. This also indicates that voxels could have representation for multiple categories, and thus be selective to more than one category. In summary, they demonstrated that intermediate responses for non-preferred categories were reflecting a fine-scale functional organization in the FFA.

Grill-Spector et al's (2006) findings have provided an insight into the results of intermediate responses in the present fMRI survey, which used a standard resolution of (~ 3mm × 3mm × 4mm). In the present survey, the intermediate responses found in the category-specific regions were also reflected by the nonpreferred activation overlapping with the FFA, PPA, and EBA. Interestingly, the FFA responded strongly to mammals and bodies, and this result is consistent with Grill-Spector et al's (2006) finding that a small proportion of face-selective voxels in the FFA are also animal-selective. However, the underlying reason for this remained unclear.

In the context of Grill-Spector et al's (2006) investigation in the FFA, there are several possible interpretations of the intermediate activation found in the PPA, and EBA in Investigation 2. It is possible that there are small patches of chairselective neurons, prepared food-selective neurons buried in the PPA. There are small patches of mammal-selective neurons, clothes-selective neurons, and bird-selective neurons buried in the EBA. Perhaps, some scene-selective neurons in the PPA, and bodies-selective neurons in the EBA are also selective to non-bodies and non-scenes

categories, suggesting that some neurons have multiple representations of several object categories. It is also possible that bodies-selective neurons in the EBA are broadly tuned to body-like stimuli. Hence, further studies using high-resolution fMRI should investigate the fine-scale functional organization in the EBA and PPA.

The issue of intermediate responses from the "non-preferred" categories (at least in the FFA) seemed to be resolved by high-resolution MRI scanning (Grill-Spector et al., 2006). However, an immediate question is whether the selective responses for the "non-preferred" category contribute to the successful recognition to the "preferred category". In addition, in terms of the general representation of objects in the ventral stream, whether the small populations of selective neurons for the "nonpreferred category" in the category-specific region are compatible with the eccentricity organization of the visual cortex. Thus, further investigation is required to examine if the selective "non-preferred" neurons in the FFA are centre-bias, and whether the selective "non-preferred" neurons in the PPA are peripheral-bias.

Another obvious question is why do some categories have more focal and more selective representation than other categories? Developmental neuroscience on face recognition provided us some insight into this question. The current evidence suggests that some regions in the visual cortex may be pre-specified innately for face representation (Farah, et al., 2000), but that these face representations also develop in specificity with experience acquired during childhood (de Haan, Johnson, & Halit, 2003; La Grand, Mondloch, Maurer, & Brent, 2003). In addition, long-term experience with faces, bodies, and scenes in particular retinal or retinotopic positions

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may have facilitated the development of such focal and bias representations (Levy, et al., 2001; Kanwisher, 2001).

### Limitations and suggestions for future studies

In the fMRI survey, apart from the FFA, PPA, and EBA, no other strongly selective regions were found in the visual cortex. There are several reasons why category selectivity might have been missed with the present techniques. It is possible that other category-selective regions may exist at a grain that is below the voxel resolution used here, or below the resolution of any technique that depends on hemodynamics to measure neural activity. In the context of Grill-Spector et al's (2006) findings, there may be a high proportion of object-selective voxels intermingled with another population of object-selective voxels. Thus, high-resolution fMRI may be able to identify a new category-selective region that may be missed by standard resolution imaging.

In addition, any type of survey depends on the selection stimuli types chosen by the experimenter. Here, this survey has explored the neural responses for object categories in the visual domain. However, apart from visual categorization of objects, it is possible that other strategies to categorize objects may be able to reveal novel category-specific regions. Despite these limitations, the present study represents the most comprehensive search for category-selective to date. Corrigenda: High-resolution fMRI revealed highly selective regions for non-face objects in the FFA.

Due to a series of analysis flaws in Grill-Spector et al's (2006) paper, their recent findings of highly selective non-face clusters buried within the highly selective face region (FFA) have been invalidated by Baker et al., (2007) and Simmons et al., (2007).

Specifically, Baker et al., (2007) claimed that voxel selection was biased to the defining category (positive weighted category in the contrast) in Grill-Spector et al's original analysis, which subsequently led to an over-estimation of selectivity for the non-face categories. To support their claim, Baker et al. (2007) used a split-half region of interest analysis (similar to that in Investigation 1 in the present thesis), and found that non-face categories did not produce selective activation in the FFA. Subsequently, to address the above concern, Grill-Spector et al., (2007) re-analyzed their data using a split-half analysis, and found that their previously reported high selectivity for non-face objects in the FFA was incorrect.

Another group of researchers (Simmons et al., 2007) reported that the formula used by Grill-Spector et al., (2006) to calculate the index of selectivity was incorrect, because lower or negative values were involved. This might have led to overestimates of the selectivity indices for all of the categories. Using the formulae proposed by Simmons et al., a re-analysis conducted by Grill-Spector et al., (2007) revealed that the original claim of high selectivity for non-face objects in the FFA was invalid

In summary, Grill-Spector et al., (2007) conclude that their original claim of a heterogeneous representation in the FFA remains valid. However, as a result of their new analyses (prompted by the recognition of their previous analysis errors), they now propose that the FFA contains highly selective "face clusters" intermingled with "non-face clusters" of lower selectivity.

### Major findings from Chapter 3

Chapter 3 investigated the face bias activation in the rIFJ. Investigations 4 and 5 demonstrated that the response patterns of the rIFJ mirrored that of the rFFA, across working memory manipulation and whole/part manipulation on objects. Investigation 6 showed a dissociation between the two regions, in which the rIFJ was sensitive to the presence of pairs of eyes, but not the rFFA. The present results, based on experiments with humans, resonate with recent results found in non-human primates (Denys et al., 2004; Freedman et al., 2003; O'Scalaidhe et al., 1997, 1999).

### Implications

Specifically, the results demonstrated that the rFFA and rIFJ could play overlapping but distinct roles in visual processing. Contrasting and comparing the neural properties of these two brain regions (Investigations 4-6) allowed us to gain an insight into their perspective roles in face representation. Some of the findings reported here are in line with other research in humans and monkeys in visual processing and working memory. In particular, many recent studies have reported the neural correlates of visual categories in the PFC and ITC, and these studies suggested that these two cortical areas are connected (Denys et al., 2004; Freedman et al., 2001,

2002, 2003; Sigala et al., 2002). Recent work and the implications of the findings from Investigations 4-6 are discussed below.

### Category representation in the prefrontal cortex

Investigations 4 and 5 demonstrated that the rIFJ, like the rFFA, elicited category-bias activation to face stimuli, the result is consistent with O'Scalaidhe et al's (1997, 1999) findings of face-selective cells in monkey's prefrontal cortex. However, O'Scalaidhe et al., did not compare activation in the prefrontal cortex with activation in the ITC, thus a functional comparison between the two regions could not be made. A direct comparison between the PFC and ITC in object representation in monkeys has been made by Freedman et al., (2003), and some of their findings can extend our understanding into the role of the human PFC in object representation. In their single unit study in monkeys, Freedman et al., (2003) compared the activation of the prefrontal cortex and inferior temporal cortex during visual categorization.

Specifically, Freedman et al., (2003) presented monkeys with a set of morphed stimuli from "dogs" to "cats"; and these stimuli were parametrically generated by a computer-morphing program. The monkeys were trained to categorize this set of visual stimuli into two categories, "dogs" or "cats". Monkeys were required to perform a match-to-sample task. First, the sample stimulus appeared in the centre, followed by a delay period, after the delay a second stimulus was presented, and then the monkeys had to respond if the first stimulus matched the second stimulus (while this second stimulus was still presented on the screen). Therefore, in this task, monkeys needed to maintain the sample object in their working memory. They found that neurons in the PFC showed stronger category-effect than the ITC, specifically,

the neurons in the PFC showed sharper between category differences relative to neurons in the ITC. From their results, they claimed that object category representations from the ITC were "copied" to the PFC through direct connections between the two regions (Ungerlieder et al., 1989; Webster, Bachevalier, & Ungerleider, 1994).

Freedman et al's (2003) findings, along with the category-bias activation in the rIFJ reported in Chapter 3, have suggested that in the human the PFC stores more explicit representation of object category, most probably by receiving object information from the visual ventral cortex. Freedman et al., (2003) also indicate that although the processing of diagnostic features may occur in the ventral regions e.g. the FFA, the process of combining those features into categorical representation may be performed by the prefrontal cortex. Furthermore, it has been proposed by some researchers that the prefrontal cortex extracts category information from the visual ventral cortex (and other sensory regions) in order to carry out appropriate behaviour (Levy and Goldman-Rakic, 2000; Miller and Cohen, 2001). Thus, it is possible that the role of the prefrontal cortex goes beyond visual categorisation, and that the prefrontal cortex in fact facilitates the processing of behaviourally relevant information from the visual ventral cortex (Riesenhuber & Poggio, 2000). In the context of IFJ's strong responses for faces, bodies, and pairs of eyes, it is speculated here that the IFJ receives visual information from the ventral region such as the FFA and/or the EBA and even the STS. Hence, it is hypothesized that the rIFJ in humans may play a role in extracting behaviourally relevant information.

Indeed, the notion of rIFJ extracting relevant information in humans is consistent with Denys, Vanduffel, Fize, Nelissen, Peuskens, and Van Essen's (2004) findings. They presented monkeys and humans with intact objects and scrambled version of these intact objects. Specifically, they found stronger bilateral activation in the PFC for intact relative to scrambled objects in both humans and monkeys. Interestingly, the magnitude of responses to objects were smaller in humans relative to monkeys, and a more restricted PFC object-related activation was also found in humans compared to monkeys. From these results, Deny et al., (2004) concluded that humans might have more conscious control over object processing, whilst monkeys might have more automatic responses to objects.

### **Behaviourally relevant information**

The idea of the PFC being involved in encoding behaviourally relevant stimuli is again supported by Freedman et al., (2003). In the match-to-sample task, monkeys were trained to judge if the sample stimulus matched with a second stimulus (test period). The experimenters then examined the match/non-match effect in both the PFC and the ITC. The match/non-match effect referred to the selective neural responses during the test period, before monkeys delivered any motor responses. They found that more neurons in the PFC showed a match/non-match effect than in the ITC, and also more neurons in the PFC showed an interaction between the match/nonmatch and category than in the ITC. This interaction suggested that there were more neurons in the PFC showing a match/non-match effect across categories relative to the ITC.

These authors concluded that the above effects reflected the process of evaluating the match/non-match status of the stimuli or the selection of the appropriate behavioural response (release or hold to indicate match or non-match). The findings of strong responses from the rIFJ to behaviourally relevant stimuli, namely faces, bodies, and eyes seemed to fit in with the above notion. The strong category-bias in rIFJ activity is also consistent with the theoretical model in visual recognition in monkeys that was proposed by Riesenhuber and Poggio, (2000). In their model, categorization takes place when the appropriately weighted inputs from stimulus selective neurons in the ITC converge or map on the PFC neurons that are dedicated for encoding behaviourally relevant information. In this context, it is possible that the rIFJ receives biased representations for faces, bodies, and eyes from the FFA, EBA, and possibly from the STS, and that the information from eyes is most behaviourally relevant. As Jellema et al., (2000) have suggested, in many social situations it could be confusing to interpret someone's action just by their body direction or head position e.g. someone's head and body could be orientated to the right, but their eyes may stare to the person or object on the left. Thus, information from the eyes can be more direct and can convey more important information, such as directions, emotions etc. Thus, strong response in the rIFJ to eyes may reflect its role in processing behaviourally relevant information from stimuli.

### Working memory

The prefrontal cortex in humans and non-human primates is known to be involved in working memory. In the human prefrontal cortex, a maintenance effect refers to a sustained robust activation during the memory delay period in a working memory task (Druzgal & D'Esposito, 2003; Haxby et al., 2000). Interestingly, such an

effect has not been found in other visual regions. Indeed, Druzgal & D'Esposito, (2003) reported a reduced activity in the FFA during the delay period. In primates, a robust maintenance effect was also found during the memory delay period in the PFC rather than the ITC (Freedman et al., 2003). There is no doubt that the PFC plays an essential role in a working memory task. However, the findings of face bias responses in both non-WM and WM tasks in the rIFJ have extended our knowledge on the functions of the PFC in humans. In the light of previous research and the results in Chapter 3, it is argued here that the rIFJ in humans is responsive to task demand, such as working memory, but also plays a significant role in representing object categories. Indeed, the response in the rIFJ seems to be biased to faces and bodies when no WM was required, and such bias for faces was then exaggerated during an 1-back WM task, even when subjects were forced to allocate attention equally across all categories (faces, bodies, tools and scenes).

As mentioned, many WM experiments used faces as stimuli; as a result many researchers observed high responses in the prefrontal region during face working memory tasks. In the context of the findings in Chapter 3, the high prefrontal responses found by previous work are likely to reflect a combined activation for faces and task demand. In other words, faces, and eyes are effective stimuli, and when a WM task required subjects to select relevant information it caused a "top-up" response for faces in the region overlapping with the rIFJ. Therefore, the high responses in the prefrontal cortex previously reported in the working memory experiment may not have reflected a pure working memory effect in the prefrontal cortex. Rather, the responses may have reflected that the rIFJ as part of the prefrontal cortex preferentially represents behaviourally relevant object information (Rainer &

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Miller; Rainer, Asaad, & Miller, 1998). In addition, with the rationale that activities in the IFJ could be driven by relevant stimuli, and since relevancy and familiarity are closely linked, it is therefore speculated here that activation in the IFJ can reflect the effect of visual experience and visual learning (Rainer & Miller, 2000; Miller et al., 2003).

### Visual learning

Faces, bodies and eyes are extremely familiar and relevant stimuli, and thus they are over-learnt stimuli. Therefore, it is possible that the strong activation in the rIFJ (part of the PFC) may have reflected the effect of visual experience and thus its activation can be used as an index of visual learning (Miller et al., 2002). This idea is supported by a single unit study of Rainer and Miller (2000), their findings provided us with an extended view of the category-bias activation in the PFC.

In their experiment monkeys were trained to perform a delayed matching task on natural objects. First, a fixation appeared, then a sample stimulus was presented (all the sample stimuli were systemically degraded by visual noise), followed by a delay period, and then a test stimulus appeared. Monkeys had to respond if the sample stimulus matched the test stimulus. In order to measure the effect of experience (or visual learning), the experimenters examined the monkeys' behaviour and neural responses when the monkeys performed the delayed matching task, and compared the monkeys' responses for familiar objects with novel objects. The monkeys were trained to familiarize with a set of stimuli on five consecutive days. Each day they had to perform five successive behavioural sessions of a delayed matching task, using the same set of objects. Another set of objects was also presented to the monkeys each

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day, but the set of objects presented in each session in this delayed matching task was totally new to the monkeys (novel objects).

Their results showed an effect of familiarity, specifically, Rainer and Miller (2000) found that the neurons in the PFC elicited less activity for familiar objects compared to novel objects. There was a reduction in the number of neurons in processing familiar objects, 24% of the neurons were selective for familiar objects, whilst 39% of neurons were selective for novel objects. They interpreted the findings as a tightening of neural representation in the PFC when the monkeys became familiar with the objects. Thus, their findings suggest that when stimuli become familiar, fewer neurons (but highly selective) are taking part in their processing. Importantly, they found that neural representation for familiar objects were more "resilient" to the degraded sample objects relative to the neural representation for novel objects. Specifically, there was a reduction in selectivity when novel objects were degraded, whilst the selectivity remained high when familiar objects were degraded. With the above results, Rainer and Miller (2000) concluded that plasticity exists in the PFC, and that the effect of visual learning can be measured by neural activities.

The above findings suggest that the PFC has greater sensitivity to objects when they become familiar through experience. The strong activation in the human rIFJ for faces, bodies, and eyes might have reflected a similar property, it is speculated thus here that the rIFJ is sensitive to highly familiar categories. Further investigations are needed to pursue the effect of visual learning in the human rIFJ.

In summary, the function of the rIFJ goes beyond simply representing object categories. Robust responses to faces, bodies and eyes in both non-WM and WM tasks suggested that the responses in the rIFJ could be driven by object categories and task demand imposed onto those test stimuli. In the light of previous work on the PFC, the maximal activation from the rIFJ could be caused by the use of effective categories (i.e. face or eyes), and/or explicit instruction to make an object category relevant to the task in hand. Present investigations illustrated that responses for eyes exceeded those for eyes masked, this is perhaps due to the fact that pairs of eyes could convey clearer information about another person's intentions and emotions (Jellema et al., 2000; Marinkovic et al., 2000). Hence, the rIFJ may play a role in representing task and behaviourally relevant information, as well as object category information.

#### Limitations and suggestions for future studies

Chapter 3 of this thesis examined the role of PFC in visual object presentation. Activation from the rIFJ was compared with the activation in the FFA, and it was found that the regions played overlapping but distinct roles in face processing. However, many studies examining the effect of WM in the PFC and the ventral cortex involved measuring the maintenance effect during a working memory task (Courtney et al., 1998; Druzgal & D'Esposito, 2003; Haxby et al., 2000; Linden et al., 2003; O'Scalaidhe et al's 1997, 1999; Rainer et al., 1998; Rainer and Miller, 2000; Rao et al., 1997). The delayed period in many experiments typically lasted for 6-12 seconds (Druzgal & D'Esposito, 2003; Linden et al., 2003; Sala et al., 2003; Sayala et al., 2006), but in Investigation 4, only a very short 1-back memory task was used to access the effect of WM in the rIFJ. Specifically, subjects had to hold each stimulus in memory for only 450 msec. With such a short delay period it was rather difficult to measure the maintenance effect in both regions. However, the main purpose of Investigation 4 was to examine if the IFJ would gain strong face-bias response in both WM and non-WM tasks, the results here not only fulfilled this aim but also showed that even with such a short maintenance period in the 1-back task, selectivity for faces remained robust. Thus, it is expected that strong face-bias activation will still be observed in a WM task with a longer delay period.

Future studies using a WM task with a longer delay period will definitely extend our knowledge on the temporal properties of the IFJ in face and object processing. Such studies will involve examining the responses from the rIFJ during a post-fixation period in a non-WM task, and during the delay period of a WM task. In the non-WM task, subjects will have to view a pre-stimuli fixation, then visual stimuli, and then a post-stimulus fixation. In the WM task, subjects will view a pre-stimulus fixation, then some sample stimuli, a delay period lasted for 6-12 seconds, and then they will have to respond if the test stimulus matches the one of the sample stimuli (Druzgal & D'Esposito, 2003; Linden et al., 2003).

As mentioned by many researchers (Avidan et al., 2002; Andrews, 2005; Grill-Spector et al., 2006), there is a heterogeneous structure in the category-specific region in the ventral cortex. The FFA contains neurons that are highly selective to the preferred category and a small population of neurons that is highly selective to other non-preferred categories. These different populations of neurons are spatially intermingled together. It is possible that the heterogeneous structure could also exist in the category-bias region in the PFC. The findings that rIFJ elicited the strongest response to faces and eyes, and strong response to body may reflect the above

heterogeneous structure, where larger population of face- and eyes-selective neurons intermingled with a smaller population of body-selective neurons in the rIFJ. In addition, if relevancy and familiarity are one of the factors that determine the representation in the PFC, then it is also possible that object categories with different levels of relevancy and familiarity are heterogeneously represented in the rIFJ. Further studies could use high-resolution fMRI to examine the response pattern to different object categories. For example, to investigate the effect of familiarity by examining the rIFJ responses to familiar and non-familiar faces relative to familiar and non-familiar object categories.

It is also possible that activation in the rIFJ can be used as an index for visual learning (Miller & Cohen, 2001); one way to test this possibility is to compare the responses to initially novel stimuli, and the responses to those stimuli when they become highly familiar and relevant to the task in hand. Recently, Op de Beeck et al., (under review) investigated the effect of training in the ventral cortex. They scanned their subjects before and after the training session (with computer generated novel stimuli), and they did not find any effects of training in the FFA. However, these researchers did not scan the prefrontal region, and therefore the effect of training in the prefrontal cortex was not examined. Thus, a similar experiment comparing responses from the prefrontal cortex and ventral cortex is needed.
Chapter 4-General Discussion

## **Summary & Conclusions**

This thesis presented the broadest fMRI survey to date to investigate object representations in the visual ventral cortex. Specifically, the fMRI survey examined the specificity of the category-selective regions, the prevalence of such categoryselective regions in the human visual cortex, and a crude division of activation between animate and inanimate objects, in the lateral and medial region of the ventral cortex. Along with the recent findings (Grill-Spector et al., 2006) of a fine-scale functional organization in the category-selective regions, it is possible that the organization of the ventral stream varied along a continuum with extreme modular organization at one end and extreme distributed organization at the other end, and that the category-specific regions landed near to the modular end of the spectrum.

The second part of the thesis pursued the intriguing face bias activation in the frontal region found in the fMRI survey. The thesis went on to explore face and object representations in the right inferior frontal junction, and has established some overlapping but distinct roles between the rIFJ and the rFFA in face representation. Along with previous experiments, it is hypothesized here that the rIFJ could play an important role in visual object representations, and extracting relevant object information, and therefore may reflect an effect of visual learning.

Given the strong connections between the PFC and the ventral cortex (Bullier et al., 1996; Jones and Powell, 1970; Kuypers et al., 1965; Ungerleider et al., 1989; O'Scalaidhe et al's 1997, 1999), it is possible that the organization in the ventral stream extends to the frontal regions, and that a heterogeneous representation of

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object category may also be found in the human prefrontal cortex. In addition, the strong rIFJ responses to faces, bodies, and eyes may reflect the fact that this region has applied top down biasing signals to some category-specific regions in the ventral stream (Miller & Cohen 2001; Corbetta & Shulman, 2002). Perhaps the rIFJ contains an "active memory" (Miller & Cohen, 2001), and that it maintains robust activities for important category information e.g. faces, bodies and eyes, all the time, and at the same time it is elastic enough to maintain other appropriate and relevant representations required by current tasks.

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Appendix



Figure A1: Sample stimuli of the 20 object categories fMRI survey.

Appendix



Figure A2: Design and stimuli presentation order of set 2. Conditions are represented in different colours and dots represent blocks of fixation. The first half and second half of this version were swapped to create the second version. The order of blocks was symmetrically counterbalanced within each version, so that the first half of each version was the mirror order of the second half.



Figure A3: Design and stimuli presentation order of set 3. Conditions are represented in different colours and dots represent blocks of fixation. The first half and second half of this version were swapped to create the second version. The order of blocks was symmetrically counterbalanced within each version, so that the first half of each version was the mirror order of the second half.



Figure A4: Samples of Greebles. Greebles were given names, gender and family. This image was retrieved from http://www-

psych.stanford.edu/~lera/psych115s/notes/lecture9/images/greebles.gif



Figure A5. Mean parameter estimate (betas) of the response to each category in the right occipital face area (OFA). Each ROI was identified individually in each subject. Error bars reflect the standard error of the mean.

The right OFA [34, -76, -15] was identified in 10 out of 12 participants (only four participants have OFA activation in both order versions). The difference between mammals and cars was non-significant t (1,9) = .30, p = .77.
									ds	lies	s	irs	thes	stals	es	_	vers	it+veg	ects	truments	mmals	crobes	spared food	otiles	snes	ders	s	apons
									bir	poq	car	cha	Co	5	fac	fist	flor	fru	ins	ins	ma	ä	pre	rep	sce	spi	to	Ň
		Avg. T	alaira	hch C	oord.																							
	mm <sup>3</sup>	X	Y	z	max(T)	mean(T)	р	Region																				
birds-all																												
1	642	42	-72	1	7.4	5.3	0.00038	R. occipitotemporal	4.88	5.65	2.71	3.50	3.86	2.45	3.79	3.19	3.65	3.01	4.53	3.16	4.76	2.60	3.40	4.31	2.16	4.25	3.61	3.69
2	50	25	23	57	5.1	4.7	0.00072	R. dorsal prefrontal	1.02	-0.40	-0.47	0.39	0.68	0.52	-0.39	-0.26	0.49	-0.02	0.43	-0.11	-0.71	0.04	0.53	-0.38	-0.24	-0.35	-0.90	-0.27
bodies-all														_							21.000.004			12				
1	1748	46	-67	1	10.9	7.0	0.00004	R. occipital temporal	3.69	4.70	1.84	2.45	3.16	1.66	2.83	2.41	2.59	2.14	3.52	2.45	3.48	1.92	2.33	3.37	1.19	3.34	2.75	2.95
2	455	42	-49	-14	7.2	6.3	0.00006	R. fusiform gyrus	2.43	3.62	2.02	1.61	2.63	1.65	3.59	1.86	1.78	2.26	2.51	2.13	2.67	1.86	2.38	2.55	2.01	2.65	1.83	2.09
3	30	37	-68	12	6.4	6.0	0.00009	R. occipitotemporal	1.35	2.52	0.87	1.25	1.44	0.62	1.33	0.82	1.19	0.97	1.53	1.39	1.41	0.58	1.02	1.53	1.45	1.34	1.52	1.21
4	378	-49	-72	0	8.7	6.7	0.00005	L. occipitotemporal	4.11	5.29	2.73	2.70	2.94	2.48	2.78	3.21	3.11	3.18	3.65	3.68	4.47	2.26	2.76	4.37	1.82	4.26	4.17	3.91
5	20	-52	-67	6	6.2	6.0	0.00009	L. occipitotemporal	2.28	3.29	1.24	0.57	1.66	1.16	1.47	1.48	1.44	1.46	2.53	2.03	2.08	1.24	1.13	2.52	0.80	1.85	2.54	2.41
cars-all														-													1.00	1.20
1	587	24	-88	-3	7.7	5.2	0.00045	R. posterior occipital	4.83	4.44	5.98	5.58	4.24	5.30	4.64	4.55	5.75	5.27	5.54	4.80	4.43	5.19	6.33	4.82	4.//	6.18	4.00	4.20
2	21	2	-36	-12	5.2	4.7	0.00069	R. colliculus	-0.94	-0.69	0.93	-0.99	-0.73	-0.39	-0.64	0.79	0.18	0.39	-0.82	0.72	-0.61	-0.81	-0.06	0.04	-0.13	-0.41	-0.56	-0.95
chairs-all	-																	2 20	2 60	2.20		2.05	F 24	2 70	6.76	2.50	2.00	2.20
1	161	29	-83	12	5.2	4.7	0.00066	R. posterior occipital	3.16	3.98	2.37	4.74	3.64	2.98	2.39	2.05	3.//	3.29	3.60	3.28	2.5/	3.65	5.34	2.70	6.36	3.60	2.86	3.30
2	872	25	-44	-6	6.9	5.1	0.00047	R. collateral sulcus	0.32	0.43	0.56	2.02	1.15	1.02	-0.14	-0.05	0.93	0.96	0.68	1.06	-0.12	1.40	1.78	0.14	4.03	-0.32	0.56	0.60
3	13	22	-80	20	4.8	4.6	0.00082	R. intraparietal sulcus	0.45	0.86	0.20	1.5/	1.05	0.6/	0.42	0.14	0.51	0.66	0.88	0.8/	0.30	0.53	1.26	0.37	2.16	0.4/	0.61	0.74
4	17	23	-12	-11	5.1	4.6	0.00075	R. anterior hippocampus / amygdala	0.57	0.45	0.46	1.11	0.91	0.63	0.43	0.16	0.06	0.74	1.29	0.44	0.45	0.39	1.39	0.55	0.44	0.29	-0.07	1.04
5	31	-25	-40	-17	5.1	4.6	0.00074	L. collateral sulcus	0.93	0./1	1.1/	2.05	1.43	1.20	0.11	0.84	0.91	1./0	1.59	1.85	0.29	1.59	2.12	0.92	2.25	1.07	1.17	1.28
6	226	-29	-88	15	5.4	4.7	0.0006/	L. intraparietal sulcus	3.66	3.95	2.88	5.13	3.41	3.69	2.00	2.55	4.03	3.80	3.52	3.80	3.51	3.00	5.24	3.18	5.50	3.84	3.81	3.05
clothes-all		-						-	0.40	0.67	0.67	0.40	0.00	0.50	0.07	0.50	0.43	0.45	0.14	0.42	0.70	0.12	0.41	0.50	0.25	0.57	0.02	0.12
1	14	59	-20	21	5.3	4.7	0.00072	R. angular gyrus	-0.40	-0.67	-0.6/	-0.43	0.28	-0.52	-0.67	-0.56	-0.42	-0.45	0.14	-0.43	-0.78	-0.13	-0.41	-0.50	-0.35	-0.57	-0.62	-0.12
2	128	47	-69	2	6.6	5.1	0.00047	R. post. occipitotemporal	4.46	5.72	2.16	2.81	3.84	1.88	2.99	3.13	3.11	2.45	4.22	2.91	4.42	2.32	2.54	4.27	1.09	4.27	3.18	3.52
3	12	38	13	40	4.9	4.6	0.00080	R. middle frontal gyrus	0.19	-0.25	-0.51	-0.11	0.63	0.39	0.45	-0.64	1.24	-0./1	-0.34	-0.89	-0.43	-0.03	-0.54	-0.2/	0.23	-0.22	-0.35	-0.54
4	28	19	31	60	5.2	4.8	0.00056	R. superior frontal gyrus	1.16	0.25	-0.20	0.46	1.44	0.97	0.23	0.33	1.24	0.49	1.03	0.41	0.18	1.18	1.01	0.34	0.21	0.50	-0.07	0.25
5	28	18	67	20	5.2	4.8	0.00064	R. frontal pole	1.14	0.59	0.34	1.08	1.55	1.22	0.20	0.59	0.32	1.02	0.97	0.23	1.04	0.03	1.26	1.50	0.43	1.74	1.50	1.40
6	61	6	-65	29	4.9	4.6	0.00082	R. posterior precuneus	-0.32	-1.08	-1.21	-0.15	0.39	-1.22	-0.91	-0.52	0.75	-1.03	-0.44	-0.72	-1.04	-0.74	-1.30	1 22	1 40	-1.24	-1.50	-1.40
7	31	6	-89	21	5.5	4.8	0.00060	R. medial posterior occipital	-1.58	-0.4/	-1.49	0.3/	1.05	-0.21	-0.39	-1.11	2 40	2 10	0.00	-0.51	-0.45	-2.00	-2.20	-1.32	-2.22	-0.70	-1.01	-4.77
8	31	-1	-/9	22	4.8	4.5	0.00085		-3.40	-4.00	-3.31	-2.22	-1.55	-2.59	-5.17	1 74	1 45	1 66	1 17	1 90	1 60	1 61	-3.20	-2.00	-0.92	-3.23	-7.07	-7.2/
9	392	-9	-88	14	6.6	5.1	0.00044	L. posterior occipital	-2.01	-2.07	-2.35	-1.1/	1.64	-1.49	-1.95	-1./4	0.65	0.21	1 14	-1.09	-1.00	0.00	0.95	0.34	0.05	0.20	0.45	0.41
10	252	-12	6/	15	5.9	4.9	0.00055	L. frontal pole	1.94	1.50	1 77	0.00	0.64	1 17	1.04	1 72	1 20	1.42	1.14	1.02	-1.50	-1.56	-1.19	-2.09	-0.52	-1.64	-1.95	-2.28
11	18	-9	-89	26	4./	4.6	0.00084	L. posterior occipital lobe	-1.80	-1.07	-1.//	-0.67	1 25	-1.1/	-1.94	-1.72	1 12	0.11	0.50	0.24	0.07	1 22	0.52	0.27	-0.10	-0.20	-0.52	0.31
12	46	-23	40	46	5.1	4./	0.00069	L. superior frontal suicus	1.02	-0.08	-0.01	0.55	1.55	0.07	-0.50	-0.21	1.15	0.11	0.50	-0.24	0.07	1.22	0.55	0.27	0.15	0.25	0.52	0.51
crystals-all	00	12	00	14	гг	4.0	0.00064	P. postorior oscipital John	2.02	1 90	3 73	2 00	2.01	3 06	3 20	3 17	3 12	3 30	3 00	2 75	2.05	2 95	4.03	2 66	3.67	4 35	2.08	1.56
1	80	13	-90	-14	5.5	4.8	0.00004	D inferior posterior occipital lobo	1.72	1.09	2.80	2.55	2.01	3.90	217	2 18	3.06	3 20	3 36	1.81	1 70	3 68	4 18	2.00	4 01	3 11	1 14	0.96
2	15	12	-80	-16	5.1	4.7	0.000/1	L posterior occipital loba	2.60	1.57	2.09	3.04	2.20	4 35	3 77	2.10	4 00	3.82	3 57	2.00	2 66	3.66	4 78	2.05	4 95	2 70	2 13	1 23
3	186	-14	-93	22	5.4	4.7	0.00000		0.56	0.56	0.34	0.36	0.69	0.05	0.02	0.38	-0.01	0.52	0.81	0.40	0.20	0.03	0.58	0.03	0.05	0.20	-0.13	-0.10
4	11	-46	-/1	33	5.3	4.8	0.00003		0.50	0.50	0.54	0.30	0.09	0.93	0.02	0.30	0.28	0.52	0.01	0.10	-0.06	0.05	0.56	0.34	0.03	0.64	0.07	0.15
5	34	-4/	-64	- 30	0.8	4.9	0.00058	L. lateral occipitotemporal	0.01	0.33	0.00	0.50	0.00	0.07	0.19	0.70	0.20	0.47	0.00	0.05	0.00	0.13	0.50	0.01	0.27	0.01	0.07	0.10

## Supplementary Table 1: Clusters of activation obtained from the whole brain analysis in Investigation 2, Chapter 2.

## Supplementary Table 2: Clusters of activation obtained from the whole brain analysis in Investigation 2, Chapter 2.

																		eg		ients	als	ss	p					s
									birds	bodies	cars	chairs	clothes	crystals	faces	fish	flowers	fruit+v	insects	instrum	mamm	microb	prepare food	reptiles	scenes	spiders	tools	weapor
		Avg. T	alaira	ch C	oord.		1																					
	mm <sup>3</sup>	X	Y	z	max(T)	mean(T)	p	Region																				
faces-all																_												
1	1197	41	-46	15	6.4	4.9	0.00057 R	. post. superior temporal sulcus	-0.11	0.19	-0.28	-0.23	-0.10	-0.32	0.62	-0.26	-0.36	0.02	-0.02	-0.17	-0.30	-0.32	-0.29	-0.29	-0.03	-0.07	-0.05	-0.17
2	369	45	9	36	6.0	4.9	0.00055 R	. inferior frontal sulcus	0.56	1.11	-0.11	0.54	1.06	0.68	1.83	0.19	-0.03	1.09	1.03	0.77	0.35	0.62	0.94	0.17	1.01	1.05	0.27	0.72
3	21	40	-8	61	4.8	4.6	0.00072 R	. dorsal precentral gyrus	0.35	1.05	0.58	0.20	0.31	0.56	1.71	0.74	0.73	1.08	0.72	0.79	0.76	0.06	1.03	0.30	1.23	1.01	0.69	0.28
4	11	41	-38	-21	4.8	4.6	0.00078 R	. fusiform gyrus	0.54	1.78	0.47	0.22	0.68	0.51	1.84	0.29	-0.14	0.49	0.84	0.68	1.07	-0.06	0.73	0.64	0.76	0.98	0.75	0.32
5	114	37	-8	50	5.8	4.8	0.00059 R	. precentral sulcus	0.26	0.57	0.15	0.09	0.29	-0.12	0.93	-0.06	0.07	0.25	0.26	0.17	0.04	0.04	0.04	0.08	0.59	0.00	0.44	0.33
6	318	37	-1	35	8.2	5.4	0.00038 R	. precentral sulcus	0.46	0.85	0.51	0.32	0.96	0.35	1.67	0.45	0.72	1.03	0.67	0.95	0.62	0.78	0.41	0.67	0.76	0.77	0.21	0.42
7	21	29	19	24	5.1	4.7	0.00071 R	. anterior insula	-0.20	0.17	-0.03	-0.30	-0.04	-0.32	0.53	-0.09	-0.62	-0.05	0.19	-0.14	-0.39	-0.20	0.08	-0.22	-0.21	-0.01	-0.13	0.00
8	27	-8	-2	2	4.8	4.6	0.00081 v	/hite matter	-0.54	0.01	-0.69	-0.25	0.17	-0.69	0.35	-0.46	-0.48	-0.31	-0.18	-0.64	-0.92	-0.33	0.03	-1.05	0.03	-0.45	0.05	-0.1/
9	111	-24	-29	7	5.8	4.7	0.00066 v	/hite matter	-0.01	0.48	0.07	-0.15	-0.25	-0.19	0.66	0.1/	-0.56	0.29	0.48	0.01	-0.09	-0.34	0.25	-0.36	0.32	0.16	0.33	-0.09
fish-all (no activations)										_		_																
flowers-all							0.00050		2.52	1.05	2.42	2.10	2.20	2.20	2.27	2.42	7 70	2.02	2.02	2 10	2.20	2.00	2 62	7.00	2.00	2.00	1.00	1.00
1	265	18	-84	-2	6.9	4.9	0.00052 R	, posterior occipital lobe	2.52	1.85	3.13	3.18	2.26	3.30	2.3/	2.42	3.30	3.03	3.03	2.19	2.38	3.06	3.62	2.60	3.08	3.00	1.88	1.93
2	11	-19	-8/	-2	4.6	4.5	0.00087 L	. posterior occipital lobe	3.33	2.3/	3.81	3.82	2.53	4.05	3.04	3.09	4.05	3./3	3.64	2.82	3.08	3./0	4.55	3.20	3.69	3.64	2.08	0.20
3	11	-52	-19	-12	5.1	4./	0.00075 L	. anterior temporal lobe	-0.25	-0.11	-0.15	-0.25	0.45	0.02	0.02	-0.17	0.70	0.15	-0.06	-0.17	-0.20	0.17	-0.27	-0.22	0.07	0.00	0.10	-0.20
prepared tood-all	140	41	20	67	0.4	E C	0.00025	lateral central culcus	0.45	0.14	-0.04	0.53	0.33	0.27	0.30	0.51	0.36	0.28	0.80	0 38	0.12	0.46	1 10	-0.16	0.05	0.16	0.40	0.23
1	7226	41	-30	02	8.4	5.0	0.00033 8	nostorior oscipital John	0.45	0.14	4.05	4.03	3.07	4.03	4.12	3.01	5.14	4.93	4 00	4 15	4.01	5.04	6.16	3 00	5.28	5.03	3 27	3 48
2	1027	24	-01	-0	11.0	5.9	0.00027 6		7.1/	2.41	7.55	3 70	3.57	3.08	1 51	2 20	3.00	3 47	2 08	3 15	2.05	3.54	4 58	2 30	4.86	2.06	2 36	2 57
3	182/	25	-40	-14	0.0	5.5	0.00057 6	amvadala	0.14	0.68	-0.03	0.75	0.74	0.75	0.47	0.11	0.63	0.27	0.91	-0.10	0.31	0.78	1 38	0.23	0.49	0.18	0.25	0.45
4 F	75	20	.00	-10	5.5	4.7	0.000071 0	ventral medial occinital	0.14	0.00	1.05	1.64	1 49	1.69	1 41	0.88	1 93	2 16	2 03	1.03	3.80	2 48	2.82	1 23	2.62	1.94	0.37	0.25
5	12	5	-30	-19	40	4.7	0.00071 P	naracentral lobule	0.00	0.05	0.27	0.27	-0.30	0.55	-0.12	0.64	0.04	0.26	0.27	0.58	-0.20	0.54	1.09	0.86	0.36	0.22	0.20	-0.32
7	40	-3	-50	16	5.4	47	0.00071	frontal nole	1.11	0.53	0.17	0.58	1.34	0.21	0.19	0.57	0.83	0.29	1.36	0.42	0.02	1.11	1.49	0.04	0.20	0.67	0.15	0.16
8	107	-10	-53	64	82	5.2	0.000431	post central avrus	-0.08	-0.21	-0.55	0.65	0.39	0.05	-0.99	-0.33	0.11	-0.31	0.91	-0.16	-0.51	-0.09	0.75	0.06	-0.26	-0.05	-0.93	0.26
9	173	-12	-84	-15	6.1	4.8	0.00061 L	ventral medial occipital	1.58	1.18	2.87	2.54	1.84	3.10	2.62	2.49	2.62	2.73	3.56	2.00	1.28	2.80	4.29	1.66	3.96	3.01	0.87	0.92
10	674	-18	31	54	7.6	5.2	0.00040 L	superior frontal sulcus	0.99	0.78	1.16	0.86	1.48	1.10	0.47	0.42	0.99	0.57	1.39	0.89	0.56	1.33	1.98	0.95	0.28	0.75	0.16	0.32
11	2464	-24	-83	-7	7.8	5.1	0.00047 L	, posterior occipital	3.39	3.02	3.84	4.01	2.90	3.99	3.05	3.17	4.10	3.91	3.92	3.36	3.21	3.96	4.85	3.27	4.28	3.86	2.94	2.45
12	29	-18	-45	63	5.2	4.7	0.00066 L	. post central gyrus	0.57	-0.36	0.04	0.49	0.42	0.19	-0.35	-0.18	0.32	-0.08	0.83	0.36	-0.09	0.20	0.91	0.43	-0.08	0.20	-0.30	0.72
13	89	-20	34	-1	6.9	4.9	0.00056 L	. orbital frontal	-0.12	-0.42	-0.14	0.34	0.22	0.26	-0.71	-0.03	0.46	0.00	0.47	-0.12	-0.17	0.71	0.96	0.13	-0.50	-0.21	-0.65	0.06
14	32	-19	3	-10	5.3	4.7	0.00067 L	. orbitofrontal	0.39	0.08	-0.13	0.35	0.48	0.46	0.22	-0.23	-0.08	0.50	1.10	-0.21	0.14	0.05	1.25	0.05	-0.34	-0.14	-0.47	0.56
15	1977	-29	-52	-15	8.3	5.4	0.00039 L	. collateral sulcus	2.71	2.54	3.20	4.20	3.25	3.84	1.84	2.86	3.89	4.30	3.67	3.86	2.44	4.35	5.55	2.97	5.34	3.43	3.11	2.87
16	125	-31	-16	-10	5.6	4.8	0.00064 L	. anterior hippocampus	0.34	0.54	0.30	0.64	0.50	0.40	0.49	0.28	0.24	0.50	0.86	0.45	0.26	0.61	1.27	0.12	0.35	0.03	0.27	0.59
17	16	-40	-29	63	5.6	4.9	0.00053 L	. lateral post central gyrus	0.61	0.22	0.06	0.47	0.56	0.82	0.57	0.55	0.35	0.77	0.59	0.55	0.65	0.75	1.26	0.48	0.26	0.50	0.71	0.89
18	111	-41	-67	-15	5.8	4.9	0.00057 L	. inferior occipital lobe	4.60	4.77	4.76	3.90	4.37	4.16	4.38	3.93	4.32	4.66	4.61	4.65	4.10	4.90	5.64	4.55	3.34	4.46	4.36	3.85
fruit & vegetables-all									_																			
1	227	42	-30	0	7.2	5.1	0.00047 F	. superior temporal sulcus	-0.34	-0.38	0.06	-0.03	-0.42	0.06	-0.17	0.18	-0.32	0.41	-0.16	0.31	-0.32	-0.49	-0.33	0.02	-0.16	0.00	-0.25	-0.52
2	185	24	-59	-31	6.7	5.1	0.00046 F	. cerebellum	0.02	-1.85	0.39	-0.01	0.28	-0.41	-2.07	-0.63	-0.48	0.91	0.05	0.85	-0.84	0.29	-0.08	-0.86	-0.55	0.30	-0.93	-0.27
3	17	19	-17	15	5.2	4.7	0.00071 F	. basal ganglia	0.06	-0.21	0.00	0.07	-0.06	-0.33	0.03	-0.04	-0.43	0.48	0.40	0.01	-0.49	-0.11	0.23	-0.24	-0.26	-0.12	-0.16	0.18
4	21	11	-24	27	5.8	4.8	0.00059 F	. corpus callosum	-0.74	-0.73	-0.15	-0.17	-0.36	-0.30	-0.03	-0.03	-0.43	0.75	-0.37	-0.06	-0.02	-0.38	-0.14	-0.37	-0.58	-0.33	-0.25	-0.29
5	16	-7	-14	27	4.7	4.6	0.00083 L	. corpus callosum	-0.04	-0.84	-0.11	0.09	-0.39	0.02	-0.38	0.18	-0.09	1.00	-0.02	0.29	0.28	0.00	0.04	0.04	-0.37	0.12	-0.25	0.25
6	28	-13	-11	26	5.3	4.7	0.00069 v	entricle	-0.27	-0.67	-0.10	-0.04	-0.40	0.05	-0.53	-0.22	-0.60	0.44	0.06	-0.02	0.06	-0.19	-0.12	-0.19	-0.45	-0.23	-0.51	-0.14
7	14	-13	-98	0	4.7	4.5	0.00089 L	. posterior occipital lobe	1.93	2.06	1.86	3.12	2.22	3.47	3.00	1.91	3.38	3.44	2.44	1.86	2.22	2.99	3.54	1.39	4.26	2.55	1.58	0.32
8	11	-16	-98	-3	4.6	4.5	0.00091 L	. posterior occipital lobe	2.69	2.38	2.64	3.60	2.42	3.56	3.16	2.66	3.5/	3.58	2.83	2.37	2.52	3.28	3.82	2.06	3.93	3.19	2.06	0.84
9	17	-25	8	30	5.0	4.7	0.00069 v	vhite matter	-0.42	-0.08	0.11	0.19	-0.22	0.03	-0.01	0.01	-0.45	0.52	0.14	0.32	0.09	-0.32	0.32	0.35	0.12	-0.05	0.05	0.01
10	390	-49	-6	26	5.4	4.7	0.00069 L	. ventral precentral gyrus	-0.08	-0.04	0.20	-0.18	0.09	0.11	0.03	0.52	-0.17	0.85	0.12	0.70	-0.01	-0.03	0.09	0.28	0.0/	0.43	0.08	0.05
11	99	-47	-29	-12	6.0	4.8	0.00059 L	. middle temporal lobe	0.05	0.24	0.18	0.02	0.30	0.21	0.07	0.21	0.09	0.08	0.31	0.58	0.16	0.16	0.30	0.23	0.28	0.12	0.02	-0.04
12	81	-57	-29	32	6.5	4.9	0.00058 L	. lateral postcentral gyrus	-0.33	-0.20	-0.29	-0.33	0.04	-0.62	-0.20	-0.1/	0.09	0.4/	0.18	0.19	-0.4/	0.00	-0.0/	0.19	-0.30	-0.09	0.00	0.59

## Supplementary Table 3: Clusters of activation obtained from the whole brain analysis in Investigation 2, Chapter 2.

									birds	bodies	cars	chairs	clothes	crystals	faces	fish	flowers	fruit+veg	insects	instruments	mammals	microbes	prepared food	reptiles	scenes	spiders	tools	weapons
		Avg. T	alaira	ch Co	ord.					_																		
	mm <sup>3</sup>	x	Y	Z	max(T)	mean(T)	р	Region																				
insects-all											2.20	2.02	2.50	2.04	2.25	2.02	2.45	2.52	4.20	2.02	4 20	2 20	2 00	4.07	1 71	2.00	2 21	2 40
1	941	44	-71	2	6.1	4.9	0.00051	R. occipitotemporal	4.45	5.44	2.29	3.02	3.58	2.04	3.35	2.93	3.15	2.53	4.20	2.83	4.30	2.28	2.80	4.03	1.71	3.90	3.31	0.20
2	26	45	-47	-30	5.1	4.7	0.00069	R. cerebellum	0.03	-0.89	-0.19	-0.19	-0.18	-0.11	-2.07	-1.53	-0.82	0.49	0.55	-0.15	2.50	-0.99	0.07	2.08	-1.24	-0.08	-1.12	-0.20
3	186	18	-94	-3	6.1	5.0	0.00049	R. occipital pole	4.12	3.55	4.//	4.4/	3.52	4.03	4.57	3.62	3.01	7.35	2.21	2.49	1.64	7.77	3.00	2.07	2.47	3.43	1.57	1 75
4	25	18	-89	-18	4.9	4./	0.00072	R. Interior occipital lobe	1.81	1.59	2.04	0.30	0.42	0.12	-0.43	0.08	0.21	-0.23	0.87	0.70	-0.11	0.27	0.51	0.26	-0.17	0.20	-0.46	-0.18
5	82	/	-45	66	5.8	4.8	0.00059	R. post central gyrus	0.17	-0.41	-0.00	-0.03	-0.18	-0.36	-0.43	-0.55	-0.59	-0.23	0.54	-0.14	0.43	-0.06	0.51	-0.29	-0.86	-0.13	-0.82	-0.06
6	52	1	13	11	5.3	4./	0.00069	ventricie	-0.40	1 61	2.04	-0.05	0.10	1 50	1.50	-0.55	-0.35	-1.90	-0.45	-2.11	-1 50	-1 21	-0.65	-2.62	-0.11	-2.66	-2.14	-2.07
7	26	-5	-92	13	5.2	4.0	0.00074	L. medial occipital	-2.10	-1.01	-0.73	-0.02	-0.09	-0.03	0.47	-0.28	-0.44	-0.36	0.45	-0.19	-2 10	-0.38	-0.14	-1.68	0.20	-0.42	-0.08	-1 10
8	231	-9	-33	42	5.8	4.9	0.00050	L. middle cingulate suicus	-0.34	-0.10	-0.44	0.50	0.19	0.03	-1 78	-0.35	-0.32	-0.44	0.94	-0.31	-0.47	-0.04	0.51	0.19	-0.73	0.02	-0.93	0.07
9	68	-10	-50	60	5.8	4.8	0.00062	L. medial post central gyrus	-0.30	-0.20	-0.05	0.09	0.10	0.15	-0.44	-0.11	-0.11	-0.06	0.40	0.08	-0.16	0.18	0.12	0.05	-0.74	-0.15	-0.26	-0.06
10	21	-13	25	0	5.0	4./	0.00071	white matter	-0.04	-0.11	-0.03	0.00	0.00	0.20	-0.79	-0.10	0.11	-0.09	0.10	-0.22	-0.41	0.20	0.18	-0.31	-0.17	-0.23	-0.19	0.13
11	104	-11	20	-0	5.1	4.0	0.00079		0.15	0.13	0.21	0.00	1.04	-0.07	0.08	-0.17	0.07	0.01	1 12	0.19	-0.02	0.50	0.58	0.04	0.08	-0.20	0.04	0.24
12	40	-16	62	1/	5.1	4.0	0.00080	L. montal pole	0.41	-0.00	0.13	0.33	0.19	0.18	-0.35	-0.13	0.27	-0.06	0.85	0.35	-0.14	0.09	0.69	0.45	-0.21	0.23	-0.30	0.55
13	/4	-17	-4/	10	5.2	4.0	0.00079	L. post central suicus	0.37	0.55	0.05	1.25	1 33	0.85	0.90	0.31	0.65	0.00	2.05	0.26	0.56	0.98	2.39	0.51	0.05	0.34	-0.03	1.42
14	97	-18	-5	-10	5.5	4./	0.00007	white matter	0.00	0.00	-0.02	0.41	0.42	0.37	0.67	0.47	-0.04	0.12	1.05	0.41	0.20	0.21	1.28	-0.17	0.39	0.01	0.02	0.22
15	20	-19	-15	-3	4.9	4.0	0.00070	I middle frontal avrus	-0.26	-0.38	-0.35	-0.19	-0.30	-0.44	-0.35	-0.58	-0.09	-0.51	0.56	-0.33	-0.89	-0.08	-0.08	-0.65	-0.37	-0.63	-0.64	-0.11
10	29	-23	-27	2/	5.0	4.9	0.00072	white matter	0.00	0.54	-0.06	-0.01	0.01	-0.20	0.56	0.24	-0.19	0.24	0.64	0.12	-0.20	-0.03	0.18	-0.45	0.38	0.00	0.41	-0.15
10	197	-20	-21	21	5.5	4.0	0.00055	Linsula	-0.08	-0.54	-0.53	-0.02	-0.22	-0.54	-0.16	-0.10	-0.45	-0.09	0.42	0.05	-0.59	-0.29	0.11	-0.25	-0.28	-0.39	-0.13	-0.01
10	20	-35	16	-14	5.0	4.9	0.00050	L temporal pole	0.68	0.32	0.09	0.89	0.79	0.78	-0.13	0.39	0.38	-0.02	1.19	0.47	0.11	0.82	0.99	0.43	0.19	0.19	-0.37	0.66
19	17	-40	4	-17	5.0	4.6	0.000077	L temporal pole	0.14	-0.31	-0.15	0.35	-0.01	0.09	-0.58	0.17	-0.09	-0.02	0.69	0.22	0.04	-0.02	0.54	-0.04	-0.32	-0.27	-0.61	0.19
20	20	-40	-1	-0	5.6	47	0.00066	L temporal pole	0.10	-0.26	-0.37	0.27	-0.05	0.29	-0.59	-0.18	-0.15	-0.47	0.53	-0.02	-0.42	-0.06	0.36	-0.16	-0.28	-0.52	-0.57	0.09
21	29	-52	-67	18	6.1	5.0	0.00049	L inferior parietal lobule	1.10	1.01	0.15	0.37	0.78	0.18	0.33	0.27	0.46	0.32	1.55	0.29	0.45	0.40	0.39	0.59	0.24	0.41	0.64	0.81
musical instruments-all	202	-52	-07	10	0.1	5.0	0.00015																					
1	134	44	-28	1	6.0	49	0.00056	R superior temporal sulcus	-0.46	-0.52	0.06	-0.22	-0.45	-0.09	-0.26	0.14	-0.39	0.32	-0.38	0.30	-0.41	-0.55	-0.49	0.11	-0.26	0.00	-0.43	-0.66
2	35	24	37	3	5.7	4.9	0.00058	R. orbital frontal	0.38	0.26	-0.16	0.44	0.61	0.39	0.17	0.18	-0.01	0.50	0.56	0.72	0.55	0.45	0.85	-0.03	0.00	0.04	-0.14	0.43
2	10	23	-14	42	6.2	5.0	0.00048	white matter	0.00	-0.11	0.12	-0.11	-0.20	0.33	0.12	0.07	-0.04	0.04	-0.24	0.45	-0.08	-0.06	-0.34	0.13	0.09	0.04	0.14	-0.48
4	21	-25	-64	22	5.0	4.6	0.00074	white matter	0.39	0.58	0.03	0.03	0.41	-0.08	0.36	-0.24	0.04	0.13	0.36	0.58	-0.22	0.39	0.12	0.02	0.78	0.02	0.58	0.24
5	118	-34	-58	2	6.7	5.1	0.00046	ventricle	0.50	0.50	0.39	0.55	0.50	0.65	0.32	0.78	0.42	0.96	0.57	1.09	0.36	0.49	0.79	0.65	0.36	0.54	0.88	0.85
6	275	-48	-32	8	6.5	5.0	0.00054	L. Heschl's avrus	0.11	-0.32	-0.05	-0.23	0.02	0.27	-0.34	-0.09	0.07	-0.03	-0.19	0.50	-0.06	-0.24	0.05	0.30	-0.21	-0.02	-0.39	-0.36
mammals-all	2/2																											
1	372	45	-71	0	10.5	5.7	0.00036	R. occipitotemporal	4.80	5.86	2.52	3.20	3.92	2.17	3.43	3.30	3.44	2.73	4.52	3.12	4.83	2.50	3.00	4.42	1.56	4.43	3.39	3.67
2	42	39	-43	-18	5.1	4.6	0.00076	R. fusiform gyrus	2.15	3.55	2.06	1.26	1.96	1.66	3.86	1.57	0.93	1.95	1.99	2.00	3.08	1.17	1.93	2.43	1.80	2.42	1.53	1.48
microbes-all																												
1	95	21	-37	-16	5.5	4.7	0.00067	R. collateral sulcus	1.14	1.30	1.66	2.32	1.86	1.94	0.77	0.97	1.91	1.97	1.57	1.86	1.01	2.47	2.69	1.46	3.43	1.02	1.47	1.62
2	11	17	10	21	5.6	4.8	0.00066	white matter	-0.20	-0.46	-0.47	-0.32	0.03	-0.54	-0.41	-0.15	0.20	-0.26	0.08	-0.35	-0.50	0.38	-0.21	-0.32	-0.50	-0.62	-0.29	-0.33
3	60	-12	-20	-30	5.7	4.9	0.00053	L. pons	0.44	-0.64	0.36	0.35	0.33	-0.37	-1.25	-0.13	1.09	0.23	0.75	0.02	-0.19	0.86	0.13	0.43	-0.08	-0.11	-0.34	0.14
4	12	-10	-72	35	5.1	4.7	0.00069	L. precuneus	-0.80	-1.28	-1.21	-0.88	-0.59	-1.49	-1.42	-0.89	-1.12	-1.24	-0.37	-0.97	-1.43	-0.36	-1.43	-0.88	-0.55	-1.19	-1.14	-1.42
5	16	-16	-28	-21	4.8	4.6	0.00081	L. cerebellum	0.13	0.04	0.23	-0.03	0.44	0.24	-1.16	-0.01	0.78	-0.32	0.47	0.07	0.44	1.68	1.20	0.77	0.11	-0.95	-0.14	0.47
6	143	-31	-76	-29	5.2	4.7	0.00067	L. cerebellum	2.08	2.21	2.80	2.02	1.91	2.40	1.17	1.29	2.93	2.98	2.60	1.00	2.14	3.14	2.48	1.65	1.28	2.78	0.54	1.39
7	126	-33	-71	-19	5.8	4.8	0.00059	L. ventral occipital	3.67	3.63	4.22	3.66	3.58	4.49	3.56	3.63	4.12	4.26	4.49	3.76	3.92	4.73	5.15	3.62	4.46	3.81	3.07	2.56
8	12	-34	6	-28	4.9	4.6	0.00073	L. temporal pole	0.51	0.06	0.07	0.49	0.71	0.52	-0.27	-0.21	0.79	-0.11	0.59	0.09	0.30	0.95	0.73	0.01	-0.03	-0.70	-0.43	0.22
9	25	-37	-4	41	5.4	4.7	0.00074	L. middle frontal gyrus	0.53	0.16	0.16	-0.12	0.60	0.23	0.45	0.14	0.14	0.22	0.47	0.77	0.02	0.91	-0.07	0.40	0.34	0.20	0.18	0.15
10	14	-40	1	40	5.0	4.7	0.00072	L. inferior frontal sulcus	0.99	0.74	0.49	-0.05	0.83	0.55	0.87	0.58	0.13	1.22	0.69	1.37	0.43	1.34	0.35	0.79	0.89	0.60	0.41	0.36
11	22	-56	-40	1	5.1	4.7	0.00070	L. middle temporal gyrus	0.26	0.15	0.36	0.21	1.05	0.50	-0.01	-0.21	0.72	-0.09	0.55	0.61	-0.11	0.86	0.46	0.22	0.16	0.14	-0.16	0.53

		4							irds	odies	ars	hairs	lothes	rystals	aces	ish	lowers	ruit+veg	nsects	nstruments	nammals	nicrobes	repared food	eptiles	cenes	piders	ools	veapons
	-		- lain	ah C	aand				2	P	U	0	U	0	4	E.	E.	-	.=	.=	-	=	٩	2	Ű	S	-5	5
		Avg. I		7		moon(T)		Pagion						-			-			-								
rantilar all	mm	~		4	max(1)	mean(1)	P	Region	-																			
1	240	13	-50	67	65	40	0.00052	P superior parietal lobe	-0 59	-0.38	0.74	-0.25	-0.47	-0.20	-0.54	0.17	-0.65	0.07	-0.22	0.28	-0.49	-0.19	-0.48	0.98	-0.79	0.51	-0.25	-0.83
sconoc-all	275	15	55	07	0.5	1.5	0.00052	N. Superior partetar ibbe	0.55	0.50	0.21	0.25	0.17	0.20	0.51	0.17	0.05	0.07	0.22	0.20	0.15	0.15	0.10	0.50	0.75	0.51	0.25	0.05
1	175	25	-76	10	97	81	0.00001	R nost intranarietal sulcus / TOS	1.03	1.88	1.55	3.16	0.97	0.81	1.48	1.13	1 39	1.43	1.57	0.98	1.65	1.46	1.30	1.49	1.68	2.52	1.63	2.09
2	2493	20	-46	-6	26.8	10.9	0.00001	R parahinpocampal	-0.19	-0.02	0.14	1 18	0.56	0.55	-0.29	-0.41	0.31	0.38	0.24	0.54	-0.54	0.62	1.01	-0.31	3 47	-0.61	-0.03	-0.05
2	10	14	-54	0	8.7	7.8	0.00000	R parieto-occipital fissure	-1 13	-1 37	-1 76	-0.61	-0.77	-0.76	-0.72	-0.99	-1 15	-0.92	-0.99	-0.97	-1 43	-1 25	-0.96	-1 37	1.81	-1 35	-1 33	-1.81
4	47	11	-87	-3	11.3	8.6	0.00001	R calcarine sulcus	1 44	-0.40	1.96	2 22	1 47	2.82	1 43	1 50	2 46	2 38	2 52	0.37	1 47	2 51	3 42	1 41	3 35	1 74	0.09	0.43
5	16	-7	-80	-6	81	7.8	0.00001	medial occipital	-7.49	-2.27	-7.48	-1.27	-0.97	-1.31	-1.08	-1.91	-1.12	-1.27	-0.47	-1.98	-2.11	-1.23	-1.02	-1.94	0.83	-1.88	-2.49	-2.40
5	708	-11	-07	2	10.0	83	0.00001		0.00	-0.06	0.12	1 42	0.90	1 51	1.08	0.05	1 46	1.20	1 25	0.12	0.26	1 31	1 77	-0.11	2 91	0.35	-0.10	-0.59
7	60	-7	-78	-12	9.0	8.0	0.00001	medial occipital	-0.80	-0.96	-0.83	0.74	0.32	0.51	0.26	-0.43	0.57	0.26	1 74	-0.66	-0.68	0.52	1 10	-0.55	2 13	-0.16	-1 35	-1.36
8	1018	-22	-48	-6	14 7	9.0	0.00001	L parahippocampal	-0.59	-0.33	-0.16	0.86	0.20	0.21	-0.48	-0.26	0.03	0.15	-0.09	0.46	-0.75	0.00	0.56	-0.70	3 11	-0.50	0.03	-0.56
0	1510	-25	-86	16	85	79	0.00000	L post intranarietal sulcus / TOS	2 32	2 73	1 49	3 70	2 52	2.53	1 15	1 20	2 77	2 51	2 48	2.45	2.26	2.59	3.88	1.79	4 58	2 10	2.61	1.92
sniders-all	10	25	00	10	0.5	1.5	0.00001	E. post. independent suices / 105	2.52	2.75	1.15	5.70	LIJE	2.00	1115	1.20	2.77	2.01	21.10	2.10	2.20	2.00	5.00	1.1.5			2.01	1.50
1	10	53	-70	35	40	4.6	0 00082	R inferior parietal lobule	-0.79	-0.44	-0.37	-0.66	-0.13	-0.63	-0.25	-0.20	-0.54	0.01	-0.17	-0.36	-0.98	-0.59	-0.59	-0.21	-0.55	0.04	-0.29	-0.47
2	50	26	-92	-2	4.8	4.6	0.00075	R. occinital pole	4.73	4.46	5.46	4.98	4.35	4.70	4.31	4.45	5.60	5.04	5.23	4.83	4.34	4.99	5.65	4.52	4.23	6.02	3.49	3.77
3	113	25	-88	-10	4.8	4.6	0.00081	R. occinital pole	3.72	3.45	5.10	4.35	3.39	4.44	3.84	3.86	4.49	4.42	4.46	4.32	3.44	4.09	4.97	3.95	3.67	5.45	3.27	3.32
4	191	-25	-93	-11	7.2	5.4	0.00036	L occinital pole	2.76	2.54	3.31	3.00	2.07	2.75	2.67	2.95	3.52	3.22	2.72	3.31	2.11	3.40	3.19	2.36	2.82	3.96	2.48	1.86
tools-all	1.91		55				0100000																					
1	29	6	-28	9	5.0	4.7	0.00067	R. splenium	-0.56	0.40	-0.85	-0.13	-0.27	-0.32	0.43	-0.18	-1.93	-0.37	0.09	-0.09	-0.54	-0.61	-0.19	-1.09	-0.07	-0.37	0.50	-0.43
2	14	-18	-44	15	5.3	4.7	0.00075	white matter	-0.92	-0.16	-0.44	-0.64	-0.67	-0.52	0.01	-0.06	-0.93	0.04	-0.48	-0.07	-0.51	-0.73	-1.02	-0.65	-0.47	-0.47	0.08	-0.65
3	23	-31	-43	41	5.2	4.7	0.00073	L post central gyrus	0.49	0.50	0.29	-0.13	0.64	0.21	0.64	0.78	0.10	0.87	0.28	0.79	0.13	0.05	0.20	0.54	0.18	0.49	1.16	0.86
4	62	-40	-33	41	6.4	4.8	0.00062	L post central gyrus	0.18	0.09	-0.35	-0.08	0.31	-0.08	0.20	-0.02	-0.05	0.24	0.36	0.25	-0.23	0.15	0.17	0.03	0.09	-0.05	0.69	0.60
weanons-all																												
1	13	14	19	13	5.9	4.9	0.00057	R. caudate nucleus	-0.15	-0.55	-0.55	0.02	0.04	-0.79	-0.72	-0.27	-0.30	-0.25	0.04	-0.14	-0.93	0.02	-0.08	-0.65	-0.63	-0.79	-0.73	0.11
2	257	-23	-62	61	6.3	5.0	0.00050	L. superior parietal lobe	0.37	0.58	0.36	0.92	0.07	-0.14	-0.33	0.55	0.13	0.32	1.06	0.53	-0.06	0.26	0.33	1.03	-0.43	0.56	1.02	1.15
。 19月1日日日前日				21/2	istra in	2.00				6223				E HOI	9635	5040		-		587A		3			3425	1	STELES	ata.
animate-inanimate		-																										
1	2321	45	-67	1	11.6	5.8	0.00031	R. ventrolateral occipitotemporal	3.72	4.66	1.94	2.39	3.02	1.67	2.86	2.45	2.53	2.16	3.46	2.45	3.61	1.94	2.23	3.40	1.26	3.38	2.75	2.96
2	252	40	-43	-19	5.7	4.7	0.00065	R. fusiform	1.64	2.81	1.49	0.85	1.51	1.25	3.07	1.09	0.66	1.37	1.64	1.40	2.37	0.73	1.42	1.81	1.34	1.92	1.13	1.00
3	47	37	-54	16	5.1	4.6	0.00079	R. superior temporal sulcus	0.37	0.63	-0.18	0.18	-0.10	-0.22	0.34	0.02	-0.16	0.24	0.30	-0.22	0.21	-0.20	-0.37	0.00	-0.05	-0.10	0.02	-0.31
4	34	5	63	36	5.5	4.9	0.00055	medial frontal pole	0.94	0.58	0.47	0.47	1.21	0.34	0.64	0.97	1.44	0.06	0.78	0.74	2.04	1.13	0.48	1.04	-0.02	1.05	0.29	-0.27
5	1684	-46	-64	8	7.3	5.2	0.00039	L STS / lateral occipitotemporal	2.04	2.61	0.98	1.01	1.34	0.87	1.31	1.37	1.21	1.27	1.94	1.63	1.96	0.96	0.87	2.12	0.74	1.94	1.84	1.86
6	340	-44	-51	-23	7.2	5.4	0.00034	L. fusiform	2.00	2.20	1.97	1.47	1.69	1.84	2.41	1.99	1.96	2.25	2.37	1.95	2.69	1.58	2.05	2.18	1.54	2.31	1.30	1.23
inanimate-animate	7769	22	-51	.7	0.0	E C	0 00033		0.56	0.86	0.88	1 70	1 20	1 35	0.23	0.53	1 10	1 34	1.10	1 36	0.40	1 48	1.95	0.67	3 25	0.41	0.76	0.85
1	7708	22	-51	-/	9.0	5.0	0.00032	L parahippocampal	0.00	0.00	1 10	2.79	1.29	1.55	0.25	0.55	1.15	1.70	1.10	1.00	0.51	1.82	2.55	0.07	3.50	1.04	1 31	1 14
2	5155	-26	-4/	-12	10.4	5.9	0.00026		0.02	2.04	1.10	2.23	2.51	2.39	1 20	1 70	2.06	1.79	2.64	2.90	2.46	2.03	4.00	0.52	4.52	2.04	2.00	7.47
3	626	-28	-84	14	6.5	4.8	0.00059	L. transverse occipital suicus	2.11	3.00	1.97	3.82	2.02	2.74	1.38	1.70	2.90	2.11	2.04	2.00	2.40	2.01	4.00	2.3/	4.52	2.50	5.00	2.43
4	38	-51	19	21	5.8	4.8	0.00065	L. lateral prefrontal	0.47	0.27	1.08	0.39	0.56	1.26	0.80	0.53	0.54	1.08	1.14	1.24	0.38	1.36	1.90	0.85	0.85	0.90	0.44	0.70

## Supplementary Table 4: Clusters of activation obtained from the whole brain analysis in Investigation 2, Chapter 2.

Notes:

Supplementary tables 1-4: All activations above minimum extent threshold of 10 mm<sup>3</sup>, from a random-effects multiple regression analysis. Contrasts were tested at a threshold of p < .001 (t = 4.43) except for scenes vs all others (t = 7.65; p < .00001) and bodies vs. all others (t = 5.875; p < .0001). Each row gives the volume of the activation, the location of the centre of activation in Talairach coordinates, the maximum and mean T value for the region, the associated p value for the region as a whole, and the approximate anatomical location of the centre of that activation. The final columns include for each activated cluster the response to all 20 categories, as measured by the betas from the regression analysis.