A SYSTEMATIC EXPLORATION OF PERCEPTUAL AND SEMANTIC DIFFERENCES IN CATEGORY-SPECIFIC OBJECT-PROCESSING USING MAGNETOENCEPHALOGRAPHY

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Thesis Summary

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In a series of experiments, we tested category-specific activation in normal participants using magnetoencephalography (MEG). Our experiments explored the temporal processing of objects, as MEG characterises neural activity on the order of milliseconds. Our experiments explored object-processing, including assessing the time-course of object naming, early differences in processing living compared with nonliving objects and processing objects at the basic compared with the domain level, and late differences in processing living compared with nonliving objects and processing objects at the basic compared with the domain level. In addition to studies using normal participants, we also utilised MEG to explore category-specific processing in a patient with a deficit for living objects.

Our findings support the cascade model of object naming (Humphreys et al., 1988). In addition, our findings using normal participants demonstrate early, category-specific perceptual differences. These findings are corroborated by our patient study. In our assessment of the time-course of category-specific effects as well as a separate analysis designed to measure semantic differences between living and nonliving objects, we found support for the sensory/motor model of object naming (Martin, 1998), in addition to support for the cascade model of object naming. Thus, object processing in normal participants appears to be served by a distributed network in the brain, and there are both perceptual and semantic differences between living and nonliving objects. A separate study assessing the influence of the level at which you are asked to identify an object on processing in the brain found evidence supporting the convergence zone hypothesis (Damasio, 1989). Taken together, these findings indicate the utility of MEG in exploring the time-course of object processing, isolating early perceptual and later semantic effects within the brain.

Key words: magnetoencephalography; category-specific deficits; semantic system; object processing; picture naming

Dedication

There are many people whom I would like to thank for their support and encouragement. Firstly, thanks to Laura Shapiro. You have always been available, offered advice, and have been a wonderful support throughout this process. You are truly a wonderful friend and supervisor, and moving to England would not have been as pleasant had you not been here to help along the way. Secondly, thanks to Gareth Barnes for your advice and counsel regarding all things MEG. You have made data analysis tolerable, which is an amazing thing. Also, thanks to the members of the Neuroimaging Research Group and my many office mates, who have offered valuable advice and suggestions along the way. Finally, special thanks to Elaine Foley and Cary Frey for patiently reading through versions of this thesis.

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I hereby certify that the work submitted for the degree of Doctor of Philosophy has not been submitted for any other academic award. In addition, I have not knowingly falsified any of the data contained within the work I am submitting. Finally, the length of the thesis is not more than 80,000 words, excluding appendices. I have clearly acknowledged in the thesis all those parts of the work which were done in collaboration with others.

Contents

List of Figures

List of Tables

CHAPTER 1

Introduction

Memory is a fundamental aspect of human cognition involving the acquisition, storage, and retrieval of information. Selective damage to one area of the memory system can produce interesting dissociations, highlighting the distributed organisation of memory in the normal brain. Some of the most striking memory deficits are the agnosias ("*loss of knowledge*"), with perhaps the most interesting being visual agnosia, referring to an inability to recognise objects or faces even though the neural architecture for converting light energy into neural signals remains intact. According to Lissauer (1890), visual agnosia ("*Seelenblindheit*") was first recognised as a clinical syndrome in 1884, and certainly his account of a patient, Gottlieb L., with a striking visual agnosia is one of the best documented historical cases in the literature. For example, when presented a large wall mirror, Gottlieb L. incorrectly reported it to be "a lamp" and when presented an illustration of a swan he incorrectly reported it to be "a giraffe." This can be contrasted with correct naming for items such as hat and horse (pp. 178-179). Importantly, based on his work with this patient, Lissauer argued that there are two stages in the recognition of objects: 1) a stage of conscious awareness of a sensory impression called *apperception*, and 2) a stage of associating what we know about objects with this sensory impression called *association*. Critically, then, visual agnosia can have three possible etiologies: 1) damage to associative processes without impairment to apperception, 2) impairment to both apperception and associative processes, and 3) selective impairment of apperception. For this patient, Lissauer argued that the deficit resulted primarily from damage to associative processes. Thus, Lissauer was the first to recognise that clinical manifestation of a visual agnosia could result from either a perceptual or semantic system deficit, or a deficit to both systems. This critical differentiation forms the basis of the research reported herein.

In a seminal book in 1946, Nielsen reported the first patients showing difficulty processing specific sub-types of objects. This pattern of deficits has come to be known as category-specific semantic deficits (first termed *category specific access dysphasia* by Warrington & McCarthy, 1983). The first patient, C. H. C., was unable to name inanimate objects by sight or touch. This included a deficit with foods presented visually until tasted, and an inability to name colours although he appeared to recognise them. What was striking about this patient was his intact recognition of faces of acquaintances, body parts, and flowers. A postmortem examination of this patient's brain showed several lesions, with the critical lesion appearing to occupy Brodmann's areas 18 and 19 in the right hemisphere. A second patient, Flora D., presented with a different pattern of deficits. She was unable to recognise hands, fingers, and any living things. She could also not recognise faces, although she was able to describe their feature colours. In complete contrast to C. H. C., Flora D. could recognise nonliving things, although the extent of her impairments was not completely understood as she died two weeks after surgery to drain

a pulmonary abscess of the left upper lobe of her brain. A postmortem examination of her brain showed a diffuse lesion affecting the left inferior occipital lobe, including Brodmann's areas 18 and 19. In a footnote to this case report, Nielsen also described a second patient with a visual agnosia for animate objects who had a focal lesion partly cortical and partly subcortical in the left occipital lobe affecting the association areas but not the projection fibre tracts. Given the three cases, Nielsen provided the most parsimonious account of category-specificity to date: the left occipital lobe recognises living/animate objects whilst the right recognises nonliving/inanimate objects. Although not supported by more recent clinical literature, Nielsen's hypothesis, then, states that category-specific deficits emerge because there are discrete category-specific recognition systems in the brain for processing living and nonliving objects (as cited in Forde & Humphreys, 2002). This idea of separate systems for processing aspects of living and nonliving objects has been described in various forms throughout the intervening sixty years.

Much of the current research on visual agnosia has focused on the semantic system (semantic memory). The semantic system is a component of our memory that stores general knowledge about things and their interrelationships, including words, objects, places, and people (Garrard, Perry, & Hodges, 1997; Hodges & Patterson, 1997), and it is thought to be located somewhere in the anterior inferior occipital and temporal lobes of the brain, in addition to other distinct brain regions (for reviews, see Martin, 2007; Patterson, Nestor, & Rogers, 2007). That the brain damage for patients with category-specific deficits involves the semantic system exclusively is inaccurate. For example, in their model of picture naming, Humphreys, Riddoch, & Quinlan (1988) highlighted that, much as Lissauer (1890) argued, category-specific effects can occur as a function of damage at different functional levels (see also Humphreys & Forde, 2001). When you are asked to name an object presented visually, you must first decipher the visual form of an object. This is followed by accessing the semantic representations associated with that object. Finally, you access the stored phonological representations in order to name the object appropriately. There is debate amongst theorists as to whether these stages occur serially or via cascade. Irregardless of this debate, damage at different levels within this system will produce fairly uniform deficits. Thus, the deficits exhibited by patients with damage at different levels of the system will appear homogeneous, but the underlying etiology is rather heterogeneous (e.g., Gerlach, 2009; Rosazza et al., 2003). This suggestion is corroborated by a review of the patient literature by Gainotti (2000). He found that a number of patients' deficits reported in the literature appeared to reflect problems with accessing the visual form of objects. For other patients, the damage seemed to occur at the level of accessing semantic representations. Finally, a final group of patients seemed to have deficits at the level of lexical decision-making. Thus, there is strong evidence that the patterning of deficits across patients is not homogeneous, but rather is a reflection of deficits at different processing levels within the object-recognition system.

Patients with category-specific impairments overwhelmingly have deficits in processing living things, with over 100 patients reported by 2003 showing deficits for living things, compared with only 25 showing deficits for nonliving things (Martin & Caramazza, 2003). Whether this 4:1 ratio simply reflects a reporting bias in the literature, or perhaps more

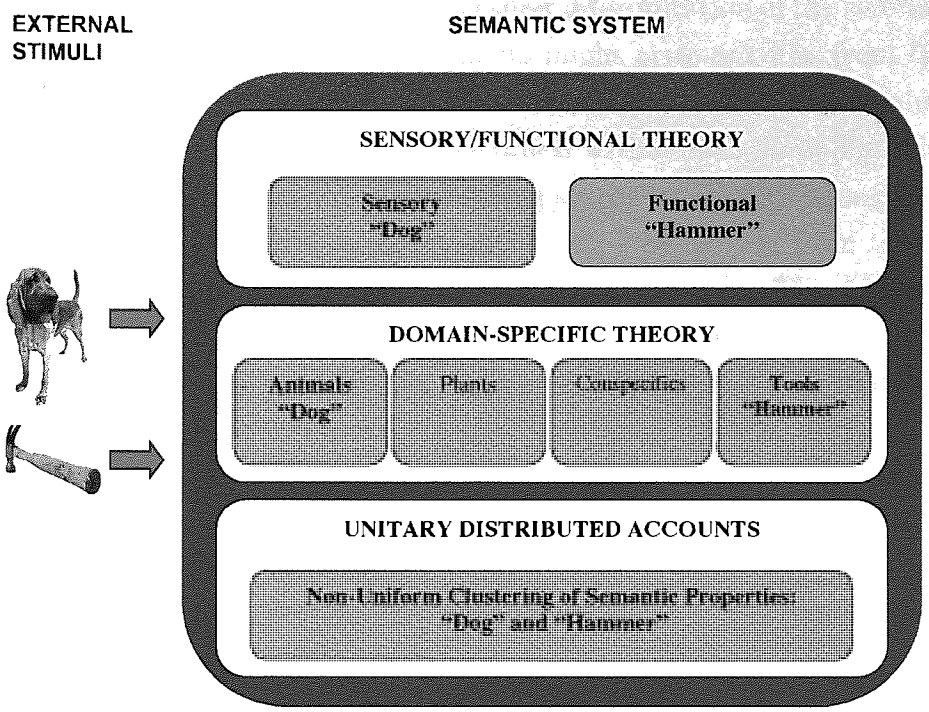
importantly, critical differences in how living and nonliving object knowledge is represented/organised in the brain remains to be seen. Certainly, there is evidence from the developmental literature that there are differences in children's acquisition of knowledge about living and nonliving things (e.g., R. Gelman, 1990; S. Gelman, 2004), and these differences might have important implications for impaired and spared knowledge following brain insult. Irregardless, that you can have impaired knowledge for specific categories of objects has led to the formulation of several theories which attempt to account for how object concepts are represented in the brain. Each of these theories is reviewed in turn.

1.1. Theories of Category-Specificity

Several theories have been proposed to describe how conceptual knowledge is organised in the brain, accounting for the pattern of deficits observed in patients. Generally, these theories fall into three broad categories (see Figure 1.1.1). The first theoretical view argues that conceptual knowledge is distributed across sensory and functional semantic processing regions (e.g., Sensory-Functional theory: Warrington & Shallice, 1984; correlated and distinguishing features account: Gonnerman et al., 1997; HIT theory: Humphreys & Forde, 2001; psychological distance account: Gaffan & Heywood, 1993). This view posits that objects can be differentiated based on the relative influence of either sensory features or functional information, and (for a subset of these theories) these are distributed across functionally and neuroanatomically distinct subsystems. The second theoretical view also argues for functionally and neuroanatomically distinct subsystems in the brain, evolved based on evolutionary pressure (Domain-Specific theory: Caramazza & Shelton, 1998). Thus this view argues that the brain has evolved specialised neural architecture for processing particular types of knowledge based on natural selection processes. The final theoretical view posits that there is a single, amodal semantic store in the brain which processes all object knowledge. Within this unitary semantic system, there is a non-uniform distribution of object properties, with similar properties clustering together (e.g., Conceptual Structure Account: Moss et al, 2002; Organised Unitary Content Hypothesis: Caramazza et al., 1990). Whilst each of these theories will be reviewed and compared in turn, it is important to note at the outset that there are several shared underlying assumptions amongst the major theoretical views. For example, all theories of category-specificity support the existence of distinct representational areas for computing distributed visual, semantic, and lexical representations. In addition, each of these theories allows for weighted mappings that determine how the representational layers influence one another as part of a dynamic and interactive system. In the following subsections, the genesis of each of these major theories is described. In addition, specific predictions made by each of these theories are explicated, in order to delineate similarities and differences amongst them.

1.1.1. The Sensory/Functional Theory. In 1983, Warrington & McCarthy described a patient, V.E.R., displaying a category-specific impairment in matching pictures of nonliving objects using a match-to-sample technique compared to foods, animals, and flowers. This was followed a year later by a paper describing four patients showing the opposite pattern of deficits, that is, relative impairment in identifying living things and

FIGURE 1.1.1. Major Theoretical Views on the Organisation of the Semantic System.



The 3 broad types of theories describing how conceptual knowledge is organised in the brain. The Sensory/Functional (SF) theory posits that living things are generally processed via the semantic subsystem, whilst nonliving things are processed by the functional semantic subsystem. The Domain-Specific (DS) theory posits that there are distinct neural systems in the brain for processing animals, plants, conspecifics, and tools. The unitary distributed accounts argue for a single semantic system having non-uniform clustering of semantic properties.

foods compared to nonliving things (Warrington & Shallice, 1984). This second paper was the first to propose a broad theory for how conceptual knowledge might be organised in the brain: the Sensory/Functional (SF) theory. The central idea of this theory is that knowledge about objects is organised by sensory features (e.g., form, motion and colour) and functional properties (e.g., motor habits related to using an object and the typical location where it may be found). There are domain-level differences in the relative importance of sensory or functional information needed to identify objects. Living things can be differentiated primarily using sensory information, whilst functional information is important for distinguishing between nonliving things. Thus, differentiating living and nonliving objects relies on separate subsystems, each dedicated to storing and processing a specific type of information (e.g., visual, motor, auditory, etc.). Thus, category-specific impairments arise from a non-categorically organised semantic system. In addition to the broad distinction of sensory versus functional information, Warrington & Shallice also noted that amongst their patients, the specific impairment was not consistent across various presentation modalities. So, for example, some patients had greater difficulty identifying specific items when presented pictorially, whilst others had difficulty identifying specific items when they were asked to define them verbally. Thus, semantic memory must also be partitioned by input modality according to these authors. Therefore, sensory information exists for both visual information and verbal information, separately. The

SF theoretical framework was the catalyst for much of the research on category-specific deficits that followed.

In 1987, Warrington & McCarthy extended their interpretation of the sensory/functional dichotomy, arguing that category-specific deficits might arise not just from the different weightings of the major sensory/functional modalities, but also as a consequence of different weighting values on more specialised channels within each modality. They posited that early segregation within the object-processing system could have concomitant effects at later processing stages, and the evidence provided by or derived from these functions might interact differentially with information from other sources. This is based on their results of testing Y.O.T., a patient with a category-specific deficit for nonliving things. In a first experiment, Y.O.T. was found to be impaired in her ability to match pictures of artefacts (67% correct) to their name compared with animals (86% correct) and flowers (86% correct). In a second experiment, this same pattern of deficits was found, but only under short time constraints. In a third experiment, the authors tested whether Y.O.T.'s impairment was specific for a sub-class of nonliving objects by testing her on manipulable and non-manipulable objects. They found that Y.O.T. was impaired in her ability to identify manipulable objects (58% correct) compared with large man-made objects (78% correct) and foods (83% correct). In a final experiment, Warrington & McCarthy showed that Y.O.T. performed more poorly on nonliving objects that were close in semantic distance rather than those that were distant. These findings led Warrington & McCarthy to argue that somatosensory information and information derived from actions might be more heavily weighted in the representations of small, manipulable objects compared with large, man-made objects. Along the same vein, Warrington & McCarthy argued that colour knowledge might be more important for recognising fruits and vegetables, whilst shape might be more important for distinguishing amongst flowers. Thus, patients might have difficulty identifying subsets of living or nonliving objects (see also Humphrey & Forde, 2001). For example, they might show an impairment in processing fruits and vegetables, whilst having relatively spared performance identifying animals.

In 2001, Humphreys & Forde proposed the Hierarchical Interactive Theory (HIT) to account for the influence of similarity on object processing. According to this theory, processing an object activates a hierarchy of stored representations, and partial activation within the hierarchy can be transmitted between processing stages. Within this model for object processing, there are three types of stored knowledge: 1) stored structural descriptions, 2) stored functional and associative information (i.e., "semantic" knowledge), and 3) name representations. When presented with an object to name, processing in the first pass is transmitted hierarchically. However, after this first pass, it is not required to continue hierarchically. When first presented a picture of an object, there is activation of stored structural descriptions and partial activation of associative/functional knowledge. In addition, there is top-down interrogation of perceptual knowledge, serving to allow differentiation of an item from its competitors. According to Humphreys & Forde (2001) additional information to distinguish living things would include form information to distinguish amongst animals, and colour and texture information to distinguish amongst fruits and vegetables. For nonliving things, additional information would include action-related functional knowledge for tools. Thus this model continues in recognising the

differential importance of sensory information for living things and functional information for nonliving things.

A central prediction of the SF theory is that damage to either the sensory or functional system should produce deficits for all items that are processed within that damaged system. So, for example, damage to the sensory system should produce impairments to all categories whose processing relies on sensory information. In the same way, damage then to the functional/motor system should produce impairment for all categories that rely on functional information. However, these clear-cut distinctions are not fully supported by patient evidence. This will be discussed further in Section 1.3 of this chapter. A second prediction of the SF theory is that patients showing disproportionate difficulties in processing visual information about objects should show greater impairment for living things. However, some patient evidence in the literature argues against this (Coltheart et al., 1998; Lambon Ralph et al., 1998). For example, Lambon Ralph et al. (1998) reported on a patient with a category-specific deficit for living things who did not have an accompanying deficit for perceptual properties of objects. In addition, another patient showed poor knowledge of perceptual properties of objects without demonstrating a category-specific deficit for living things. Other clinical reports have described patients with category-specific deficits who show impairments in all knowledge related to a given object category. For example, patients with category-specific deficits for living things have shown equal impairment in their visual and functional knowledge about living things using property verification tasks in which questions about visual and functional knowledge have been equated for difficulty (Caramazza & Shelton, 1998; Laiacona, Barbarotto, & Capitani, 1993; Laiacona, Capitani, & Barbarotto,1997; Lambon-Ralph et al., 1998; Moss et al., 1998; Samson, Pillon, & De Wilde, 1998). Difficulties in reconciling the clinical findings with the theoretical predictions of this theory have led to the formulation of alternative accounts for how living and nonliving knowledge is organised/represented in the brain.

1.1.2. The Domain-Specific Theory. In 1998, an alternative theory describing the organisation of conceptual knowledge was proposed by Caramazza & Shelton: the Domain-Specific (DS) theory. This theory proposes a phylogenetic account for how concepts are organised in the brain. According to the theory, evolutionary pressure and natural selection have resulted in dedicated neural circuitry for processing animals, conspecifics, plant life, and possibly tools (for a discussion on the phylogenetically recent evolution of a tool-specific domain, see Santos & Caramazza, 2002). In addition, more recent research has questioned whether there might also be separate neural circuitry for processing fruits and vegetables (Samson & Pillon, 2003). These systems could then, in turn, be organised by property (Mahon & Caramazza, 2003; Mahon et al., 2007). Caramazza and Shelton's theory is based on the study of patient E.W., a patient showing a category-specific deficit for living things (specifically, impairment with animals). E.W.'s impairment was not restricted to visually presented stimuli, but encompassed auditory and language comprehension as well. Therefore, E.W.'s impairment seemed to encompass the semantic system, and did not simply reflect a deficit for visual recognition or word production. In addition, E.W.'s impairment with living things encompassed both

functional and visual attributes, suggesting that the damage was not modality-specific. Caramazza & Shelton went on to review the overall patterns of deficits in the category-specific literature, noting that within the domain of living things, the category of animals can be damaged or spared relatively independently of fruits, vegetables, and plants (e.g., Caramazza & Shelton, 1998; Hillis & Caramazza, 1991; Hart & Gordon, 1992). In fact, E.W. was found to have an impairment identifying animals specifically, whilst her ability to name fruits and vegetables remained relatively intact. In addition to this pattern, fruits and vegetables (combined) and plants can be damaged selectively compared to other living and nonliving items (e.g., Crutch & Warrington, 2003; Farah & Wallace, 1992; Hart, Berndt, & Caramazza, 1985; Samson & Pillon, 2003).

Based on the idea that deficits for living things can accompany both visual and functional information, and that nonliving things deficits can also accompany both types of knowledge, Caramazza & Shelton (1998) suggested the DS theory could properly account for the pattern of deficits seen in patients with category-specific impairments. In support of an evolutionary model for category-specific semantic subsystems, Caramazza & Shelton highlighted developmental research which shows that infants can distinguish living from nonliving things by as young as 3 months of age (Bertenthal, Proffitt, & Cutting, 1984; Leslie, 1982). This early distinction is used to support the notion that these biological subsystems are innate.

There are several important predictions made by the DS theory. The first is that category-specific deficits occur only to those categories which have dedicated neural circuitry as a function of evolution, namely animals, plant life, and tools (but also fruits and vegetables; e.g., Samson & Pillon, 2003). The second is that category-specific impairments for either living or nonliving things should show comparable visual and functional attribute impairments. A third prediction of the DS theory is that damage to specific semantic systems should produce selective deficits for only the category of objects which rely on that system. So, for example, damage to the neural system responsible for processing animals should produce a category-specific impairment for only animals and no other category. Support for this assertion that category-specific deficits should be selective for a particular category exists in the patient literature. For example, patients have been described whose deficits are selective within the domain of living things for fruits and vegetables and not animals (e.g., Farah & Wallace, 1992; Hart, Berndt, & Caramazza, 1985). In addition, a patient has been reported whose damage was selective for animals but not fruits and vegetables (Caramazza & Shelton, 1998).

1.1.3. Unitary Distributed Accounts. The third major theoretical view for how living and nonliving object knowledge is represented in the brain proposes that different levels of interconnections exist between perceptual and functional features in living and nonliving things, and these may be more important than the relative weighting of either attribute for object identification (e.g., Caramazza et al., 1990; Garrard et al., 1998; Moss et al., 1998). Many of these theories have been proposed to directly account for the over-representation of living things relative to nonliving things deficits in the literature. For example, living things have many properties and a portion of these are shared amongst all members of a category (e.g., animals breathe, eat, can see, etc.). In essence, semantic

space is not uniform and similar things tend to share similar properties. Thus, features tend to co-occur more often within a category than across categories, and these features might cluster together in semantic space. Damage to one area of semantic space might then produce disproportionate impairments for one category of knowledge over others. Therefore, category-specific deficits emerge from a non-categorical, feature-based organisation (for a review, see Moss et al., 2002). One of the first theories to argue for a unitary semantic system, not organised by category or modality, was the Organised Unitary Content Hypothesis (OUCH) model, proposed by Caramazza et al. (1990). OUCH argues that salient parts of objects activate both perceptual and functional attributes in semantic memory during visual object processing. However, for nonliving things, there is a strong correlation between visual features and functional use. This strong correlation leads to direct activation of action-related information, which aids in recognition of nonliving objects relative to living objects. This strong correlation between visual and functional information then serves to preserve aspects of nonliving knowledge relative to living knowledge, and Caramazza et al. argued this might explain the larger proportion of living things deficits in the literature (see De Renzi & Lucchelli, 1994 for a similar proposition).

An extension to the idea that correlated features are important for object recognition has been described by Moss, Tyler, and colleagues (Moss, Tyler, & Jennings, 1997; Moss et al., 1998; Tyler & Moss, 1997). Their account has been called the Conceptual Structure Account, and it argues that the nature of distinctive features varies between living and nonliving objects. In particular, distinctive features of nonliving objects are correlated with an object's functional use, whilst common perceptual features of living objects are weakly associated with their functional properties. This difference leads to an advantage for nonliving things following brain damage, because the features that correlate with functional properties may be better preserved than those having only weak correlations. Moss, Tyler, & Devlin (2002) note that this account differs from the SF theory because it does not suggest that functional information is necessarily more important for nonliving things. Rather, there is a difference across living and nonliving objects as to the *kind* of functional information that is most strongly correlated with objects, and the nature of this kind of information produces a higher likelihood of living than nonliving object knowledge impairment following brain damage. To test their hypothesis, Moss et al. constructed a small-scale connectionist model having living and nonliving semantic representations, in order to demonstrate that random damage within a distributed semantic system can produce selective deficits for one type of knowledge compared with another. Their findings showed that "lesioning" of a small number of interconnections (semantic vectors) led to a disadvantage for living things, as these items were less distinctive. That is, the distinctive functional information associated with nonliving things remained, and therefore led to an advantage in identifying nonliving things. However, more widespread "lesioning" produced a more selective deficit for nonliving things, because both shared properties and form-function correlations were damaged, with only shared biological functional correlations remaining to allow the system to distinguish amongst living things.

1.2. Exploring the Factors that Vary Between Living and Nonliving Objects

Much research has explored the specific factors that vary between living and nonliving objects. This research has aimed to explain the nature of category-specific deficits. Several factors have been identified that vary between living and nonliving things. These include differences in visual form, similarity, and the importance of visual versus functional information for discriminating living and nonliving objects.

1.2.1. Visual Form. There are differences in the importance of visual form for distinguishing living and nonliving objects. For example, research by Sergent (1987) suggests that low-spatial frequency components of an image are processed more quickly than high-spatial frequency components. Importantly, global shape is transmitted via low-spatial frequency information in an image, whilst local details are transmitted via high-spatial frequency information. So a critical differentiation is that global shape rather than local details in an image might be recognised more quickly. Thus, objects whose differentiation relies more on global shape will be recognised more quickly than objects whose differentiation relies on local detail. This has important implications for living/nonliving objects as research suggests that access to global shape information in impoverished images leads to a behavioural advantage for living things (Gerlach, 2001; Lloyd-Jones & Luckhurst, 2002). However, under normal viewing conditions, these same researchers found performance was better for nonliving things because participants could use full internal detail in order to make a decision. These data then suggest that global shape is more critical for recognition of living than nonliving objects, whereas internal detail may be more important for recognising nonliving things.

In addition to differences in local/global shape, research has indicated that important visual cues such as colour, texture, and shape might play an important role in category-specificity. For example, research has indicated a strong behavioural advantage for naming items presented having congruent colour and texture cues, and that this advantage is larger for living than nonliving things (e.g., Price & Humphreys, 1989; Tanaka & Presnell, 1999). Thus, colour and texture might be more heavily weighted in the representations of living than nonliving things because they aid in recognition when overall shape is highly similar amongst category members. In addition, colour and texture help to differentiate living things because they are diagnostic, whereas for nonliving things colour and texture are usually irrelevant. Consider, for example, the range of tomatoes and other fruits and vegetables we encounter in the grocery store. For selecting the "best" fruit, we often use colour cues and the firmness of the item to aid in selection. However, in selecting from a range of hammers, colour and texture information is not often tied so closely to our final choice. Thus, colour and texture are reliable cues that are diagnostic for living things, whereas the same is not true for nonliving things (Tanaka & Presnell, 1999). Studies have also demonstrated that colour is more important for object naming than categorisation (Davidoff & Ostergaard, 1988; Price & Humphreys, 1989), and that surface detail is more important for living than nonliving things (Price & Humphreys, 1989).

1.2.2. Similarity. One of the most investigated factors thought to vary between living and nonliving objects is the level of similarity amongst category members. Similarity

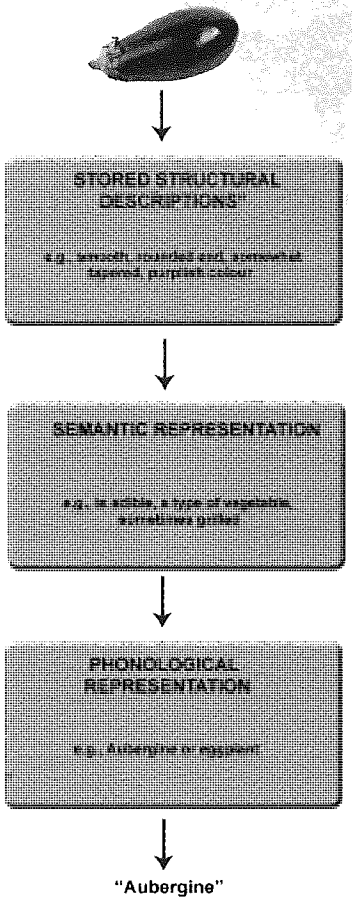
can relate to structural/visual similarity and semantic similarity, although these two items are thought to overlap significantly, and therefore are traditionally measured together.

Humphreys et al. (1988) asked participants to list the number of common parts across different categories of objects, and they also measured the amount of contour overlap on outlines of standardised and size-normalised drawings of objects. On both of these measures, they found higher ratings for living compared with nonliving objects, suggesting higher structural similarity for living compared with nonliving things. Indeed, in studies using normal participants, many researchers have found an advantage for nonliving compared with living things (e.g., Humphreys et al., 1988; Snodgrass & Yuditsky, 1996), thought to relate to the amount of structural similarity amongst living compared with nonliving things. In addition, research using monkeys has shown that stimulus-response learning was slower for living than nonliving things, and this disadvantage increased as the stimulus set increased (Gaffan & Heywood, 1993).

Humphreys et al. (1988) articulated a theory to describe the influence of similarity at different levels of object processing. When you are asked to name an object presented visually, there are a series of stages that are consistently regarded as important in object processing. These stages have been described earlier in the chapter, and include accessing stored structural descriptions, accessing semantic representations, and accessing phonological representations. There is debate amongst researchers in the field as to how these stages proceed. In the more traditional view, picture naming occurs through a series of discrete stages (e.g., Snodgrass, 1984) (see Figure 1.2.1). However, more recent findings suggest that a model where picture naming occurs via a cascade process might better explain findings in the literature (Humphreys et al., 1988) (see Figure 1.2.2). For example, research has indicated that under speeded response deadlines, normal participants will often produce the names of items that are visually and semantically related to the target item (i.e., producing the name of an object that is visually similar and within the same category as the target item; e.g., "fox" for "dog" or "tin opener" for "bottle opener"; see Vitkovitch & Humphreys, 1991; Vitkovitch et al., 1993). Simulated data has also indicated that greater competition will produce longer reaction times (Humphreys, Lamonte, & Lloyd-Jones, 1995). This competition occurs because items that are structurally similar to the target are co-activated when an object is initially presented, and this set of items is then constrained by semantic information derived from the target object (Humphreys, Riddoch, & Forde, 2002). This competition then produces a behavioural disadvantage for items that have many shared features, and thus greater competition.

Under speeded naming conditions, naming errors of participants often involve production of names of structurally similar items (Lamberts & Freeman, 1999; Rumiati & Humphreys, 1998; Vitkovitch & Humphreys, 1991; Vitkovitch et al., 1993). For example, Vitkovitch et al. (1993) asked participants to name pictures that had previously been categorised (see Humphreys et al., 1988) as either structurally similar or dissimilar under a speeded response condition. Structurally similar items were all drawn from living things (animals, birds, insects, fruits, and vegetables), whilst all but one category of dissimilar items were drawn from nonliving things (living things: body parts; nonliving things: building parts, clothing, furniture, household items, kitchen utensils, tools, toys, vehicles, and weapons). Vitkovitch et al. counted the number of different names produced in error

FIGURE 1.2.1. Discrete Stage Account of Picture Naming.

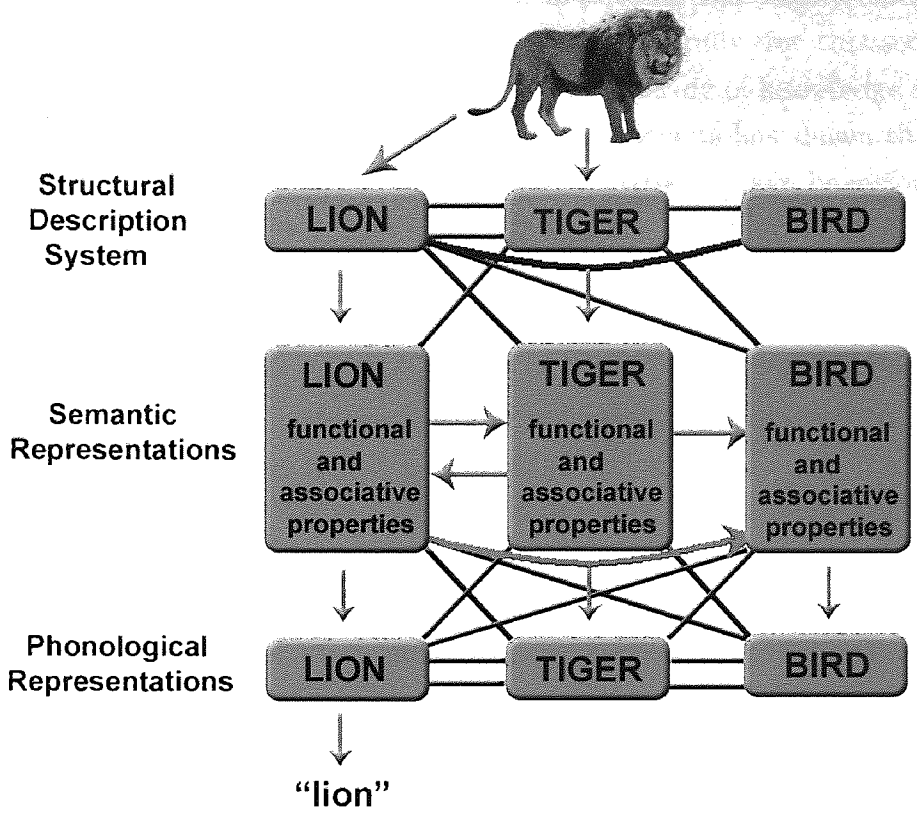


Schematic of discrete stage theory of picture naming, showing sequential activation from accessing structural descriptions through to accessing phonological representations (adapted from Humphreys et al., 1988).

(e.g., "zebra" called "tiger", "giraffe", or "horse") for each item, and found that there were more incorrect names produced for the structurally similar items than dissimilar items, and that the types of errors involved producing names of items that were visually and semantically related to the target item.

1.2.3. Visual Versus Functional Knowledge. In proposing the SF hypothesis to describe category-specific effects, Warrington & Shallice (1984) argued that differences in the importance of visual/perceptual and functional knowledge might underlie the deficits exhibited by patients. In particular, they argued that perceptual information might be more relevant for living things, whilst functional information might be more relevant for nonliving things. This prediction was tested empirically by Farah & McClelland (1991), who asked participants to indicate the visual and functional attributes of living and nonliving things in their dictionary definitions. For living things, the researchers found greater levels of visual information indicated in the definitions, whilst for nonliving things they found greater functional information indicated. Importantly, however, Caramazza & Shelton (1998) criticised the methodology used by Farah & McClelland because the definition of functional attributes ('What is the object used for?') was biased against the kind of functional information relevant for living things. This is because the type of functional information often associated with living things categories typically relates to a different sort of non-visual knowledge (e.g., eating, breathing, running, etc.) than how

FIGURE 1.2.2. Cascade Processing Account of Picture Naming.



Schematic of cascade theory of picture naming, showing parallel activation from accessing structural descriptions through to accessing phonological representations (adapted from Humphreys et al., 1988).

you would use an object instrumentally. In trying to overcome this limitation, McRae, de Sa, & Seidenberg (1997) simply asked participants to generate properties for various living and nonliving objects, and then assessed how many of these properties belonged to either visual/sensory or non-sensory features. For living and nonliving things, they found sensory information was listed roughly equally. However, for nonliving things, they found far greater non-sensory features were listed. Thus, these findings are still in line with theories that posit a crucial difference between visual and non-visual/functional knowledge in differentiating living and nonliving things.

1.3. What are the "Categories" Showing Impairment in Category-Specific Deficits?

It has been mentioned previously that the pattern of impairments displayed by patients with category-specific deficits does not always closely follow a living-nonliving dichotomy. A review of the patient literature by Gainotti (2000) supports this assertion. He reviewed the case histories of patients with category-specific deficits reported in the literature. Of these 57 patients, he subsequently performed a detailed assessment of the patterns of semantic impairments exhibited in a subset of 19 patients having selective deficits for living things. He found that impairment with animals and plants tended to co-occur with deficits for foods (a category representing man-made foods, hence considered to reflect nonliving items) and musical instruments. In addition, for many of these patients who had living things deficits, they tended to have spared knowledge for body parts, which

is typically thought of as belonging to living things. For a second subset of 10 patients having selective deficits for nonliving things, their pattern was highly similar to those reported for the patients with living things deficits. Generally, for this second subset, there was impairment with body parts knowledge with sparing of knowledge about foods. In addition, research on patients with category-specific deficits has shown that there can be even more fine-grained distinction. For example, patients have been found to have selective impairment with either plants (Farah & Wallace, 1992; Forde et al., 1997; Hart et al., 1985) or animals (Caramazza & Shelton, 1998; Hart & Gordon, 1992).

Findings such as these have led some researchers to explore the patterning of knowledge impairment and how it might relate to other important factors. For example, Cree & McRae (2003) identified several trends in 10 previously reported cases of patients with category-specific deficits. These trends were highly similar to those reported by Gainotti (2000, 2002). The first is that within the domain of living things, animals and fruits and vegetables can be selectively impaired independently of other items within the domain (and independently of each other). In addition, fruit and vegetable knowledge is sometimes impaired along with nonliving things knowledge. Within the domain of nonliving things, musical instruments and foods can also be selectively impaired independently of other items within the domain (and independently of each other). Foods and musical instruments knowledge can also sometimes be impaired in patients with deficits for living things. To explore the relevant factors of object knowledge which best explains this pattern of deficits, they looked at correlations amongst a large set of feature norms for living and nonliving objects. Their findings suggest that extending the SF theory to include other important factors could adequately account for the pattern of deficits observed in patients. These factors include some recognition of the informativeness of various object features, visual complexity, and both visual and semantic similarity (although their analysis of visual similarity showed no significant effects). In addition, concept familiarity and frequency also accounted to some degree for the pattern found. Finally, they found no important role for feature correlations, contrary to what many of the theories arguing for an amodal semantic store suggest (e.g., Devlin et al., 1998; Gonnerman et al., 1997; Tyler & Moss, 2001).

In addition to the patterning of impairments across categories, other evidence suggests that there can be damage at different levels within the visual object-recognition system. In traditional views of object naming, there are three key stages that occur. The first of these is accessing the structural/visual information of an item. The second is accessing the semantic system and stored knowledge about objects. The final stage is applying the appropriate name to an object (see Humphreys et al., 1988; Snodgrass, 1984). Evidence that damage at different levels of the naming system can produce selective impairments exists. For example, Riddoch & Humphreys (1987a)reported an agnosic patient, HJA, having a deficit recognising many common objects by sight. HJA's impairment was worse for living than nonliving things. Despite this problem, HJA showed intact stored knowledge for living things, in that he could accurately draw and provide detailed definitions from memory. In addition to HJA, there have been nine other cases of category-specific impairments where the deficit appears to precede the semantic system (ELM: Dudek, Arguin, & Bub, 1994; Felicia: De Renzi & Lucchelli, 1994; Helga: Mauri et al., 1994;

Giuletta: Sartori et al., 1993; IL: Arguin et al., 1996a; JB: Riddoch & Humphreys, 1987b; LH: Farah et al., 1989; Michelangelo: Sartori & Job, 1988; SRB: Forde et al., 1997). For all of these patients, the resultant category-specific impairments are more pronounced for living than nonliving objects. In addition, except for JB, all of the patients showed impaired retrieval of stored visual information when that information was probed using either visual or verbal input, suggesting that damage for these patients was at the level of stored structural descriptions. There is also clear evidence in the literature that some patients with category-specific deficits have damage at the level of the semantic system (e.g., Adam: Farah & Rabinowitz; EW: Caramazza & Shelton, 1998; GA: Humphreys & Riddoch, 2003).

1.4. Where are the Critical Neuroanatomical Regions for Category-Specific Deficits?

Researchers have attempted linking lesion data from patients with category-specific deficits to the specific type of knowledge impairment (broadly, living versus nonliving) exhibited, in the hope that it would shed light on exactly how object concepts are organised in the brain. Unfortunately, the results are murky at best. An extensive investigation of 30 patients with a single, focal lesion resulting in a category-specific deficit found that impairment in processing animals (living things) was associated with damage to the left anterior inferotemporal region of the brain (Damasio et al., 1996; see also Tranel, Damasio, & Damasio, 1997 and Nielsen, 1958 for evidence of medial occipital lobe involvement in category-specific semantic deficits for animals). These researchers also found that impairment in processing tools (nonliving things) was associated with damage to the posterolateral inferotemporal area and the junction of the temporal-occipital-parietal cortices. A second study by Damasio et al., (2004) assessed the neural systems impaired in a large cohort of patients (N=169) with unilateral brain damage in either the left (N=105) or right (N=64) hemisphere. The lesions resulted from a range of etiologies, including cerebrovascular disease, herpes simplex encephalitis (HSE), and temporal lobectomies. The authors tested the patients on their ability to name stimuli from a broad range of categories, including persons, animals, tools, vegetables, and musical instruments. Using a lesion-difference mapping approach, the authors founds that naming of unique persons was associated with lesions in the left temporal pole, and naming of animals with lesions in left anterior inferior temporal cortex, anterior insula, and dorsal temporo-occipital junction, close to area MT. Difficulty with naming tools was associated with damage in the posterior lateral temporo-occipito-parietal junction (classical area MT), the inferior pre- and post-central gyri, and the insula. In a separate study assessing the neural correlates of conceptual knowledge for actions, Tranel et al. (2003) found there was partial overlap between neural systems supporting conceptual knowledge for tools and the neural systems supporting conceptual knowledge for actions in the vicinity of MT. Damasio et al. also found that difficulty naming vegetables was associated with damage in inferior pre- and post-central gyri and anterior insula, and difficulty with musical instruments was associated with lesions to the temporal polar region and anterior inferior temporal cortex, the posterolateral temporal region, the insula, and the inferior pre- and post-central gyri. Another study by Gainotti et al. (1995) found that bilateral medial temporal lobe damage

was often associated with impairments in processing living things, whilst left frontoparietal damage resulted in deficits for nonliving things (see also Gainotti, 2000). A further study by Moss & Tyler (2000) found that diffuse rather than focal brain damage produced a category-specific deficit.

Part of the difficulty in understanding the direct relationship between structure-function is that seeming category-specific impairments can arise from a number of different etiologies, as mentioned previously. For example, a survey of 57 patients with category-specific impairments by Gainotti (2002) found that semantic impairments for living things (N=47) resulted mostly from HSE (55%), closed head trauma (CHT; 18%), and semantic dementia (SD; 14%), whilst only 2 patients suffered cerebrovascular accident. However, of the 10 patients with selective deficits for nonliving things, all were affected by large infarcts in the territory of the left middle cerebral artery. For the three main causes of selective impairment for living things (HSE, CHT, and SD), lesions were usually bilateral and involved the anterior parts of the temporal lobes. In cerebrovascular accidents, lesions were usually unilateral and did not involve the anterior parts of the temporal lobes. Interestingly, the patients with selective impairments for living things often showed difficulty for animals and plants (living) as well as difficulty with foods and musical instruments (nonliving), whilst knowledge for body parts (living things), was spared. For patients with impairments for nonliving things, animals and plants (living things) as well as food (nonliving) were spared, whilst body parts (living) knowledge was frequently impaired. This suggests that there is not a clear-cut distinction between living-nonliving semantic knowledge, and its representation in the brain might not be organised purely by category.

1.5. Neuroimaging Evidence for Category-Specificity in Normal Participants

Functional neuroimaging studies of object-processing have consistently demonstrated that the temporal lobes are a critical site for stored object representations (for a review, see Martin, 2007). Specifically, the fusiform gyrus on the ventral surface of the temporal lobes shows preferential responses to real objects compared to scrambled images (van Turennout, Ellmore, & Martin, 2000; Vuilleumier et al., 2002). Within the fusiform gyrus, studies using functional brain imaging have provided evidence that there might be fine-grained patterns of activity related to object category. Specifically, direct comparisons of pictures of faces, houses, animals, and tools have shown that the fusiform face area (FFA) on the lateral aspect of the fusiform gyrus might be specialised for processing faces, and the parahippocampal place area (PPA) on the anterior medial surface might be specialised for processing houses (Kanwisher et al., 2001; Martin, 2001). In addition, Chao, Haxby, & Martin (1999) have shown that viewing pictures of animals activates more lateral aspects of fusiform gyrus, whilst viewing pictures of tools activates more medial aspects. Importantly, however, studies suggest that these "category-specific" regions in ventral temporal cortex also respond, though to a lesser extent, for objects from other categories. Thus, there is debate as to whether these activations are in fact functionally significant. Finally, pattern analysis techniques have demonstrated object category-related patterns of activity can be observed over a relatively large expanse of occipito-temporal cortex, and that these patterns are stable when subjects are tested over multiple sessions as well as between subjects (Haxby et al., 2001).

A study by Price et al. (2003) explored category-specific differences in fusiform cortex. They were particularly interested in responses in the category-sensitive fusiform region reported by Chao and colleagues (e.g., Chao et al., 1999; Chao et al., 2002) and a more anterior mid-fusiform area identified by a range of other researchers as important in the retrieval of semantic information (e.g., D'Esposito et al., 1997; Martin et al., 1995). Their findings showed that the bilateral posterior fusiform gyrus showed greater category-specific activation when the stimuli presented were pictures of objects relative to written object names. The authors suggest that this finding supports the idea that these effects are driven by bottom-up processing of a stimulus. In addition, they found that the lateral fusiform gyrus often found to be more active for animals relative to tools was also activated for fruits and vegetables relative to tools. Their findings also indicated that the more anterior mid-fusiform region involved in semantic retrieval serves as a polymodal association area. This is based on their finding that this region showed increased activation both when participants retrieved object colour from names presented auditorily and retrieved information about object size from names presented auditorily. In addition, they also found no posterior fusiform activation during a semantic retrieval task, leading the authors to argue that visual information can be retrieved from the polymodal association cortex in more anterior fusiform cortex without requiring top-down re-activation of the category-sensitive regions in posterior fusiform cortex.

In addition to activation within the ventral visual object-processing stream, there is evidence that tools activate left middle temporal gyrus and regions in left premotor cortex that include the intraparietal and ventral premotor cortices (Chao & Martin, 2000; Chao, Weisberg, & Martin, 2002). These are near tool motion associated areas of cortex, and thus researchers have hypothesised that viewing pictures of tools co-activate regions important in manipulating and knowing how to use an item (Martin, 2001). In addition, pictures of animals and faces tend to activate superior temporal sulcus (Martin & Chao, 2001). This is a region known to be active during the perception of biological motion (Bonda et al., 1996; Puce et al., 1998), thus researchers hypothesise that this region is recruited even when viewing static images of animals.

Many neuroimaging studies lend support to the idea that object concepts are grounded in perception and action, thus providing evidence that concepts might be organised according to the SF theory (e.g., Barsalou, 1999; Gallese & Lakoff, 2005). However, consistent with the DS theory, these studies also suggest that some regions for representing object properties might be organised by category. A recent review of 17 functional imaging studies of normal participants comparing visual processing for animals and tools found object representations in the brain to be widely distributed but also categorically organised (Chouinard & Goodale, 2010). In particular, Chouinard & Goodale found that naming animals activated visual areas in the occipital lobe to a greater extent than naming tools. These regions included the left cuneus, lingual gyrus, middle occipital gyrus, and lateral occipital area. In addition, outside of visual areas of the brain, animals activated left anterior cingulate to a greater extent than tools. Tools, in contrast, activated visual areas in left middle temporal gyrus, right superior temporal gyrus, and bilateral medial fusiform gyrus to a greater extent than animals. In addition to these visual area, tools also activated a left ventral premotor area, left post-central gyrus, and left anterior superior parietal

lobule to a greater extent than animals. To further muddle the debate, however, a second recent review of 20 functional imaging studies using normal participants comparing visual processing of living and nonliving objects found no single area to be consistently activated for a given category across studies (Gerlach, 2007). In his review, Gerlach argued that this inconsistency might be due to adopting liberal statistical thresholds when analysing neuroimaging data. These liberal thresholds then might produce a large number of false-positive activations. In addition, Gerlach argued that many studies suffer from reduced sensitivity due to limited sampling of the signal (i.e., a low number of trials) resulting in too few observances. Finally, Gerlach also criticised a number of studies for failing to match the critical categories of comparison on confounding variables such as familiarity and visual complexity. So, of the most consistent activations found, none appeared to be selective for either living or nonliving things. These findings, then, are compatible with theories of category-specificity that assume a widely distributed conceptual system not organised by category. Thus, there is debate in the literature as to the importance of so called "category-specific" activations in the cortex.

1.6. Our Aims

We set out to reconcile some of the apparent differences between behavioural studies of category-specificity and the neuroimaging evidence. In particular, we observed that much of the neuroimaging research to date explored differences in the semantic representations of living and nonliving things. Whilst this is understandable given the temporal constraints of the most frequently used imaging techniques (e.g., functional magnetic resonance imaging: fMRI, positron emission tomography: PET), we felt that simply focusing on the semantic system ignored the range of behavioural evidence indicating that deficits at different levels within the object-processing system (i.e., structural descriptions, semantic representations, phonological representations; see Humphreys et al., 1988) could produce clinically-similar manifestations. The approach taken in these behavioural studies is consistent with the account of aphasia first provided by Lissauer in 1890. In addition to a general lack of neuroimaging evidence of category-specific effects at different levels of the object-processing system, we also felt that alternative neuroimaging techniques could be exploited to help resolve some contradictions within the category-specific literature. We therefore opted to use magnetoencephalography (MEG) to explore the time-course of processing living and nonliving objects, addressing a series of relevant questions within four primary studies. The rationale and design of each of these studies is explained within the ensuing chapters.

We were interested in using the cascade model of picture naming (Humphreys et al., 1988) as a framework for investigating object recognition processes. This model takes into account perceptual processes, as well as semantic processes, involved in identifying living and nonliving objects. In addition, the model does an adequate job of explaining the behavioural and patient findings mentioned previously. Importantly, the time-course of object processing is particularly important within the cascade model framework. We therefore set out to exploit the temporal benefits of MEG to measure the time-course of activation in the brain in response to naming pictures of objects. We had three main aims. First, we were interested in assessing the time-course of object recognition generally.

Second, we were interested in assessing when processing diverges for objects based on factors which have been indicated to be important in object-processing. The first factor we were interested in studying was differences based on the category of objects (i.e., living or nonliving), and the second factor we were interested in assessing was the influence of the level at which you were asked to identify an object (i.e., basic level or domain level) on processing. Our third main aim was to assess later processing differences between living and nonliving objects, as well as later differences in object processing based on the level at which you are asked to identify objects.

In Chapter 2, we begin by addressing our first aim. Specifically, we exploited the temporal information available in MEG to measure the time-course of object processing. This will allow us to determine whether the cascade model (Humphreys et al., 1988) is supported by the pattern of activation in the brain across time for naming objects. In Chapter 3, we describe a set of experiments in which living and nonliving objects were presented, where we assessed when living and nonliving object-processing diverges within the ventral visual object-processing stream. This study supports our second main aim: to measure when living and nonliving object processing diverges. The rationale for this analysis approach is that, if the processing of living and nonliving objects diverges before the semantic system, these findings could provide an alternative account for category-specificity other than discrete semantic subsystems. Specifically, if processing diverges before reaching the semantic system, this could cause apparent category-specificity within a distributed semantic system. In Chapter 4, we sought to utilise MEG to measure semantic processing associated with identifying living and nonliving objects. This chapter addresses our third main aim: to measure semantic differences between living and nonliving objects. MEG allows us to separate semantic processing from earlier, perceptual processing. In Chapter 5, we sought to measure the time-course of category-specific processing. This analysis is designed to bring together our second and third aims. In Chapter 6, we sought to measure differences between categorising objects at the basic level compared with the domain level. We compared basic to domain-level naming using a long time window, in line with our third aim: to measure later differences in processing objects. In Chapter 7, we utilised the temporal benefits of MEG to measure the time-course of identifying objects at each level of specificity, addressing our second and third aim. Finally, in Chapter 8, we utilised MEG to measure perceptual differences between living and nonliving objects in a patient with a documented deficit for living things. This addresses our second aim, providing a further analysis of perceptual processing in a patient with known damage to the semantic system. Before describing each of the studies in detail in the ensuing chapters, a brief discussion of MEG and its benefits are provided.

1.6.1. What is MEG?. MEG, like its sister technique electroencephalography (EEG), is a completely non-invasive technique for characterising electrical activity within the brain. Unlike EEG, MEG measures magnetic fields emanating from the brain. It does so using superconducting quantum interference devices (SQUIDs). These magnetic fields emanate from the ionic current flow of dendrites of neurons during synaptic transmission, and are the net result of changes over a population of neurons. Approximately 50,000 active neurons are needed to produce a signal that is detectable (Okada, 1983). MEG

measures observable magnetic fields emanating from pyramidal cells located on the sulci of the cortex that have orientations parallel to the surface of the head.

MEG offers several benefits over EEG. Firstly, MEG does not require application of electrodes, so setup is much faster. Secondly, MEG is less sensitive to muscle artifacts. Finally, and most importantly, sources of activity in the brain are much easier to estimate. Details of conductivity geometry and actual conductivity values have a small effect on localising sources. This is because magnetic signals pass unimpeded through the skull. Hence, there is no need to account for bone conductivity and differences in bone density in solving the inverse problem.

One difficulty with MEG, however, arises from the inverse problem. That is, measured magnetic fields outside of the head must be inverted in order to localise sources of activation within the brain. Unfortunately, there is no unique solution to this inversion, which has led to it being described as an ill-posed problem (Hadamard, 1902). That is, the measured distribution of magnetic fields can arise from an infinite number of possible current distributions. Thus, to try to resolve this problem, we have utilised a beamforming strategy to localise sources of cortical activity for each of our analyses.

1.6.1.1. *What is Beamforming?* Beamforming is a procedure whereby a weighted sum of field measurements is applied as a spatial filter to localise source power at predetermined locations in the brain (Cheyne et al.,2006; Robinson & Vrba, 1998; Robinson, 2004; Sekihara et al., 2001; Van Veen et al., 1997). Thus, this filter acts as a tuner to each voxel in the brain. The benefit of this approach is that the filtering procedure is data driven. The approach taken by synthetic aperture magnetometry (SAM), the beamformer that we have adopted for our data analyses, is to maximise power at each given location in the brain by minimising other correlated power across the entire brain. The result is a set of weighting parameters tuned to each specified location (i.e., voxel) in the brain. This calculation can be computed over the entire brain in order to produce a volumetric image of source power within a given frequency range and a specified time window. SAM has been used successfully to image activity that is both phase-locked and non-phase-locked, including event-related synchronisation (ERS) and event-related desynchronisation (ERD) (Pfurtscheller & Lopes da Silva, 1999; Pfurtscheller, Stancak, & Neuper, 1996).

Beamforming has many advantages over other MEG source-localisation methods (see Van Veen et al., 1997 for a more detailed review). In particular, unlike dipole modelling, there is no *a priori* assumption about the number of active sources in the brain during a given time interval (Supek & Aine, 1993). In addition, the estimate of power at each voxel is made independently of all other voxels in the brain, thus there is no influence of other voxels on the estimate (Van Veen et al., 1997). Also, unlike other approaches (e.g., minimum norm approaches), there is no weighting of source depth that might influence final source location (e.g, localising sources more superficially based on the weighting used in the analysis) (Grave de Peralta-Menendez & Gonzales-Andino, 1998). Finally, because the beamformer solution of the inverse problem depends on the data covariance, this solution can then be used to assess changes in spectral power that are not phase-locked to stimulus onset (Pfurtscheller & Lopes da Silva, 1999).

The disadvantages of beamforming, particularly using the SAM algorithm, are that it will fail to localise spatially separate sources that are highly correlated (Mosher & Leahy,

1998; Mosher, Lewis, & Leahy, 1992; Van Veen et al., 1997). That is, because the SAM algorithm tunes activation at each voxel by suppressing correlated power across the brain, two highly correlated sources will prove problematic for SAM to image properly. However, simulations have shown that the temporal correlation between two sources must be relatively high (>0.7) before cancellation occurs (Van Veen et al., 1997). A solution to overcome this problem is to use long temporal windows of data when constructing the covariance matrix, as this will minimise the amount of correlation between sources. That is, stimulus-related correlated firing between two regions of cortex is likely to be transient, so that using longer time windows will reduce the correlation magnitude. A second problem with beamforming is that the resultant statistical parametric images (SPMs) are both inhomogeneously smooth spatially and anisotropic (e.g., Barnes & Hillebrand, 2003). This can lead to unpredictable effects during group imaging. In order to overcome this issue, we have utilised a novel approach to MEG group imaging that assesses the distribution of image peaks across participants, which we describe in detail below.

1.6.1.2. *Investigating the Distribution of Image Peaks: Peakomatic.* One problem in conventional MEG group analysis is that the individual beamformer images are not homogeneously smooth; the images are information rich around strong sources, yet very smooth elsewhere (Barnes & Hillebrand, 2003; Gross et al., 2001). These smoothness differences can range over two orders of magnitude within an image (Barnes et al., 2004). This inverse relationship between source strength and smoothness leads to unpredictable effects at a group imaging level. For example, consider an electrical source which varies in spatial location by 3 cm across the participant group. As the source power increases from zero to above the noise level, a group effect will become apparent (as the change in each image will be very smooth), but this effect will disappear as the signal-to-noise ratio is increased (and the sources become more focal). This effect will be further compounded in a realistic situation as there will be no homogeneity of smoothness across voxels from different participants. This problem of non-isotropic or inhomogeneous smoothness has been studied in the context of functional magnetic resonance imaging (fMRI) to correct for cluster size statistics in cases where, for example, the underlying isotropic image has been inhomogeneously resampled onto a cortical surface (Hayasaka et al., 2004; Worsley et al., 1999). Similar solutions have been proposed for MEG (Barnes & Hillebrand, 2003; Pantazis et al., 2005), however these are computationally intensive as the MEG volumes have to be constructed on a very fine mesh in order to make accurate local smoothness estimates.

In order to address some of these issues, we used a simple, non-parametric technique (hereafter, *peakomatic*) to look at the distribution of image peaks across participants (Gilbert, Shapiro, & Barnes, submitted). It is based on the assumption that, under the null hypothesis, the top P (number of peaks of importance) image peaks across participants will be no more closely grouped across participants than any random selection of peaks. The algorithm is as follows. Step 1: rank order (largest positive or negative peak first) the image peaks for each participant and store their corresponding locations. Step 2: compute the N smallest ellipsoids which contain the top P peaks across participants (without replacement) and participant sub-groups. Step 3: establish if these ellipsoids are smaller (in terms of maximum radius) than one would expect by chance. This is done by

randomly assigning ranks to peak locations and repeating step 2 above 500 times. This produces a distribution of ellipsoids which one would expect due to chance (if peak rank were not important).

The technique has a number of advantages over existing techniques. It is immune to smoothness variation, immune to amplitude variation across participants, and indeed it makes no assumptions about the underlying image properties. In addition, the null distributions (of locations) are constructed from the data itself and the randomisation testing naturally takes into account the multiple comparisons problem (for a pre-specified P, see Appendix A). An added bonus is that subgroup statistics are naturally available, so, for example, bounds for any 5 of the 10 participants having significantly clustered peaks can automatically be tested. Another benefit is that the program uses true peak locations across participants, allowing one to naturally revert to region of interest (ROI) analysis on a per participant level. The disadvantage clearly is that the technique will not be sensitive to truly spatially extended regions of electrical activity which are not artefacts of smoothness. In addition, it requires the arbitrary parameter P of the number of peaks which could be important (see Appendix A for methodological considerations in defining P). Setting this parameter too low (e.g., 2 or 3) could result in large volumes surviving statistical significance. Whilst the mean power across the group of participants would be relatively high (because this analysis includes only the largest amplitude peaks from the resultant images), the spatial extent of the ellipsoid might have little anatomical consistency. In addition, setting this parameter too high (e.g., 30 or so), would result in ellipsoids that have good anatomical consistency, but it would include lower-magnitude peaks in the analysis (by definition, less important regions). Therefore, setting this parameter adequately is important to the analysis outcomes. We have opted to test a range of P values for each comparison, and then to assess statistical significance after correcting for multiple comparisons (see Appendix A). We considered regions as showing a significant effect if they survived a statistical threshold of $p<0.01$ corrected.

CHAPTER 2

On The Time-Course of Object Naming

2.1. Introduction

Many models of picture naming posit at least three key serial stages (e.g., Humphreys, Riddoch, & Quinlan, 1988; Ratcliff & Newcombe, 1982; Snodgrass, 1980). When first presented with an image, perceptual features of an object are compared and matched to stored structural descriptions. After this stage, semantic information about an object is retrieved. Finally, the phonological form is retrieved. There is debate in the literature as to how naming occurs, whether each stage occurs serially, or whether activation can occur in parallel. For example, Levelt (1989) proposed that activation during naming occurs in a serial fashion. Whilst multiple 'nodes' at each stage of object-processing can potentially activate for a given picture, only a single node will then transmit information to the next stage. In addition, information is transmitted to the next stage only after processing at the current stage is completed. In contrast to a discrete stage model, Humphreys et al. (1988) argue in their cascade model of picture naming that information between these stages is transmitted via a cascade process. In their model, multiple 'nodes' at each stage can spread activation to the next stage (e.g., multiple lexical nodes can activate their corresponding phonological nodes), and that activation at each stage can proceed in parallel.

A critical stage in picture naming involves the retrieval of semantic information about objects (e.g., Levelt et al., 1991; Vitkovitch & Humphreys, 1991). Vitkovitch & Humphreys (1991) used a speeded naming procedure to demonstrate that naming pictures of objects generally involves the co-activation of competing items from within the same semantic category. When participants were asked to name items under a speeded response condition, the types of errors mainly consisted of retrieving the names of other items from within the same semantic category. In particular, errors often consisted of producing the name of related (prime) pictures. These perseverative naming errors were not found when participants were asked to read aloud printed names of primes or when they were asked to categorise picture primes. This suggests that correct naming involves a stage at which you must select the name of the item from amongst related and/or competing items. In essence, the speeded condition produced residual activation in the route from accessing semantic knowledge to applying the appropriate name code, a route used in picture naming but not in categorisation or word naming.

Much research has focused on the neural structures supporting object naming. These studies include assessing impaired versus spared functioning in patients with lesions, in addition to functional imaging studies (primarily PET and fMRI) of both patients and normal participants. Both of these techniques have demonstrated posterior to anterior object-processing along the ventral stream. Posterior regions tend to support early visual

processing, whilst more anterior regions support more detailed and higher-level object-processing. Patient studies, for example, have indicated that bilateral occipital lobe lesions produce impaired form discrimination and apperceptive visual agnosia (e.g., Campion, 1987; Farah, 1990; Frackowiak et al., 1997). More anteriorly, overlapping regions of the fusiform gyri and inferior occipito-temporal cortices are thought to be involved in higher-order visual processing, up to and including the level of accessing structural descriptions of objects (e.g., Allison et al., 1999; Liu et al., 2009; for a review of neuroimaging and lesion studies, see Whatmough & Chertkow, 2002). Neuroimaging studies with normal participants, for example, have shown involvement of these regions during object naming. Martin et al. (1996) showed activation in a region straddling anterior occipital cortex and posterior fusiform cortex for processing nonsense objects compared to visual noise. Thus these regions are involved in fairly early stages of object recognition. That is, these regions are involved in recognising whether something is an object at all. Moving anteriorly into medial and lateral fusiform cortex, Martin et al. (1996) showed activation for real objects compared with nonsense objects. Indeed, Moore & Price (1999) showed activation in a region in anterior fusiform gyrus (anterior to the region identified by Martin et al.) that responded more to multicomponent real objects than simple objects. Taken together, these findings support a crucial role for the ventral stream in both visual object-processing and retrieving semantic information about objects. These findings also suggest a trend for more anterior regions to be involved when "higher level" or semantic processing is required.

In addition to regions in ventral temporal cortex, studies of semantic memory using naming paradigms have shown involvement from a host of brain regions. Critically, studies have indicated involvement from regions in frontal cortex (e.g., Bar et al., 2006; Kirchner et al., 2009; Thorpe et al., 1996) as well as parietal cortex (e.g., Levelt et al., 1998). In the frontal lobe, a principle region in object naming studies is the left inferior frontal lobe (for a review, see Cabeza & Nyberg, 2000). This region is thought to be involved in semantic search processes (Gabrieli et al., 1996). In addition, Rosen et al. (2000) reported increased fMRI activation in Broca's area during covert naming of pictures (see also Kertesz, 1999 for lesion evidence for Broca's role in speech programming/articulation). In addition to inferior frontal regions, studies have reported activation in pre-motor and motor cortices during object naming (e.g., Rosen et al., 2000; Zelkowicz et al., 1998). Lesion evidence has demonstrated that speech initiation, selection and activation processes arise from the supplementary motor area located on the medial surface of the frontal lobe (Kertesz, 1994). In addition to frontal cortex, Levelt et al. (1998) demonstrated increased activity in a region in the left posterior lobe which they consider to be Wernicke's area. They argue that this region is recruited during the phonological encoding of objects whilst naming (see also Bookheimer et al., 1998).

There is some evidence from the literature as to the timing of cortical activation across the brain during object-naming. For example, Levelt et al. (1998) used MEG to measure the time course of object naming. Based on their own previous work, they predicted that cortical activation during object naming would proceed serially rather than in cascade. They based their timing on previous ERP evidence and behavioural predictions in the literature, and thus chose *a priori* time windows in which to analyse MEG activation

patterns. Recognising the visual object and accessing the lexical concept, the first two stages in Levelt et al.'s theory of object naming, were hypothesised to occur within the first 150 ms of seeing a picture. From 150-275 ms, lemma selection then occurs. From 275-400 ms, phonological encoding occurs. Finally, from roughly 400-600 ms after seeing a picture, phonetic and articulatory processing occur. Using MEG, Levelt et al. assessed the primary locations of activity in each of these time windows. Within 150 ms of seeing a stimulus, the visually evoked magnetic fields (dipole locations) were localised to occipital cortex, primarily in the right hemisphere. Within the lemma selection window, activity was more variable, with approximately 50% of sources localised to occipital cortex. In addition, localised activity occurred in the right parietal cortex, along the posterior end of the superior temporal sulcus, and occasionally in temporal areas. Within the phonological encoding time period, sources of activity were localised to the posterior third of the superior temporal gyrus and the temporo-parietal junction. This was in agreement with the site of classical Wernicke's area. Finally, phonetic and articulatory processes were quite scattered, with a sizable concentration localised in sensory-motor cortex and in the parietal and temporal lobes.

In addition to MEG evidence in humans, Thorpe & Fabre-Thorpe (2001) reviewed studies assessing the time course of visual processing of stimuli in monkeys. Initial visual processing within the retina is projected to visual cortex in the occipital lobe via the lateral geniculate nucleus (LGN), and spiking occurs in the LGN at roughly 50 ms after a stimulus is displayed. The LGN then projects to visual cortex, and spiking of cells in area V1 (i.e., primary visual cortex) occurs at roughly 60 ms after a picture is shown. This information is transmitted to V2 at about 70 ms. Within 80 ms of stimulus presentation, spiking occurs in area V4, an area in the monkey that is responsive to visual form. Continuing in a feedforward manner, cells in the posterior inferior temporal cortex begin to show spiking around 90 ms after a picture is shown, followed by spiking in anterior inferior temporal cortex. Anterior inferior temporal cortex in monkeys seems to be a critical region for higher-level object processing. Spiking activity in this region seems to be category-specific, with responses in this region demonstrating selectivity for particular types of objects. Because of this pattern of spiking activity, this region is thought to be analogous to the human fusiform gyrus. Anterior inferior temporal cortex in monkeys then projects to prefrontal cortex (PFC), and spiking occurs there at roughly 130 ms after a picture is displayed. This region is thought to be involved in decision-making or forming categorical judgements. From PFC, information is transmitted to pre-motor cortex and motor cortex by approximately 160 ms and 190 ms respectively for tasks involving some motor output (e.g., pressing a button in response to a visually-presented stimulus). The motor command then gets transmitted via motor cortex to the spinal cord, and spiking activity occurs there at roughly 220 ms after a picture. Thus, within 300 ms of a visual stimulus, monkeys can produce the motor output necessary for the task. Thorpe & Fabre-Thorpe point out that the monkey brain is considerably smaller than humans, and thus similar activity within the human brain would occur at longer latencies. This is due to limits in the conduction velocity of intracortical axons, with suggestions that it is roughly 1 to 2 m/s (Nowak & Bullier, 1997). For example, Thorpe, Fize, & Marlot (1996) demonstrated a frontal negativity in ERP data in humans that

developed at roughly 150 ms after stimulus onset. This negativity was specific to no-go trials on a go/no-go categorisation task using a rapid serial visual presentation (RSVPs) technique with pictures. This effect involved an almost linear increase in the voltage difference between go and no-go trials from 150-200 ms after stimulus presentation, and the authors suggest that the effect was a consequence of inhibitory mechanisms within frontal areas. Thus, according to their data, the necessary visual processing for decision-making in humans must occur within the first 150 ms of stimulus presentation; this is roughly 50 ms longer than spiking activity within the monkey PFC.

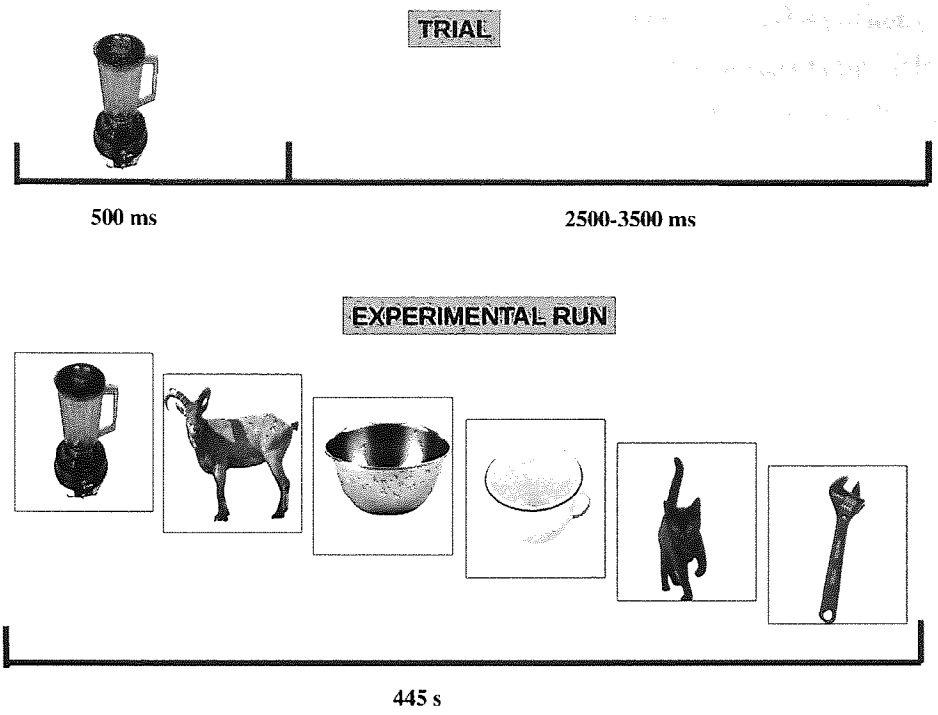
Given the range of studies mentioned previously, we were compelled to design an MEG study to assess the time course of picture naming in humans. This is because the temporal benefits of MEG would allow us to clearly assess the cortical regions showing significant activation across time. Whilst Levelt et al (1998) have already used MEG to assess the timing of cortical regions in a picture naming task, their selection of a priori time windows does not demonstrate sufficiently the entire network of cortical regions involved in object naming. In addition, advances in MEG analysis, namely the introduction of event-related beamforming (discussed more thoroughly in the methods), allow for more precise localisation of cortical regions across time (Brookes et al., 2010). Thus, we aimed to use event-related beamforming to explore the time-course of naming both living and nonliving objects in the human brain, to better understand the timing of neural activation across the brain. In particular, we wanted to understand whether picture naming occurs serially in the brain, as predicted by Levelt (1989), or whether it occurs in a parallel, as predicted by the cascade model (Humphreys et al., 1988). If picture naming is serial, then each region involved in the process should only show activation at a given time point, as information is thought to be transmitted to the next stage only after completion of processing at the previous stage. If picture naming can occur in parallel, then multiple regions can be activated at a given time point, and we should see re-activation of regions (via a top-down process) recruited to perform the task.

2.2. Methods

2.2.1. Study Procedures. Ten right-handed volunteers (Mean Age=31.9 years, range=24 41, 2 males) gave written informed consent following Aston University ethical guidelines and participated in the MEG study. Identical informed consent procedures were utilised for all studies reported in this thesis (see Appendix B for details on ethical guidelines followed in all studies). During scanning, participants were asked to silently name pictures of objects and to press a button as they named each item (see Figure 2.2.1). Participants were first shown a picture of an object, followed by a variable inter-stimulus interval (ISI). Participants were instructed to respond by button press as quickly as possible, pressing the left button with their right index finger as they named each item.

Target objects included 60 exemplars drawn from the categories of animals (living) and tools (nonliving). For each exemplar, we displayed 2 separate images during scanning. For this study, we matched stimuli across domain on word frequency. Word frequency can be considered to reflect a mixture of name and concept familiarity (see Cree & McRae, 2003). We therefore gathered frequency counts for each item from the British National Corpus (BNC, Burnard, 2000; on-line search engine: http://corpus.byu.edu/bnc/x.asp).

FIGURE 2.2.1. Study 3 Design



Participants were shown a target object for 500 ms, followed by a variable inter-stimulus interval (2500, 3000, or 3500 ms). They were instructed to name each item covertly as quickly and accurately as possible, and to press a button as they named the item.

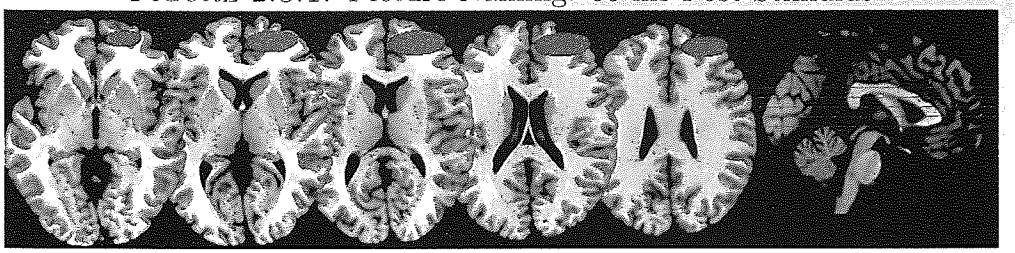
The BNC is a linguistic corpus of 90 million written and 10 million spoken words in British English from the 1980s to 1993. To control for outliers in the final set of stimuli, we used the natural logarithm of the word frequency counts for statistical comparison (similar procedures have been used extensively in a range of behavioural studies). An independent-samples t-test was then used to compare the two lists of words. This analysis showed no significant differences between animals (Mean=6.4, SD=1.5) and tools (Mean=6.2, SD=1.7) on word frequency counts $|t(58)=-0.515,\ p=0.609|$. Each target object was shown once during scanning, resulting in a total of 120 trials during the entire scan. The presentation order was randomised across participants.

2.2.2. MEG Data Acquisition and Analyses. Neuromagnetic data were recorded at a 600 Hz sampling rate with a bandwidth of 0-150 Hz using a CTF 275 MEG system (VSM MedTech Ltd., Canada) composed of a whole-head array of 275 radial 1st order gradiometer channels housed in a magnetically shielded room (Vacuumschmelze, Germany). Synthetic 3rd gradient balancing was used to remove background noise online. Fiducial coils were placed on the nasion, left preauricular, and right preauricular sites of each participant. These coils were energised before each run to localise the participant's head with respect to the MEG sensors. Total head displacement was measured after each run and could not exceed 5 mm for inclusion in the source analysis. Prior to scanning, participants' head shapes and the location of fiducial coils were digitised using a Polhemus Isotrak 3D digitiser (Kaiser Aerospace Inc.). These were then coregistered to high-resolution T1-weighted anatomical images for each participant acquired with a 3-Tesla while-body scanner (3T Trio, Siemens Medical Systems) using in-house coregistration software.

Data for each participant were edited and filtered to remove environmental and physiological artefacts. An event-related beamforming technique was then used to assess the source locations of evoked power for all objects across time. Event-related synthetic aperture magnetometry (ER-SAM) was used to assess sources of activity across time. ER-SAM involves time-domain averaging of estimated source activity and has the benefit of allowing more precise temporal resolution for beamforming (Cheyne, Bakhtazad, & Gaetz, 2006; Robinson, 2004). To begin, a single covariance matrix was calculated over unaveraged 500 ms epochs of both living and nonliving target object trials (120 trials in total), from picture onset to 500 ms after, with a 5-45 Hz bandpass filter. We then selected time points at which to compute the source analysis using the averaged data across the 500 ms window following picture onset. Specific time-points at which source projections were computed included: 65 ms, 120 ms 165 ms, 195 ms 235 ms, 265 ms, 295 ms, 335 ms 365 ms, 390 ms, 420 ms, 440 ms, and 475 ms. We began with 65 ms as Thorpe & Fabre-Thorpe (2001) suggested that typical average spiking rates in V1 in the monkey begin at roughly this time. In order to select time points beyond this, we first averaged signals across all sensors for a small number of subjects from stimulus onset to 500 ms after. Based on these averaged time courses, we then selected time points at which fluctuations in the signal occurred. We aimed to use identical time points across our group of subjects, and we also wanted adequate sampling of sources of activation across the entire 500 ms window we used. Whilst subjects did not tend to respond until almost 800 ms, we thought that most stimulus-specific processing required to correctly name an object would occur by around 500 ms after the picture. At each of the selected time points, source power was projected using a single-state, pseudo-Z approach. This approach is different from all other analyses reported in this thesis, as all other analyses compute differences in spectral power between two conditions. In the ER-SAM analysis, the beamformer weights are normalised in order to correct for spatial distortions in the volumetric images due to the white-noise gain of the weights. Thus, the images that are produced are not in units of source amplitude (i.e., not in nAm). Each participant's data were then normalised and converted to Talairach space using statistical parametric mapping (SPM99, Wellcome Department of Imaging Neuroscience, London, UK, http://www.fil.ion.ucl.ac.uk/spm) for group-level comparisons.

For group-level analyses, we utilised peakomatic to assess the distribution of image peaks across our participants. We tested a ranged of P values from 2 to 20 and after multiple comparisons correction were left with a number of significant clusters of positive peaks across our selected time points. We chose a small range of P values to test compared with other experiments reported in subsequent chapters because the number of peaks within a participant's resultant volumetric image were significantly reduced using the ER-SAM analysis. Therefore, we set P to its maximum value, with the constraint that all images contained at least P peaks. In addition, ER-SAM results in only positive peaks across the brain, and we thus only tested positive values in the peakomatic analysis. If a region was identified as showing a significant effect across a range of P values, we chose the region for reporting purposes that yielded the largest N. In cases where several P values yielded the same N, we then chose the volume that had the smallest spatial extent.

FIGURE 2.3.1. Picture Naming: 65 ms Post-Stimulus



Region in right middle frontal gyrus showing significant event-related power increases at 65 ms post stimulus onset (centre= 25, 52, 15). This region was identified using the top 11 peaks per image; 9 participants had a peak in the volume (maximum radius=24.6 mm).

2.3. Results

2.3.1. Behavioural Findings. Behaviourally, participants responded on average at 787.7 ms (SD=194.6 ms). Their accuracy rates were relatively high, with button-press responses to 113.5/120 trials on average (94.6%, range=108-119). These results are in-line with previous studies of overt picture naming. For example, Kan & Thompson-Schill (2004) found that overt naming of pictures having high name agreement occurred at approximately 795 ms for a group of participants. Thus, our covert naming with button-press findings mirror findings using overt naming paradigms, and suggest that our participants were performing the task in the instructed manner.

2.3.2. Source-Level Findings. We used ER-SAM to identify sources of event-related power changes for all objects at specified time points. These time points included: 65 ms, 120 ms 165 ms, 195 ms 235 ms, 265 ms, 295 ms, 335 ms 365 ms, 390 ms, 420 ms, 440 ms, and 475 ms. We then used peakomatic to determine significantly clustered peaks across our group of participants (see Appendix C for time-frequency information from all regions identified). We will review the locations of significant activation at each time point that was selected.

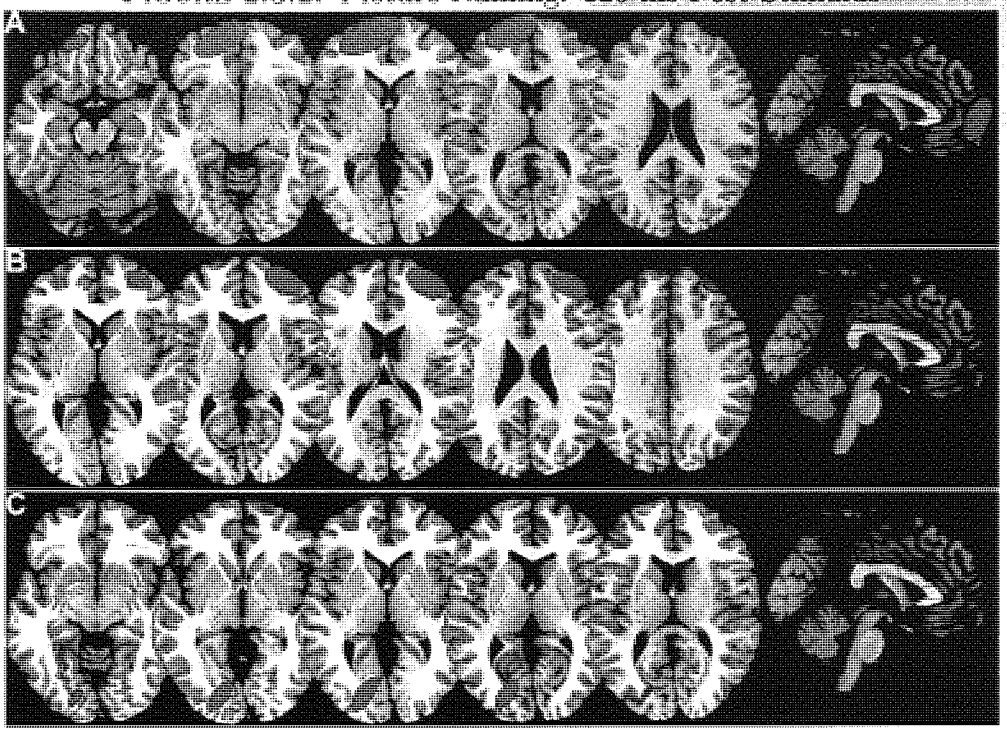
At 65 ms after picture onset, we found a single region showing significant event-related power increases. This region was in right middle frontal gyrus (N=9, P=11, peak activation=30.5) (see Figure 2.3.1).

At 120 ms after picture onset, we found significant event-related power increases in right middle to superior frontal gyrus (N=8, P=13, peak activation=25.5) (see Figure 2.3.2). In addition, we found a region in left cuneus (N=6, P=5, peak activation=43.0) showing significant event-related power increases across our group (see Figure 2.3.2).

At 165 ms after picture onset, we found significant event-related power increases in the occipital lobe, centred on the left lingual gyrus (N=9, P=3, peak activation=63.7) (see Figure 2.3.3). We also found a region in medial frontal gyrus (N=6, P=2, peak activation=66.5) showing event-related power increases across our group, in addition to a region in right middle temporal gyrus (N=6, P=12, peak activation=55.2) (see Figure 2.3.3).

At 195 ms after picture onset, we found significant event-related power increases in right middle temporal gyrus (N=7, P=13, peak activation=57.4) (see Figure 2.3.4). In

FIGURE 2.3.2. Picture Naming: 120 ms Post-Stimulus



Regions identified as showing significant event-related power increases at 120 ms post-stimulus. A) Left superior frontal gyrus (centre= -15, 59, 2). This region was identified using the top 11 peaks per image; 10 participants had a peak in the volume (maximum radius=26.5 mm). B) Right middle frontal gyrus (centre= 32, 52, 16). This region was identified using the top 13 peaks per image; 8 participants had a peak in the volume (maximum radius=18.9 mm). C) Left cuneus (centre= -19, -82, 2). This region was identified using the top 5 peaks per image; 6 participants had a peak in the volume (maximum radius=15.5 mm).

addition, we found a region in the left middle occipital gyrus (N=6, P=3, peak activation=76.8) showing event-related power increases across our group (see Figure 2.3.4).

At 235 ms after picture onset, we found a single region showing significant event-related power increases. This region was in right inferior frontal gyrus (N=9, P=16, peak activation=50.6) (see Figure 2.3.5).

At 265 ms after picture onset, we found significant event-related power increases in right precentral gyrus (N=7, P=19, peak activation=52.7) (see Figure 2.3.6). In addition, we found a region in left cuneus (N=6, P=19, peak activation=63.9) showing event-related power increases across our group (see Figure 2.3.6).

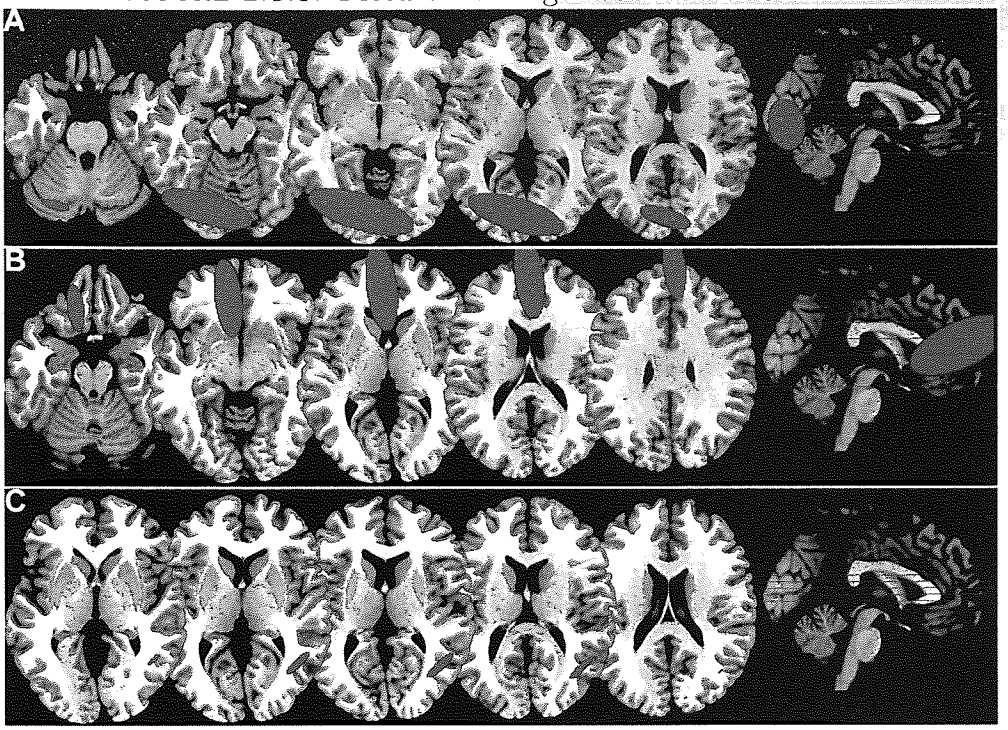
At 295 ms after picture onset, we found a single region showing significant event-related power increases. This region was in left inferior parietal lobule (N=9, P=18, peak activation=52.7) (see Figure 2.3.7).

At 335 ms after picture onset, our peakomatic analysis did not identify any regions showing significant event-related power increases across our group of participants.

At 365 ms after picture onset, we found significant event-related power increases in right middle temporal gyrus (N=8, P=9, peak activation=72.4) (see Figure 2.3.8). In addition, we found a region in left anterior superior temporal gyrus (N=6, P=16, peak activation=61.1) showing event-related power increases across our group (see Figure 2.3.8).

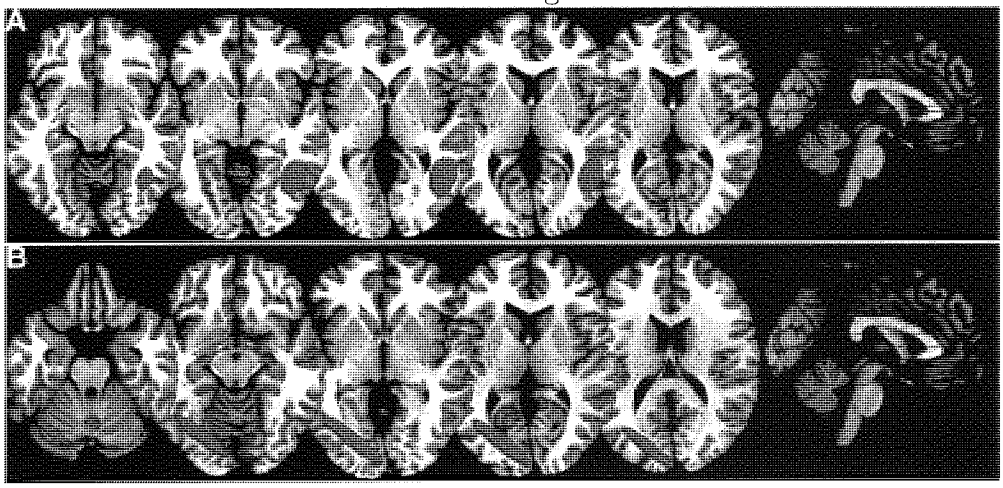
At 390 ms after picture onset, we found a single region showing significant event-related power increases. This region was in right middle temporal gyrus (N=10, P=15,

FIGURE 2.3.3. Picture Naming: 165 ms Post-Stimulus



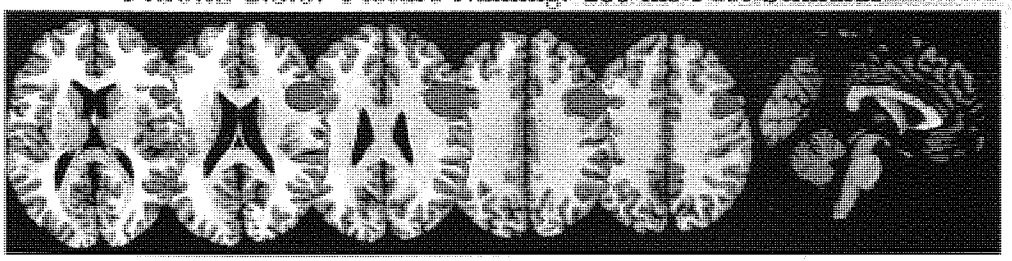
Regions identified as showing significant event-related power increases at 165 ms post-stimulus. A) Left lingual gyrus (centre= -14, -80, -4). This region was identified using the top 3 peaks per image; 9 participants had a peak in the volume (maximum radius=45.4 mm). B) Medial frontal gyrus (centre= -5, 50, 8). This region was identified using the top 2 peaks per image; 6 participants had a peak in the volume (maximum radius=45.6 mm). C) Right middle temporal gyrus (centre= 43, -60, 10). This region was identified using the top 12 peaks per image; 6 participants had a peak in the volume (maximum radius=15.6 mm).

FIGURE 2.3.4. Picture Naming: 195 ms Post-Stimulus



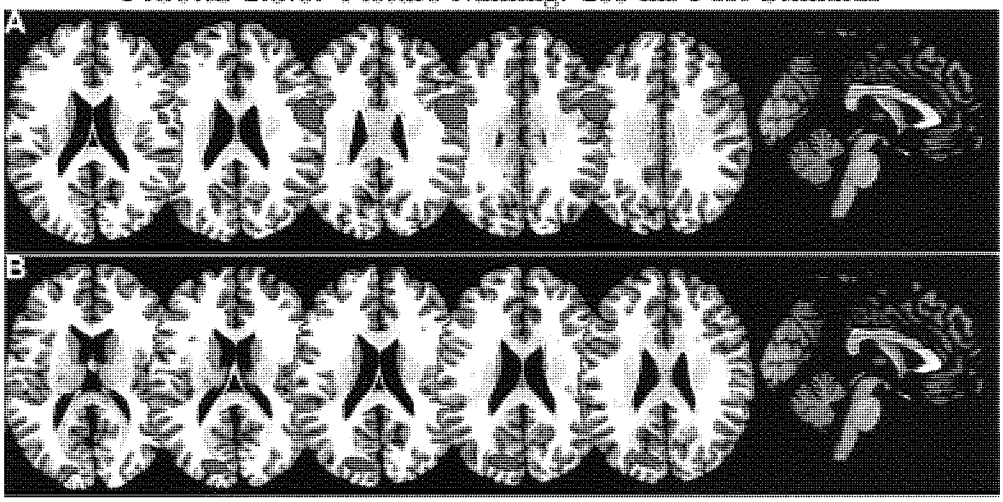
Regions identified as showing significant event-related power increases at 195 ms post-stimulus. A) Right middle temporal gyrus (centre= 44, -55, 0). This region was identified using the top 13 peaks per image; 7 participants had a peak in the volume (maximum radius=16.7 mm). B) Left middle occipital gyrus (centre= -24, -75, 1). This region was identified using the top 3 peaks per image; 6 participants had a peak in the volume (maximum radius=34.9 mm).

FIGURE 2.3.5. Picture Naming: 235 ms Post-Stimulus



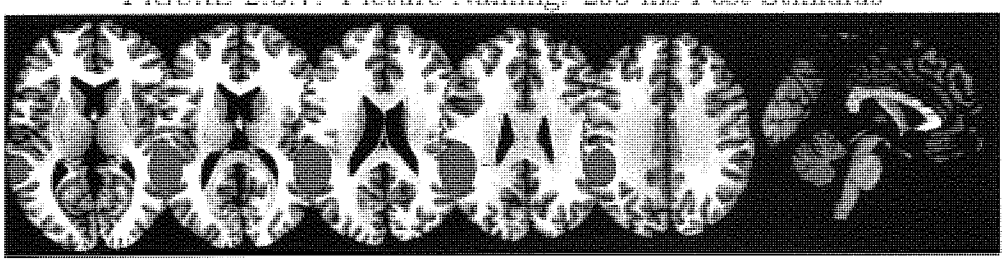
Region in right inferior frontal gyrus showing significant event-related power increases at 235 ms post stimulus onset (centre= 48, 11, 28). This region was identified using the top 16 peaks per image; 9 participants had a peak in the volume (maximum radius=17.7 mm).

FIGURE 2.3.6. Picture Naming: 265 ms Post-Stimulus



Regions identified as showing significant event-related power increases at 265 ms post-stimulus. A) Right precentral gyrus (centre= 54, 2, 28). This region was identified using the top 19 peaks per image; 7 participants had a peak in the volume (maximum radius=15.3 mm). B) Left cuneus (centre= -15, -82, 23). This region was identified using the top 19 peaks per image; 6 participants had a peak in the volume (maximum radius=11.7 mm).

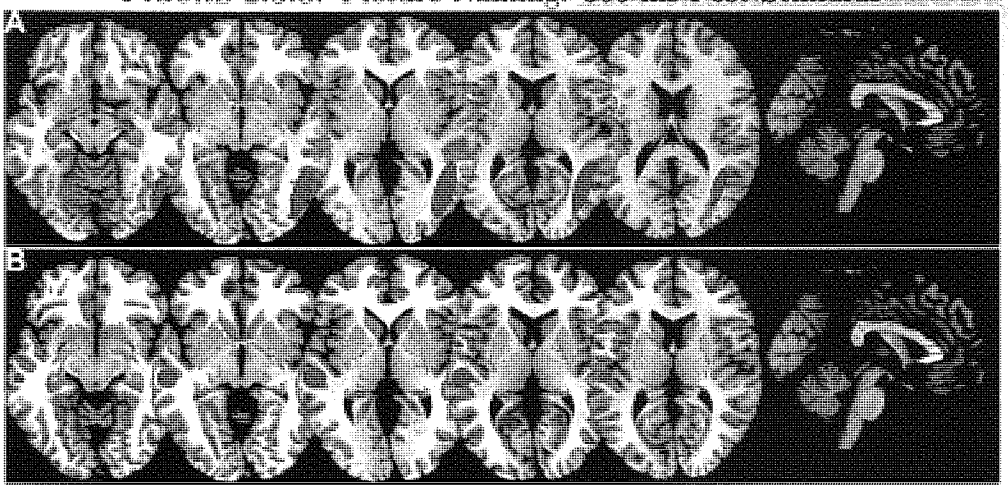
FIGURE 2.3.7. Picture Naming: 295 ms Post-Stimulus



Region in left inferior parietal lobule showing significant event-related power increases at 295 ms post stimulus onset (centre= -54, -40, 24). This region was identified using the top 18 peaks per image; 9 participants had a peak in the volume (maximum radius=19.6 mm).

peak activation=70.4) (see Figure 2.3.9). At 420 ms after picture onset, we again found a single region in right middle temporal gyrus (N=10, P=11, peak activation=73.4) across

FIGURE 2.3.8. Picture Naming: 365 ms Post-Stimulus



Regions identified as showing significant event-related power increases at 365 ms post-stimulus. A) Right middle temporal gyrus (centre= 44, -62, 2). This region was identified using the top 9 peaks per image; 8 participants had a peak in the volume (maximum radius=22.3 mm). B) Left superior temporal gyrus (centre= -58, -23, 1). This region was identified using the top 16 peaks per image; 6 participants had a peak in the volume (maximum radius=12.6 mm).

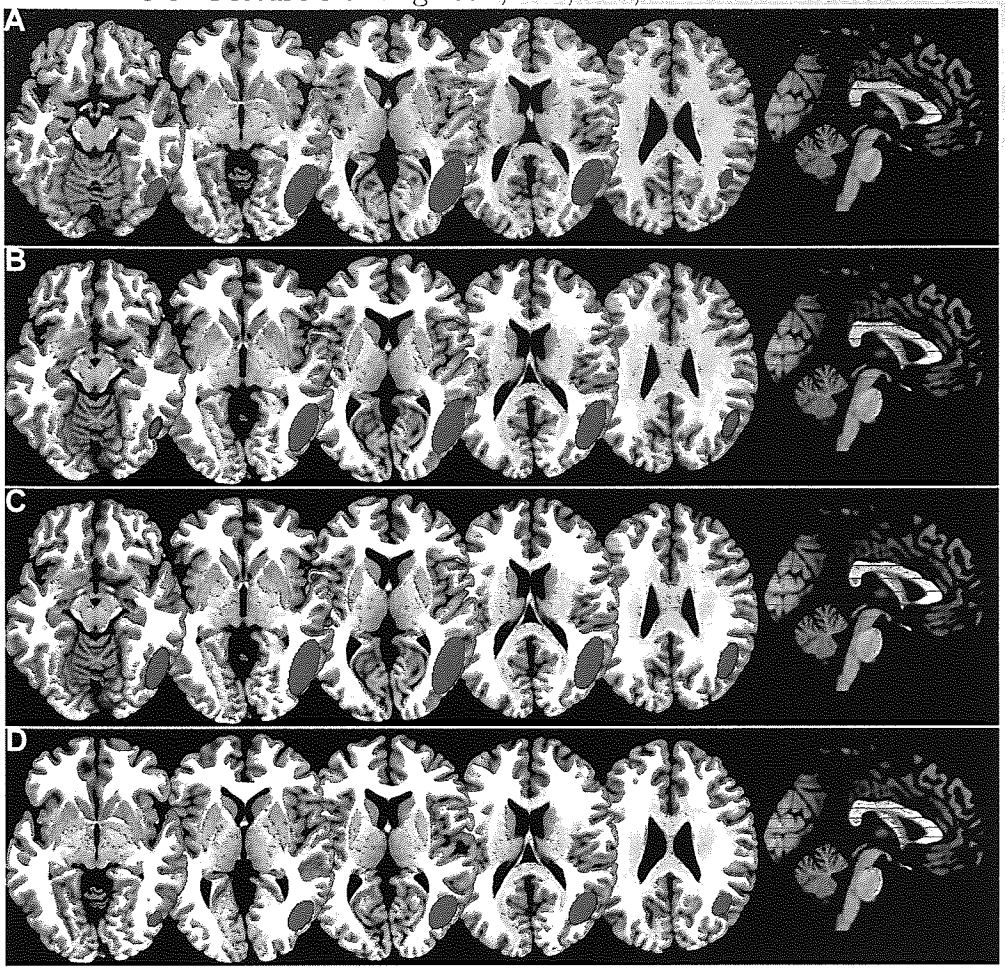
our group of participants (see Figure 2.3.9). This same region continued to show significant event-related power increases at 440 ms after picture onset (N=9, P=9, peak activation=82.5) and again at 475 ms after picture onset (N=8, P=13, peak activation=80.3) (see Figure 2.3.9).

2.4. Discussion

We set out to explore the time course of processing living and nonliving objects in humans. We identified regions in the brain that showed event-related activation to pictures of both living and nonliving objects using event-related SAM across time. We selected a range of time points at which to assess cortical locations of significant event-related activity, beginning at 65 ms after a picture and ending at 475 ms after a picture. This allowed us to map significant cortical activation in response to naming pictures of living and nonliving objects across time. Our results demonstrate very early activation in frontal cortex in response to pictures of objects. This was followed by activation in early visual areas in the ventral stream and more anterior regions of ventral-temporal cortex. We then found activation again in frontal cortex, corresponding to pre-motor areas, followed by activation in inferior parietal lobule to superior temporal gyrus. This was followed by significant activation in middle temporal gyrus for the remainder of our sampling time.

We found very early activation in right frontal cortex for objects. The peaks across our group of participants centred on a region in right middle frontal gyrus at 65 ms post stimulus onset. Given that Thorpe & Fabre-Thorpe (2001) predicted feedforward activation beginning in primary visual cortex at roughly 60 ms after a picture, our results are surprising. However, recent evidence has also demonstrated very early activation in frontal cortex in response to visual stimuli in humans (Kirchner et al., 2009). Kircher et al. (2009) recorded from implanted electrodes in the frontal eye fields (FEF) of 11 epileptic patients being evaluated for surgical resection. They found that activation in the FEF

FIGURE 2.3.9. Picture Naming: 390, 420, 440, and 475 ms Post-Stimulus



Regions in right middle temporal gyrus identified as showing significant event-related power increases from 390-475 ms post-stimulus. A) 390 ms post-stimulus (centre= 46, -60, 4). This region was identified using the top 15 peaks per image; 10 participants had a peak in the volume (maximum radius=25.0 mm). B) 420 ms post-stimulus (centre= 47, -60, 8). This region was identified using the top 11 peaks per image; 10 participants had a peak in the volume (maximum radius=23.3 mm). C) 440 ms post-stimulus (centre= 46, -60, 6). This region was identified using the top 9 peaks per image; 9 participants had a peak in the volume (maximum radius=27.8 mm). D) 475 ms post-stimulus (centre= 42, -65, 11). This region was identified using the top 13 peaks per image; 8 participants had a peak in the volume (maximum radius=20.5 mm).

in response to flashing checkerboard stimuli was very fast, at approximately 45 ms after stimulus onset. In addition, a subset of 4 patients were presented with natural scenes containing faces, and these stimuli were shown to activate the FEF at approximately the same time as the checkerboard stimuli. Thus, their results indicate that the FEF responds to complex stimuli. In addition, recordings from monkeys have demonstrated that the FEF has a modulatory role on lower-order visual areas (Ekstrom et al., 2008). In addition, tracing studies have indicated that FEF has both afferent and feedforward connections with early visual processing area V4 (Barone et al., 2000). Thus, this early activation in frontal cortex potentially reflects FEF responses to both the living and nonliving pictures at roughly 65 ms post-stimulus.

Bar et al. (2006) have also demonstrated early activation in frontal cortex. They used MEG to measure cortical activity in humans in response to line drawings of nameable

objects that were presented briefly between two masks. They then assessed cortical activation to recognised versus non-recognised stimuli. They found differential activation in left posterior orbital gyrus at roughly 130 ms after stimulus onset. Responses in this region were diagnostic for recognised compared with non-recognised objects. They also demonstrated that this early differential activation developed prior to significant activation in both right and left fusiform cortex. In fact, recognition-related activation occurred in fusiform cortex at roughly 180 ms after a stimulus. We also demonstrate early activation in frontal cortex at 120 ms post-stimulus. In addition to the region in right middle frontal gyrus previously mentioned, we find activation in left anterior superior frontal gyrus, extending into orbito-frontal cortex. Also at this time, we also show significant activation in early visual cortices, centred on the left cuneus. These findings are in line with ERP findings from Allison et al. (1999), which showed the ERP generators of the N100 and P100 to localise to striate and peristriate cortex. Importantly, only 6 of our participants had a peak in left cuneus at this early time window, suggesting that it is not as robust an effect as the frontal activation across our group of participants. This finding is then in line with Bar et al.'s prediction that significant frontal activation occurs prior to activation in visual object-processing areas in the ventral stream.

At roughly 165 ms post-stimulus we found significant event-related activation in the occipital lobe. Given the range of studies reporting object-specific activation in this region roughly 170 ms post-stimulus, our findings are not surprising. In fact, visual object-processing in the ventral stream is the most consistent activation across our group of participants at this time. Liu et al. (2009) recorded from intracranial electrodes implanted in occipital, temporal, frontal, and parietal regions in 11 patients undergoing evaluation of epileptic discharge foci. They presented participants with grayscale photographs of nameable objects. Using a support vector machine classifier, they were able to demonstrate object-category related activation in visual cortex from single trial data beginning at roughly 100 ms post-onset. Critically, classification performance peaked in visual cortex at roughly 170-180 ms post-stimulus onset. This timing mirrors the timing we find for visual object-processing in our study. In addition to early visual cortex activation, we continue to see activation in medial regions of frontal cortex, extending into orbito-frontal cortex. We also begin to find consistent activation extending into more anterior regions in the fusiform gyrus (right middle temporal gyrus), although only 6 of our participants had a peak in this region at this time.

Allison et al. (1999) recorded ERPs from 98 epilepsy patients with implanted electrodes who were being monitored for surgical intervention. They presented their participants with a range of grayscale photographs of faces and nameable objects, and measured cortical responses. In addition to localising early sources of ERP activation, they were primarily interested in the generator of the N200 response to faces and objects. They found that the ERP generators of the N200 response to faces and objects localised to the ventral surface of the fusiform gyrus (although they find the ERP generators for faces and other objects to be in slightly different locations, they both localised to medial regions of the ventral surface of the fusiform gyrus, although less pronounced for objects than faces). Our findings for event-related activation for living and nonliving objects in middle

temporal gyrus at roughly 195 ms post-stimulus are in line with Allison et al.'s findings. Allison et al. suggest that this early stage of processing might reflect the structural encoding of a stimulus (Bruce & Young, 1986; Perrett et al., 1987).

Beginning at roughly 235 ms post-stimulus, we found significant event-related activation in the right inferior frontal gyrus. This activation in frontal cortex continues at 265 ms post-stimulus. Thorpe et al. (1996) measured ERP signals from 15 participants whilst they were shown a series of pictures briefly. Their task was a go/no-go task, in which they released a button when they saw a picture containing an animal. Measuring from a series of electrodes in frontal regions, Thorpe et al. found consistent differences between the go/no-go trials at roughly 171 ms after stimulus onset, with significance increasing until it peaked at 237 ms post-stimulus. Our timing in frontal cortex then is in accord with Thorpe et al.'s findings. These timings are also in accord with Thorpe & Fabre-Thorpe's (2001) predictions that conduction velocity should result is approximately 50 ms timing differences between monkey and human neural activity in frontal regions. Thorpe & Fabre-Thorpe noted that typical average spiking within monkey pre-motor cortex in response to visual categorisation tasks is around 160 ms, whilst spiking in motor cortex begins at roughly 190 ms. This would place human activation in these regions at roughly 210 and 240 ms respectively. Thus, this activation in right inferior cortex to the precentral gyrus probably reflects anticipatory motor processes related to the visual stimulus. That is, participants are preparing to make a motor response to the visually-presented stimulus (i.e., press a button).

At 295 ms and 365 ms, we found significant event-related activation in a region extending from left inferior parietal lobule to the superior temporal gyrus. Our timing in this region corresponds to Levelt et al.'s (1998) MEG recordings during their picture naming task. They assessed the dipole source locations of activation in a window from 275 to 400 ms post-stimulus onset, a window in time they felt best reflected phonological encoding. The localisation of these sources were primarily in inferior parietal to superior temporal gyrus, in strong accord with our findings. They argue that their localisation appears to be within the site of classic Wernicke's area in the left hemisphere of their participants, with right-hemisphere sources in the same time window at more remote areas. In fact, none of Levelt's participants showed a dipole localisation to the right-hemisphere homologue of Wernicke's area. These findings are in agreement with our results, as our event-related activation at this time interval was in the left hemisphere.

Beginning at 365 ms post-stimulus, we found event-related activation across our group of participants in right middle temporal gyrus. Activation in this region continued at each of the subsequent time samples, to 475 ms post-stimulus. Allison et al. (1999) showed a VP350 face-specific component in their ERP recordings that localised to similar regions in the ventral surface of the fusiform gyrus as the N200 component. In some cases, this later component was adjacent to the N200 localisation sites, suggesting that later face processing might be carried out in similar regions as the early component. Our MEG findings would support this hypothesis, as the regions identified in right middle temporal gyrus at 165 ms and 195 ms post-stimulus are in close correspondence with these later regions identified in our analysis. Certainly, lesion evidence in patients suggest that the temporal lobes may be a principal site for storage of perceptual information about

objects and their attributes (e.g., Hillis & Caramazza, 1991; Gainotti, 2000; Warrington & McCarthy, 1987). Thus, it appears that feedback projections might cause re-activation of this region during the phonetic and articulatory processing necessary to name an object.

Our results then support very early differences in the FEF and anterior medial regions of frontal cortex extending into orbito-frontal cortex, followed by more elaborative processing of the living and nonliving objects through the ventral stream, from early visual areas to more anterior activation in middle temporal gyrus. Whilst the activation in the ventral stream might proceed in a bottom-up fashion, our results indicate that frontal cortex could conceivably provide some top-down modulatory control on the visual processing, in line with other recent findings in the literature. After initial processing in the ventral stream we found significant activation in inferior frontal and pre-motor regions of the brain, suggestive of motor-preparatory behaviour. This was followed by activation in left superior temporal to inferior parietal lobule, a region implicated in phonological processing. Finally, we found activation again in more anterior regions of the ventral stream, suggestive of re-activation of stored object representations during the phonetic and articulatory processes of our task. Critically, our results indicate that activation at each region of the brain is not completed prior to activation at later stages. Thus, our findings provide some support for models of object-naming that posit that activation at each of the stages proceeds in a parallel fashion, rather than in serial (e.g., Humphreys et al., 1988).Therefore, these findings provide a basis for looking at perceptual and semantic differences in processing objects separately. Critically, according to the cascade model, there will be important interactions both within and between the perceptual and semantic system, and therefore it is critical to use a neuroimaging strategy that allows us to measure the time-course of object processing.

CHAPTER 3

When does Processing of Living and Nonliving Objects Diverge in the Ventral Object-Processing Stream?

3.1. Introduction

Reports of striking dissociations in patients' recognition and naming of living and nonliving objects have been used to formulate theoretical accounts of the organisation of semantic knowledge. Many of these accounts assume that the organisation of knowledge in semantic memory is innately constrained (either by category-specific subsystems: Caramazza & Shelton, 1998; or modality-specific subsystems: Warrington & Shallice, 1984; see Mahon & Caramazza, 2007 for a review of these theories; see Chapter 1 for greater discussion). Although separate subsystems provide a neat account of the most commonly reported patterns of deficits observed in patients, there is a growing body of evidence suggesting that living/nonliving dissociations are not clear-cut, and may be more consistent with a distributed conceptual system (Gainotti, 2002). In addition, a recent review of functional imaging studies using normal participants found no single brain region to be consistently activated for a given object category (Gerlach, 2007). Again, these findings are more compatible with theories of category specificity that assume a widely distributed conceptual system not organised by category (e.g, Garrard et al., 1998; Moss et al., 1998; Tyler et al., 2000).

A crucial question when deciding between subsystems and distributed accounts of semantic knowledge is whether processing of living and nonliving objects diverges before reaching the semantic system, thus providing an alternative to separate semantic subsystems accounts of category-specific effects. Behavioural studies using normal participants have suggested that perceptual characteristics of living and nonliving things may cause processing differences in the visual object recognition system (e.g., Farah & McClelland, 1991; Gerlach, 2001; Humphreys & Forde, 2001; Humphreys, Riddoch, & Quinlan, 1988; Humphreys, Riddoch, & Forde, 2002; Lamberts & Shapiro, 2002; Lloyd-Jones & Luckhurst, 2002; Shapiro & Olson, 2005; Tanaka & Presnell, 1999). Differences in perceptual processing could have knock-on effects on semantic processing, revealing a crucial dimension underlying a distributed semantic system. A few neuroimaging studies (e.g., Kiefer, 2001; Martin et al., 1996; Perani et al., 1999; Price et al., 2003; Rogers et al., 2005; VanRullen & Thorpe, 2001) suggest that it is likely that living and nonliving things make different demands on our perceptual system. However, as yet, there is no direct evidence of the timing of category-specific differences in brain regions dedicated to visual object processing. The current study therefore aims to pinpoint the time and cortical location of the earliest processing stage at which category-specific effects occur using magnetoencephalography (MEG). This will address the key question of whether accounts based on perceptual processing can provide a serious alternative to separate semantic subsystems.

3.1.1. Evidence of Perceptual Processing Differences for Living and Nonliving Objects. A range of characteristics of living and nonliving objects have been isolated as a potential cause of processing differences. Specifically, research has shown that living and nonliving objects differ in the relative importance of visual form (e.g., Farah & McClelland, 1991; Humphreys Riddoch, & Forde, 2002; Tanaka & Presnell, 1999) and global shape (e.g., Gerlach, 2001; Gerlach et al., 2004; Gerlach et al., 2006; Lloyd-Jones & Luckhurst, 2002; Thomas et al., 2002), as well as the amount of perceptual similarity amongst category members (Humphreys et al., 1988; Humphreys & Forde, 2001; Lamberts & Shapiro, 2002; Shapiro & Olson, 2005).

3.1.1.1. *The Relative Importance of Visual Form and Global Shape.* Previous research has demonstrated that visual form might be more critical for differentiating between living than nonliving things. For example, Farah & McClelland (1991) used computer simulations of damage to either visual or functional semantic memory units to demonstrate that visual knowledge is critical for differentiating between living things, whilst functional knowledge is critical for differentiating between nonliving things. They also highlighted that dictionary definitions of animals depend on visual feature information to differentiate amongst members of the category, unlike definitions of nonliving things. Caramazza & Shelton (1998) criticised their approach (i.e., asking 'What does the item do or what is it used for?') as being biased toward nonliving things (see also Humphreys & Forde, 2001). However, McRae, de Sa, & Seidenberg (1997) found when they asked participants to simply list properties of objects that the frequency of sensory properties was roughly equal between living and nonliving things, whilst more non-sensory features (e.g., used for cutting) were listed for nonliving things (see also McRae & Cree, 2002). Tanaka & Presnell (1999) used a naming task comparing naming performance for coloured, achromatic, and incongruently coloured pictures to show that colour and texture are reliable, diagnostic cues for living things and help to differentiate living things from competitors (see also Price & Humphreys, 1989). For this reason, colour and texture might be more strongly weighted in the representations of living things than nonliving things (Humphreys et al., 2002).

Gerlach (2001) and Lloyd-Jones & Luckhurst (2002) compared participants' recognition of living and nonliving objects under different viewing conditions. When conditions were sub-optimal and participants could only use global shape to make their decisions, they found an advantage for living things. However, when conditions were optimal, and participants were required to make full use of internal details of the object in order to make a decision, performance was better for nonliving things. These data support the hypothesis that global shape is more critical for recognition of living than nonliving objects, whereas internal detail may be more important for recognising nonliving things. In support of this hypothesis, Thomas et al. (2002) described an integrative visual agnosic patient, DW, who had difficulty accessing the overall shape of objects and therefore relied on local features in order to identify things. DW performed significantly worse when naming line drawings of living things compared with nonliving things, suggesting that a deficit in global shape can disproportionately affect recognition of living things.

3.1.1.2. *Perceptual Similarity.* Humphreys, Riddoch, & Quinlan (1988) demonstrated that living things have higher within-category perceptual similarity than nonliving things,

using two measures: ratings of the number of common parts and the amount of contour overlap (also see Lamberts & Shapiro, 2002). Humphreys et al. support their conclusion with evidence from a patient whose selective deficit for living objects appears to be caused by problems with naming highly similar objects (see also Arguin, Bub, & Dudek, 1996b; Moss et al., 1998; Warrington & Shallice, 1984). In addition, Shapiro & Olson (2005) demonstrated the impact of high levels of similarity on normal recognition of novel images from both living and nonliving categories, suggesting that perceptual similarity, and not semantic category, underlies object recognition performance.

In sum, these studies indicate that there are perceptual attributes that vary systematically with semantic category. These attributes alone might cause differences in the way in which structural descriptions of living and nonliving objects are accessed, before semantic representations are activated (Humphreys et al., 1988).

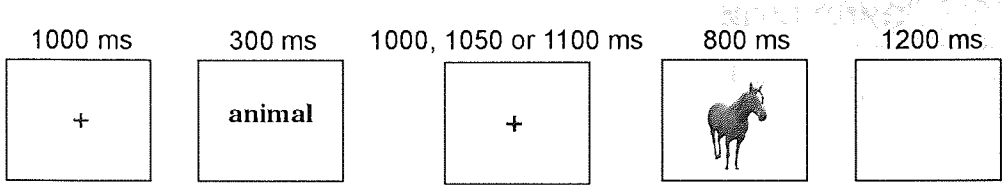
3.1.2. Current Studies. Two event-related potential (ERP) studies have reported an early difference in processing living and nonliving objects (Kiefer, 2001; VanRullen & Thorpe, 2001). For both studies, this difference reflected a larger N1 (negative-going deflection at approximately 180 ms in posterior sensors) for living compared to nonliving objects, occurring independent of task manipulation, suggesting greater activity in perceptual processing areas for pictures of living objects. Importantly, however, Kiefer (2001) only found this difference for pictures of nameable objects and not for the written name of an object, suggesting that this effect is more likely to arise from bottom-up processing of a stimulus. However, it was not possible to accurately localise these effects using EEG. MEG allows more accurate localisation of these electrical changes with the same high temporal resolution. Thus, we have two main aims. Firstly, we will examine whether this early difference can also be observed using MEG, and whether there is greater activity for living things. Secondly, we aim to examine whether these early differences occur in visual object-recognition areas of the brain. We will address these aims in a series of three studies. Each of these studies utilises a different task manipulation, and thus allow us to test whether early divergence in the visual object-processing system is task-specific, or whether it is a phenomenon that occurs in a range of tasks. If we see divergence of visual object-processing within the ventral stream in some tasks but not others, then the greater activity for living objects reported in the previously mentioned studies would most likely be a direct result of the task manipulation, and thus we could not argue that this effect is a function of visual object-processing per se. If, however, we find increased activity for living objects in each of our task manipulations, this gives us greater ability to argue that the difference seen is a reflection of task-independent differences in how the brain processes pictures of living and nonliving objects.

3.2. Methods

3.2.1. Study Procedures.

3.2.1.1. *Study 1.* Ten right-handed volunteers (Mean Age=29.4 years, range=20-36 years; 2 males) participated in the MEG study. Using an adaptation of Kiefer's (2001) design, participants were first shown a superordinate category name as a probe, followed by a target object (see Figure 3.2.1). Participants were instructed to respond by button

FIGURE 3.2.1. Example Trial from Study 1.



Participants were shown a 1000 ms red fixation cross, followed by a 300 ms category probe. After a variable (1000, 1050, or 1100 ms) delay interval, participants were shown a target object for 800 ms. They were instructed to decide as quickly and accurately as possible if the target object was a member of the previously presented category probe by pressing a button.

press as quickly and accurately as possible, identifying whether the target object matched the category probe. Participants responded using a 2-button response box held in their right hand. They were instructed to respond by pressing the left button with their right index finger for "yes" (i.e., congruent trial) and the right button with their middle finger for "no" (i.e., incongruent trial).

Target objects included 78 exemplars drawn from 3 living (plants, animals, fruits and vegetables; note that we collapsed fruits and vegetables into a single superordinate category given difficulties in distinguishing the two, see e.g., Snodgrass & McCullough, 1986) and 3 nonliving (tools, transport, and furniture) categories (see Table 1 for a list of exemplars). One common criticism of previous research on category-specificity has been that confounding variables including word frequency, stimulus familiarity, age of acquisition of an object's name, and visual complexity have not always been adequately controlled. For this reason, all selected images had a pre-test naming consistency rate of greater than 65 percent. In addition, in separate behavioural sessions using a different group of participants, we collected data on naming speed, familiarity, typicality, and visual complexity for a large set of living and nonliving objects. For the naming speed task, we simply asked participants to name each item aloud as quickly and accurately as possible, and measured response time. For familiarity, typicality, and visual complexity, participants were asked to rate stimuli from 1 (Low) to 5 (High), using a procedure similar to that employed by Snodgrass & Vanderwart (1980). For the current study, we then selected stimuli that were matched on pre-test naming speed (Living=1232.9 ms, Nonliving=1247.7 ms), familiarity (Living=3.46, Nonliving=3.63), and typicality (Living=3.83, Nonliving=3.75) (see Table 2). Unfortunately, in this study, we were not able to match visual complexity between living and nonliving objects, however the ratings were relatively close. In his review of functional imaging studies of category specificity, Gerlach (2007) argued that adequate control of visual complexity and the number of common parts across domain might eliminate category-specific activations in certain regions of the brain. His criticism specifically described the type of category being compared (for example, animal versus tool, where animals are typically rated as more visually complex; Snodgrass & Vanderwart, 1980). The living and nonliving categories we selected were broadly balanced for complexity since 2 categories from each domain were rated as high in complexity (plants and animals versus furniture and vehicles), and 1 category from each domain was rated as low in complexity (fruits and vegetables versus tools).

TABLE 1. Living and Nonliving Object Exemplars from Study 1.

LIVING			NONLIVING		
Plants	Animals	Fruits/Vegetables	Tools	Transport	Furniture
Cactus	Cow	Apple	Axe	Aeroplane	Armchair
Clover	Deer	Broccoli	Drill	Boat	Bunk beds
Dandelion	Eagle	Cauliflower	File	Bicycle	Bed
Daffodil	Goat	Cucumber	Garden Fork	Camper van	Chair
Grass	Hippo	Grapes	Hammer	Limousine	Chandelier
Palm	Leopard	Lemon	Pen	London Bus	Chest
Rose	Monkey	Lettuce	Saw	Lorry	Chest of Drawers
Sunflower	Peacock	Orange	Scissors	Skateboard	Deck Chair
Thistle	Penguin	Peach	Screw	Submarine	Desk
Toadstool	Pike	Pear	Screwdriver	Taxi	Shelves
Tree	Rabbit	Pepper	Spanner	Train	Sofa
Water-lily	Raccoon	Potato	Tape Measure	Tram	Table
Wheat	Wolf	Strawberry	Workbench	Van	Wardrobe

TABLE 2. Naming Speed, Familiarity, Typicality, and Complexity Ratings for Living and Nonliving Objects from Study 1.

Measure	N	Living Mean (SD)	Nonliving Mean (SD)
Naming Speed (ms)	23	1232.9 (270.6)	1247.7 (297.7)
Familiarity (/5)	21	3.46 (0.59)	3.63 (0.61)
Typicality (/5)	21	3.83 (0.39)	3.75 (0.34)
Complexity (/5)*	20	2.84 (0.38)	2.46 (0.30)

For all tasks, participants were instructed to respond as quickly and accurately as possible. For the Naming Speed task, participants were presented pictures of objects in random order and were asked to name each item aloud. For Familiarity, Typicality, and Complexity, participants were asked to rate each picture on a scale from 1 (Low) to 5 (High). Paired samples t-tests showed that complexity is the only measure that is significantly different between living and nonliving objects, * $p<0.01$.

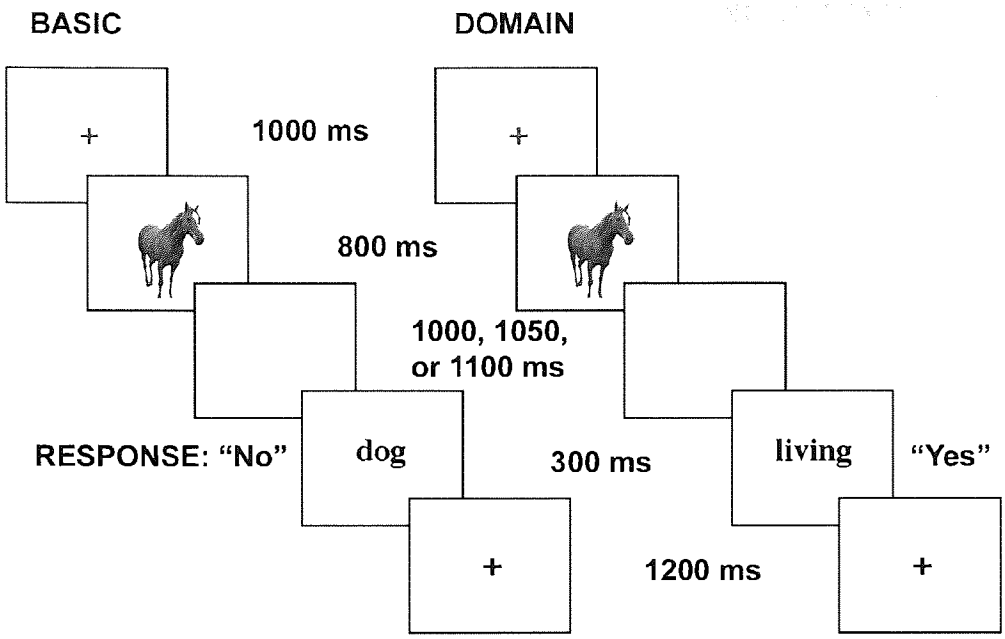
Each target object was presented twice, once as a congruent trial ("yes", e.g., target dandelion preceded by a flower superordinate category label) and once as an incongruent trial. For incongruent trials, each image was associated with either a within or across-domain label. For example, a target dandelion with an animal superordinate category label would be classed as within-domain incongruent whereas a target dandelion with a tool superordinate category label would be classed as across-domain incongruent. Throughout the entire run, there were equal chances of having a within or across-domain incongruent label. Across participants, we counterbalanced whether a given item had a within or across-domain incongruent label. A total of 156 trials were shown during the scan, half

of which included a living target object and the other half a nonliving target object. The order of trial presentation was randomised across participants.

3.2.1.2. *Study 2.* In a second study, nine right-handed volunteers (Mean Age=31.3 years, range=22-41 years, 5 males) participated in the MEG study. During scanning, participants performed a categorisation task in which they were asked to categorise pictures of objects at either the basic level or the domain level (see Figure 3.2.2). Participants were first shown a picture of a target object, and after a brief variable delay, they were presented with either a basic-level object name or a domain-level name. This order was reversed from study 1. We reversed the presentation because we felt that presenting a label prior to the target object contaminated the 'baseline' period used for comparison purposes. Specifically, we were interested in processing in the brain as a function of the target object, and so we wanted to compare this time period with a period where participants were not doing any task. However, seeing a category probe prior to target object onset meant that participants were retaining this probe name in memory during this period. This new design ensured that there was no task (i.e., retaining the probe name in short-term memory) during the period just prior to target onset. As with study 1, participants were instructed to respond by button press as quickly and accurately as possible, indicating whether the basic or domain-level name matched the target object. Again, participants responded using a 2-button response box held in their right hand. In this study, we blocked trials by level of processing, whilst allowing category membership to vary across each block (see Chapter 6 for further explanation on the motivation for this experimental design). Therefore, participants were first shown a screen indicating at which level of specificity they would be required to categorise the subsequent pictures (i.e., "basic-level name" or "living/nonliving"), followed by a series of 20 pictures. A total of six blocks were shown during the entire scan, with blocks alternating between the basic and domain levels. Across participants, we then varied the presentation time of basic and domain-level blocks in order to minimise any potential practise and/or timing effects. As with study 1, participants were instructed to respond by pressing the left button with their right index finger for "yes" (i.e., congruent) and the right button with their right middle finger for "no" (i.e., incongruent).

Target objects included 60 exemplars drawn from 3 living (plants, animals, fruits and vegetables) and 3 nonliving (tools, transport, furniture) categories (see Table 3 for a list of exemplars). For this study, we again ensured that all selected images had a pre-test naming consistency rate of greater than 65%. In addition, stimuli were matched on pre-test naming speed (Living=1220.7 ms, Nonliving=1222.8 ms), familiarity (Living=3.56, Nonliving=3.72), typicality (Living=3.86, Nonliving=3.96), and visual complexity (Living=2.69, Nonliving=2.52) (see Table 4). During scanning, each target object was presented four times. On 2 occasions, the target object was shown with a domain-level label, and on 2 occasions it was shown with a basic-level label. For both of these conditions, the target object was congruently matched with its appropriate label (e.g., dog picture presented with either "dog" or "living" label) once, and incongruently matched with another label (e.g., dog picture presented with either "lily" or "nonliving" label) once. For incongruent trials at the basic-level, we ensured that the non-matching label did not come from the same general category. So, for example, a picture of an item from the animal

FIGURE 3.2.2. Example Trial from Study 2.



Participants were shown a 1000 ms red fixation cross, signalling the beginning of a trial. They then saw a target object for 800 ms, followed by a variable delay (1000, 1050, or 1100 ms). Participants then saw a 300 ms probe at either the basic level (i.e., "dog") or domain level (i.e., "living"), followed by a black fixation cross for 1200 ms. They were instructed to decide as quickly and accurately as possible if the probe matched the target object and respond via button press.

category would be presented with a basic-level label drawn from either plants or fruits and vegetables. We did this to ensure that participants were still required to access the semantic system at the same level for basic-level congruent and incongruent trials, whilst not increasing the difficulty for incongruent trials by having the label come from the same general category (e.g., dog picture presented with "cat"). We also felt that presenting an across-domain non-matching exemplar name (e.g., dog picture with an exemplar name from tools, transport or furniture) would not be equated with the basic-level task for difficulty, and thus we wanted to ensure participants were making basic-level comparisons. A total of 240 trials were shown during the scan, half of which included a living target object and the other half a nonliving target object. The order of trial presentation was randomised across participants.

3.2.1.3. *Study 3.* In a third study, ten right-handed volunteers (Mean Age=31.9 years, range=24-41, 2 males) participated in the MEG study. During scanning, participants were asked to silently name pictures of objects and to press a button as they named each item (see Figure 3.2.3). Participants were first shown a picture of an object, followed by a variable inter-stimulus interval (ISI). As with both study 1 and 2, participants were instructed to respond as quickly as possible, pressing the left button with their right index finger as they named each item.

Target objects included 60 exemplars drawn from the categories of animals (living) and tools (nonliving). (see Table 5 for a list of exemplars). We chose to use stimuli from only two categories in this study, because we felt that this would provide for greater control in assessing differences in living and nonliving object processing. That is, we would not have to worry about variability across different categories within a single domain. In

TABLE 3. Living and Nonliving Object Exemplars from Study 2.

LIVING			NONLIVING		
Plants	Animals	Fruits/Vegetables	Tools	Transport	Furniture
Clover	Cow	Apple	Axe	Aeroplane	Armchair
Daffodil	Deer	Cucumber	Drill	Bicycle	Bed
Dandelion	Eagle	Lemon	Garden Fork	Boat	Bunk beds
Grass	Goat	Lettuce	Hammer	Limousine	Chair
Palm	Hippo	Orange	Saw	London Bus	Chest
Rose	Penguin	Peach	Scissors	Lorry	Chest of Drawers
Sunflower	Pike	Pear	Screwdriver	Taxi	Deck Chair
Tree	Rabbit	Pepper	Spanner	Train	Desk
Water-lily	Raccoon	Potato	Tape Measure	Tram	Table
Wheat	Wolf	Strawberry	Workbench	Van	Wardrobe

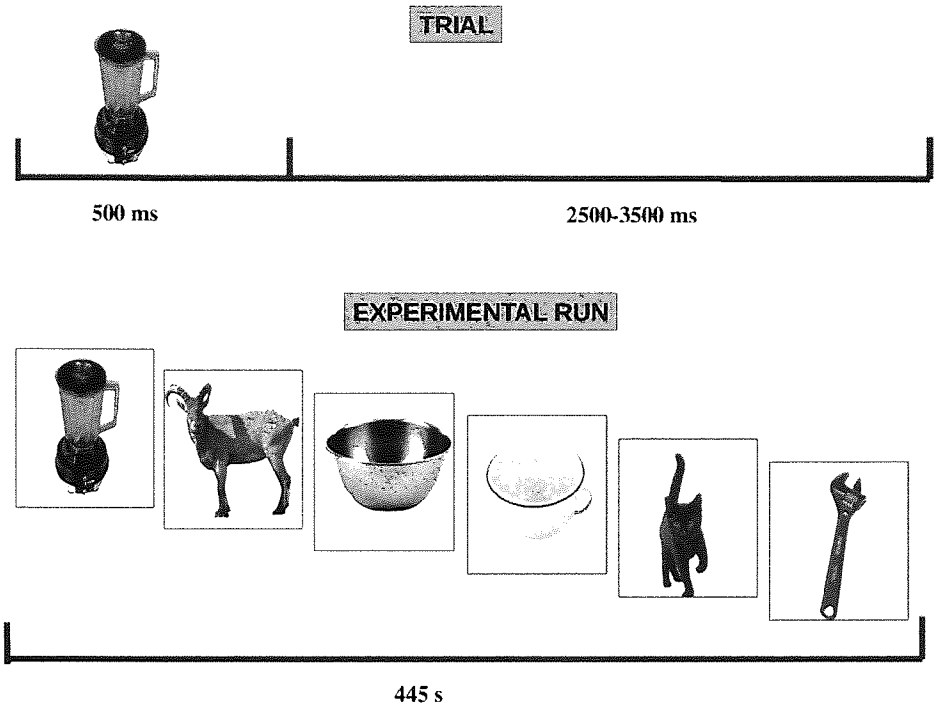
TABLE 4. Naming Speed, Familiarity, Typicality, and Complexity Ratings for Living and Nonliving Objects from Study 2.

Measure	N	Living Mean (SD)	Nonliving Mean (SD)
Naming Speed (ms)	23	1220.7 (274.4)	1222.8 (278.4)
Familiarity (/5)	21	3.56 (0.61)	3.72 (0.59)
Typicality (/5)	21	3.86 (0.39)	3.96 (0.34)
Complexity (/5)	20	2.69 (0.37)	2.52 (0.30)

For all tasks, participants were instructed to respond as quickly and accurately as possible. For the Naming Speed task, participants were presented pictures of objects in random order and were asked to name each item aloud. For Familiarity, Typicality, and Complexity, participants were asked to rate each picture on a scale from 1 (Low) to 5 (High). Paired samples t-tests showed that there were no significant differences between living and nonliving objects on any measure.

addition, these are the most frequent categories used in the neuroimaging literature to assess category-specific effects. For each exemplar, we displayed 2 separate images during scanning. For this study, we matched stimuli across domain on word frequency, but did not measure naming consistency, familiarity, complexity, or typicality as in studies 1 and 2. Rather, we selected 30 items from each category that were matched on word frequency, as word frequency can be considered to reflect a mixture of name and concept familiarity (see Cree & McRae, 2003), which we felt were the most critical factors. We gathered frequency counts for each item from the British National Corpus (BNC, Burnard, 2000; on-line search engine: http://corpus.byu.edu/bnc/x.asp). The BNC is a linguistic corpus of 90 million written and 10 million spoken words in British English from the 1980s to 1993. To control for outliers in the final set of stimuli, we used the natural logarithm of the word frequency counts for statistical comparison (similar procedures have been used extensively in a range of behavioural studies). An independent-samples t-test was then used to compare the two lists of words. This analysis showed no significant differences

FIGURE 3.2.3. Study 3 Design.



Participants were shown a target object for 500 ms, followed by a variable inter-stimulus interval (2500, 3000, or 3500 ms). They were instructed to name each item covertly as quickly and accurately as possible, and to press a button as they named the item.

between animals (Mean=6.4, SD=1.5) and tools (Mean=6.2, SD=1.7) on word frequency counts [t(58)=-0.515, p=0.609]. Each target object was shown once during scanning, resulting in a total of 120 trials during the entire scan. The presentation order was again randomised across participants.

3.2.2. MEG Data Acquisition and Analyses. Neuromagnetic data were recorded at a 600 Hz sampling rate with a bandwidth of 0–150 Hz using a CTF 275 MEG system (VSM MedTech Ltd., Canada) composed of a whole-head array of 275 radial 1st order gradiometer channels housed in a magnetically shielded room (Vacuumschmelze, Germany). Synthetic 3rd gradient balancing was used to remove background noise online. Fiducial coils were placed on the nasion, left preauricular, and right preauricular sites of each participant. These coils were energised before each run to localise the participant's head with respect to the MEG sensors. Total head displacement was measured after each run and could not exceed 5 mm for inclusion in the source analysis. Prior to scanning, participants' head shapes and the location of fiducial coils were digitised using a Polhemus Isotrak 3D digitiser (Kaiser Aerospace Inc.). These were then coregistered to high-resolution T1-weighted anatomical images for each participant acquired with a 3-Tesla whole-body scanner (3T Trio, Siemens Medical Systems) using in-house coregistration software.

Data for each participant were edited and filtered to remove environmental and physiological artefacts. A beamforming technique was used to assess sources of early, category-specific differences in processing living and nonliving objects. Synthetic Aperture Magnetometry (SAM), an adaptive beamformer technique, was used to produce 3-dimensional images of cortical power changes. For each study, a wide-band (1-80 Hz) SAM analysis

TABLE 5. Living and Nonliving Object Exemplars from Study 3.

LIVING	NONLIVING
Antelope	Blender
Bear	Bowl
Buffalo	Chisel
Bull	Crowbar
Camel	Cup
Cat	Dishwasher
Cow	Drill
Deer	Fork
Dog	Hammer
Donkey	Knife
Elephant	Ladle
Fox	Level
Giraffe	Mixer
Goat	Nails
Hippo	Pan
Horse	Pencil
Leopard	Plate
Lion	Pliers
Monkey	Pot
Moose	Rolling pin
Mouse	Ruler
Penguin	Saw
Rabbit	Screwdriver
Raccoon	Spatula
Rhino	Spoon
Sheep	Square
Squirrel	Stove
Tiger	Sieve
Wolf	Toaster
Zebra	Wrench

was computed using a 100 ms window surrounding the M170 (120-220 ms) for living ('active') compared to nonliving ('control') target objects. This technique was used because it provided a good approximation of an ERP-style technique, centred on the N1. Spectral power changes between the 'active' and 'passive' periods were calculated as a pseudo t-statistic (Vrba & Robinson, 2001). Each participant's data were then normalised and

converted to Talairach space using statistical parametric mapping (SPM99, Wellcome Department of Imaging Neuroscience, London, UK, http://www.fil.ion.ucl.ac.uk/spm) for group-level comparisons.

For group-level analyses, we utilised peakomatic to assess the distribution of image peaks across our participants. We tested a range of P values from 2 to 40 and after multiple comparisons correction were left with a number of significant clusters of positive and negative peaks. The remaining volumes decreased in size spatially as P increased, so if a region was identified as showing a significant difference across a range of P values, we chose the region for reporting purposes that yielded the largest N. In cases where several P values yielded the same N, we then chose the volume that had the smallest spatial extent.

Virtual electrodes were constructed at the peak locations identified for each participant in the peakomatic analysis for the region in left occipito-temporal cortex for each of the three studies. These virtual electrodes were based on a covariance matrix constructed using a 1 second window from 500 ms prior to target picture onset, to 500 ms after the target object, using a wide band (1-80 Hz). Time-frequency plots were then computed on the virtual electrodes using the Stockwell Transform (Stockwell, Mansinha, & Lowe, 1996) for a window beginning 100 ms prior to 500 ms after target picture onset. Power change from baseline (the 500 ms preceding target object onset) was computed at each frequency from 0-60 Hz for both living and nonliving target objects to assess mean (across epochs and participants) power increases and decreases for living and nonliving target objects. In addition, living and nonliving target objects were directly contrasted at each region of interest for a window from 100 ms prior to 500 ms after target object onset across each group of participants, thresholded at $p<0.01$ uncorrected.

3.3. Results

3.3.1. Study 1.

3.3.1.1. *Behavioural Findings.* Behaviourally, we found no difference in performance between living and nonliving objects. Both reaction time [t(9)=-0.055] and accuracy rates [t(9)=0.318] were not significantly different for living (mean=715 ms, SD=99 ms; accuracy=72.9/78, 93.5%, SD=2.5) and nonliving (mean=717 ms, SD=115 ms; accuracy=72.5/78, 92.9%, SD=2.2) target objects.

3.3.1.2. *Source-Level Findings.* We used SAM to identify sources of differential activity between living and nonliving objects during the 100 ms window surrounding the M170, using a wide frequency band (1-80 Hz). We then used peakomatic to define significantly clustered peaks across our group of participants. We found five distinct regions showing significant differences between living and nonliving objects (see Table 3). These included 2 regions showing significantly greater power for living objects and 3 regions showing significantly greater power for nonliving objects during this 100 ms time window.

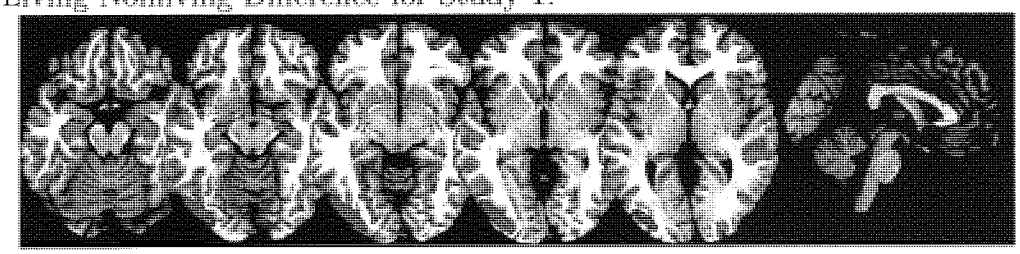
The analysis of positive peaks using peakomatic identified a region in left occipito-temporal cortex (inferior occipital gyrus) showing greater power for living than nonliving objects (see Figure 3.3.1). Using the top 8 positive peaks in each image, 7 of our 10 participants were found to have a peak falling within the region (maximum radius=22.3 mm, mean value=1.84). In addition to this region, when using the top 15 positive peaks

TABLE 6. Regions Showing Significant Differences Between Living and Nonliving Objects from Study 1.

Location	N	P	Coordinates of Centre (x, y, z) [MNI]	Volume (mm^3)	Max Radius (mm)	Absolute Mean Value	Sign
Left Inferior Occipital Gyrus	7	8	-40.2, -81.0, -6.9	4,147	22.3	1.84	p
Right Superior Temporal Gyrus	6	15	49.0, 5.0, -13.5	1,608	12.4	1.70	p
Right Inferior Parietal Lobule	10	9	51.2, -30.1, 27.0	36,945	30.4	1.69	n
Left Occipito-Parietal Cortex	8	3	-19.1, -65.3, 20.0	85,552	46.0	2.12	n
Left Frontal Cortex	6	3	-34.1, 12.0, 20.9	56,414	37.0	2.34	n

All regions identified as showing a significant group-level difference between living and nonliving objects during the 100 ms window surrounding the M170. N=number of participants (out of 10) identified as having a peak within the volume. P=number of peaks used to identify the region. The sign column indicates the peak polarity: p=positive, n=negative. Positive values identify those regions showing significantly greater power for living objects, and negative values are those showing significantly greater power for nonliving objects.

FIGURE 3.3.1. Region in Left Occipito-Temporal Cortex Showing an Early Living-Nonliving Difference for Study 1.

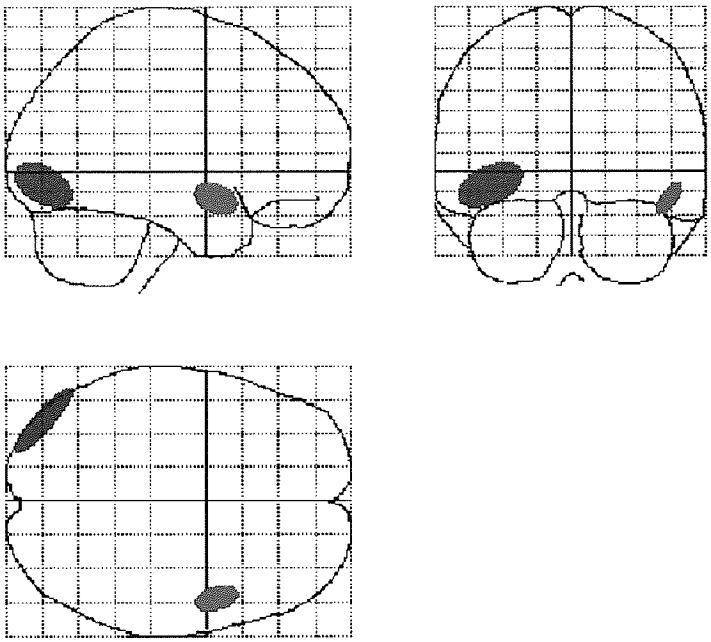


Inferior to superior axial slices through the region in left occipito-temporal cortex identified as showing a significant group effect in the wide-band (1-80 Hz) SAM comparison of living to nonliving target objects (Talairach coordinates of centre= -40, -81, -7). This volume was identified with P set to the top 8 positive peaks for each participant; 7 participants had a peak falling within this region (maximum radius=22.3 mm).

in each image (i.e., a less stringent magnitude criterion), 6 of our 10 participants were found to have a peak falling within a region in right superior temporal gyrus (maximum radius=12.4 mm, mean value=1.7) (see Figure 3.3.2).

The analysis of negative peaks using peakomatic identified three separate regions showing greater power for nonliving objects, although these regions were more spatially extensive than those identified for living objects, with the smallest region having a maximum radius of 30.4 mm (see Figure 3.3.3). Of these regions, two were found to have clusters of peaks closer than one would expect by chance when considering only the top 3 negative

FIGURE 3.3.2. Regions Identified by Peakomatic as Showing Greater Power for Living Objects in Study 1.



The two regions identified by peakomatic as showing significantly greater power for living compared with nonliving objects. Blue=Inferior Occipital Gyrus; Red=Superior Temporal Gyrus.

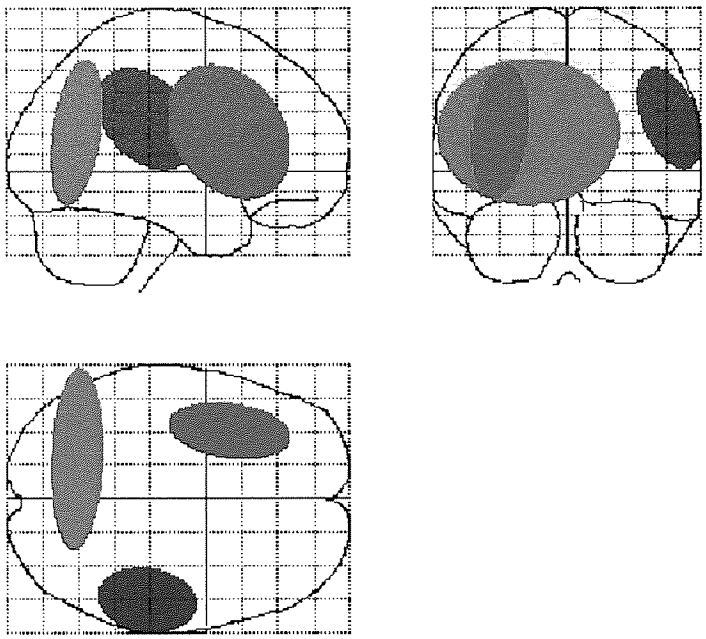
image peaks. Given the spatial extent of both of these regions (maximum radius of the smallest region=37 mm), it seems plausible that there might, in fact, be different anatomical regions being identified across the group of participants. Thus one methodological consideration for the peakomatic analysis might be to begin with a larger P (such as 5) so as to rule out significant clusters which have little anatomical consistency. Using this criterion, the only remaining area showing significantly greater power for nonliving objects is a region in right inferior parietal lobule (maximum radius=30.4 mm, mean value=1.69). Interestingly, all of our participants had a peak at this location when using the top 9 negative peaks in each image.

3.3.1.3. *Time-Frequency Findings.* We constructed virtual electrodes to map the time-frequency characteristics of the region in left occipito-temporal cortex for the subgroup of 7 participants identified in the peakomatic analysis. Group-level time-frequency findings from this region showed that this category-specific effect is due to greater low-frequency (approximately 10-20 Hz) power for living compared with nonliving objects at this location in the brain (see Figure 3.3.4). This early domain-level difference peaked at roughly 160-180 ms after onset of the target object across our group of participants.

3.3.2. Study 2.

3.3.2.1. *Behavioural Findings.* Behaviourally, we found a significant advantage for living things (mean=842.8 ms, SD=208.8 ms) compared with nonliving things (mean=919.9 ms, SD=227.5 ms) [$F(1, 8)=14.882$, $p<0.01$]. In addition, we found a significant advantage for categorising objects at the basic level (mean=801.4 ms, SD=198.6 ms) compared

FIGURE 3.3.3. Regions Identified by Peakomatic as Showing Greater Power for Nonliving Objects in Study 1.



The three regions identified by peakomatic as showing significantly greater power for nonliving compared with living objects. Blue=Inferior Parietal Lobule; Red=Frontal Cortex; Green=Occipito-Parietal Cortex.

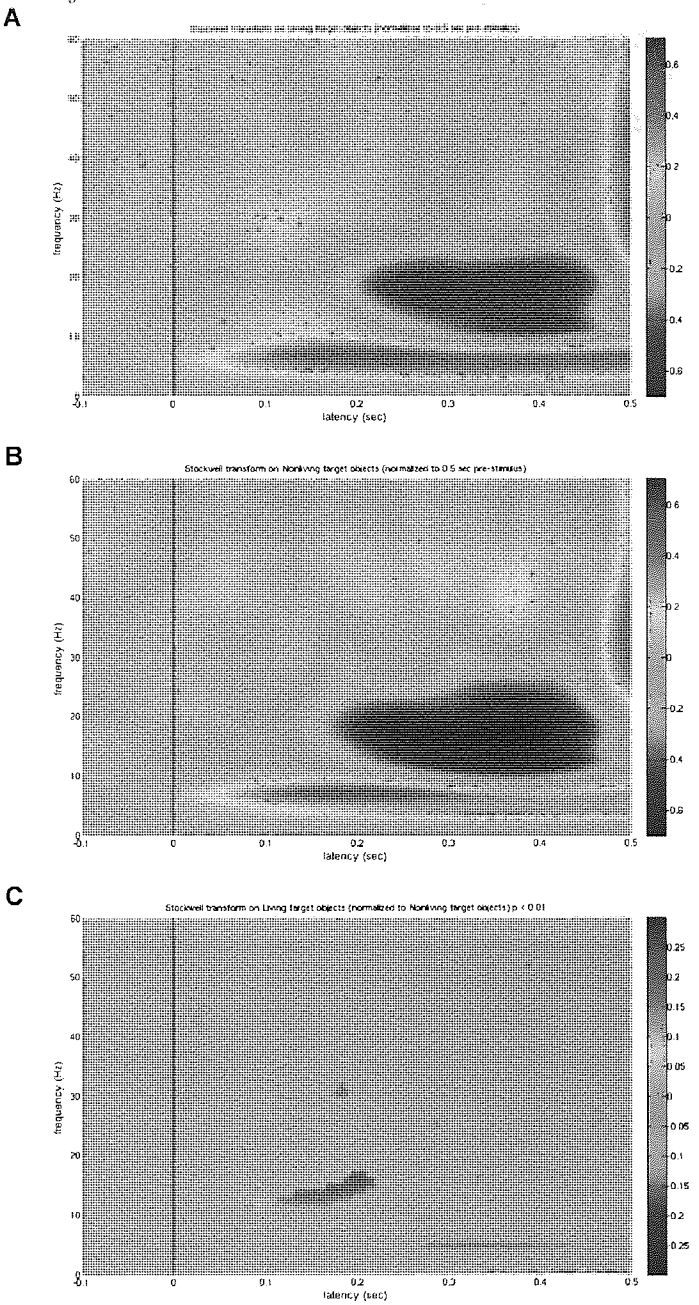
with the domain level (mean=961.3 ms, SD=238.2 ms). More importantly, we found an interaction between category and level of processing [$F(1, 8)=15.916$, $p<0.01$]. This effect seems to be driven by faster reaction times when categorising living things at the domain level compared with nonliving things (see Figure 3.3.5). This pattern was not observed in accuracy scores, as we found no difference in accuracy rates for living (accuracy=106.6/120, 88.8%, SD=8.4) and nonliving (accuracy=105.3/120, 87.8%, SD=5.9) target objects [$F(1,8)=0.191$, $p=0.674$].

3.3.2.2. *Source-Level Findings.* Again, we used SAM to identify sources of differential activity between living and nonliving objects during the 100 ms window surrounding the M170, using a wide frequency band (1-80 Hz). We then used peakomatic to define significantly clustered peaks across our group of participants. We found four distinct regions showing significant differences between living and nonliving objects (see Table 7). These included a single region showing greater power for living objects and 3 regions showing significantly greater power for nonliving objects during this 100 ms time window.

The analysis of positive peaks using peakomatic identified a single region showing significantly greater power for living compared with nonliving objects. This was a region in left occipito-temporal cortex (middle occipital gyrus) (see Figure 3.3.6). Using the top 28 positive peaks in each image, all 9 of our participants were found to have a peak falling within the region (maximum radius=18.7 mm, mean value=1.21).

The analysis of negative peaks using peakomatic identified three separate regions showing greater power for nonliving objects (see Figure 3.3.7). These included a region in left

FIGURE 3.3.4. Time-Frequency Findings from Left Occipito-Temporal Cortex for Study 1.



Time-frequency findings in left occipito-temporal cortex for the group of 7 participants identified in study 1 as showing greater power for living compared to nonliving objects. Target object onset is denoted by the solid line. A=Living objects compared to baseline; B=Nonliving objects compared to baseline; C=Direct comparison of living to nonliving objects thresholded at $p<0.01$. Note the region in C (approximately 10-20 Hz) showing increased power for living compared to nonliving objects, peaking at roughly 160-180 ms after an object is shown.

inferior parietal lobule identified using the top 5 negative peaks in each image; 7 participants were found to have a peak in this region (maximum radius=25.9 mm, mean value=1.89). In addition, 6 participants were found to have a peak in right middle to inferior frontal gyrus when using the top 5 negative peaks in each image (maximum radius=28.8 mm, mean value=1.77). Finally, a region in right superior temporal gyrus was found to have a peak in 6 participants when using the top 16 negative peaks within each image (maximum radius=15.1 mm, mean value=1.78).

FIGURE 3.3.5. Study 2: Participants' Performance During MEG Scanning

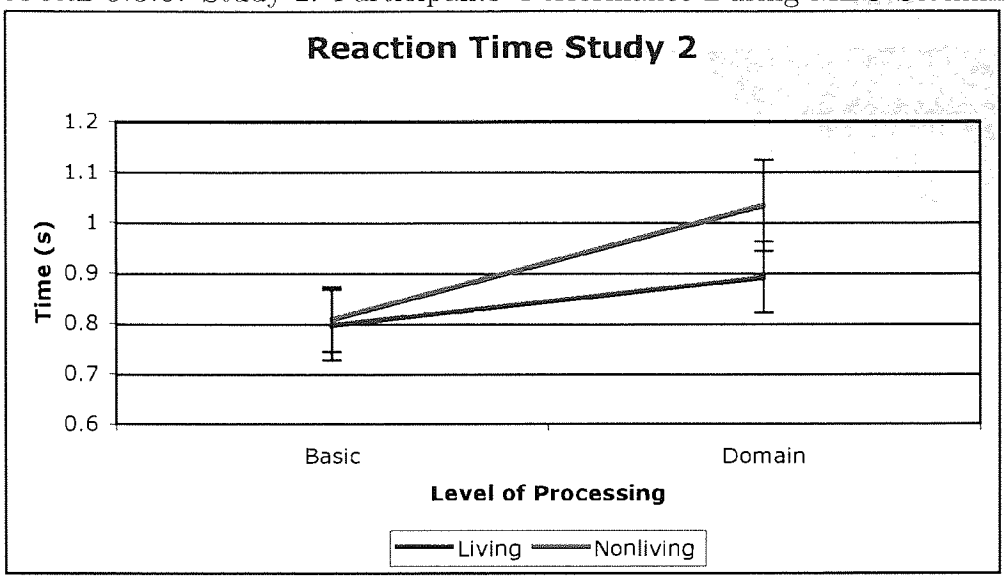


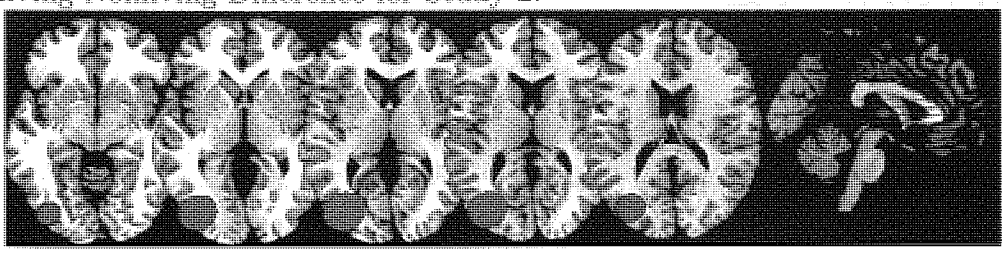
TABLE 7. Regions Showing Significant Differences Between Living and Nonliving Objects from Study 2.

Location	N	P	Coordinates of Centre (x, y, z) [MNI]	Volume (mm^3)	Max Radius (mm)	Absolute Mean Value	Sign
Left Middle Occipital Gyrus	9	28	-35.7, -79.0, 6.3	16,235	18.7	1.21	p
Left Inferior Parietal Lobule	7	5	-40.2, -35.6 42.0	22,019	25.9	1.89	n
Right Middle to Inferior Frontal Gyrus	6	5	37.5, 44.20, 5.0	33,719	28.8	1.77	n
Right Superior Temporal Gyrus	6	16	52.5, -42.0, 9.5	7,890	13.1	1.78	n

All regions identified as showing a significant group-level difference between living and nonliving objects during the 100 ms window surrounding the M170. N=number of participants (out of 9) identified as having a peak within the volume. P=number of peaks used to identify the region. The sign column indicates the peak polarity; p=positive, n=negative. Positive values identify those regions showing significantly greater power for living objects, and negative values are those showing significantly greater power for nonliving objects.

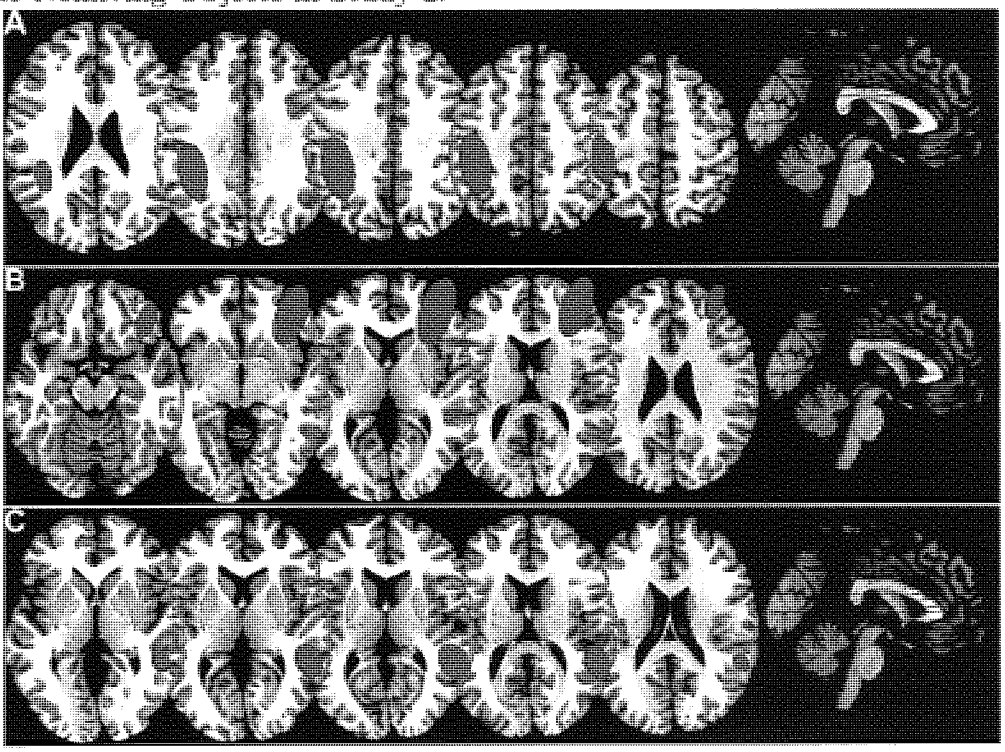
3.3.2.3. *Time-Frequency Findings.* We constructed virtual electrodes to map the time-frequency characteristics of the region in left occipito-temporal cortex for all 9 participants. Group-level time-frequency findings from this region showed that this category-specific effect is due to greater low frequency (approximately 10-20 Hz) power for living compared with nonliving objects at this location in the brain (see Figure 3.3.8). This early domain-level difference peaked at roughly 160-180 ms after onset of the target objects across our group of participants.

FIGURE 3.3.6. Region in Left Occipito-Temporal Cortex Showing an Early Living-Nonliving Difference for Study 2.



Inferior to superior axial slices through the region in left occipito-temporal cortex identified as showing a significant group effect in the wide band (1-80 Hz) SAM comparison of living to nonliving target objects (Talairach coordinates of centre= -36, -79, 6). This volume was identified with P set to the top 28 positive peaks for each participant; all 9 participants had a peak falling within this region (maximum radius=18.7 mm).

FIGURE 3.3.7. Regions Identified by Peakomatic as Showing Greater Power for Nonliving Objects in Study 2.



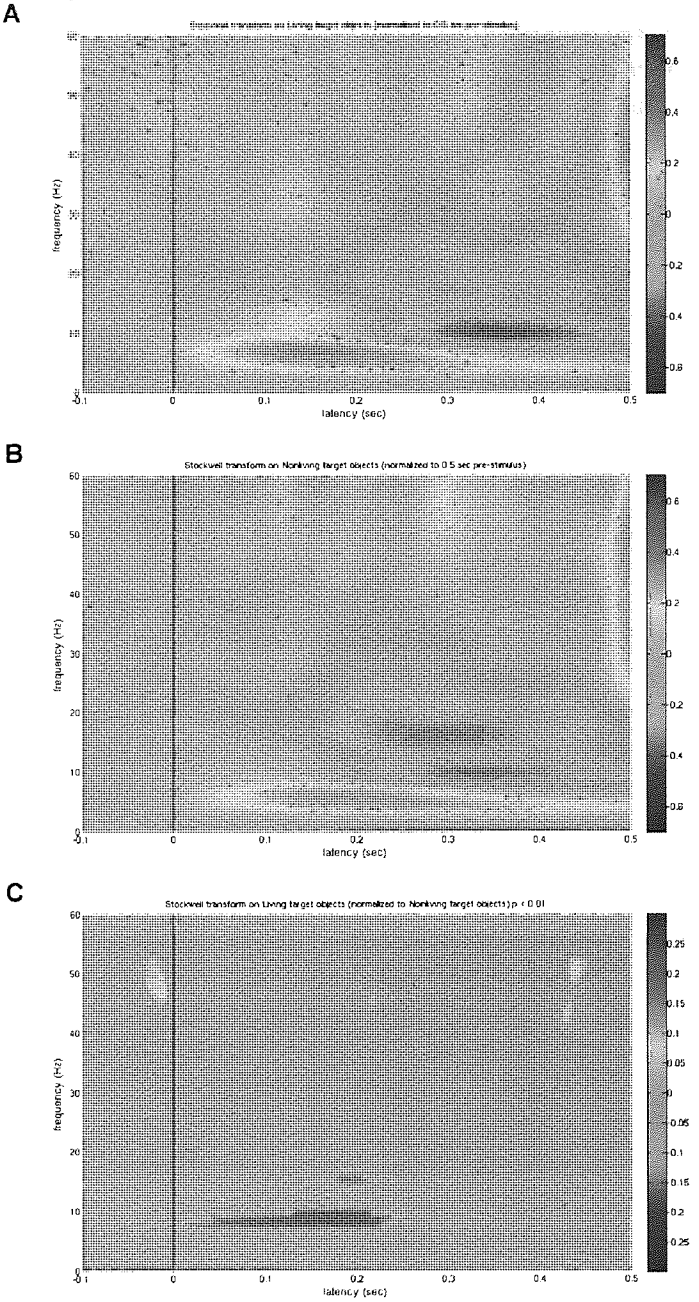
The three regions identified by peakomatic as showing significantly greater power for nonliving compared with living objects. A) Left inferior parietal lobule; B) Right middle to inferior frontal gyrus; C) Right superior temporal gyrus.

3.3.3. Study 3.

3.3.3.1. *Behavioural Findings.* Behaviourally, we found no difference in performance between living and nonliving objects. Both reaction time [t(9)=0.929] and accuracy rates [t(9)=-2.002] were not significantly different for living (mean=778 ms, SD=206 ms; accuracy=57.5/60, 95.8%, SD=1.8) and nonliving (mean=798 ms, SD=194 ms; accuracy=56/60, 93.3%, SD=2.2) target objects.

3.3.3.2. *Source-Level Findings.* We again used SAM to identify sources of differential activity between living and nonliving objects during the 100 ms window surrounding the M170, using a wide frequency band (1-80 Hz). We then used peakomatic to define

FIGURE 3.3.8. Time-Frequency Findings from Left Occipito-Temporal Cortex for Study 2.



Time-frequency findings in left occipito-temporal cortex for all 9 participants identified in study 2 as showing greater power for living compared to nonliving objects. Target object onset is denoted by the solid line. A=Living objects compared to baseline; B=Nonliving objects compared to baseline; C=Direct comparison of living to nonliving objects thresholded at $p<0.01$. Note the region in C (approximately 10 Hz) showing increased power for living compared to nonliving objects, peaking at roughly 150 ms after an object is shown.

significantly clustered peaks across our group of participants. We found four distinct regions showing significant differences between living and nonliving objects (see Table 8). These included 3 regions showing significantly greater power for living objects and 1 region showing significantly greater power for nonliving objects during this 100 ms time window.

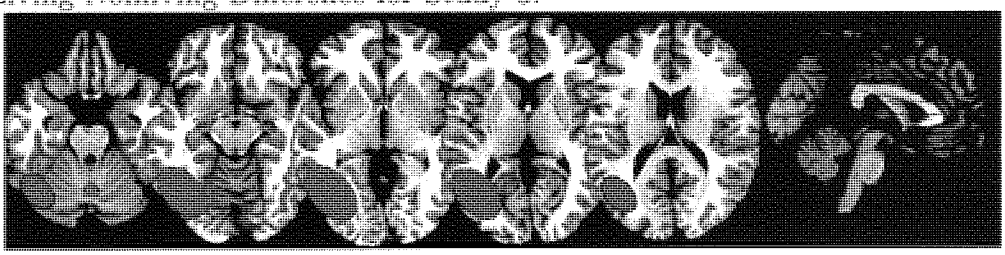
The analysis of positive peaks using peakomatic identified a region in left occipito-temporal cortex showing greater power for living than nonliving objects (see Figure 3.3.9).

TABLE 8. Regions Showing Significant Differences Between Living and Nonliving Objects from Study 3.

Location	N	P	Coordinates of Centre (x, y, z) [MNI]	Volume (mm^3)	Max Radius (mm)	Absolute Mean Value	Sign
Left Occipito-Temporal Cortex	8	8	-41.3, -63.4, -2.3	43,139	26.5	2.00	p
Right Cuneus	9	17	16.0, -85.3, 4.7	16,882	19.6	1.82	p
Left Postcentral Gyrus	6	8	-41.5, -30.5, 38.0	10,908	19.6	1.91	p
Right Occipital Cortex	8	3	18.8, -66.8, 19.1	183,141	47.7	1.88	n

All regions identified as showing a significant group-level difference between living and nonliving objects during the 100 ms window surrounding the M170. N=number of participants (out of 10) identified as having a peak within the volume; P=number of peaks used to identify the region. The sign column indicates the peak polarity; p=positive, n=negative. Positive values identify those regions showing significantly greater power for living objects, and negative values are those showing significantly greater power for nonliving objects.

FIGURE 3.3.9. Region in Left Occipito-Temporal Cortex Showing an Early Living-Nonliving Difference for Study 3.

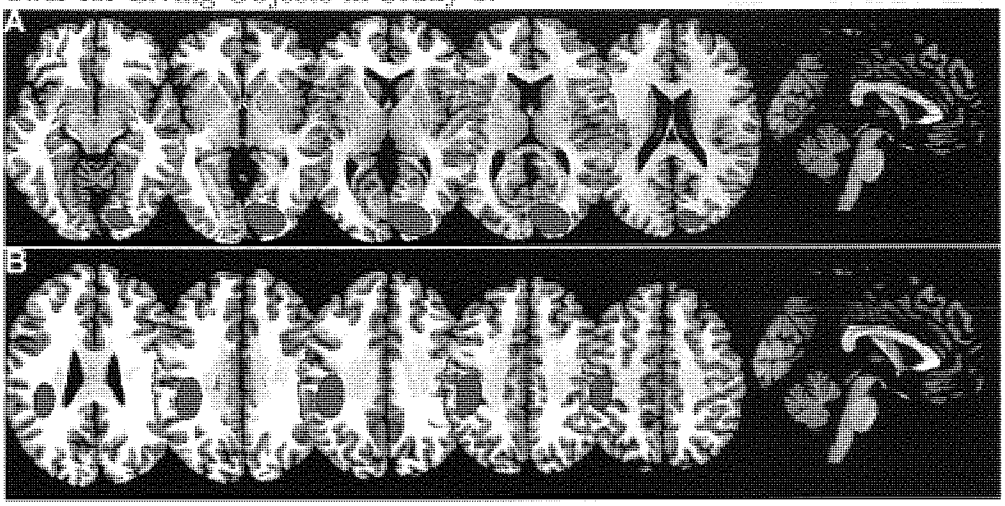


Inferior to superior axial slices through the region in left occipito-temporal cortex identified as showing a significant group effect in the wide band (1-80 Hz) SAM comparison of living to nonliving target objects (Talairach coordinates of centre= -41, -63, -2). This volume was identified with P set to the top 8 positive peaks for each participant; 8 participants had a peak falling within the region (maximum radius=26.5 mm).

Using the top 8 positive peaks in each image, 8 of our 10 subjects were found to have a peak falling within the region (maximum radius=30.3 mm, mean value=2.10). In addition to this region, when using the top 17 positive peaks in each image, 9 of our 10 participants were found to have a peak falling within a region in right cuneus (maximum radius=19.6 mm, mean value=1.82) (see Figure 3.3.10). Finally, there was also a region in left postcentral gyrus having a peak for 6 of our subjects when using the top 8 positive peaks in each image (maximum radius=19.6 mm, mean value=1.91).

The analysis of negative peaks using peakomatic identified a single region in right occipital cortex showing greater power for nonliving than living objects (see Figure 3.3.11). Using the top 3 negative peaks within each image, 8 of our 10 subjects were found to have a peak falling within the region (maximum radius=47.7 mm, mean value=1.88). Given

FIGURE 3.3.10. Regions Identified by Peakomatic as Showing Greater Power for Living Objects in Study 3.



The two additional regions identified by peakomatic as showing significantly greater power for living compared with nonliving objects. A) Right cuneus; B) Left postcentral gyrus.

FIGURE 3.3.11. Regions Identified by Peakomatic as Showing Greater Power for Nonliving Objects in Study 3.

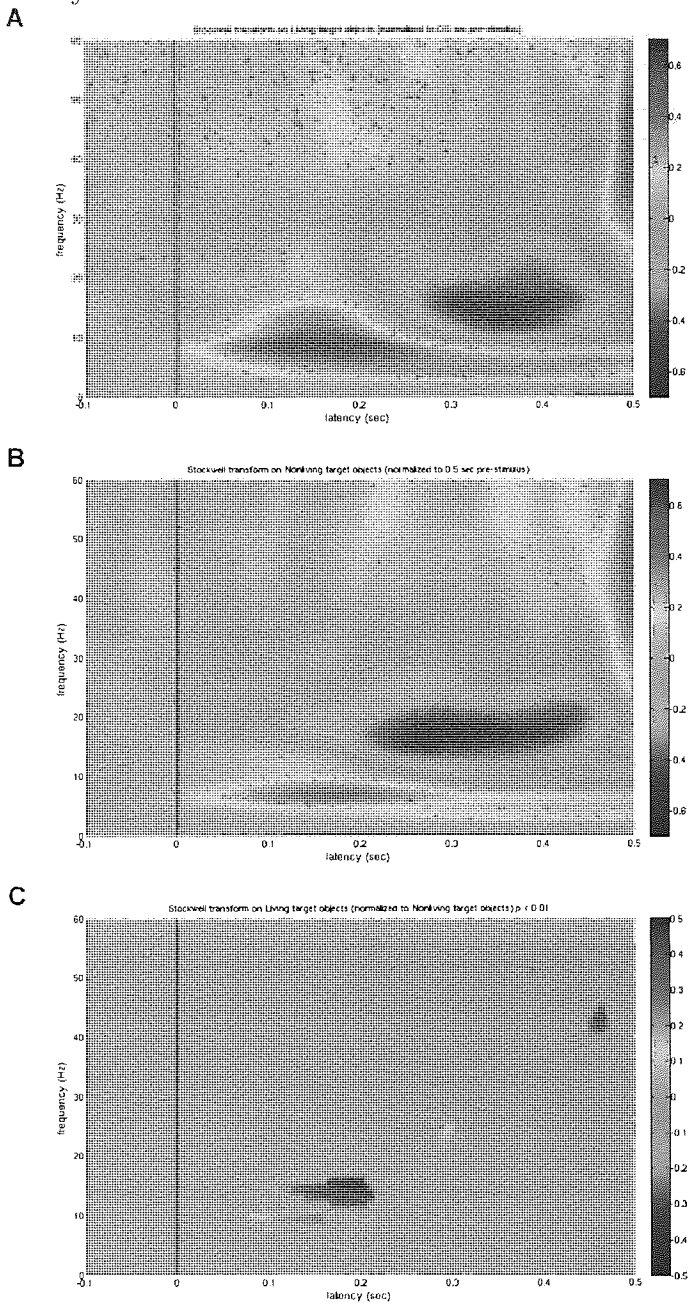
The region identified by peakomatic as showing significantly greater power for nonliving compared with living objects in right occipital cortex.

the spatial extent of this region, it seems again plausible that there might be different anatomical regions being identified across the group of participants. Thus, again, it would be advantageous to consider a larger P value so as to rule out significant clusters which have little anatomical consistency. This criterion would eliminate this region, and thus no meaningful clusters were identified when looking at negative peaks within each image.

3.3.3.3. *Time-Frequency Findings.* We constructed virtual electrodes to map the time-frequency characteristics of the region in left occipito-temporal cortex for the subgroup of 8 participants identified in the peakomatic analysis. Group-level time-frequency findings from this region showed that this category-specific effect is due to greater low-frequency (approximately 10-20 Hz) power for living compared with nonliving objects at this location in the brain (see Figure 3.3.12). This early domain-level difference peaked at roughly 180 ms after onset of the target object across our group of participants.

3.3.4. Overlap in Left Occipito-Temporal Cortex. All 3 studies identified a region in left occipito-temporal cortex showing greater power for living compared to nonliving target objects, although the precise location of the volume varied across all 3 studies. To confirm that there was overlap in these volumes, we overlaid the regions onto a single template brain (see Figure 3.3.13). This figure shows a high degree of overlap between

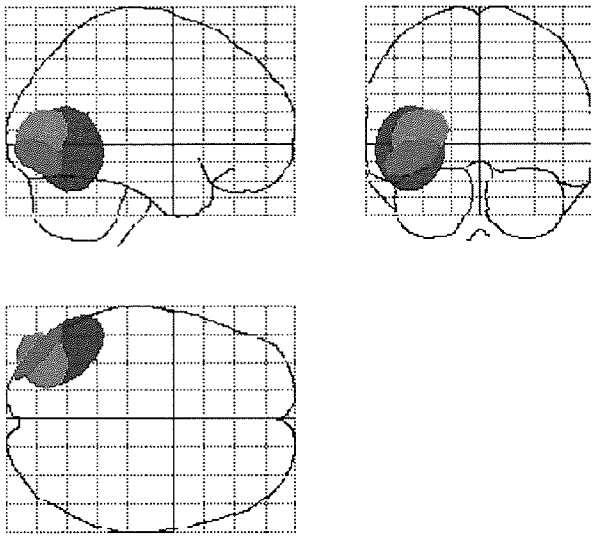
FIGURE 3.3.12. Time-Frequency Findings from Left Occipito-Temporal Cortex for Study 3.



Time-frequency findings in left occipito-temporal cortex for the group of 8 participants identified in study 3 as showing greater power for living compared to nonliving objects. Target object onset is denoted by the solid line. A=Living objects compared to baseline; B=Nonliving objects compared to baseline; C=Direct comparison of living to nonliving objects thresholded at $p<0.01$. Note the region in C (approximately 10-20 Hz) showing increased power for living compared to nonliving objects, peaking at roughly 180 ms after an object is shown.

the regions identified in each study, suggesting that we are probably localising the same region in all three studies. Importantly, there were no other regions that were consistently activated across all three studies. For example, right superior temporal gyrus showed significant differences in study 1 and 2, although this region showed greater power for living objects in study 1 and greater power for nonliving objects in study 2. In addition, inferior parietal lobule was found in studies 1 and 2, although it was in the right hemisphere in

FIGURE 3.3.13. Region in Left Occipito-Temporal Cortex Showing an Early Living-Nonliving Difference for Studies 1, 2, and 3.



The regions in left occipito-temporal cortex identified by peakomatic as showing significantly greater power for living than nonliving objects from 120-220 ms after an object is displayed for studies 1, 2, and 3. Red=Study 1; Green=Study 2; Blue=Study 3.

study 1 and the left hemisphere in study 2. Thus, this region is the only region that seems to be responding in a task-independent manner.

3.4. Discussion

We used MEG to investigate early perceptual processing differences between living and nonliving objects. Our analysis identified several regions showing significant differences between living and nonliving objects during the 100 ms window surrounding the M170 across our 3 studies. Critically, of these regions, we consistently found an early difference localised to left occipito-temporal cortex, with 7, 9, and 8 participants showing greater power for living compared to nonliving objects at this location for studies 1, 2, and 3 respectively. Given our predictions about early, perceptual differences between living and nonliving objects, and the high consistency of this region across studies, we have focused on this region in more detail in subsequent time-frequency analyses.

Our findings in left occipito-temporal cortex support previous neuroimaging studies of living and nonliving object processing that show an early, domain-level difference in posterior regions of the brain (e.g., Kiefer, 2001; Martin et al., 1996; Perani et al., 1999; VanRullen & Thorpe, 2001). Importantly, our source localisation results demonstrate that this early, domain-level difference localises to left occipito-temporal cortex, with the largest difference peaking at approximately 180 ms after an image is shown. Our time-frequency findings from this region of the brain also demonstrate that this effect is driven by low-frequency (approximately 10-20 Hz) processing differences between living

and nonliving objects. These finding are in line with previous ERP studies examining living and nonliving objects (Kiefer, 2001; VanRullen & Thorpe, 2001).

Previous research has already shown that there are differences in the importance of visual form and specific features for differentiating amongst objects. Research has shown that visual form is more critical for differentiating between living things (e.g, Farah & McClelland, 1991). For example, to differentiate a zebra and horse, one critical diagnostic feature is the presence or absence of black and white stripes. It could be the case that our differences are partially the result of the reliance on visual form to identify living things. In a PET study of category-specific effects in normal participants, Moore & Price (1999) found that a region in occipito-temporal cortex (although in right hemisphere) showed greater activation to objects having multicomponent parts, and they suggest that this region might play a role in visual configuration. They found maximum activation in this region for animals and least activation for simple man-made objects. Importantly, however, there was not greater activation in this region for animals than other multicomponent non-objects. This finding suggests this area might be responding to an object's complexity or the structure of its parts. In addition to visual form, other feature-based differences between living and nonliving things might account for this early processing difference. All our images were presented as full-colour pictures, without any manipulation of texture or form. Research has shown that colour and texture are more diagnostic for living than nonliving things (e.g., Tanaka & Presnell, 1999). Again, our difference could reflect a reliance on extracting the visual features of an object, which would result in greater perceptually-driven processing demands for living than nonliving things.

Previous research has also shown that there are differences in the relative importance of global shape and internal detail for identifying living and nonliving things (e.g., Gerlach, 2001; Lloyd-Jones & Luckhurst, 2002; Thomas et al., 2002). Importantly, global shape is more critical for differentiating living things. Gerlach et al., (2004) argued that object recognition involves both shape configuration (the binding of shape components into more elaborate descriptions) and selecting the appropriate object name from amongst competing representations in memory. Shape configuration is more important for living things because their texture, colour, and overall location of component parts are much less variable than for nonliving objects. Gerlach et al. (2006) used PET to show that shape configuration is mediated by posterior and ventral regions of the brain, including the inferior occipital gyri and the posterior portion of the fusiform gyri. More recently, Gerlach (2009) has developed a pre-semantic account of category effects (PACE) in visual object recognition. In this paper, he separated the visual object recognition process into two stages: shape configuration and selection. He argued that the first stage, binding of shape elements into shape descriptions, is easier for living objects, since their structural features are more stable and highly correlated. In contrast, the second stage, selecting amongst competing representations, is harder for living objects due to their high within-category similarity. Our superordinate categorisation task obviously demands both shape configuration and selection, but poses fairly low demands on the second process since participants are not required to select between highly similar exemplars. Gerlach argued that shape configuration is likely to be mediated by posterior and middle parts of the fusiform gyri and/or regions of peristriate cortex, to include Brodmann's area 19. More

specifically, the PACE model predicts greater activation in this region for nonliving things during tasks that tax shape configuration. We did not find these effects, perhaps because our task posed low demands on shape configuration. Instead, our findings in left occipito-temporal cortex are in line with the hypothesis that regions involved with early stages of object recognition (including shape configuration) may be activated to a greater degree for living objects since this stage is more important for their recognition. In line with this, our findings might support the accessing of shape configurations to identify the living objects.

In addition to differences in visual form, previous research has shown that there is a strong effect of similarity for living objects compared to nonliving objects (e.g., Humphreys et al., 1988; Lamberts & Shapiro, 2002; Shapiro & Olson, 2005). For example, animals all have similar features, and therefore it is harder to differentiate between members of the category. It could be the case that this region in left occipito-temporal cortex is more active for living things because of the higher visual discrimination required for living things compared to nonliving things. Support for this hypothesis comes from a PET study conducted by Rogers et al. (2005). In this study, the authors found posterior fusiform activation was greater for animals than for vehicles, but only when participants categorised pictures at intermediate levels of specificity (e.g, dog, car). They suggest that these regions are recruited when items must be discriminated from many visually-similar competitors. What is interesting is that we find this area to be activated when objects are categorised at the superordinate level, contrary to the Rogers et al. findings. In their cascade model of object recognition, Humphreys et al. (1988) proposed that, when naming items, we first access structural descriptions that describe the visual form of an object. These structural descriptions then allow access to semantic and phonological representations of objects. Competition occurs when choosing between perceptually similar structural descriptions, and this competition is greater for living objects. Humphreys & Forde (2001) went on to suggest that processing of living things also suffers at a later stage, because perceptual knowledge is more likely to require "re-activation" to resolve competition between functionally and perceptually similar representations. Since we did not compare the naming of items at different levels of specificity (basic versus superordinate versus domain), it is impossible to differentiate at what levels of specificity the posterior fusiform is recruited. It could be the case that this region is being recruited during both the accessing of structural descriptions and at a later processing stage. Perhaps, then, Rogers et al. (2005) were observing the re-activation of this region to resolve competition between perceptually similar objects, whereas our findings are more likely to reflect the initial accessing of structural descriptions. In addition, that this region is recruited in all three studies argues against similarity as the cause for this effect. For example, if similarity were causing greater activation in this region, we should find differential activation when we ask participants to name objects rather than categorise them at the superordinate or domain level. In fact, we should find that this region is recruited to a lesser degree during superordinate or domain-level categorisation if this region is responding to high similarity. However, we find this region during all three tasks, suggesting that similarity cannot account for this category-specific effect.

One area for debate is whether our findings reflect a difference in visual complexity between living and nonliving objects, as our sets of items are not balanced across domains in studies 1 and 3. In study 1, for example, behavioural pre-testing found our living stimuli were rated as slightly more visually complex than our nonliving stimuli. Higher complexity for living things has been demonstrated elsewhere (e.g., Gaffan & Heywood, 1993; Snodgrass & Vanderwart, 1980). However, complexity is unlikely to account for the pattern of results we have found, since visual complexity was balanced for living and nonliving objects in study 2. In addition, other research has found differences in left occipito-temporal cortex even for images that have no internal visual detail. For example, a PET study using silhouettes of animals and tools found greater left medial occipital activity for naming animals compared to tools (Martin et al., 1996), suggesting that the complexity of the item is not responsible for the differential activation. In addition, using fMRI, Price et al. (2003) showed category-specific effects in bilateral posterior fusiform for both pictures of animals and fruits compared with tools. The relatively simple structure of fruits would argue against visual complexity as the sole reason for enhanced activation in this region of cortex.

Since important factors such as naming speed, familiarity (studies 1, 2, and 3), typicality (studies 1 and 2), and visual complexity (study 2) have been controlled for, it seems highly plausible that this effect is the result of perceptually-driven processing differences between living and nonliving objects. It is also striking how consistent this effect is, as we have found differences in this region for two matching tasks (studies 1 and 2) and for a task involving silent-naming (study 3). Our findings suggest that activation in this region is task-independent. We therefore conclude that due to the relative importance of form (in particular, global shape, colour and texture), and the high similarity within living objects, early visual regions are recruited to a higher degree when presented with living objects compared to nonliving objects. If this is true, then patients with damage to this region should show a selective impairment for living things. Evidence for this comes from a review of patients showing greater category-specific deficits by Tranel et al. (1997). Using a lesion-overlap comparison, they found that patients showing deficits for animals had damage in a left mesial occipital region, in addition to damage in right mesial occipital/ventral temporal cortex. They suggest that these regions might play an intermediary role in object-concept retrieval, serving as regions best suited by feedforward and feedback projections to areas subtending visual perception and those that represent conceptual knowledge. In this view, the left occipito-temporal cortex region might serve as an intermediate area between early visual cortex and the conceptual representation of living objects in more anterior regions of the ventral object-processing stream.

In summary, we found early perceptually-driven processing differences between living and nonliving objects. Given that these perceptually-driven differences are consistent with increased processing demands for living compared to nonliving objects, a crucial remaining question is how this might influence later, semantic processes in more anterior regions of ventral-temporal cortex. For example, one prediction is that visual information for living objects arrives later because of the increased early processing demands. If so, this is likely to influence activity in ventral temporal cortex. Thus, differences in the way living and nonliving objects are processed in the visual object recognition system could

provide a crucial organising factor underlying the semantic system, supporting distributed accounts of conceptual knowledge.

CHAPTER 4

Exploring the Semantic Processing of Living and Nonliving Objects.

4.1. Introduction

Our first set of findings of category-specific processing showed significant differences between living and nonliving objects at an early time point, located in a posterior region of the ventral object-processing stream. These findings mirrored findings reported in the literature (e.g., Kiefer, 2001; VanRullen & Thorpe, 2001). The source location of this region was anatomically early within the ventral stream. The location and timing of these effects have led us to hypothesise that these differences reflect perceptual rather than semantic processing differences between living and nonliving objects. Thus, this category-specific difference might reflect differences in accessing the structural descriptions of living and nonliving objects, with living things requiring greater visual (perceptual) processing at this early time point. In addition to examining perceptual differences between living and nonliving objects, we also sought to examine semantic differences between living and nonliving object processing. A range of neuroimaging methods have now been used to explore category-specific differences; the majority of these studies have utilised either PET or fMRI. Given the limited temporal resolution of these methods, we speculate that many of the effects being measured by these imaging techniques reflect semantic differences between living and nonliving objects. Given the temporal benefits of MEG, in addition to reasonably good spatial resolution, we therefore set out to explore differences in the semantic processing of living compared with nonliving objects. We can utilise the temporal information provided by MEG, therefore we can more closely tie information processing to the stages of object recognition derived from the behavioural data (e.g., cascade model: Humphrey et al., 1988). We will review a number of findings from PET and fMRI studies of category-specificity, as well as their implications in terms of the major theoretical views described in the literature.

The first imaging study of category-specificity reported in the literature was by Perani et al. (1995). They utilised PET to measure changes in oxygen metabolism in the brain whilst participants performed a same-different matching task of living and nonliving objects. Stimuli included line drawings of animals and tools. When the authors contrasted living to nonliving objects, differential activation was seen in visual areas of the brain. Specifically, there was enhanced activity in both left fusiform gyrus and bilateral lingual gyri when participants matched living compared to nonliving objects, although this activation difference was only detected at a sub-threshold significance level. There were no reported regions showing the opposite pattern, that is, enhanced activity for nonliving compared to living objects. Perani et al. concluded that their study provided evidence of specialised semantic systems in the brain for identifying living and nonliving things.

A second PET study by Martin et al. (1996) also showed greater activation in the left lingual gyrus for animals relative to tools. In addition, this study identified a region in left posterior middle temporal cortex showing greater activation for tools relative to animals. These findings, and a range of others, led Martin and colleagues to propose the *sensory/motor model of semantic knowledge* (first proposed by Martin, 1998). This was the first model to describe category-specific differences in terms of the differential pattern of activation seen in the brain for each type of object. In this model, the brain is organised such that there are neural systems for processing both the perceptual and functional (i.e., motor-related) information related to an object. That is, humans learn specific sensory and motor-related properties associated with objects, and the learning of these properties are supported by distinct neural circuitry in the brain. These properties are thought to be universal, restricted in number, and accessed implicitly and automatically (in a top-down fashion) when we are presented with an object. Therefore, when we require additional information about objects in order to perform a task, our stored representations are accessed in a top-down fashion. These representations are stored in the sensory and motor systems of the brain. According to the theory, these brain systems are activated when we initially encounter and learn about objects. So, for example, information about object form and motion is processed in the visual processing system, whilst knowledge about motor properties associated with using an object reside in the motor/action-related system (Martin, 2001). Evidence for specific neural systems supporting sensory and motor processing of objects comes from a range of studies. For example, neuroimaging studies have demonstrated that living things activate the lateral portion of the fusiform gyrus, in addition to regions of the superior temporal sulcus and medial prefrontal cortex (e.g., Chao et al., 1999; Chao et al., 2002; Kanwisher, McDermott, & Chun, 1997; Martin et al., 1996; Price et al., 2003). Nonliving things, especially tools, have been found to activate regions in medial fusiform gyrus, middle temporal gyrus, intraparietal sulcus, and premotor cortex (e.g., Beauchamp & Martin, 2007; Decety et al., 1994; Grafton et al., 1996; Grafton et al., 1997; Martin et al., 2000; Rizzolatti, Fadiga, Matelli, et al., 1996b). This evidence will be reviewed in turn.

Living things in contrast to nonliving things tend to activate a network of regions in the brain. For example, Chao et al. (2002) showed that pictures of animals activated more lateral regions of the fusiform gyrus bilaterally. A similar region was identified by Kan et al. (2003) when they imaged normal participants whilst they performed a property verification task using either true (e.g., cat–whiskers) or false (e.g., mouse–stinger) trials. Importantly, during the false trials, items could either be associative (e.g., cat, litter) or unassociative (e.g., mouse–stinger). The authors hypothesised that associative false trials would require accessing semantic information about objects, whilst unassociative trials could be performed without accessing the semantic system. As predicted, Kan et al. found activation in the left fusiform gyrus only when true trials were intermixed with associated false trials, but not when they were mixed with unassociated false trials. The authors suggest that these findings lend support to the hypothesis that conceptual knowledge is organised visually and grounded in the perceptual system, a prediction of the sensory/motor model. In addition to the fusiform gyrus, Chao et al. reported that animals relative to tools activated a region in superior temporal sulcus in about half of

their participants, stronger on the right than the left (see also Kanwisher et al., 1997). A similar region has been shown to be activated when participants view faces (Kanwisher et al., 1997), human movements (Beauchamp et al., 2004; Rizzolatti, Fadiga, Gallese, et al., 1996a), and mouth and eye movements (Puce et al., 1998). Finally, studies of category-specificity have reported greater activation for living things in left inferior frontal gyrus (left ventral prefrontal cortex; Chouinard & Goodale, 2010). This region has been shown to be activated for tasks requiring selection amongst competing alternatives (Kan et al., 2006; Kan & Thompson-Schill, 2004; Thompson-Schill et al., 1997).

Nonliving things in contrast to living things also tend to activate a network of regions in the brain. For example, Chao et al. (2002) showed that pictures of tools activated more medial aspects of the fusiform gyrus bilaterally. Also, Chao et al. reported that tools relative to animals activated a region in middle temporal gyrus in most subjects, stronger on the left than right (see also Beauchamp & Martin, 2007). This same region has been shown to be activated when participants are asked to retrieve action verbs (Martin, Ungerleider, & Haxby, 2000). In addition, activation of premotor cortex for tools has been reported in a number of studies (e.g., Decety et al., 1994; Grafton et al., 1996; Grafton et al., 1997; Martin et al., 1996; Rizzolatti et al., 1996b). For example, Decety et al. (1994) reported activation in left premotor cortex when participants imagined grasping objects with their right hands (see also Grafton et al., 1996). In support of motor-related properties serving to shape category-specific representations, Mahon et al. (2007) scanned participants whilst they silently named pictures of animals, tools (e.g., hammer), arbitrary manipulable objects (defined as a manipulable object where the relationship between motor output and object use are arbitrary; e.g., book), and nonmanipulable man-made objects (e.g., fence). Using a repetition suppression (RS) paradigm, the authors found that neural specificity in left medial fusiform gyrus tracked with the motor-relevant properties of the object. That is, the largest RS effects were found for tools, followed by arbitrary manipulable and nonmanipulable objects, then animals. In fact, the only object type for which a significant RS was found in this region was for tools. This same pattern of results was found in bilateral inferior parietal sulcus. In addition, activation in left inferior parietal lobule was found only for tools, and as with the other regions, this region showed a significant RS effect for tools. A functional connectivity analysis showed that the RS for tools in the left medial fusiform gyrus predicted the RS effects for tools in both the left inferior parietal lobule and left middle temporal gyrus. In addition to the fMRI findings using normal participants, the authors explored lesion overlap patterns in 42 patients whose primary impairments involved identifying and using tools. The authors found that lesions to the left inferior parietal lobule and left middle temporal gyrus modulated any behavioural priming effects during repeated stimulus presentations. On the basis of these findings, the authors suggest that neural specificity for tools in the medial fusiform gyrus is determined by motor-relevant "similarity" metrics computed in left inferior parietal lobule and left middle temporal gyrus. Finally, a region in inferior frontal gyrus centred on the pars opercularis has also been shown to be activated more for nonliving things (e.g., Chouinard & Goodale, 2010; Kan et al., 2006).

Even with this evidence for specialised neural systems in the brain for processing living and nonliving objects, a range of other neuroimaging findings suggest these effects might

be spurious or related to other attributes of the stimuli typically used in experiments of category-specificity (e.g., differences in visual complexity between the living and nonliving stimuli; e.g., Gerlach, 2007). For example, a review of neuroimaging studies on category-specificity by Price & Friston (2002) found that the only category-specific region across 14 neuroimaging studies utilising either PET or fMRI that was consistently present was the left posterior middle temporal cortex. This region showed increased activation for tools relative to other categories of objects. However, the authors found no clear evidence across neuroimaging studies for differential activation for living objects relative to nonliving objects in the brain. A similar finding was reported by Gerlach (2007) in his review of 20 functional neuroimaging studies of category-specificity (however, see Chouinard & Goodale, 2010 for criticism of his methodology and alternative findings). Findings such as these argue against specialised semantic subsystems in the brain for processing living and nonliving objects, and rather lend support to theories which argue for a unitary semantic store that processes knowledge about all types of objects.

Neuroimaging support for a unitary semantic system comes from Tyler et al. (2003). They imaged normal participants whilst they performed a semantic categorisation task using pictures of living (animals and fruits and vegetables) and nonliving (tools and vehicles) objects. In line with previous findings, Tyler et al. found the inferior occipital gyrus was more active for animals, but not fruits and vegetables, compared with nonliving things. The authors suggested that this effect was a consequence of bottom-up visual processing of the stimuli, rather than top-down activity in order to perform the task as predicted by the sensory/motor model. Price et al. (2003) reached a similar conclusion, arguing that posterior fusiform regions (slightly anterior to the region reported by Tyler et al.) were driven by bottom-up visual input. They found that these regions showed enhanced activation for animals and fruits relative to nonliving objects only when the stimuli presented were pictures of objects. There was no category-specific activation in this region for objects presented as either written or auditory words. In addition, Price et al. found enhanced activation in a more anterior left-lateralised mid-fusiform region during the retrieval of visual information from object names. However, this region did not show category-specific effects, leading the authors to suggest that this more anterior region serves as a polymodal associative region in the brain. Similar findings were reported by Tyler et al. In addition to category-specific effects in the inferior occipital gyrus, Tyler et al. found widespread activity in a network of regions including occipital, temporal, parietal, and frontal areas, however there were no category-specific differences within this network. Thus, Tyler et al. concluded that these findings support a unitary semantic system for processing both living and nonliving objects.

An interesting recent imaging study suggests that bottom-up processing of a stimulus does not serve to organise the representations in ventral temporal cortex, contrary to the findings reported by Price et al. (2003) and Tyler et al. (2003). Mahon et al. (2009) scanned 24 participants (21 sighted; 3 congenitally blind) whilst they either viewed pictures of animals, tools, and nonmanipulable man-made objects (sighted participants) or performed a size judgement task to auditorily-presented words from the same categories of objects (both sighted and blind participants with their eyes closed). In line with previous findings using normal participants, the authors found a region in lateral fusiform

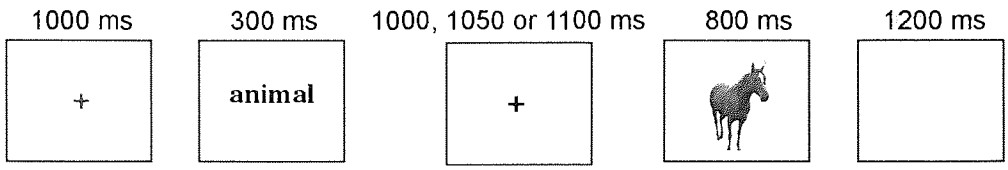
that responded more to animals, whilst a region in medial fusiform responded more to nonliving (both tools and non-manipulable man-made objects) objects. This region was anterior to the region reported by both Price et al. and Tyler et al. This differential activation occurred for both the picture naming and the size judgement task, and in both sighted and congenitally-blind participants. Thus, the authors argue that these findings are not compatible with theories that suggest visual experience serves to shape category-specific activations in the ventral stream. Rather, the authors suggest these findings are in line with a distributed domain-specific hypothesis (first proposed by Mahon & Caramazza, 2009). The distributed domain-specific hypothesis suggests that category-specific activations in the ventral stream are part of a broader network of brain regions that are innately disposed to handle information about different categories of objects.

It should be clear from this debate that no consensus has been reached as to the semantic organisation of object concepts in the brain. Specifically, contrasting evidence from neuroimaging studies both support and refute the idea that there are specialised systems in the brain for representing living and nonliving objects. In addition, it should be fairly clear that one set of findings (e.g., medial to lateral activation in fusiform gyrus for tools relative to animals) can be used to support contrasting theories about how object concepts are represented in the brain (e.g., both the sensory/motor model and distributed domain-specific theory would predict this finding). In addition, given the rather sluggish nature of the hemodynamic signal, it is hard to precisely indicate which effects are a consequence of bottom-up versus top-down processing (e.g., whether the left inferior occipital gyrus as reported by Tyler et al., 2003 for animals, or the posterior fusiform gyrus as reported by Price et al., 2003 for animals and fruits, is a consequence of bottom-up processing). Thus, given this intense debate, we sought to utilise the temporal benefits of MEG to explore semantic differences between living and nonliving objects. We predicted that if unitary distributed accounts of category-specificity are correct, we should find no differential activation for living compared with nonliving objects using a relatively long window (1 s) in which we directly contrast objects drawn from the two domains. However, if the sensory/motor model is correct, we should find differential activation in visual processing areas for living objects and motor-related areas for nonliving objects. That is, we should find greater activation for living things in lateral regions of the fusiform gyrus and superior temporal sulcus. In addition, we should find greater activation for nonliving things in medial fusiform gyrus, middle temporal gyrus, and premotor cortex. A similar pattern might exist according to the distributed domain-specific hypothesis, thus our findings cannot differentiate between these two theories of neural representations of category-specificity.

4.2. Methods

4.2.1. Study Procedures. We utilised data collected from Study 1 (see Chapter 3) for the analyses presented here. In this study, ten right-handed volunteers (Mean Age=29.4 years, range=20-36 years; 2 males) participated in the MEG study. Using an adaptation of Kiefer's design, participants were first shown a superordinate category name as a probe, followed by a target object (see Figure 4.2.1). Participants were instructed to respond by button press as quickly and accurately as possible, identifying whether

FIGURE 4.2.1. Example Trial.



Participants were shown a 1000 ms red fixation cross, followed by a 300 ms category probe. After a variable (1000, 1050, or 1100 ms) delay interval, participants were shown a target object for 800 ms. They were instructed to decide as quickly and accurately as possible if the target object was a member of the previously presented category probe by pressing a button.

the target object matched the category probe. Participants responded using a 2-button response box held in their right hand. They were instructed to respond by pressing the left button with their right index finger for "yes" (i.e., congruent trial) and the right button with their middle finger for "no" (i.e., incongruent trial).

Target objects included 78 exemplars drawn from 3 living (plants, animals, fruits and vegetables) and 3 nonliving (tools, transport, and furniture) categories. We ensured that all selected images had a pre-test naming consistency rate of greater than 65 percent. In addition, we selected stimuli that were matched on pre-test naming speed, familiarity, and typicality (see Chapter 3 for further discussion). Unfortunately, we were not able to match items of visual complexity, however the ratings were close.

Each target object was presented twice, once as a congruent trial ("yes", e.g., target dandelion preceded by a flower superordinate category label) and once as an incongruent trial. For incongruent trials, each image was associated with either a within or across-domain label. For example, a target dandelion with an animal superordinate category label would be classed as within-domain incongruent whereas a target dandelion with a tool superordinate category label would be classed as across-domain incongruent. Throughout the entire run, there were equal chances of having a within or across-domain incongruent label. Across participants, we counterbalanced whether a given item had a within or across-domain incongruent label. A total of 156 trials were shown during the scan, half of which included a living target object and the other half a nonliving target object. The order of trial presentation was randomised across participants.

4.2.2. MEG Data Acquisition and Analyses. Neuromagnetic data were recorded at 600 Hz sampling rate with a bandwidth of 0-150 Hz using a CTF 275 MEG system (VSM MedTech Ltd., Canada) composed of a whole-head array of 275 radial 1st order gradiometer channels housed in a magnetically shielded room (Vacuumschmelze, Germany). Synthetic 3rd gradient balancing was used to remove background noise online. Fiducial coils were placed on the nasion, left preauricular, and right preauricular sites of each participant. These coils were energised before each run to localise the participant's head with respect to the MEG sensors. Total head displacement was measured after each run and could not exceed 5 mm for inclusion in the source analysis. Prior to scanning, participants' head shapes and the location of fiducial coils were digitised using a Polhemus Isotrak 3D digitiser (Kaiser Aerospace Inc.). These were then coregistered to high-resolution T1-weighted anatomical images for each participant acquired

with a 3-Tesla whole-body scanner (3T Trio, Siemens Medical Systems) using in-house coregistration software.

Data for each participant were edited and filtered to remove environmental and physiological artefacts. Again, we applied a beamforming technique to assess sources of category-specific differences in processing living and nonliving objects. For these analyses, meant to assess semantic differences in processing living and nonliving objects, we utilised overlapping SAM frequency bins (1-10, 5-15, 10-20, 15-25, 20-30, 25-35, and 30-60 Hz) in which we directly contrasted living ('active') compared to nonliving ('passive') objects from target object onset to 1 second after. This analysis strategy is different from the analysis strategy utilised in Chapter 3, which was meant to assess differences in living and nonliving object-processing at an early time window based on findings reported in the literature. In the analyses described in this chapter, we were interested in later, semantic differences between living and nonliving objects, and thus we chose a long time window in specified frequency bands from which to construct our covariance matrix. As with the procedures reported in Chapter 3, spectral power changes between the 'active' and 'passive' periods were again calculated as a pseudo t-statistic (Vrba & Robinson, 2001). Each participant's data were then normalised and converted to Talairach space using statistical parametric mapping (SPM99, Wellcome Department of Imaging Neuroscience, London, UK) for group-level comparisons.

For group-level analyses, we again utilised peakomatic to assess the distribution of image peaks across our participants. We tested a range of P values from 2 to 40 and after multiple comparisons correction were left with a number of significant clusters of positive and negative peaks. As with our previous analyses, if a region was identified as showing a significant difference across a range of P values, we chose the region for reporting purposes that yielded the largest N. In cases where several P values yielded the same N, we then chose the volume that had the smallest spatial extent. In addition, because we used overlapping frequency bins, a region could be identified as showing a significant effect across a range of frequency bins. In this case, we again chose to report the region that yielded the largest N, however, we also reported the entire frequency range over which the region showed significant differences.

We again used virtual electrodes to probe the time-frequency characteristics of areas showing group-level effects in our peakomatic analyses. These virtual electrodes were based on a covariance matrix constructed using a 2 second window from 1 second prior to target picture onset, to 1 second after the target object, using a wide band (1-65 Hz). Time-frequency plots were then computed on the virtual electrodes using the Stockwell Transform (Stockwell, Mansinha, & Lowe, 1996) for a window beginning 1 second prior to 1 second after target picture onset. Percent power change from baseline (the 100 ms preceding target object onset) was computed at each frequency from 0-60 Hz for both living and nonliving target objects to assess mean (across epochs and participants) power increases and decreases for living target objects compared to baseline and nonliving target objects compared to baseline. In addition, living and nonliving target objects were directly contrasted at each region of interest across our group of participants for a window from 100 ms prior to 1 second after target object onset, thresholded at $p<0.01$ uncorrected.

4.3.1. Behavioural Findings. As mentioned previously, we found no behavioural difference in performance between living and nonliving objects (see Chapter 3). Both reaction time and accuracy rates were not significantly different for living and nonliving target objects.

4.3.2. Source-Level Findings. We used SAM to identify sources of differential activity between living and nonliving target objects during the 1 s window after target object onset. This longer window was chosen to assess semantic differences between living and nonliving object-processing. We then used peakomatic to define significantly clustered peaks across our group of participants. We found 14 distinct regions showing significant differences between living and nonliving target objects (see Table 1). These included 6 regions showing significantly greater power for living target objects and 8 regions showing significantly greater power for nonliving target objects during this 1 s window.

The analysis of positive peaks using peakomatic identified a region centred on right superior temporal gyrus showing greater power for living compared with nonliving objects (see Figure 4.3.1). Using the top 6 positive peaks in each image, all 10 of our participants were found to have a peak falling within this region (maximum radius=39.2 mm, mean value=1.25). In addition to this region, we also found a region in the right posterior inferior parietal lobe showing greater power for living compared with nonliving objects (see Figure 4.3.2). Using the top 12 peaks in each image, all 10 of our participants were found to have a peak falling within this region (maximum radius=28.7 mm, mean value=1.13). We also found a region centred on the precuneus showing greater power for living compared with nonliving objects (see Figure 4.3.3). Using the top 14 peaks in each image, all 10 of our participants were found to have a peak falling within this region (maximum radius=21.5 mm, mean value=1.06). The analysis of positive peaks also identified a region in left inferior frontal gyrus showing greater power for living compared with nonliving objects (see Figure 4.3.4). Using the top 11 positive peaks in each image, 8 of our 10 participants were found to have a peak falling within this region (maximum radius=21.0 mm, mean value=1.25). We also found a region in right inferior frontal gyrus showing greater power for living compared with nonliving objects (see Figure 4.3.5). Using the top 6 peaks in each image, 7 of our 10 participants were found to have a peak falling within this region (maximum radius=24.5 mm, mean value=1.12). In addition, we also found a region in right dorsomedial prefrontal cortex showing greater power for living compared with nonliving objects (see Figure 4.3.6). Using the top 11 peaks in each image, 7 of our 10 participants were found to have a peak falling within this region (maximum radius=18.4 mm, mean value=1.29).

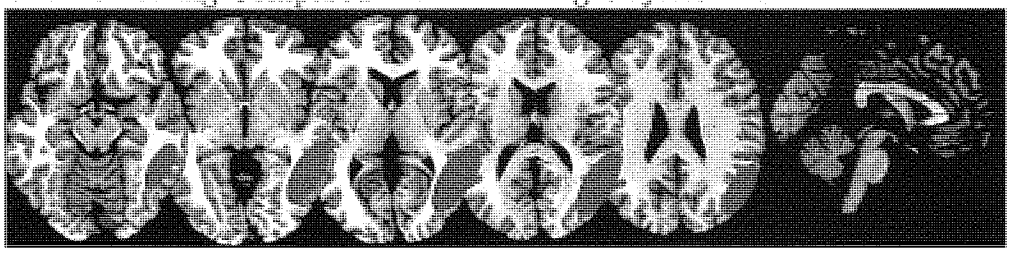
The analysis of negative peaks using peakomatic identified a region in right dorsolateral prefrontal cortex showing greater power for nonliving compared with living objects (see Figure 4.3.7). Using the top 6 positive peaks in each image, all 10 of our participants were found to have a peak falling within this region (maximum radius=34.0 mm, mean value=1.47). In addition to this region, we also found a region in right postcentral gyrus showing greater power for nonliving compared with living objects (see Figure 4.3.8). Using the top 19 peaks in each image, all 10 of our participants were found to have a peak

TABLE 1. Regions Showing Significant Differences Between Living and Nonliving Objects.

Location	N	P	Coordinates of Centre (x, y, z) [MNI]	Max Radius (mm)	Absolute Mean Value	Sign	Frequency Range (Hz)
Right Superior Temporal Gyrus	10	6	46.8, -52.5, 12.0	39.2	1.25	p	10-20
Right Posterior Inferior Parietal Lobe	10	12	36.0, -62.7, 24.6	28.7	1.13	p	15-25
Precuneus	10	14	7.8, -50.1, 48.6	21.5	1.06	p	15-25
Left Inferior Frontal Gyrus	8	11	-28.1, 34.1, 15.4	21.0	1.25	p	5-15
Right Inferior Frontal Gyrus	7	6	39.9, 27.0 9.0	24.5	1.12	p	30-60
Right Dorsomedial Prefrontal Cortex	7	11	14.6, 50.1, 15.4	18.4	1.29	p	1-10
Right Dorsolateral Prefrontal Cortex	10	6	35.7, 19.5, 30.3	34.0	1.47	n	20-30
Right Postcentral Gyrus	10	19	41.1, -28.5, 50.4	16.2	1.02	n	15-25
Left Occipito-Temporal Cortex	10	22	-21.0, -80.7, 1.5	20.6	1.05	n	20-30
Left Supramarginal Gyrus	8	7	-38.3, -53.6, 38.3	24.5	1.25	n	20-30
Right Superior Temporal Gyrus to Inferior Parietal Lobule	8	7	40.5, -22.9, 24.4	26.8	1.17	n	30-60
Right Precuneus	8	33	26.6, -77.3, 34.5	11.4	0.83	n	1-10
Left Inferior Parietal Lobule	7	6	-44.6, -33.0, 47.6	24.6	1.3	n	10-20
Left Frontal Cortex	6	16	-25.5, 29.5, 23.5	12.3	1.03	n	10-20

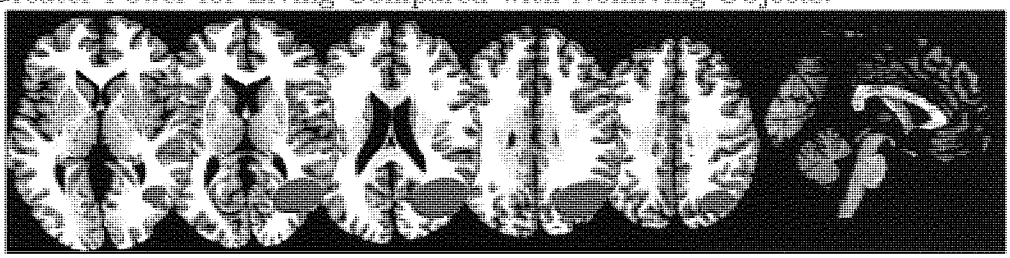
All regions identified as showing a significant group-level difference between living and nonliving objects during the 1 s window following target object onset. N=number of participants (out of 10) identified as having a peak within the volume. P=number of peaks used to identify the region. For regions identified in several of the overlapping bins, we chose the region yielding the largest N and report the associated P value. The sign column indicates the peak polarity: p=positive, n=negative. Positive values indicate those regions showing significantly greater power for living objects, and negative values indicate those showing significantly greater power for nonliving objects. Frequency range indicates the range of frequencies (in 10 Hz bins) over which each region was identified as showing a significant difference.

FIGURE 4.3.1. Region in Right Superior Temporal Gyrus Showing Greater Power for Living Compared with Nonliving Objects.



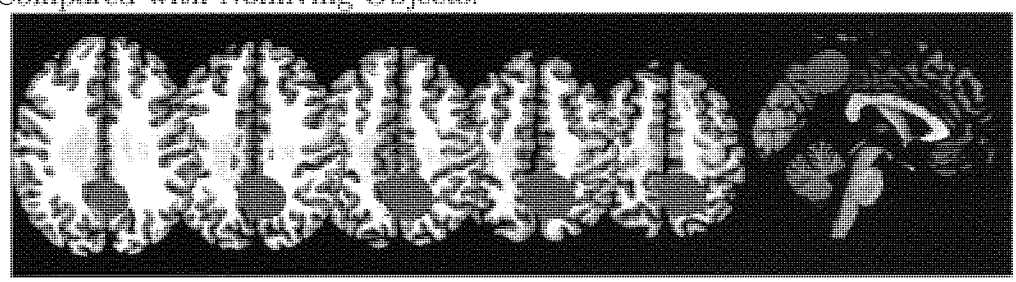
Axial slices through the region in right superior temporal gyrus identified as showing a significant group effect from 10-20 Hz in our SAM comparison of living to nonliving target objects (Talairach coordinates=46.8, -52.5, 12.0). This volume was identified with P set to the top 6 positive peaks for each participant; all 10 of our participants had a peak falling within this region (maximum radius=39.2 mm).

FIGURE 4.3.2. Region in Right Posterior Inferior Parietal Lobe Showing Greater Power for Living Compared with Nonliving Objects.



Axial slices through the region in right posterior inferior parietal lobe identified as showing a significant group effect from 15-25 Hz in our SAM comparison of living to nonliving target objects (Talairach coordinates=36.0, -62.7, 24.6). This volume was identified with P set to the top 12 positive peaks for each participant; all 10 of our participants had a peak falling within this region (maximum radius=28.7 mm).

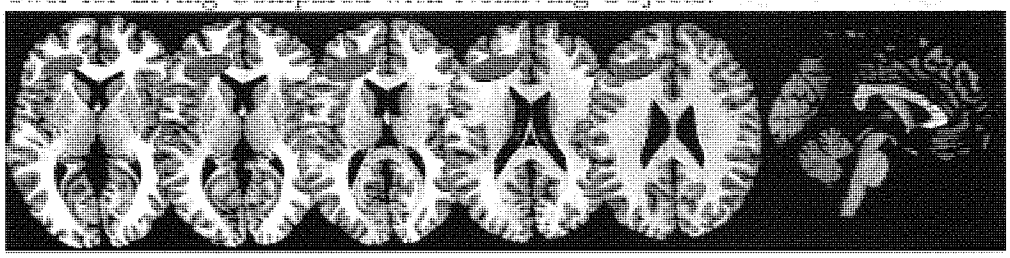
FIGURE 4.3.3. Region in Precuneus Showing Greater Power for Living Compared with Nonliving Objects.



Axial slices through the region in precuneus identified as showing a significant group effect from 15-25 Hz in our SAM comparison of living to nonliving target objects (Talairach coordinates=7.8, -50.1, 48.6). This volume was identified with P set to the top 14 positive peaks for each participant; all 10 of our participants had a peak falling within this region (maximum radius=21.5 mm).

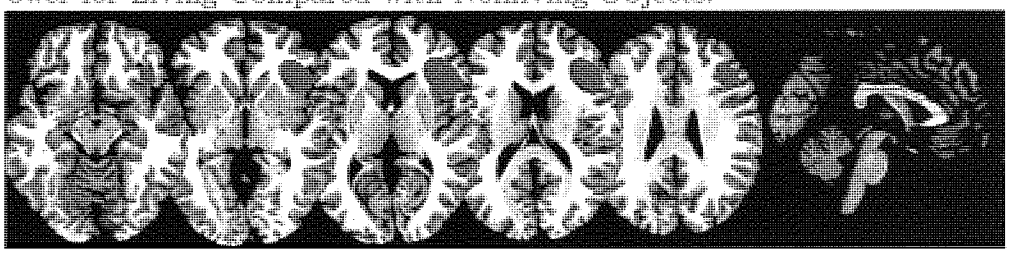
falling within this region (maximum radius=16.2 mm, mean value=1.02). We also found a region in left occipito-temporal cortex showing greater power for nonliving compared with living objects (see Figure 4.3.9). Using the top 22 peaks in each image, all 10 of our participants were found to have a peak falling within this region (maximum radius=20.6 mm, mean value=1.05). The analysis of negative peaks also identified a region in the left supramarginal gyrus showing greater power for nonliving compared with living objects (see

FIGURE 4.3.4. Region in Left Inferior Frontal Gyrus Showing Greater Power for Living Compared with Nonliving Objects.



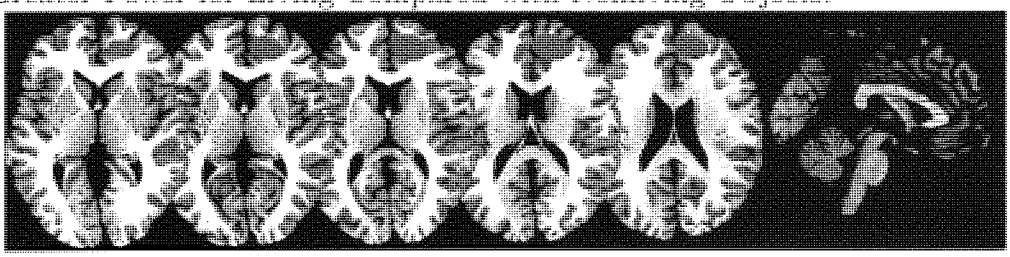
Axial slices through the region in left inferior frontal gyrus identified as showing a significant group effect from 5-15 Hz in our SAM comparison of living to nonliving target objects (Talairach coordinates= -28.1, 34.1, 15.4). This volume was identified with P set to the top 11 positive peaks for each participant; 8 of 10 participants had a peak falling within this region (maximum radius=21.0 mm).

FIGURE 4.3.5. Region in Right Inferior Frontal Gyrus Showing Greater Power for Living Compared with Nonliving Objects.



Axial slices through the region in right inferior frontal gyrus identified as showing a significant group effect from 30-60 Hz in our SAM comparison of living to nonliving target objects (Talairach coordinates=39.9, 27.0, 9.0). This volume was identified with P set to the top 6 positive peaks for each participant; 7 of 10 participants had a peak falling within this region (maximum radius=24.5 mm).

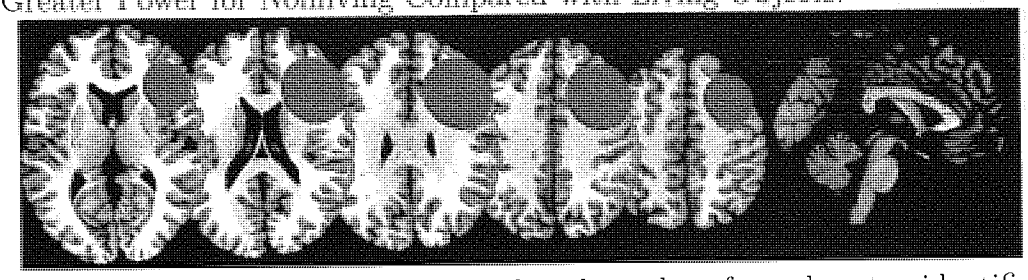
FIGURE 4.3.6. Region in Right Dorsomedial Prefrontal Cortex Showing Greater Power for Living Compared with Nonliving Objects.



Axial slices through the region in right dorsomedial prefrontal cortex identified as showing a significant group effect from 1-10 Hz in our SAM comparison of living to nonliving target objects (Talairach coordinates=14.6, 50.1, 15.4). This volume was identified with P set to the top 11 positive peaks for each participant; 7 of 10 participants had a peak falling within this region (maximum radius=18.4 mm).

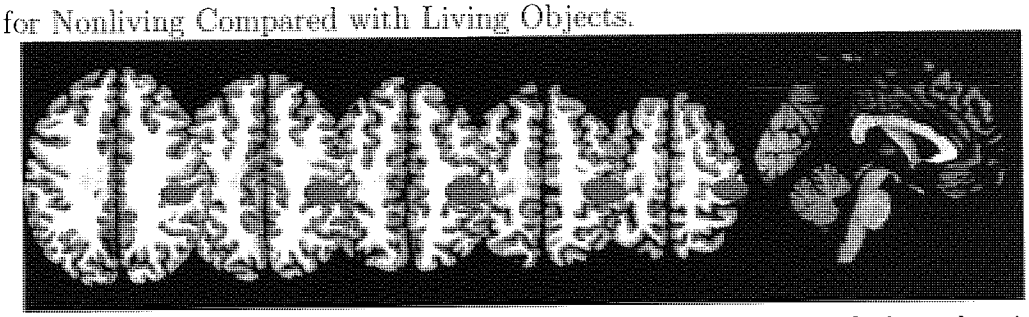
Figure 4.3.10). Using the top 7 peaks in each image, 8 of our 10 participants were found to have a peak falling within this region (maximum radius=24.5 mm, mean value=1.25). We also found a region in right superior temporal gyrus to inferior parietal lobule showing greater power for nonliving compared with living objects (see Figure 4.3.11). Using the top 7 peaks in each image, 8 of our 10 participants were found to have a peak falling within this region (maximum radius=26.8 mm, mean value=1.17). The analysis of negative peaks also identified a region in right precuneus showing greater power for nonliving compared

FIGURE 4.3.7. Region in Right Dorsolateral Prefrontal Cortex Showing Greater Power for Nonliving Compared with Living Objects.



Axial slices through the region in right dorsolateral prefrontal cortex identified as showing a significant group effect from 20-30 Hz in our SAM comparison of living to nonliving target objects (Talairach coordinates=35.7, 19.5, 30.3). This volume was identified with P set to the top 6 negative peaks for each participant; all 10 of our participants had a peak falling within this region (maximum radius=34.0 mm).

FIGURE 4.3.8. Region in Right Postcentral Gyrus Showing Greater Power for Nonliving Compared with Living Objects.

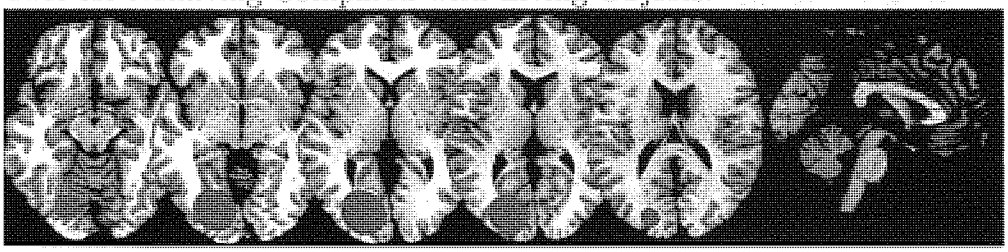


Axial slices through the region in right postcentral gyrus identified as showing a significant group effect from 15-25 Hz in our SAM comparison of living to nonliving target objects (Talairach coordinates=41.1, -28.5, 50.4). This volume was identified with P set to the top 19 negative peaks for each participant; all 10 of our participants had a peak falling within this region (maximum radius=16.2 mm).

with living objects (see Figure 4.3.12.). Using the top 33 negative peaks in each image, 8 of our 10 participants were found to have a peak falling within this region (maximum radius=11.4 mm, mean value=0.83). We also found a region in left inferior parietal lobule showing greater power for nonliving compared with living objects (see Figure 4.3.13). Using the top 6 negative peaks in each image, 7 of our 10 participants were found to have a peak falling within this region (maximum radius=24.6 mm, mean value=1.3). In addition, we found a region showing significantly greater power for nonliving compared to living objects in left frontal cortex (see Figure 4.3.14). Using the top 16 negative peaks in each image, 6 of our 10 participants were found to have a peak falling within this region (maximum radius=12.3 mm, mean value=1.03).

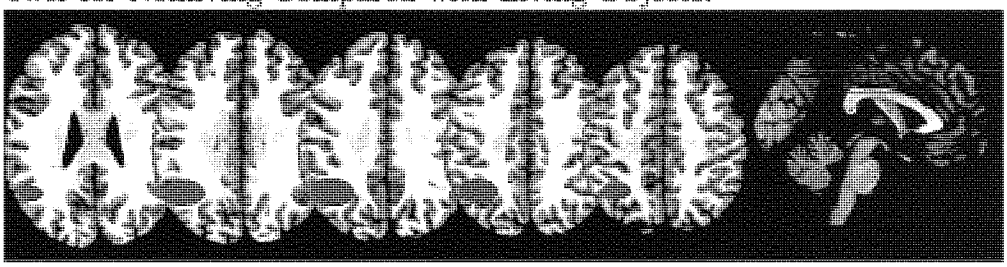
4.3.3. Time-Frequency Findings. We constructed virtual electrodes to map the time-frequency characteristics of the regions in right superior temporal gyrus, right posterior inferior parietal lobe, precuneus, and left inferior frontal gyrus for the the subgroup of participants identified as having a peak in each volume. These are regions showing greater power for living objects compared with nonliving objects. For the regions showing the opposite patter, that is greater power for nonliving compared with living objects, we constructed virtual electrodes in right dorsolateral prefrontal cortex, right postcentral gyrus, left occipito-temporal cortex, left supramarginal gyrus, right superior temporal

FIGURE 4.3.9. Region in Left Occipito-Temporal Cortex Showing Greater Power for Nonliving Compared with Living Objects.



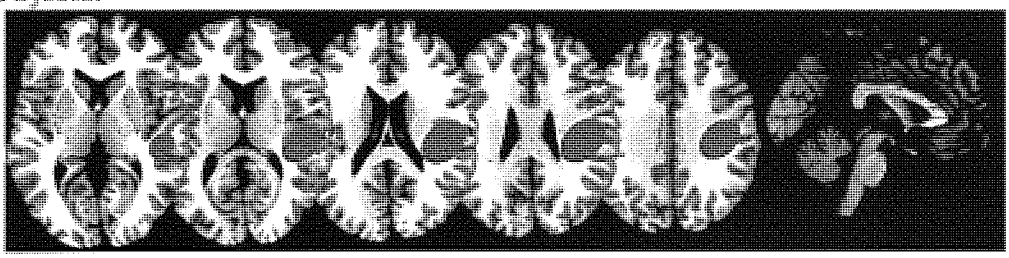
Axial slices through the region in left occipito-temporal cortex identified as showing a significant group effect from 20-30 Hz in our SAM comparison of living to nonliving target objects (Talairach coordinates= -21.0, -80.7, 1.5). This volume was identified with P set to the top 22 negative peaks for each participant; all 10 of our participants had a peak falling within this region (maximum radius=20.6 mm).

FIGURE 4.3.10. Region in Left Supramarginal Gyrus Showing Greater Power for Nonliving Compared with Living Objects.



Axial slices through the region in left supramarginal gyrus identified as showing a significant group effect from 20-30 Hz in our SAM comparison of living to nonliving target objects (Talairach coordinates= -38.3, -53.6, 38.3). This volume was identified with P set to the top 7 negative peaks for each participant; 8 of our 10 participants had a peak falling within this region (maximum radius=24.5 mm).

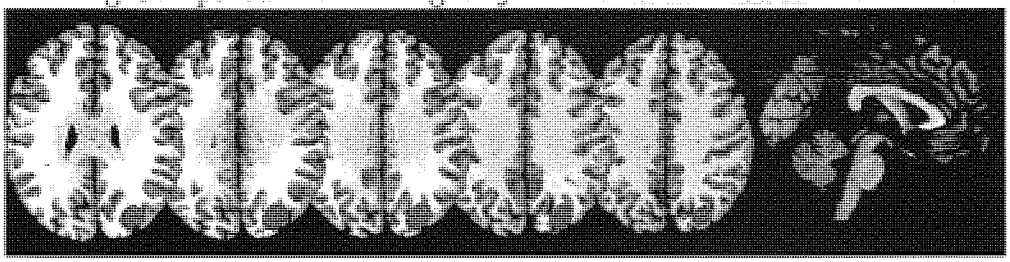
FIGURE 4.3.11. Region in Right Superior Temporal Gyrus to Inferior Parietal Lobule Showing Greater Power for Nonliving Compared with Living Objects.



Axial slices through the region in right superior temporal gyrus to inferior parietal lobule identified as showing a significant group effect from 30-60 Hz in our SAM comparison of living to nonliving target objects (Talairach coordinates= 40.5, -22.9, 24.4). This volume was identified with P set to the top 7 negative peaks for each participant; 8 of our 10 participants had a peak falling within this region (maximum radius=26.8 mm).

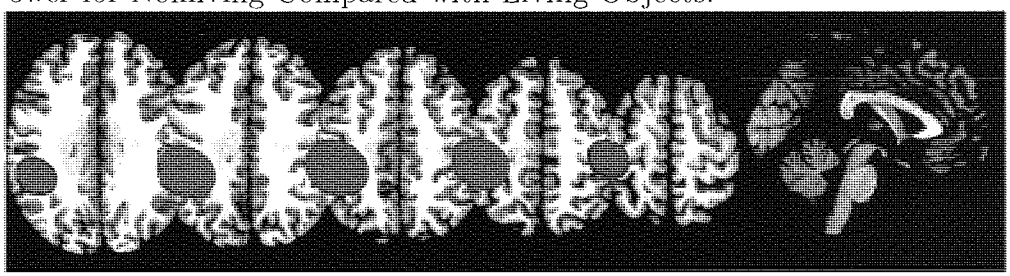
gyrus to inferior parietal lobule, and right precuneus. Again, we constructed the virtual electrodes for only those participants identified as having a peak in the volume. We chose these 10 regions to focus on for further analysis because of the large number of participants having a peak in each region (i.e., 8 and greater). Whilst this might seem arbitrary, the larger number of participants suggests that these regions show greater consistency across our group of participants.

FIGURE 4.3.12. Region in Right Precuneus Showing Greater Power for Nonliving Compared with Living Objects.



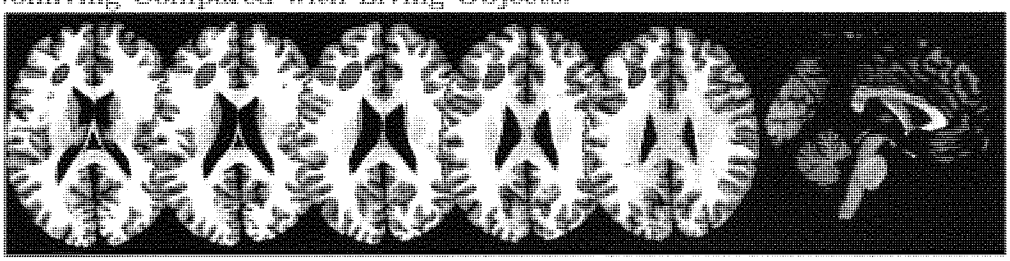
Axial slices through the region in right precuneus identified as showing a significant group effect from 1-10 Hz in our SAM comparison of living to nonliving target objects (Talairach coordinates=26.6, -77.3, 34.5). This volume was identified with P set to the top 33 negative peaks for each participant; 8 of our 10 participants had a peak falling within this region (maximum radius=11.4 mm).

FIGURE 4.3.13. Region in Left Inferior Parietal Lobule Showing Greater Power for Nonliving Compared with Living Objects.



Axial slices through the region in right inferior parietal lobule identified as showing a significant group effect from 10-20 Hz in our SAM comparison of living to nonliving target objects (Talairach coordinates= -44.6, -33.0, 47.6). This volume was identified with P set to the top 6 negative peaks for each participant; 7 of our 10 participants had a peak falling within this region (maximum radius=24.6 mm).

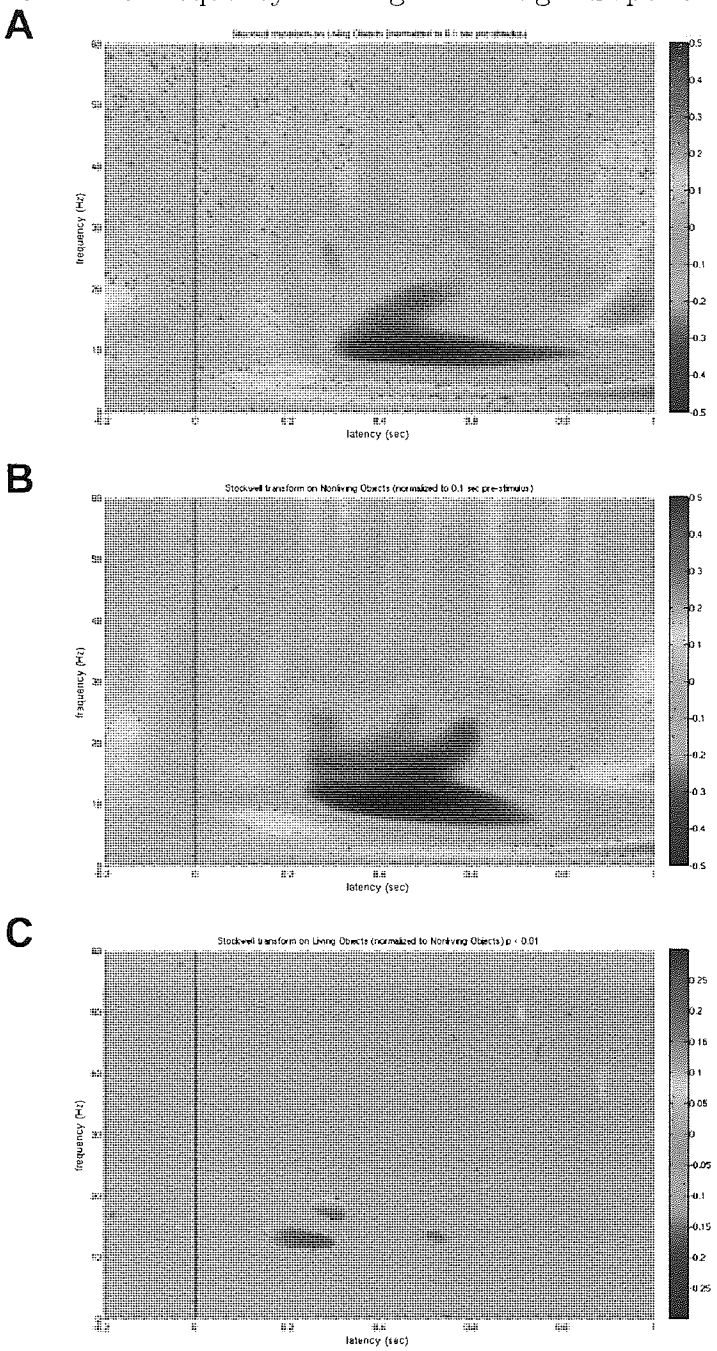
FIGURE 4.3.14. Region in Left Frontal Cortex Showing Greater Power for Nonliving Compared with Living Objects.



Axial slices through the region in left frontal cortex identified as showing a significant group effect from 10-20 Hz in our SAM comparison of living to nonliving target objects (Talairach coordinates= -25.5, 29.5, 23.5). This volume was identified with P set to the top 16 negative peaks for each participant; 6 of our 10 participants had a peak falling within this region (maximum radius=12.3 mm).

In the region in right superior temporal gyrus (see Figure 4.3.1 for source location), we found differences between living and nonliving objects beginning around 200 ms after target object onset (see Figure 4.3.15). This difference appears to be initially caused by a greater increase in power for living compared with nonliving objects. At a slightly later time (approximately 300-400 ms post target onset), this difference is a consequence of

FIGURE 4.3.15. Time-Frequency Findings from Right Superior Temporal Gyrus.

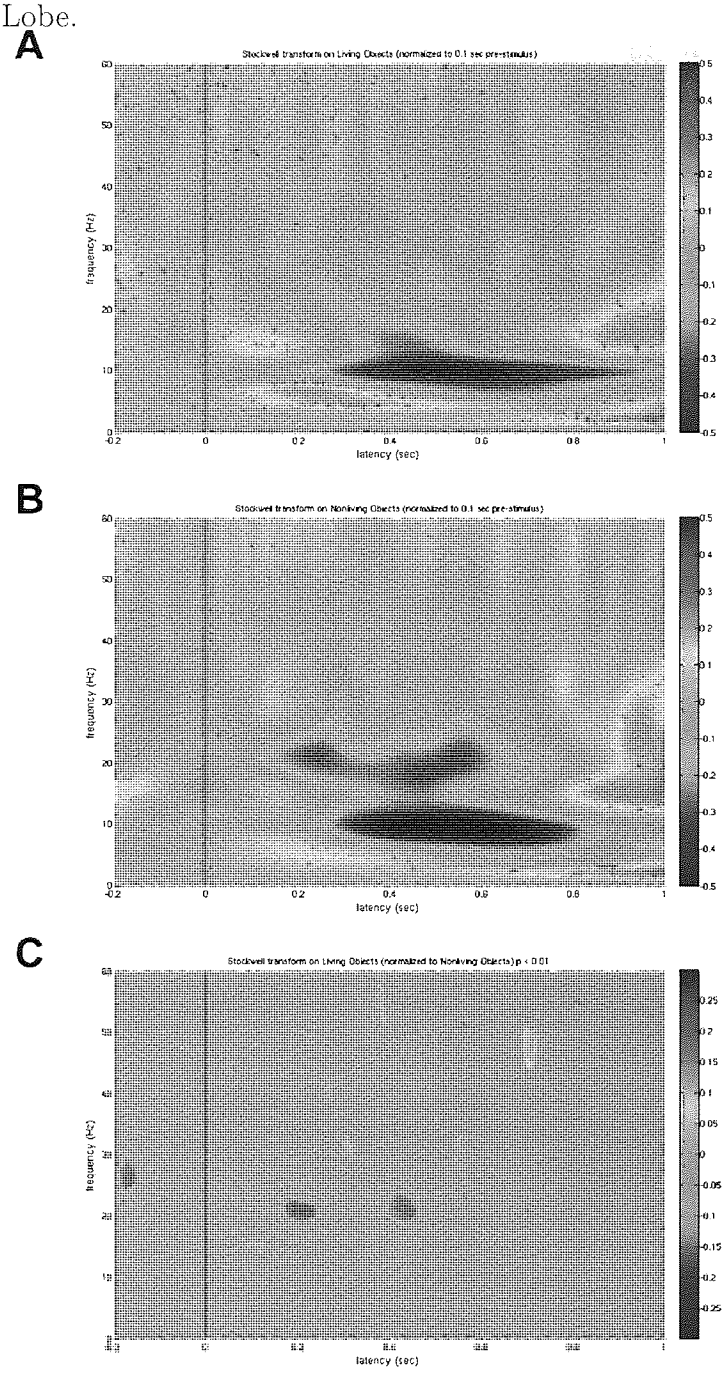


Time-frequency findings in right superior temporal gyrus for all 10 participants. Target object onset is denoted by the solid line. A) Living objects compared to baseline; B) Nonliving objects compared to baseline; C) Direct comparison of living to nonliving objects thresholded at $p<0.01$ uncorrected. Note the difference in C (approximately 200 ms post-stimulus, 10-20 Hz) showing greater power for living compared to nonliving objects.

greater desynchronisation (i.e., a greater loss of power) for nonliving compared to living objects within the alpha to low-beta frequency range.

In the region in right posterior inferior parietal lobe (see Figure 4.3.2 for source location), we found differences between living and nonliving objects beginning around 150-200 ms after target object onset (see Figure 4.3.16). This difference appears to be initially caused by a greater increase in power for living compared with nonliving objects. At

FIGURE 4.3.16. Time-Frequency Findings from Right Posterior Inferior Parietal Lobe.

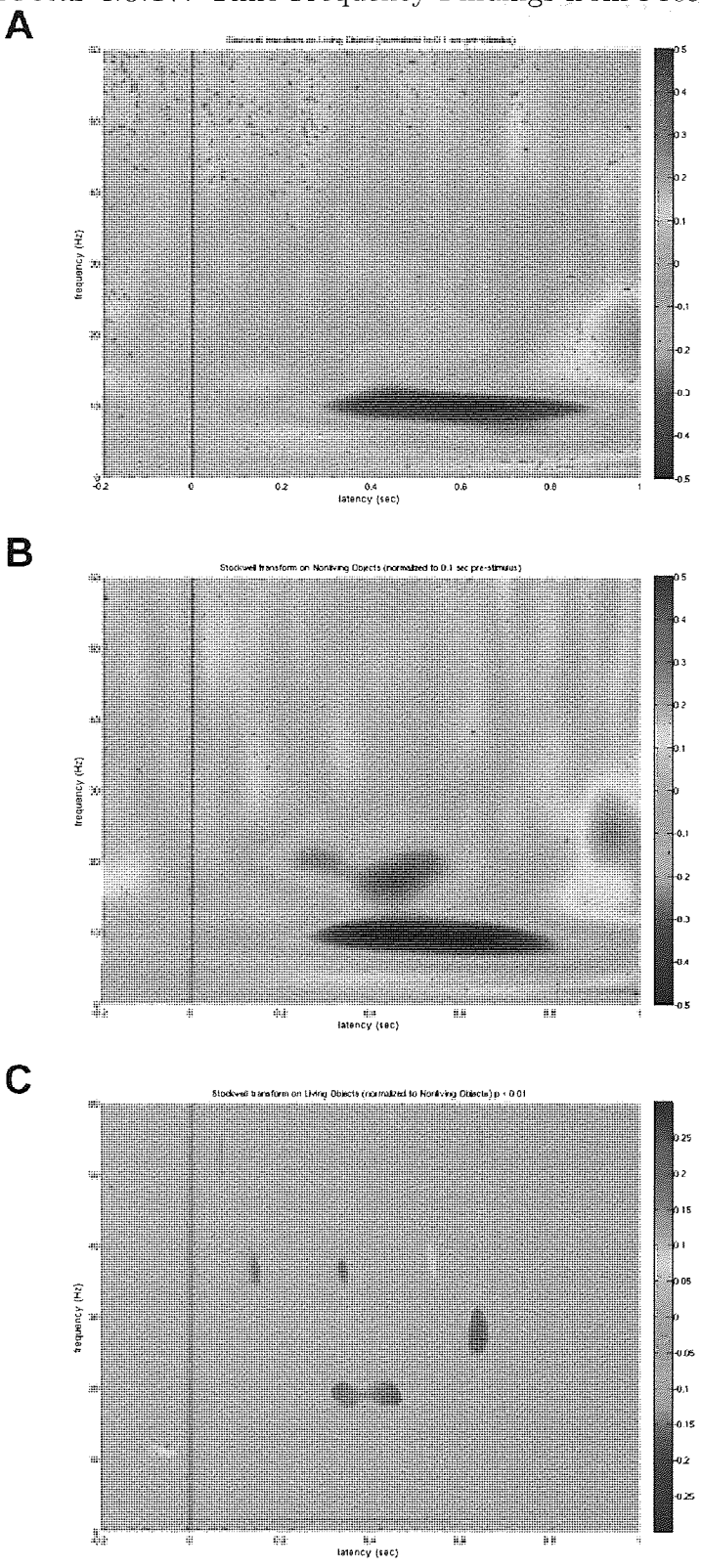


Time-frequency findings in right posterior inferior parietal lobe for all 10 participants. Target object onset is denoted by the solid line. A) Living objects compared to baseline; B) Nonliving objects compared to baseline; C) Direct comparison of living to nonliving objects thresholded at $p<0.01$ uncorrected. Note the difference in C (approximately 150-20 ms post-stimulus, 15-25 Hz) showing greater power for living compared to nonliving objects.

a slightly later time (approximately 200 ms post target onset), this difference is a consequence of greater desynchronisation for nonliving compared to living objects within the beta frequency range.

In the region in precuneus (see Figure 4.3.3 for source location), we found differences between living and nonliving objects beginning around 300 ms after target object onset (see Figure 4.3.17). This difference appears to be caused by greater desynchronisation for nonliving compared with living objects.

FIGURE 4.3.17. Time-Frequency Findings from Precuneus.



Time-frequency findings in the precuneus for all 10 participants. Target object onset is denoted by the solid line. A) Living objects compared to baseline; B) Nonliving objects compared to baseline; C) Direct comparison of living to nonliving objects thresholded at $p<0.01$ uncorrected. Note the difference in C (approximately 300 ms post-stimulus, 15-25 Hz) showing greater power for living compared to nonliving objects.

In the region in left inferior frontal gyrus (see Figure 4.3.4 for source location), we found differences between living and nonliving objects beginning within 100 ms of target object onset (see Figure 4.3.18). This difference appears to be caused by a greater increase in power for living compared to nonliving objects.

In the region in right dorsolateral prefrontal cortex (see Figure 4.3.7 for source location), we found differences between living and nonliving objects beginning around 100 ms after target object onset (see Figure 4.3.19). This difference appears to be caused by a greater increase in power for nonliving compared to living objects. At a slightly later time (approximately 600 ms post target onset), this difference is a consequence of greater desynchronisation for living compared with nonliving objects.

In the region in right postcentral gyrus (see Figure 4.3.8 for source location), we found differences between living and nonliving objects beginning around 200 ms after target object onset (see Figure 4.3.20). This difference appears to be caused by greater desynchronisation for living compared to nonliving target objects.

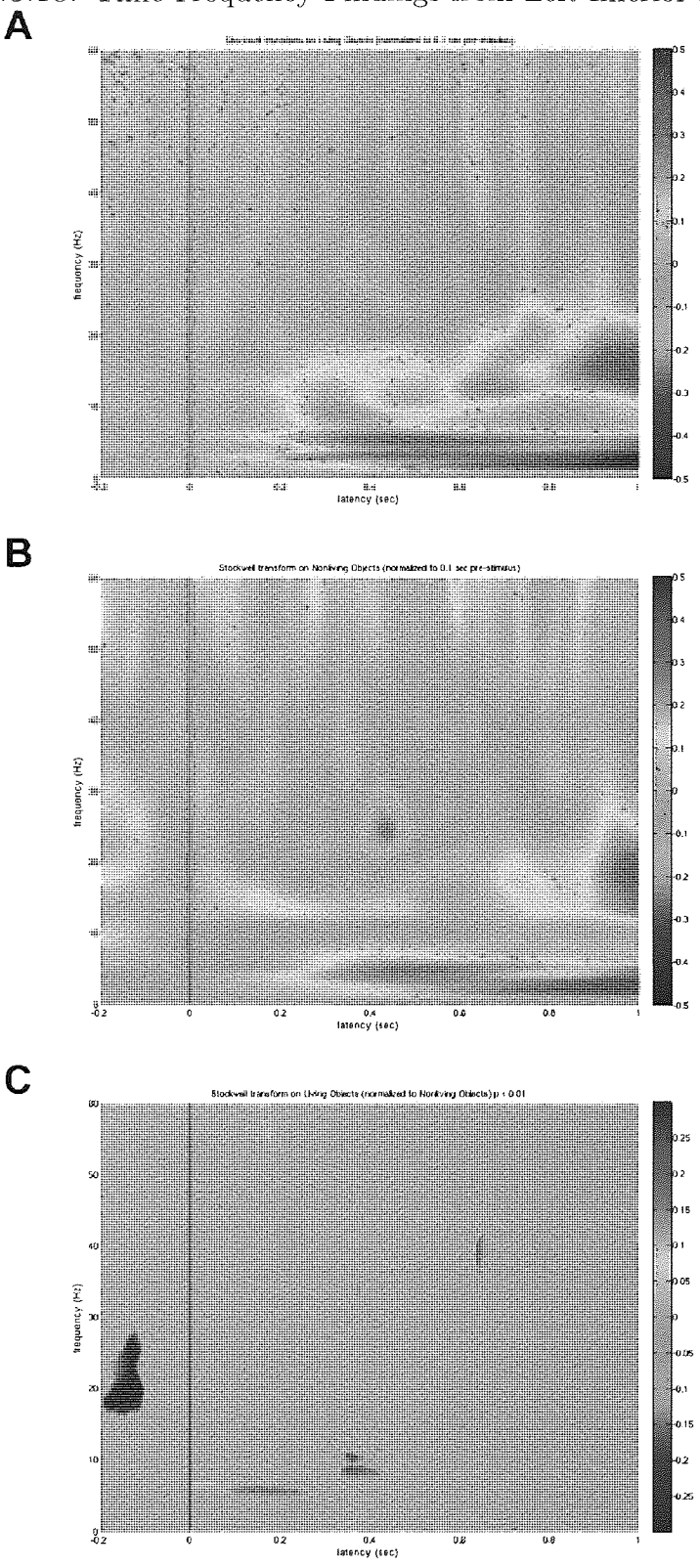
In the region in left occipito-temporal cortex (see Figure 4.3.9 for source location), we found differences between living and nonliving objects beginning around 200 ms after target object onset (see Figure 4.3.21). This difference appears to be caused initially by an increase in power for nonliving objects, which does not occur for living objects. This is then followed by a desynchronisation for both living and nonliving objects, with greater desynchronisation around 450 ms post-stimulus for living compared to nonliving target objects.

In the region in left supramarginal gyrus (see Figure 4.3.10 for source location), differences in the 20-30 Hz range (the range in which the source analysis identified significant differences) were found between living and nonliving objects beginning around 900 ms after target object onset (see Figure 4.3.22). This difference appears to be caused by a greater increase in power for nonliving compared to living objects. In addition to the 20-30 Hz frequency band, the time-frequency findings suggest greater power for nonliving compared to living objects in the gamma range as well. This difference begins at approximately 350 ms post target onset and appears to also be caused by a greater increase in power for nonliving compared with living objects.

In the region in right superior temporal gyrus to inferior parietal lobule (see Figure 4.3.11 for source location), differences in the 30-60 Hz range (the range in which the source analysis identified significant differences) were found between living and nonliving objects beginning around 800 ms after target object onset (see Figure 4.3.23). This difference appears to be caused by an increase in power for nonliving compared to living objects. In addition to the 30-60 Hz frequency band, the time-frequency findings suggest greater power for nonliving compared to living objects in the beta range as well. This difference begins at approximately 400 ms post target onset and appears to be caused by greater desynchronisation for living compared to nonliving objects.

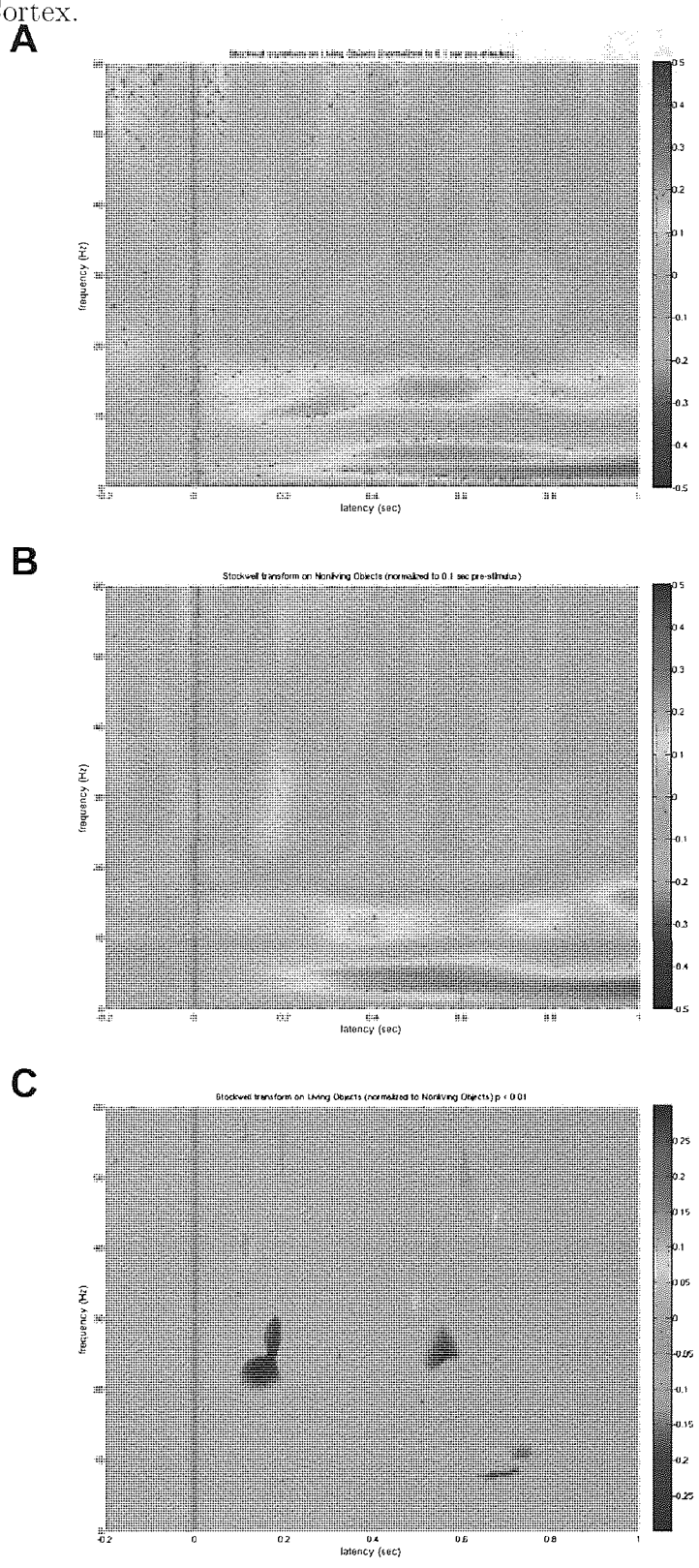
In the region in right precuneus (see Figure 4.3.12 for source location), our time-frequency analysis did not identify time points or frequencies in which there was greater power for nonliving compared with living objects (see Figure 4.3.24).

FIGURE 4.3.18. Time-Frequency Findings from Left Inferior Frontal Gyrus.



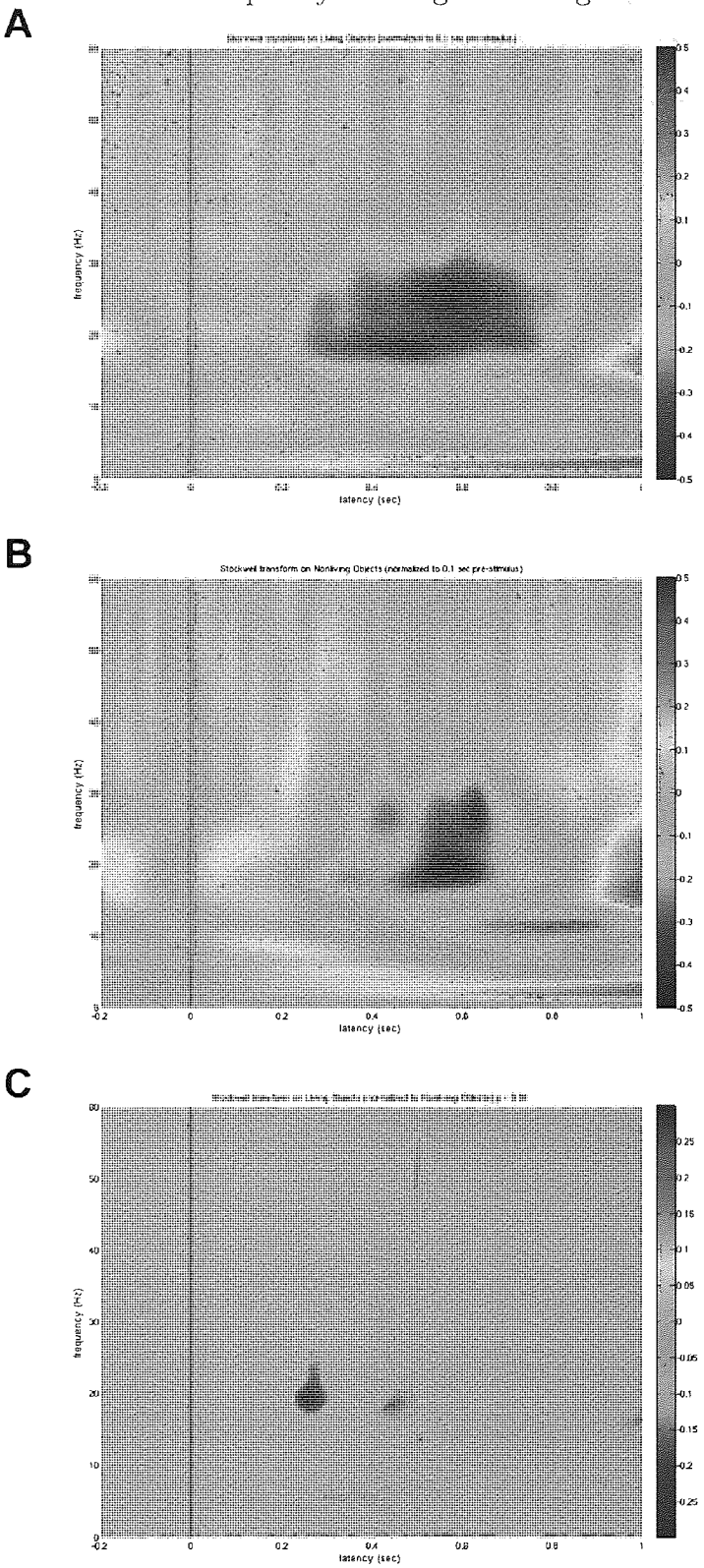
Time-frequency findings in left inferior frontal gyrus for 8 of 10 participants. Target object onset is denoted by the solid line. A) Living objects compared to baseline; B) Nonliving objects compared to baseline; C) Direct comparison of living to nonliving objects thresholded at $p<0.01$ uncorrected. Note the difference in C (within 100 ms post-stimulus, 5-15 Hz) showing greater power for living compared to nonliving objects.

FIGURE 4.3.19. Time-Frequency Findings from Right Dorsolateral Prefrontal Cortex.



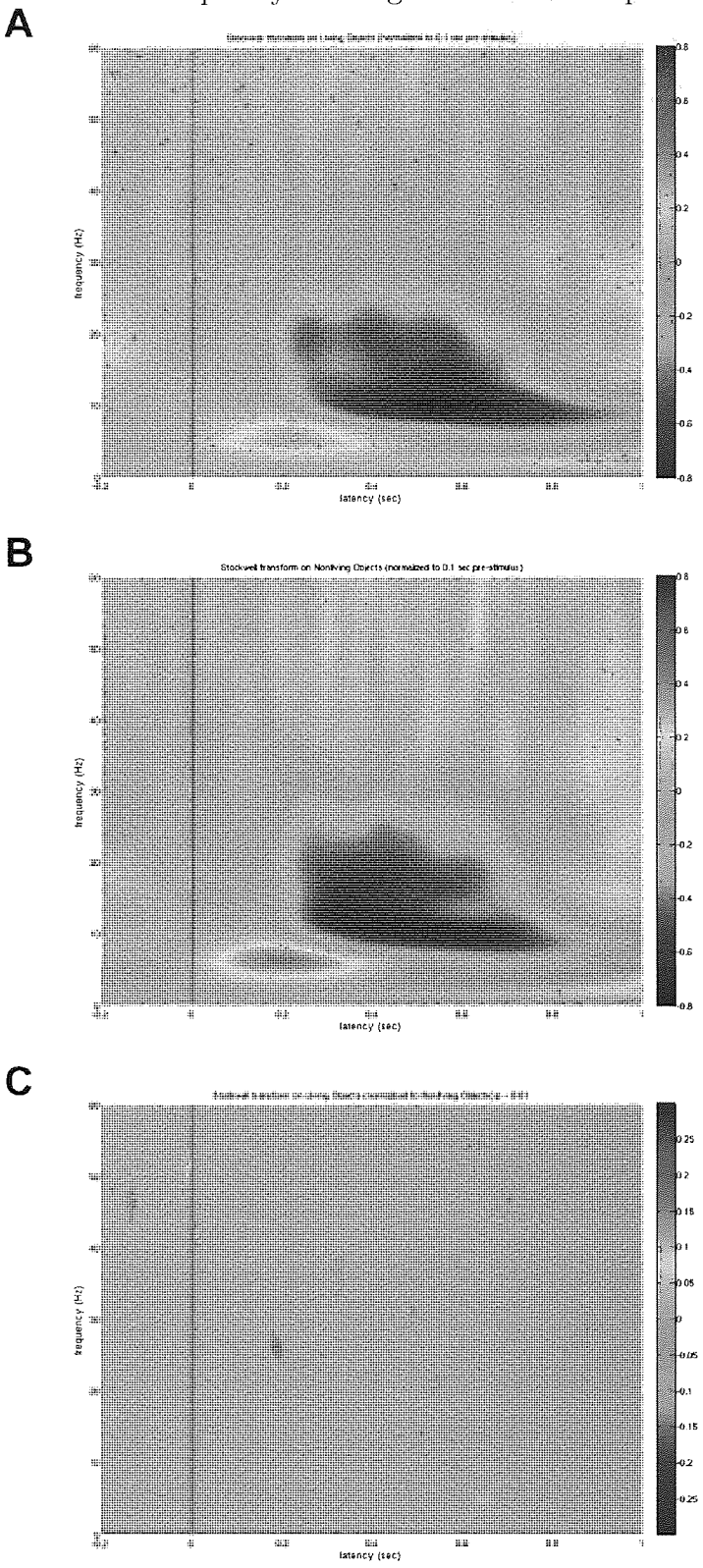
Time-frequency findings in right dorsolateral prefrontal cortex for all 10 participants. Target object onset is denoted by the solid line. A) Living objects compared to baseline; B) Nonliving objects compared to baseline; C) Direct comparison of living to nonliving objects thresholded at $p<0.01$ uncorrected. Note the difference in C (approximately 100-200 ms post-stimulus, 20-30 Hz) showing greater power for nonliving compared to living objects.

FIGURE 4.3.20. Time-Frequency Findings from Right Postcentral Gyrus.



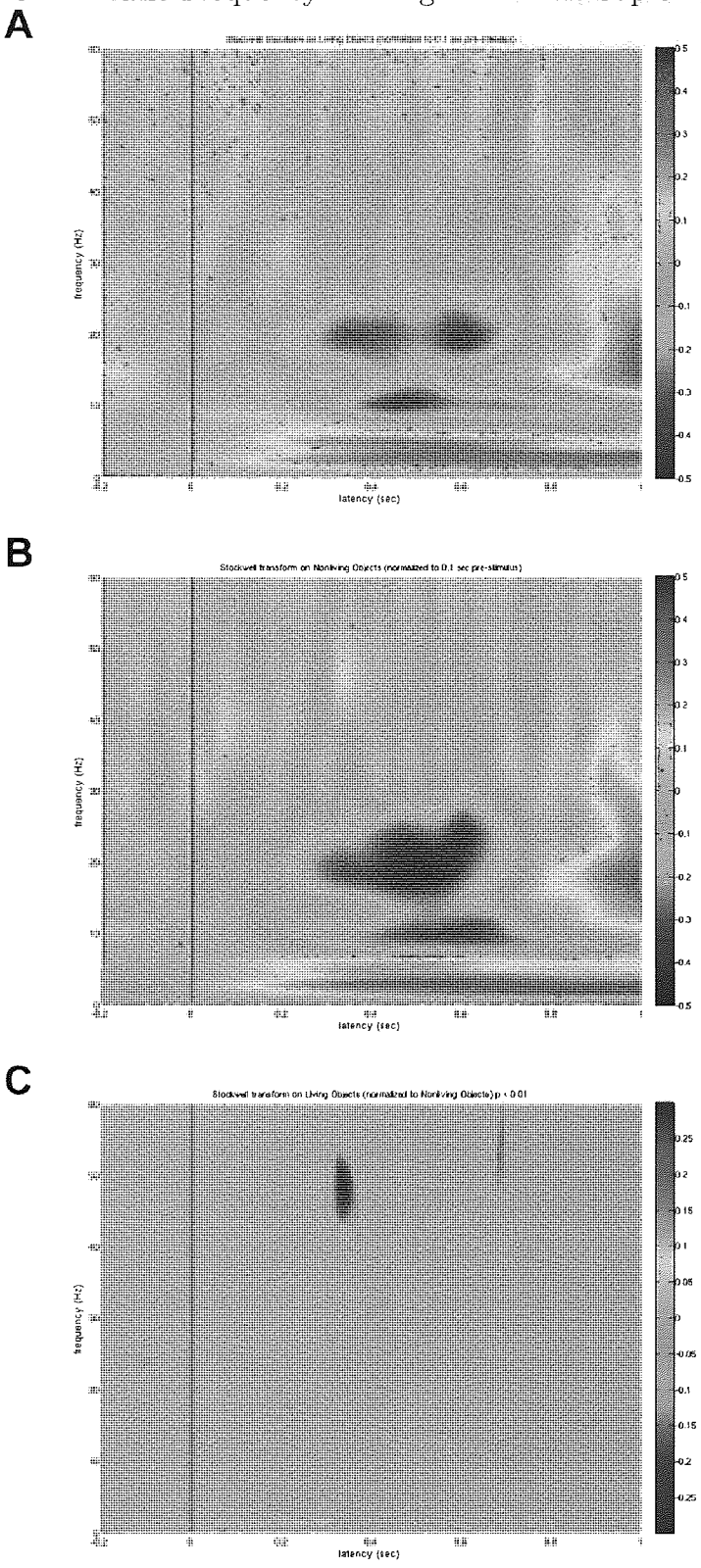
Time-frequency findings in right postcentral gyrus for all 10 participants. Target object onset is denoted by the solid line. A) Living objects compared to baseline; B) Nonliving objects compared to baseline; C) Direct comparison of living to nonliving objects thresholded at $p<0.01$ uncorrected. Note the difference in C (approximately 200 ms post-stimulus, 15-25 Hz) showing greater power for nonliving compared to living objects.

FIGURE 4.3.21. Time-Frequency Findings from Left Occipito-Temporal Cortex.



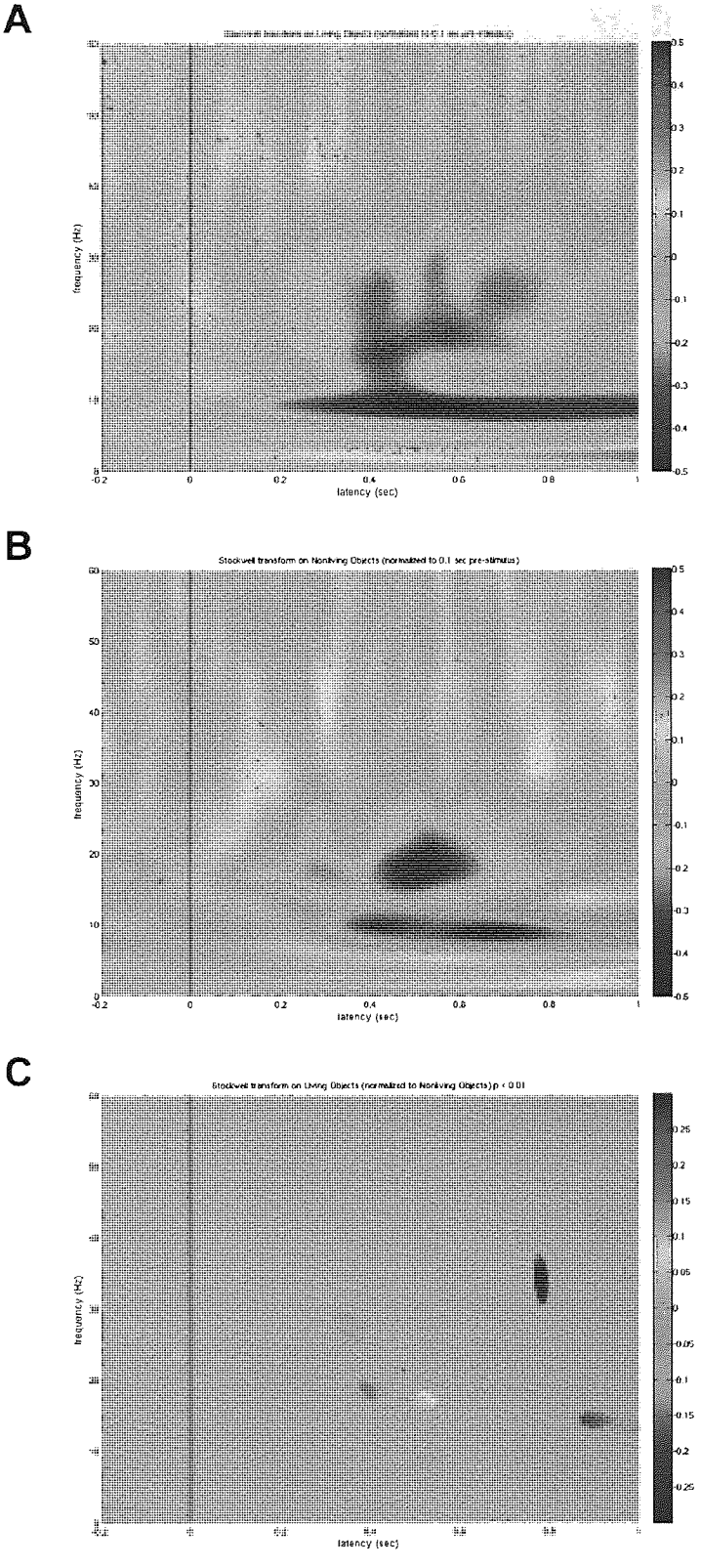
Time-frequency findings in left occipito-temporal cortex for all 10 participants. Target object onset is denoted by the solid line. A) Living objects compared to baseline; B) Nonliving objects compared to baseline; C) Direct comparison of living to nonliving objects thresholded at $p<0.01$ uncorrected. Note the difference in C (approximately 200 ms post-stimulus onset, 20-30 Hz) showing greater power for nonliving compared to living objects.

FIGURE 4.3.22. Time-Frequency Findings from Left Supramarginal Gyrus.



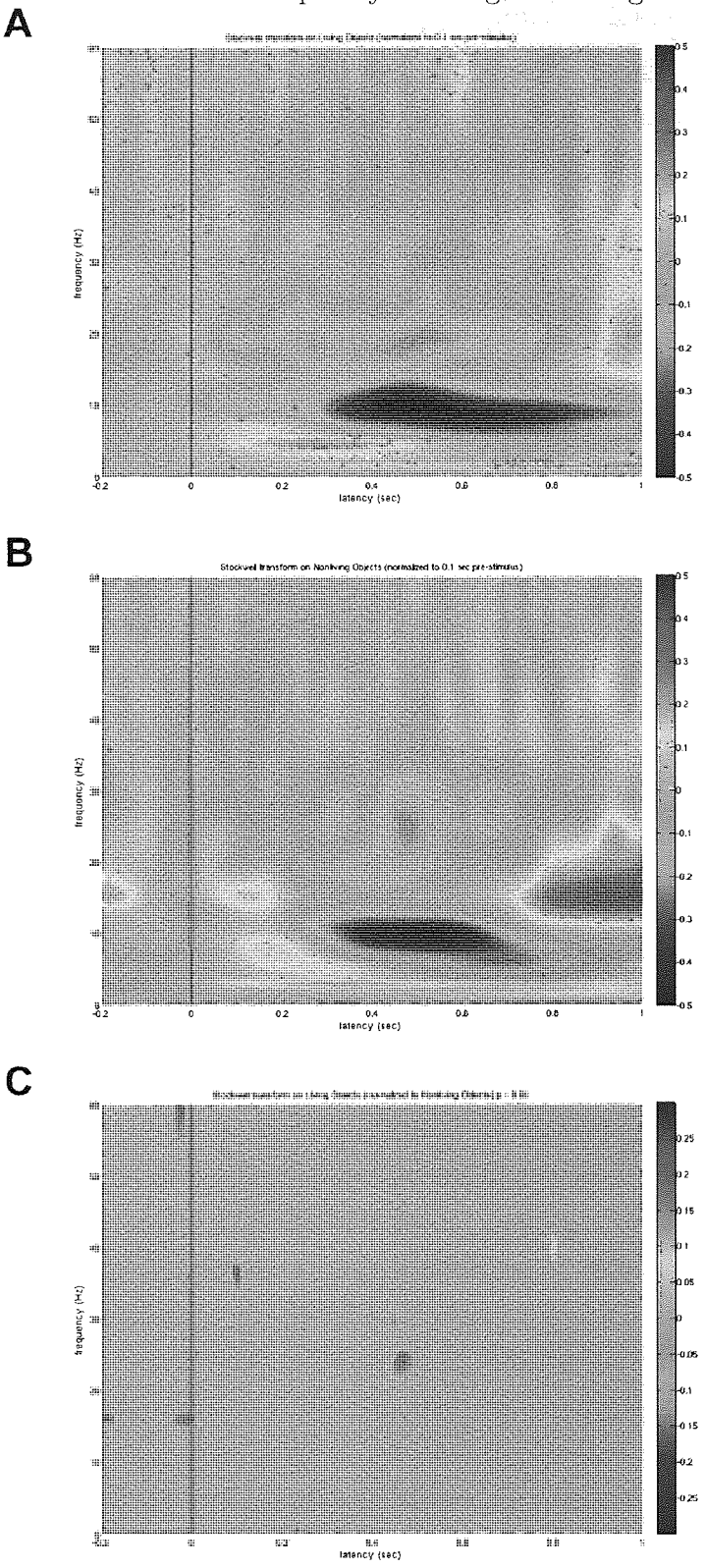
Time-frequency findings in left supramarginal gyrus for 8 of 10 participants. Target object onset is denoted by the solid line. A) Living objects compared to baseline; B) Nonliving objects compared to baseline; C) Direct comparison of living to nonliving objects thresholded at $p<0.01$ uncorrected. Note the difference in C in two separate bands (approximately 900 ms post-stimulus; 20-30 Hz; 300 ms post-stimulus; 30-60 Hz) showing greater power for nonliving compared to living objects.

FIGURE 4.3.23. Time-Frequency Findings from Right Superior Temporal Gyrus to Inferior Parietal Lobule.



Time-frequency findings in right superior temporal gyrus to inferior parietal lobule for 8 of 10 participants. Target object onset is denoted by the solid line. A) Living objects compared to baseline; B) Nonliving objects compared to baseline; C) Direct comparison of living to nonliving objects thresholded at $p<0.01$ uncorrected. Note the differences in C in two separate bands (approximately 800 ms post-stimulus, 30-60 Hz; 400 ms post-stimulus; 15-30 Hz) showing greater power for nonliving compared to living objects.

FIGURE 4.3.24. Time-Frequency Findings from Right Precuneus.



Time-frequency findings in right precuneus for 8 of 10 participants. Target object onset is denoted by the solid line. A) Living objects compared to baseline; B) Nonliving objects compared to baseline; C) Direct comparison of living to nonliving objects thresholded at $p<0.01$ uncorrected. Note that there are no times/frequencies in which there is greater power for nonliving compared to living objects post-stimulus.

4.4. Discussion

We used MEG to investigate semantic processing differences between living and nonliving objects. Our analysis identified several regions showing significant differences between living and nonliving objects during the 1 s window following target object onset. These included right superior temporal gyrus, right posterior inferior parietal lobe, precuneus, bilateral inferior frontal gyrus, and right dorsomedial prefrontal cortex, all showing greater power for living compared with nonliving objects. In addition, left occipito-temporal cortex, right postcentral gyrus, left supramarginal gyrus, right precuneus, bilateral inferior parietal lobule, right dorsolateral prefrontal cortex, and left frontal cortex showed greater power for nonliving compared with living objects.

A number of these regions have been identified previously in neuroimaging studies of category-specificity. For example, many neuroimaging studies of category-specificity have reported differences between living and nonliving objects within the temporal lobes in ventral temporal cortex and the superior temporal gyrus (e.g., Chao & Martin, 2000; Martin et al., 1996). Outside of the temporal lobes, studies have shown category-specific differences in inferior frontal gyrus, ventral dorsolateral prefrontal cortex, and premotor and motor cortices in the frontal lobes (e.g., Chao & Martin, 2000; Martin et al., 1996) and the cuneus in parietal cortex (Chouinard & Goodale, 2010).

A number of regions have come out of this analysis which have not been routinely recognised in neuroimaging studies of category-specificity. For example, we found greater power for living compared to nonliving things in a region in the right posterior inferior parietal lobe. Although not completely overlapping, some studies of category-specificity have reported activation in the middle occipital gyrus (e.g., Chouinard & Goodale, 2010) for living compared with nonliving things. For example, an ALE meta-analysis of category-specific effects by Chouinard & Goodale (2010) showed greater activation in right middle occipital gyrus to living things in studies contrasting animal to tool picture naming. It might be the case that the more limited spatial resolution of MEG has not allowed us to fully localise effects accurately. Therefore, it would certainly be advantageous to explore combining methodologies to increase spatial resolution (i.e., scanning participants with both MEG and fMRI, and using the fMRI as a prior to aid with source localisation).

Mapping the time-frequency characteristics of regions showing category-specific effects highlighted a number of interesting findings. For example, the first region showing category-specific differences temporally is left inferior frontal gyrus (IFG). Within 100 ms of seeing an object, there was greater power in this region for living compared with nonliving objects. Many studies have indicated an important role for this region in semantic processing (e.g., Kan & Thompson-Schill, 2004; Martin et al., 1996; Petersen et al., 1998). Thompson-Schill and colleagues have proposed that left IFG is involved in selecting semantic information from competing alternatives (e.g., Kan & Thompson-Schill, 2004; Thompson-Schill et al., 1997). For example, Thompson-Schill et al. (1997) used fMRI to measure activation in IFG as participants performed a verb generation task, a semantic classification task, or made a comparison between a target and several probe words. In addition, they varied each task so that there was a high selection and low selection condition. On all tasks, IFG was recruited to a higher degree during the high

selection condition, leading the authors to argue that IFG is involved in selecting amongst competing alternatives, rather than simply responding to semantic content. Thus, one could argue that IFG should be recruited during picture naming to a greater degree for living than nonliving things, as there would be enhanced competition based on structural similarity (see Chapter 1 and Chapter 3 for discussion), in line with our findings.

A second interesting finding from our analysis is that left occipito-temporal cortex showed greater power for nonliving compared with living things, which initially appears contrary to the findings reported in left occipito-temporal cortex in the previous chapter. However, the source location of these effects is not overlapping. Our source localisation in Chapter 3 resulted in a more lateral area showing greater power for living than nonliving objects. Interestingly, when we mapped the time-frequency characteristics at this location, we found this power difference to be caused by greater desynchronisation (i.e., a greater loss of power) for living compared with nonliving objects at around 200 ms post-stimulus. The increased desynchronisation suggests perhaps that there are greater processing demands for living than nonliving things at this time point (e.g., Singh et al., 2002). These findings, then, are in line with our findings from the previous chapter, although the mechanisms behind this effect (i.e., relative power increase compared with desynchronisation) differ between the two regions. In terms of the debate about bottom-up versus top-down processing, this region seems to be responding in a top-down fashion to the stimulus. That is, there is an initial increase in power to the stimulus for both living and nonliving objects, which appears to be time-locked and phase-locked (i.e., evoked) to the target object. Then, slightly later, there is desynchronisation for both living and nonliving things. Since this desynchronisation reflects a decrease in observable power in this frequency range, which does not appear to be time-locked and phase-locked to the stimulus, it suggests a top-down difference in processing living and nonliving objects.

In a region centred on right postcentral gyrus, we find an initial increase in power for nonliving objects compared to baseline. This does not exist for living objects. Later, for both living and nonliving objects, there is desynchronisation, with relatively greater desynchronisation for living compared to nonliving things. The early increase in power for nonliving objects seems to shift the subsequent desynchronisation temporally, and perhaps this early power increase fits with the sensory-motor model of object-processing. Certainly this region is involved in motor behaviour, and it would follow that this region would be recruited for nonliving things because that is how they are typically identified (i.e., through motor-associated behaviour), according to the model. The early increase in power for nonliving objects is relatively weak, however, and this may have to do with the nature of the categories we included. Nonliving objects included not only tools, which have tightly constrained motor-related properties, but also furniture and types of transport, whose motor-related properties are not as tightly mapped. Therefore, we cannot fully support the sensory-motor model. However, this might be a consequence of our experimental design. It would have benefited us to increase the number of items drawn from each category within our sample, to test specific predictions about motor-affordances and activation in motor-associated areas of cortex. Nevertheless, a cursory look at the time-frequency representation suggests greater power initially for nonliving than living objects at this location.

One rather interesting finding is that we do not detect medial temporal gyrus activation for either living or nonliving objects. Again, one could argue that the limited number of items from the nonliving domain that had closely mapped motor affordances could have reduced the chances of observing an effect for the entire group. Perhaps, again, if we had an increased the number of images from each category, it would have been beneficial to directly contrast manipulable and non-manipulable nonliving objects, to see whether we might detect medial temporal gyrus for the manipulable objects (e.g., Beauchamp & Martin, 2007; Chao et al., 2002; Mahon et al., 2007).

In sum, our analyses identified several regions showing category-specific differences between living and nonliving objects. Many of these regions have been reported in previous studies. In general, our findings indicate that different regions of cortex do respond differentially to living and nonliving objects during the 1s window following target object onset, failing to support theories of category-specificity that suggest all objects are processed in a unitary semantic store. In addition, some of the regions showing category-specific effects have been identified as regions involved in visual and motor processing generally, lending tentative support to the sensory-motor model of object processing

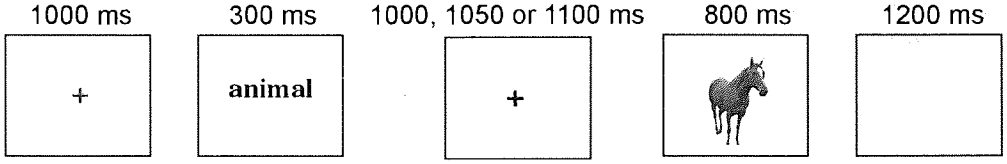
CHAPTER 5

On the Time-Course of Category-Specific Processing of Living and Nonliving Objects

5.1. Introduction

Our findings have shown both perceptual and semantic processing differences between living and nonliving objects using MEG. We focused our original set of source-level analyses on a pre-determined time window because of specific questions about when living and nonliving objects diverge in the visual object-processing stream (and based on EEG/ERP evidence of divergence at around the N1; see Chapter 3). Therefore, we did not exploit fully the temporal benefits of MEG to measure the evolution of neural processing of living and nonliving objects in the brain. In addition, whilst our second set of source-level analyses allowed us to explore the semantic processing of living and nonliving objects, we discarded temporal information in order to gain greater source-level detection capabilities. Research has indicated that this is advantageous, as the amount of data used in constructing the covariance matrix (which source-localisation is based on) can severely impact on the accuracy of the beamformer in estimating source location (e.g., Brookes et al., 2008). In addition, as the SAM algorithm is designed to maximise power at a given voxel in the brain by minimising all other correlated sources across the brain, we should use relatively long windows of activity in order to minimise correlation amongst competing sources (see Chapter 1 for further discussion). We obviously are interested in an accurate representation of signal power across the brain. However, one critical benefit to using a technique such as MEG is to gain temporal resolution. Therefore, some compromise must be reached between the amount of data (i.e., length of the time window used to construct the covariance matrix) and the temporal precision of the analysis. For example, it is possible that in giving away temporal information to enhance source reconstruction, a temporal shift in activity between comparison conditions at a particular location could be missed. That is, if there is no amplitude difference between living and nonliving objects over an entire 1s window, but rather a temporal shift in processing, using a long time window might result in no detection of this difference between the two conditions. This is certainly more a risk for our type of analysis, which directly contrasts two 'active' periods in the brain. That is, event-related (phase-locked and non phase-locked) activity is occurring for both of the conditions that we contrast. Whereas, in other types of designs, activity is compared to some baseline condition (i.e., activation in the brain in response to all objects compared with pre-stimulus). Thus, there could indeed be processing differences between living and nonliving objects which we are not detecting in our current analysis. Therefore, we set out to examine in a more detailed manner differences in processing living and nonliving objects in the brain across time. We utilised a shorter time window in which we directly

FIGURE 5.2.1. Example Trial.



Participants were shown a 1000 ms red fixation cross, followed by a 300 ms category probe. After a variable (1000, 1050, or 1100 ms) delay interval, participants were shown a target object for 800 ms. They were instructed to decide as quickly and accurately as possible if the target object was a member of the previously presented category probe by pressing a button.

contrasted living to nonliving objects, and increased our frequency range of interest, in order to maximise accuracy within this shortened window.

5.2. Methods

The study procedures reported in this chapter are identical to those described in the previous chapter (Chapter 4). In addition, the MEG data acquisition is identical to those previously reported, however the MEG analyses differ from those described previously. For clarity of reading and understanding, all methods used are reported again in this chapter.

5.2.1. Study Procedure. Ten right-handed volunteers (Mean Age=29.4 years, range=20-36 years; 2 males) participated in the MEG study. Participants were first shown a superordinate category name as a probe, followed by a target object (see Figure 5.2.1). Participants were instructed to respond by button press as quickly and accurately as possible, identifying whether the target object matched the category probe. Participants responded using a 2-button response box held in their right hand. They were instructed to respond by pressing the left button with their right index finger for "yes" (i.e., congruent trial) and the right button with their middle finger for "no" (i.e., incongruent trial).

Target objects included 78 exemplars drawn from 3 living (plants, animals, fruits and vegetables) and 3 nonliving (tools, transport, and furniture) categories. We ensured that all selected images had a pre-test naming consistency rate of greater than 65 percent. In addition, we selected stimuli that were matched on pre-test naming speed, familiarity, and typicality (see Chapter 2 for further discussion). Unfortunately, we were not able to match items of visual complexity, however the ratings were close.

Each target object was presented twice, once as a congruent trial ("yes", e.g., target dandelion preceded by a flower superordinate category label) and once as an incongruent trial. For incongruent trials, each image was associated with either a within or across-domain label. For example, a target dandelion with an animal superordinate category label would be classed as within-domain incongruent whereas a target dandelion with a tool superordinate category label would be classed as across-domain incongruent. Throughout the entire run, there were equal chances of having a within or across-domain incongruent label. Across participants, we counterbalanced whether a given item had a within or across-domain incongruent label. A total of 156 trials were shown during the scan, half

of which included a living target object and the other half a nonliving target object. The order of trial presentation was randomised across participants.

5.2.2. MEG Data Acquisition and Analyses. Neuromagnetic data were recorded at 600 Hz sampling rate with a bandwidth of 0-150 Hz using a CTF 275 MEG system (VSM MedTech Ltd., Canada) composed of a whole-head array of 275 radial 1st order gradiometer channels housed in a magnetically shielded room (Vacuumschmelze, Germany). Synthetic 3rd gradient balancing was used to remove background noise online. Fiducial coils were placed on the nasion, left preauricular, and right preauricular sites of each participant. These coils were energised before each run to localise the participant's head with respect to the MEG sensors. Total head displacement was measured after each run and could not exceed 5 mm for inclusion in the source analysis. Prior to scanning, participants' head shapes and the location of fiducial coils were digitised using a Polhemus Isotrak 3D digitiser (Kaiser Aerospace Inc.). These were then coregistered to high-resolution T1-weighted anatomical images for each participant acquired with a 3-Tesla whole-body scanner (3T Trio, Siemens Medical Systems) using in-house coregistration software.

Data for each participant were edited and filtered to remove environmental and physiological artefacts. We then applied a beamforming technique to assess sources of category-specific differences in processing living and nonliving objects. For this analysis, we aimed to identify the time course of processing living and nonliving objects. In order to do this, we used 100 ms windows in which we directly contrasted living ('active') to nonliving ('passive') objects using a wide frequency range (1-80 Hz). Our first window began at target object onset, and we then slid this window every 50 ms until 400-500 ms after target object onset. Spectral power changes between the 'active' and 'passive' periods were calculated as a pseudo t-statistic (Vrba & Robinson, 2001). Each participant's data were then normalised and converted to Talairach space using statistical parametric mapping (SPM99, Wellcome Department of Imaging Neuroscience, London, UK) for group-level comparisons.

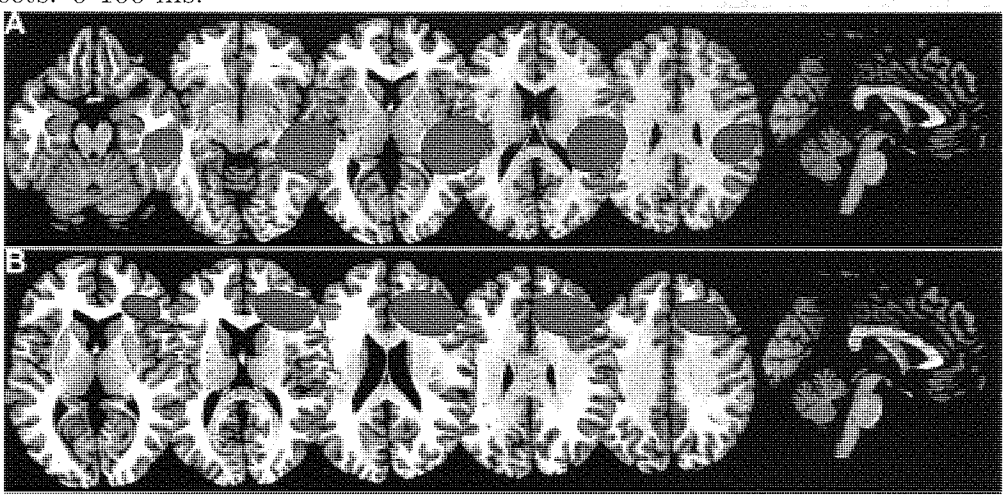
For group-level analyses, we utilised peakomatic to assess the distribution of image peaks across our participants. We tested a range of P values from 2 to 40 and after multiple comparisons correction were left with a number of significant clusters of positive and negative peaks. As with our previous analyses, if a region was identified as showing a significant difference across a range of P values, we chose the region for reporting purposes that yielded the largest N. In cases where several P values yielded the same N, we then chose the volume that had the smallest spatial extent.

5.3. Results

5.3.1. Behavioural Findings. As mentioned previously, we found no behavioural difference in performance between living and nonliving objects (see Chapter 3). Both reaction time and accuracy rates were not significantly different for living and nonliving target objects.

5.3.2. Source-Level Findings. We used SAM to identify sources of differential activity between living and nonliving objects using a 100 ms window slid every 50 ms.

FIGURE 5.3.1. Regions Showing Significantly Greater Power for Living Objects: 0-100 ms.



Regions identified as showing significantly greater power for living compared with nonliving objects from 0-100 ms. A) Right superior temporal gyrus (centre=49.3, -26.7, 5.7). This region was identified using the top 4 positive peaks per image; 9 of 10 participants had a peak in the volume (maximum radius=34.4 mm). B) Right frontal cortex (centre=28.3, 29.7, 24.3). This region was identified using the top 10 positive peaks per image; 9 of 10 participants had a peak in the volume (maximum radius=27.6 mm).

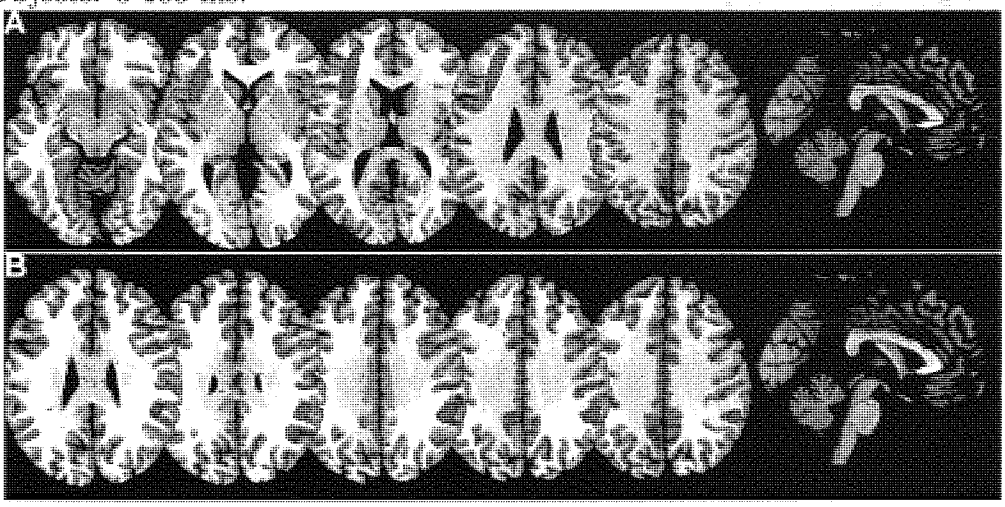
The first window began at target object onset, and the right-hand edge of the last window was at 500 ms after target object onset. Thus, we assessed differences in living and nonliving object-processing within 500 ms of seeing a picture. Source differences in each of these 100 ms windows are discussed separately below.

Within the first 100 ms (time window: 0-100 ms) of seeing either a living or nonliving object, our peakomatic analysis identified four regions showing significant category-related differences. Two of these regions showed greater power for living objects, whilst the other 2 showed greater power for nonliving objects. The first region showing greater power for living objects was rather extensive spatially, and it was centred on the right superior temporal gyrus (N=9, P=4, peak activation=2.1) (see Figure 5.3.1). In addition, a region in right frontal cortex showed greater power for living compared with nonliving objects (N=9, P=10, peak activation=1.78) (see Figure 5.3.1). The first region showing greater power for nonliving objects was located in left frontal cortex (N=6, P=3, peak activation=2.25) (see Figure 5.3.2). In addition, a region in the right supramarginal gyrus showed greater power for nonliving compared with living objects (N=6, P=29, peak activation=1.2) (see Figure 5.3.2).

From 50-150 ms after seeing either a living or nonliving object, our peakomatic analysis identified two regions showing significant category-related differences. One of these regions showed greater power for living objects, whilst the other region showed greater power for nonliving objects. The region showing greater power for living objects was centred on the right angular gyrus (N=7, P=6, peak activation=1.79) (see Figure 5.3.3). The region showing greater power for nonliving objects was located in the right occipital lobe centred on the right posterior cingulate (N=8, P=5, peak activation=1.72) (see Figure 5.3.4).

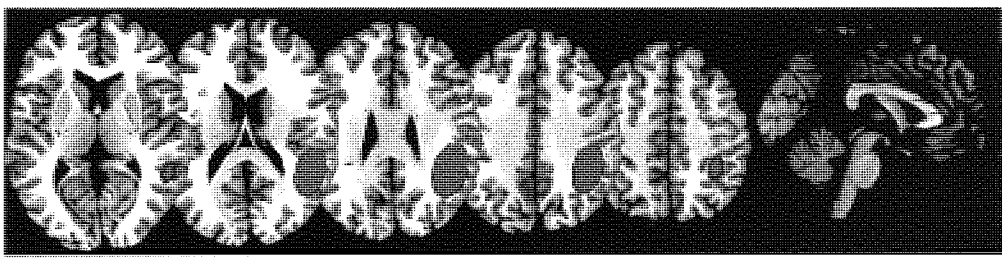
From 100-200 ms after seeing either a living or nonliving object, our peakomatic analysis identified three regions showing significant category-related differences. Two of

FIGURE 5.3.2. Regions Showing Significantly Greater Power for Nonliving Objects: 0-100 ms.



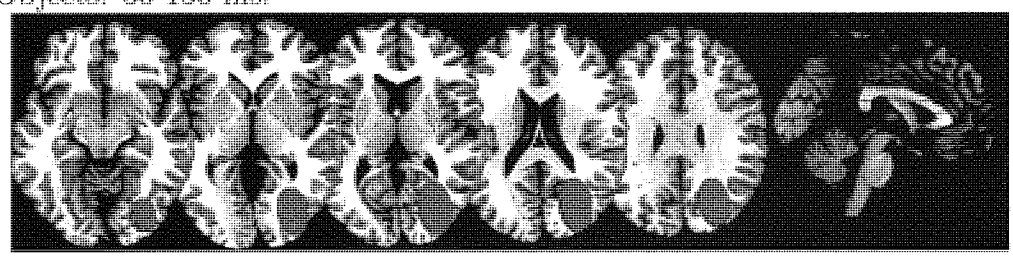
Regions identified as showing significantly greater power for nonliving compared with living objects from 0-100 ms. A) Left inferior to middle frontal cortex (centre= -33.5, 29.0, 14.0). This region was identified using the top 3 negative peaks per image; 6 of 10 participants had a peak in the volume (maximum radius=34.9 mm). B) Right supramarginal gyrus (centre=50.5, -41.5, 34.0). This region was identified using the top 29 positive peaks per image; 6 of 10 participants had a peak in the volume (maximum radius=8.6 mm).

FIGURE 5.3.3. Region Showing Significantly Greater Power for Living Objects: 50-150 ms.



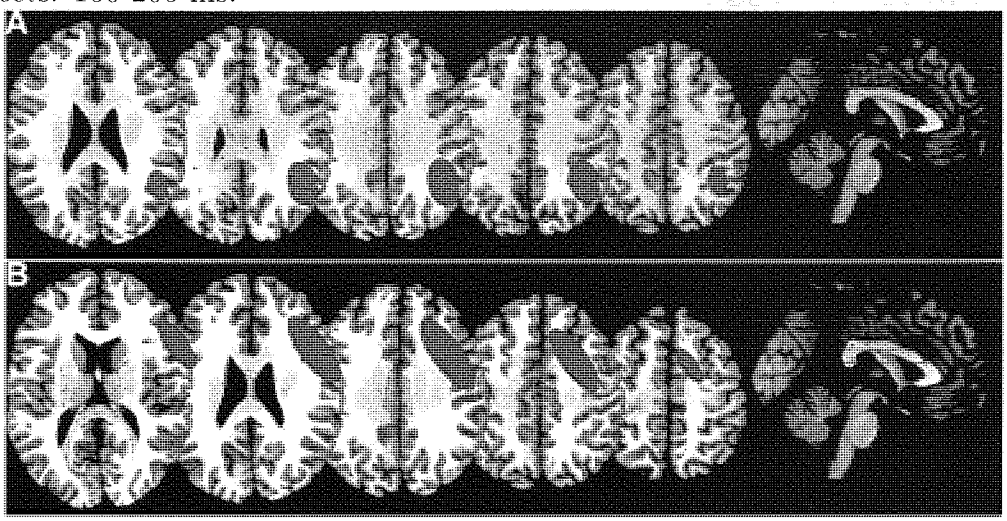
Region in right angular gyrus (centre=43.3, -43.7, 28.7) identified as showing significantly greater power for living compared with nonliving objects from 50-150 ms. This region was identified using the top 6 positive peaks per image; 7 of 10 participants had a peak in the volume (maximum radius=24.3 mm).

FIGURE 5.3.4. Region Showing Significantly Greater Power for Nonliving Objects: 50-150 ms.



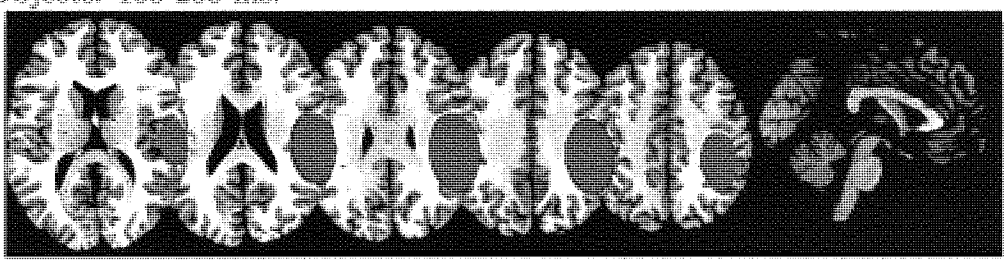
Region in right occipital cortex (centre=28.5, -72.4, 15.0) identified as showing significantly greater power for nonliving compared with living objects from 50-150 ms. This region was identified using the top 5 negative peaks per image; 8 of 10 participants had a peak in the volume (maximum radius=33.7 mm).

FIGURE 5.3.5. Regions Showing Significantly Greater Power for Living Objects: 100-200 ms.



Regions identified as showing significantly greater power for living compared with nonliving objects from 100-200 ms. A) Right angular gyrus (centre=42.6, -49.5, 34.8). This region was identified using the top 24 positive peaks per image; all 10 of our participants had a peak in the volume (maximum radius=18.6 mm). B) Right middle frontal gyrus (centre=37.3, 11.0, 33.3). This region was identified using the top 5 positive peaks per image; 9 of 10 participants had a peak in the volume (maximum radius=39.7 mm).

FIGURE 5.3.6. Region Showing Significantly Greater Power for Nonliving Objects: 100-200 ms.

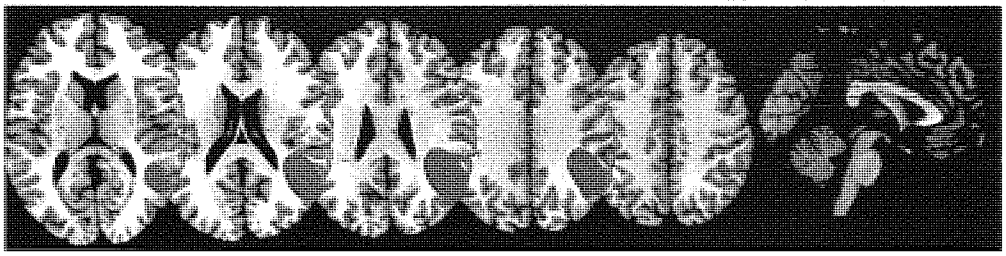


Region in right inferior parietal lobule (centre=47.3, -28.7, 31.3) identified as showing significantly greater power for nonliving compared with living objects from 100-200 ms. This region was identified using the top 7 negative peaks per image; 9 of 10 participants had a peak in the volume (maximum radius=32.3 mm).

these regions showed greater power for living objects, whilst 1 region showed greater power for nonliving objects. The first region showing greater power for living objects was centred again on the right angular gyrus (N=10, P=24, peak activation=1.56), as was seen during the 50-150 ms time window (see Figure 5.3.5). In addition, a region in right middle frontal gyrus showed greater power for living compared with nonliving objects (N=9, P=5, peak activation=1.74) (see Figure 5.3.5). The region showing greater power for nonliving objects was centred on the right inferior parietal lobule (N=9, P=7, peak activation=1.77) (see Figure 5.3.6).

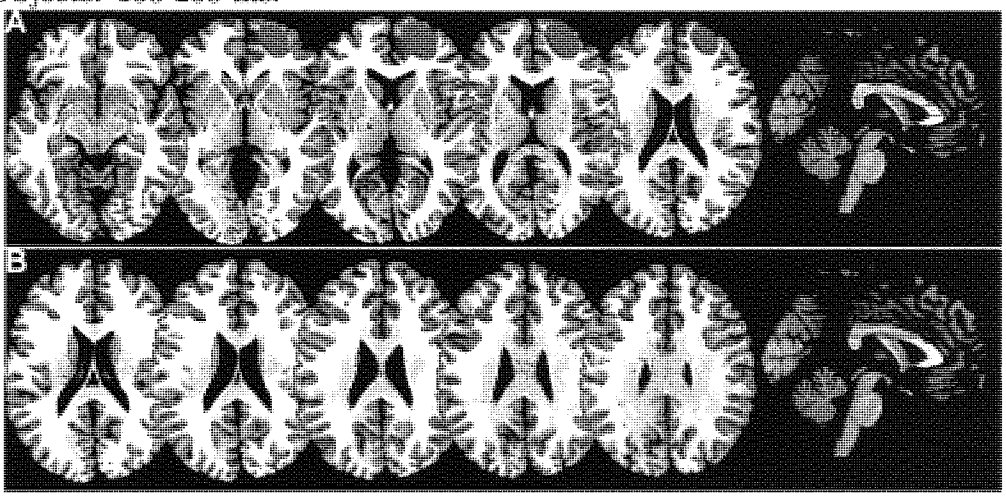
From 150-250 ms after seeing either a living or nonliving object, our peakomatic analysis identified three regions showing significant category-related differences. One of these regions showed greater power for living objects, whilst 2 regions showed greater power for nonliving objects. The region showing greater power for living objects was centred on the right angular gyrus (N=7, P=6, peak activation=1.83), as was seen in the

FIGURE 5.3.7. Region Showing Significantly Greater Power for Living Objects: 150-250 ms.



Region in right angular gyrus (centre=44.6, -49.7, 27.0) identified as showing significantly greater power for living compared with nonliving objects from 150-250 ms. This region was identified using the top 6 positive peaks per image; 7 of 10 participants had a peak in the volume (maximum radius=23.5 mm).

FIGURE 5.3.8. Regions Showing Significantly Greater Power for Nonliving Objects: 150-250 ms.

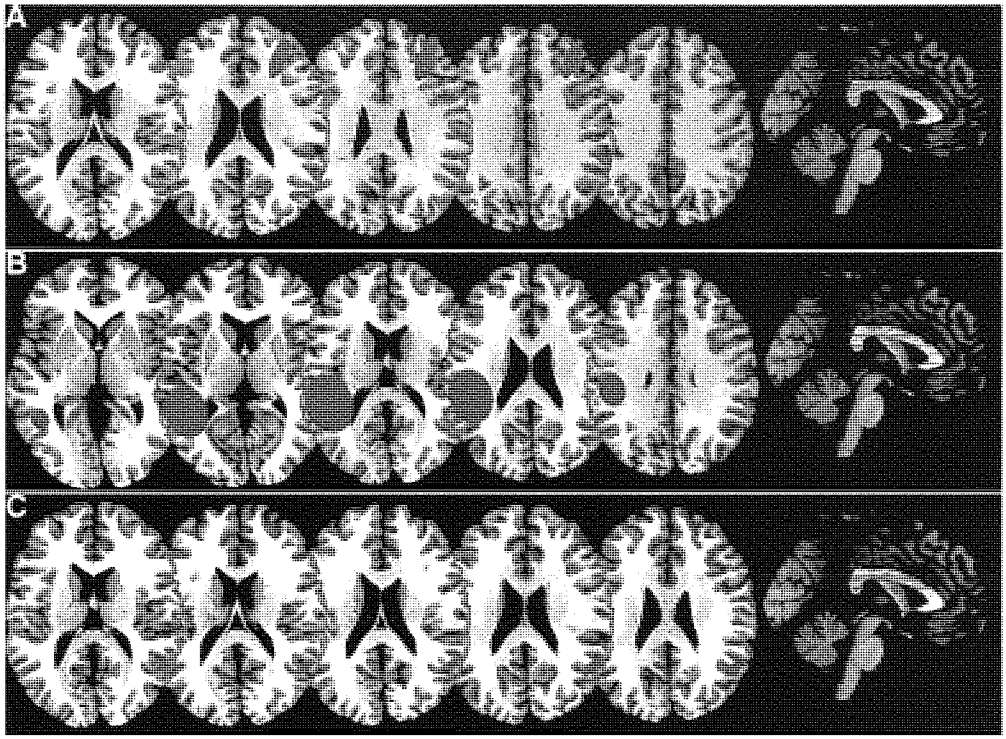


Regions identified as showing significantly greater power for nonliving compared with living objects from 150-250 ms. A) Right anterior superior frontal gyrus (centre=43.1, 14.3, 11.3). This region was identified using the top 11 negative peaks per image; 8 of 10 participants had a peak in the volume (maximum radius=24.5 mm). B) Left inferior frontal cortex (centre= -31.7, 27.4, 25.7). This region was identified using the top 37 negative peaks per image; 7 of 10 participants had a peak in the volume (maximum radius=8.5 mm).

previous two time windows (see Figure 5.3.7). The first region showing greater power for nonliving objects was located in right anterior superior frontal gyrus (N=8, P=11, peak activation=1.49) (see Figure 5.3.8). In addition, a region in left inferior frontal cortex showed greater power for nonliving compared with living objects (N=7, P=37, peak activation=1.29) (see Figure 5.3.8).

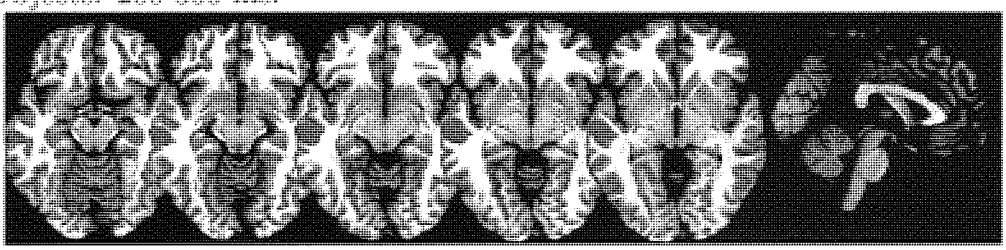
From 200-300 ms after seeing either a living or nonliving object, our peakomatic analysis identified four regions showing significant category-related differences. Three of these regions showed greater power for living objects, whilst 1 region showed greater power for nonliving objects. The first region showing greater power for living objects was located in right middle frontal gyrus (N=8, P=10, peak activation=1.55) (see Figure 5.3.9). In addition, a region centred on the left angular gyrus showed greater power for living compared with nonliving objects (N=6, P=5, peak activation=1.83), as did a region located in the right angular gyrus (N=6, P=19, peak activation=1.47) (see Figure 5.3.9).

FIGURE 5.3.9. Regions Showing Significantly Greater Power for Living Objects: 200-300 ms.



Regions identified as showing significantly greater power for living compared with nonliving objects from 200-300 ms. A) Right middle frontal gyrus (centre=31.9, 37.5, 27.8). This region was identified using the top 10 positive peaks per image; 8 of 10 participants had a peak in the volume (maximum radius=18.2 mm). B) Left angular gyrus (centre= -46.0, -39.0 17.0). This region was identified using the top 5 positive peaks per image; 6 of 10 participants had a peak in the volume (maximum radius=28.7 mm). C) Right angular gyrus (centre=51.5, -55.0, 23.0). This region was identified using the top 19 positive peaks per image; 6 of 10 participants had a peak in the volume (maximum radius=10.5 mm).

FIGURE 5.3.10. Region Showing Significantly Greater Power for Nonliving Objects: 200-300 ms.

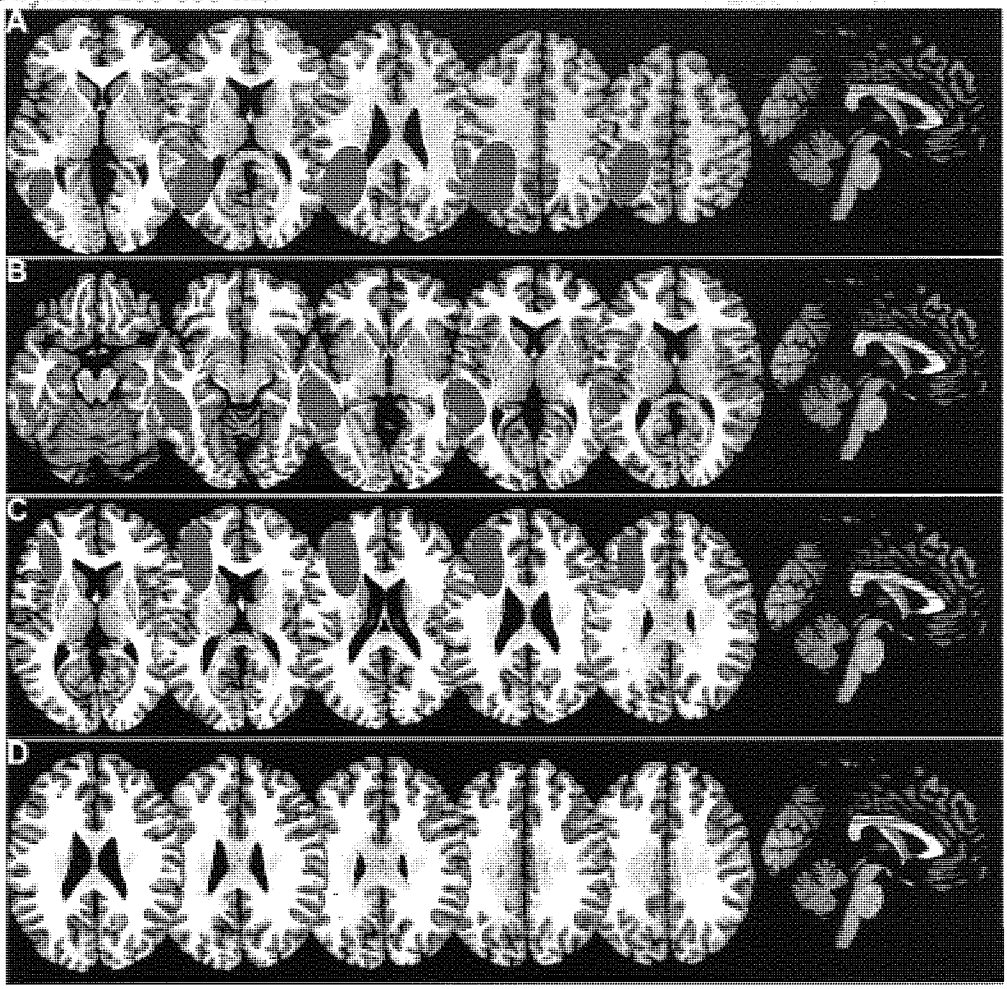


Region in left middle temporal gyrus (centre= -61.3, -18.0, -6.0) identified as showing significantly greater power for nonliving compared with living objects from 200-300 ms. This region was identified using the top 24 positive peaks per image; 6 of 10 participants had a peak in the volume (maximum radius=12.1 mm).

The region showing greater power for nonliving objects was located in the lateral extent of left middle temporal gyrus (N=7, P=24, peak activation=1.31) (see Figure 5.3.10).

From 250-350 ms after seeing either a living or nonliving object, our peakomatic analysis identified six regions showing significant category-related differences. Four of these regions showed greater power for living objects, whilst 2 regions showed greater power for nonliving objects. The first region showing greater power for living objects was

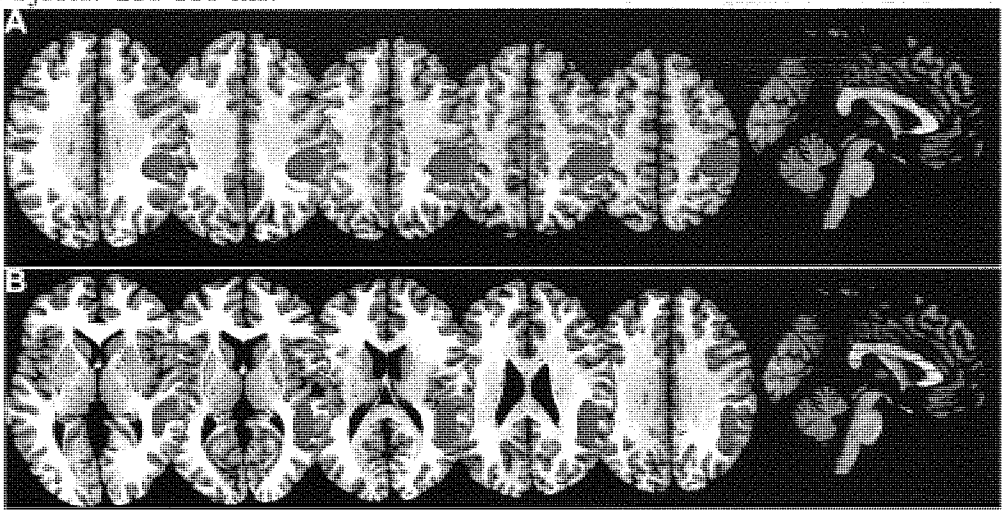
FIGURE 5.3.11. Regions Showing Significantly Greater Power for Living Objects: 250-350 ms.



Regions identified as showing significantly greater power for living compared with nonliving objects from 250-350 ms. A) Left parietal cortex (centre= -37.2, -48.9, 32.7). This region was identified using the top 5 positive peaks per image; all 10 of our participants had a peak in the volume (maximum radius=42.6 mm). B) Left middle temporal gyrus (centre= -54.0, -36.6, -0.9). This region was identified using the top 15 positive peaks per image; all 10 of our participants had a peak in the volume (maximum radius=23.2 mm). C) Left frontal cortex (centre= -32.5, 29.5, 21.0). This region was identified using the top 4 positive peaks per image; 6 of 10 participants had a peak in the volume (maximum radius=29.6 mm). D) Right middle frontal gyrus (centre=38.5, 25.0, 33.5). This region was identified using the top 19 positive peaks per image; 6 of 10 participants had a peak in the volume (maximum radius=11.9 mm).

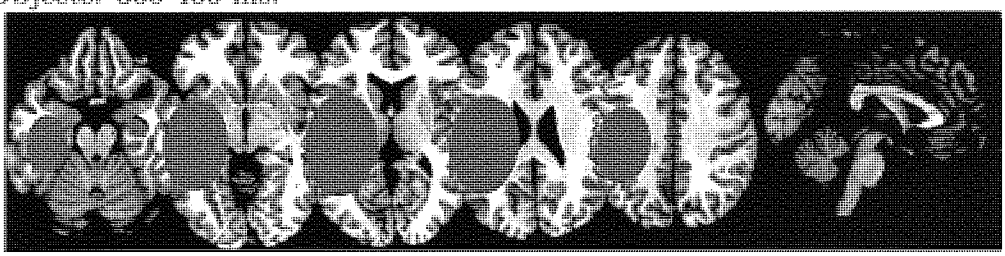
located in left parietal cortex (N=10, P=5, peak activation=1.96) (see Figure 5.3.11). In addition, a region located in left middle temporal gyrus showed greater power for living compared with nonliving objects (N=10, P=15, peak activation=1.67) (see Figure 5.3.11). Also, a region in left frontal cortex showed greater power for living compared with nonliving objects (N=6, P=4, peak activation=1.86), as did a region in right middle frontal gyrus (N=6, P=19, peak activation=1.31) (see Figure 5.3.11). The first region showing greater power for nonliving objects was located in right inferior parietal lobule (N=10, P=23, peak activation=1.17) (see Figure 5.3.12). In addition, a region located in right angular gyrus showed greater power for nonliving compared with living objects (N=6, P=9, peak activation=1.56) (see Figure 5.3.12).

FIGURE 5.3.12. Regions Showing Significantly Greater Power for Nonliving Objects: 250-350 ms.



Regions identified as showing significantly greater power for nonliving compared with living objects from 250-350 ms. A) Right inferior parietal lobule (centre=43.8, -32.7, 45.9). This region was identified using the top 23 negative peaks per image; all 10 of our participants had a peak in the volume (maximum radius=19.7 mm). B) Right angular gyrus (centre=46.0, -41,0, 19.5). This region was identified using the top 9 negative peaks per image; 6 of 10 participants had a peak in the volume (maximum radius=20.7 mm).

FIGURE 5.3.13. Region Showing Significantly Greater Power for Nonliving Objects: 300-400 ms.

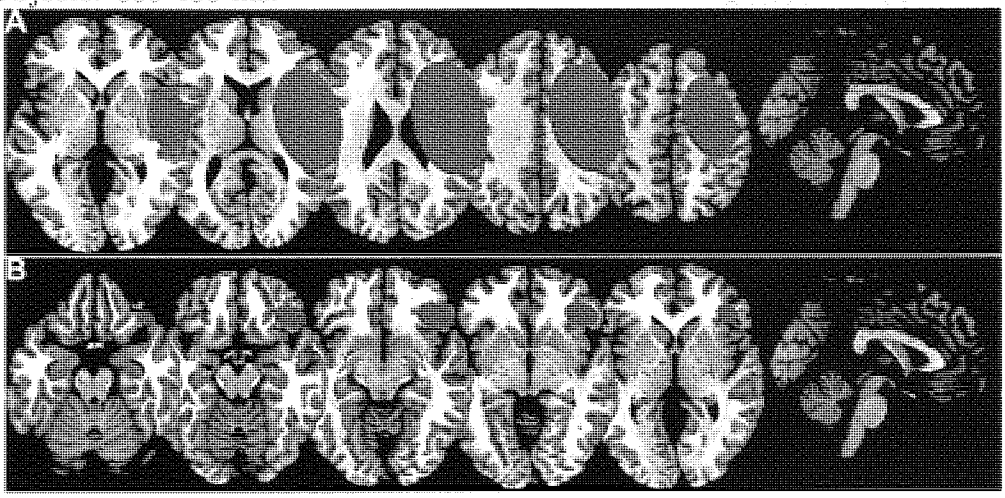


Region in left temporal to inferior parietal cortex (centre= -38.6, -24.4, 13.1) identified as showing significantly greater power for nonliving compared with living objects from 300-400 ms. This region was identified using the top 4 negative peaks per image; 8 of 10 participants had a peak in the volume (maximum radius=40.3 mm).

From 300-400 ms after seeing either a living or nonliving object, our peakomatic analysis identified a single region showing significant category-related differences. This region showed greater power for nonliving objects, and occupied a large extent of left temporal to inferior parietal cortex (N=8, P=4, peak activation=1.71) (see Figure 5.3.13).

From 350-450 ms after seeing either a living or nonliving object, our peakomatic analysis identified five regions showing significant category-related differences. Two of these regions showed greater power for living objects, whilst 3 regions showed greater power for nonliving objects. The first region showing greater power for living objects was located in right parietal to frontal cortex, centred on the right precentral gyrus (N=10, P=4, peak activation=1.86) (see Figure 5.3.14). In addition, a region located in right inferior frontal gyrus showed greater power for living compared with nonliving objects (N=6, P=13, peak activation=1.43) (see Figure 5.3.14). The first region showing greater power for nonliving objects was located in right parietal cortex, centred on the postcentral

FIGURE 5.3.14. Regions Showing Significantly Greater Power for Living Objects: 350-450 ms.



Regions identified as showing significantly greater power for living compared with nonliving objects from 350-450 ms. A) Right parietal to frontal cortex (centre=39.0, -4.5, 27.0). This region was identified using the top 5 positive peaks per image; all 10 of our participants had a peak in the volume (maximum radius=44.6 mm). B) Right inferior frontal gyrus (centre=41.5, 32.0, -9.5). This region was identified using the top 13 positive peaks per image; 6 of 10 participants had a peak in the volume (maximum radius=14.8 mm).

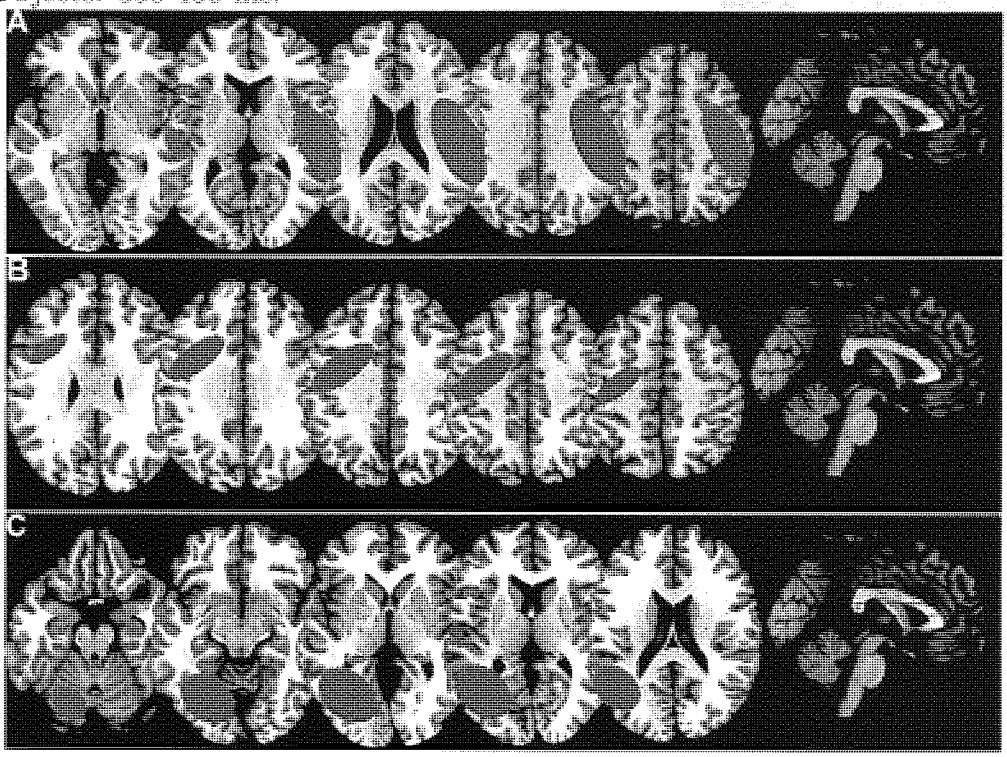
gyrus (N=9, P=5, peak activation=1.68) (see Figure 5.3.15). In addition, a region located in left frontal/premotor cortex showed greater power for nonliving compared with living objects (N=9, P=8, peak activation=1.53), as did a region centred on the posterior aspect of left middle temporal gyrus (N=7, P=4, peak activation=2.12) (see Figure 5.3.15).

From 400-500 ms after seeing either a living or nonliving object, our peakomatic analysis identified five regions showing significant category-related differences. One of these regions showed greater power for living objects, whilst 4 regions showed greater power for nonliving objects. The region showing greater power for living objects was centred on the right supramarginal gyrus (N=8, P=8, peak activation=1.69) (see Figure 5.3.16). The first region showing greater power for nonliving objects was located in left inferior frontal gyrus (N=7, P=6, peak activation=1.84) (see Figure 5.3.17). In addition, a region located in right precentral gyrus showed greater power for nonliving compared with living objects (N=7, P=12, peak activation=1.39) (see Figure 5.3.18). Also, a region centred on the left anterior cingulate showed greater power for nonliving compared with living objects (N=6, P=7, peak activation=1.61), as did a region in the right inferior parietal lobule (N=6, P=13, peak activation=1.56) (see Figure 5.3.18).

5.4. Discussion

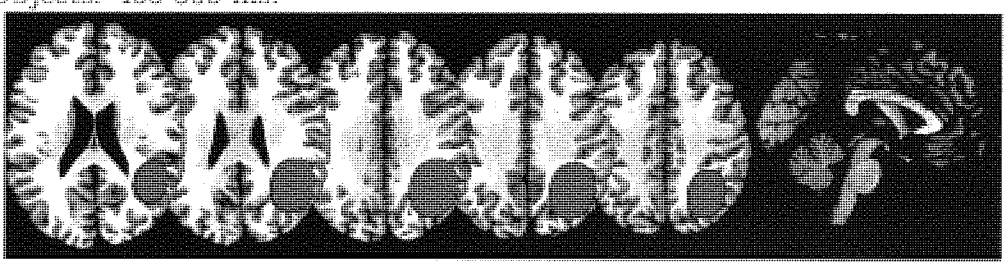
We sought to determine the time-course of category-specificity by directly contrasting living to nonliving objects in small, overlapping windows. Our findings show very early category-specific differences in the brain. Within 100 ms of seeing an object, regions in right superior temporal gyrus and right frontal cortex showed greater power for living objects, whilst regions in left inferior to middle frontal cortex and right supramarginal gyrus showed greater power for nonliving objects. This was followed by greater power for living objects from 50-150 ms in right angular gyrus, and greater power for nonliving

FIGURE 5.3.15. Regions Showing Significantly Greater Power for Nonliving Objects: 350-450 ms.



Regions identified as showing significantly greater power for nonliving compared with living objects from 350-450 ms. A) Right parietal cortex (centre=46.3, -21.0, 28.7). This region was identified using the top 9 negative peaks per image; 9 of 10 participants had a peak in the volume (maximum radius=39.4 mm). B) Left frontal/premotor cortex (centre= -34.0, -2.7, 40.7). This region was identified using the top 8 negative peaks per image; 9 of 10 participants had a peak in the volume (maximum radius=29.6 mm). C) Left middle temporal gyrus (centre= -35.6, -59.1, 12.4). This region was identified using the top 4 negative peaks per image; 7 of 10 participants had a peak in the volume (maximum radius=32.8 mm).

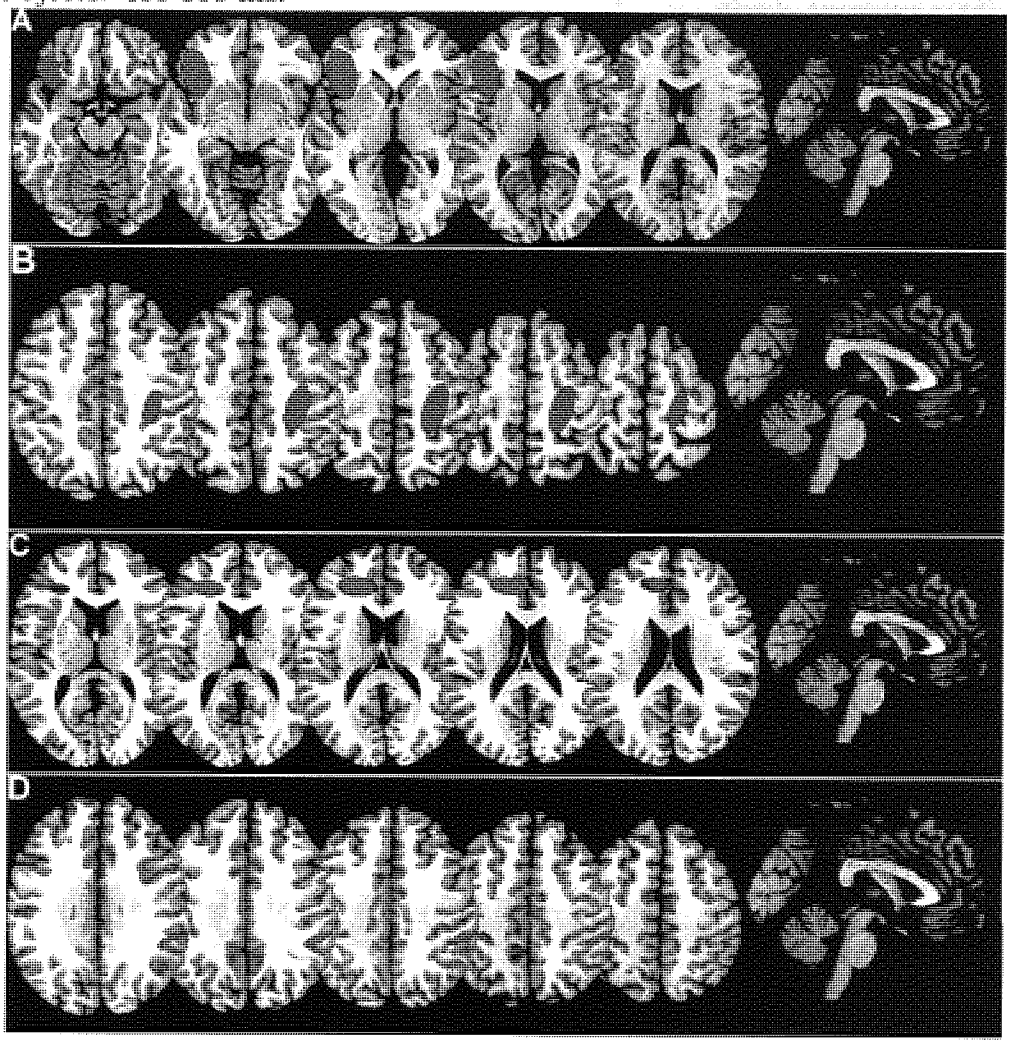
FIGURE 5.3.16. Region Showing Significantly Greater Power for Living Objects: 400-500 ms.



Region in right supramarginal gyrus (centre=36.0, -54.0, 33.4) identified as showing significantly greater power for living compared with nonliving objects from 400-500 ms. This region was identified using the top 8 positive peaks per image; 8 of 10 participants had a peak in the volume (maximum radius=25.3 mm).

objects at this same time point in right occipital cortex. From 100-200 ms, we found greater power again in right angular gyrus for living objects, as well as greater power for living objects in right middle frontal gyrus. From 100-200 ms, there was greater power for nonliving objects in right inferior parietal lobule. Again, at 150-250 ms we found greater power for living objects in right angular gyrus, whilst a region in right anterior superior frontal gyrus and left inferior frontal cortex showed greater power for

FIGURE 5.3.17. Regions Showing Significantly Greater Power for Nonliving Objects: 400-500 ms.



Regions identified as showing significantly greater power for nonliving objects compared with living objects from 400-500 ms. A) Left inferior frontal gyrus (centre= -4.29, 39.0, 20.6). This region was identified using the top 6 negative peaks per image; 7 of 10 participants had a peak in the volume (maximum radius=29.7 mm). B) Right precentral gyrus (centre=26.1, -26.1, 55.3). This region was identified using the top 12 negative peaks per image; 7 of 10 participants had a peak in the volume (maximum radius=17.9 mm). C) Left anterior cingulate (centre= -19.5, 38.0, 18.0). This region was identified using the top 7 negative peaks per image; 6 of 10 participants had a peak in the volume (maximum radius=18.4 mm). D) Right inferior parietal lobule (centre=51.0, -37.5, 41.5). This region was identified using the top 13 negative peaks per image; 6 of 10 participants had a peak in the volume (maximum radius=13.1 mm).

nonliving objects. At 200-300 ms, we again saw greater power for living objects in the right angular gyrus, as well as greater activation for living objects in right middle frontal gyrus and left angular gyrus. During this same time window, we found greater power for nonliving objects in left middle temporal gyrus. From 250-350 ms, we found greater power for living objects again in right middle frontal gyrus, as well as regions in left parietal cortex, left middle temporal gyrus, and left frontal cortex. At this same time point, we found greater power for nonliving objects in the right inferior parietal lobule and right angular gyrus. From 300-400 ms, we found greater power for nonliving objects in an extensive region from left temporal to inferior parietal cortex, whilst no regions showed greater power for living objects. From 350-450 ms, we found greater power for

living objects in an expansive region in right frontal to parietal cortex, as well as a region in right inferior frontal gyrus. During this same time window, we found greater power for nonliving objects in right parietal cortex, left frontal cortex including premotor cortex, and left middle temporal gyrus. Finally, at 400-500 ms, we found greater power for living objects in right supramarginal gyrus. In addition, at this same time point, we found greater power for nonliving objects in left inferior frontal gyrus, right precentral gyrus, left anterior cingulate, and right inferior parietal lobule.

Our findings suggest that the earliest differences between living and nonliving objects occur in more dorsal regions of the brain. We found greater power for living objects in a region in right superior temporal gyrus and right frontal cortex within the first 100 ms of target object onset, whilst we found greater power for nonliving objects in left inferior to middle frontal cortex and right supramarginal gyrus. We continued to find greater power within the dorsal stream for living objects (right angular gyrus) from 150-250 ms post target object onset, and we began to see the earliest differences in the ventral stream at this time point, with greater power for nonliving objects in occipital cortex.

Looking within ventral temporal cortex, we found an interesting pattern of activation unfolding over time. The first region showing category-specific differences was a region in occipital cortex in the right hemisphere that showed greater power for nonliving than living objects from 50-150 ms post-stimulus. We then found a region in more lateral middle temporal gyrus in the left hemisphere showing greater power for nonliving objects from 200-300 ms, followed by a region located more medially showing greater power for living objects from 250-350 ms post target object onset. This is followed by a region in left middle temporal gyrus showing greater power for nonliving objects from 350-450 ms post target object onset. It is important to be cautious about interpreting the direction of these effects. As demonstrated in Chapters 3 and 4, different mechanisms can produce a similar effect. For example, we do not know if greater power for nonliving objects initially is a consequence of differences in the level of synchrony exhibited (i.e., increased power for both objects), or whether it is a consequence of a difference in the level of desynchronisation within the region (i.e., decreased power for both objects). What is interesting, given the cascade model framework, is that there seems to be early and later differences within the ventral stream. These findings are in line with the cascade model, which predicts both bottom-up and top-down effects during object naming (Humphreys et al., 1988). That is, perceptual differences between living and nonliving things can have a knock-on effect into the semantic system. In much the same way, enhanced competition within the semantic system for one class of objects (i.e., living things) will mean that stored structural descriptions will be re-accessed in order to resolve the conflict. Therefore, our findings of both early and later effects within the ventral stream support this model of naming. Importantly, these regions should be explored further with time-frequency spectrograms, to gain a better sense of the direction and timing of these effects.

Within regions thought to be associated with motor-related properties of objects, we also found an interesting pattern of activation. For example, we found a region in right inferior parietal lobule showing greater power for nonliving objects from 100-200 ms post target object onset, and again at 250-350 ms post target object onset. We then found a region in left premotor cortex showing greater power for nonliving objects from 350-450

ms post target object onset. Again at 400-500 ms, we found greater power for nonliving objects compared to living objects in right precentral gyrus. We need to again be cautious with our interpretation, as we do not know whether these differences reflect increased or decreased power for living and nonliving objects. Again, probing these regions to assess the direction and specific timing of these effects is warranted. However, that we find motor-associated regions of the cortex showing differences suggests tentative support for the sensory/motor model (Martin, 1998) of object processing.

One other important region showing differences between living and nonliving objects is right superior temporal gyrus. This region exhibited greater power for living than nonliving objects within the first 100 ms of seeing a target object. Certainly, Chao et al. (2002) reported greater activation in this region using fMRI for living than nonliving objects. In addition, this region has been shown to be activated to biological motion (e.g., Beauchamp et al., 2004). According to the sensory/motor model, this region is recruited because of the biological motion associated with living things (Martin, 1998). It is interesting that this region shows a very early difference between living and nonliving objects. Again, it is important to be cautious because we do not know the direction of the difference (i.e., synchronisation or desynchronisation), however these findings are also supportive of the sensory/motor model.

Taken together, these findings suggest that there are temporal differences in the processing of living and nonliving objects. Generally, there are early differences within the dorsal stream, with differences within the ventral stream occurring at a slightly later time. Our findings lend support to the cascade model of object processing, as we find early and later effects within the ventral stream, suggesting an initial activation of stored structural descriptions, activation within the semantic system, and re-activation of the structural description system to resolve conflict (Humphreys et al., 1988). The specific timing and direction of these effects should be explored further using time-frequency spectrograms. In addition, we find regions showing category-specific differences that have been shown previously to respond differentially to living and nonliving objects. These regions lend support the sensory/motor model of object processing (Martin, 1998), as we find regions in motor cortex and motion-related areas of the brain, in addition to differences within ventral temporal cortex. These regions should also be explored further to assess the direction and specific timing of these effects.

CHAPTER 6

How Does Level of Processing Influence Living and Nonliving Object-Processing?

6.1. Introduction

Objects can be categorised at many different levels. For example, if presented with a picture of a dog, you would be correct in identifying it as living, an animal, a dog, or even providing the specific breed of dog (e.g., Dalmatian). Interestingly, several studies have shown that patients with category-specific impairments in identifying objects at the basic level (e.g., "dog") can have relatively intact performance when the given task requires them to sort items into their respective categories (e.g., "animal", Farah & Wallace, 1992;Forde et al., 1997; Moss et al., 1998). In addition, the types of errors made by these patients often involve producing semantically-related responses (e.g., saying "cat" for "dog"; Caramazza & Shelton, 1998). This suggests that, for at least a portion of patients, the impairment might occur as a result of distinguishing amongst highly similar items, which is not an issue when subjects are asked to provide the category or domain name of an item. In addition to evidence from patients, research has demonstrated this effect for normal participants under speeded conditions (e.g., Vitkovitch, Humphreys, & Lloyd-Jones, 1993). For example, Vitkovitch et al. (1993) asked participants to name pictures that had previously been categorised (see Humphreys et al., 1988) as either structurally similar or dissimilar under a speeded response condition. Structurally similar items were all drawn from living things (animals, birds, insects, fruits, and vegetables), whilst all but one category of dissimilar items were drawn from nonliving things (living things: body parts; nonliving things: building parts, clothing, furniture, household items, kitchen utensils, tools, toys, vehicles, and weapons). Vitkovitch et al. counted the number of different names produced in error (e.g., "zebra" called "tiger", "giraffe", or "horse") for each item, and found that there were more incorrect names produced for the structurally similar items than dissimilar items, and that the types of errors involved producing names of items that were visually and semantically related to the target item. This effect of high similarity has previously been discussed in Chapter 1.

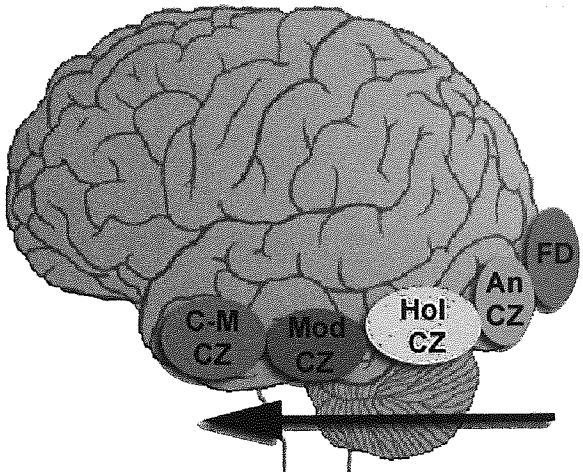
Theories of object naming have been proposed that attempt to explain this effect of high similarity on naming performance. Perhaps the most complete account is the "convergence zone" (CZ) hypothesis, first proposed by Damasio in 1989. This hypothesis has been elaborated to explain category-specific effects in particular (Barsalou, 1999; Simmons & Barsalou, 2003). We will first describe the hypothesis and its elaboration, and then discuss how this model of object naming attempts to account for the influence of similarity. According to this hypothesis, processing an object activates sensorimotor regions associated with its different attributes, along with an intermediate region that binds features together. So, for example, if you were presented with a picture of a dog,

hierarchically organised neurons in the visual system would respond to the visual features of the image ("feature detectors": e.g., line orientations, surface textures, colour, and orientation). The pattern of activation across these feature detectors would represent the dog in visual perception (Palmer, 1999; Zeki, 1993). Similar patterns of activation in other regions of the brain would represent other modality-specific information (e.g., touch: "soft", "furry"; sound: "woof"). In higher level association areas of the brain, neuronal firing then serves to conjoin patterns of activation across these various modalities. In addition, when required to recall information about an item seen previously (e.g., during imagery, conceptual processing, and other cognitive tasks), this region then serves to reactivate the patterns of firing within the various sensorimotor regions (Barsalou, 1999). These higher-level regions have been termed *convergence zones*.

The CZ theory was elaborated by Simmons & Barsalou (2003), who proposed in their Conceptual Topography theory that CZs are structured hierarchically such that, for visual processing, more posterior cortical regions bind features of a specific type (e.g., visual shape) whilst more anterior regions combine features into more complex configurations (e.g., visual shape, colour and visual motion) (see Figure 6.1.1). This organisational hierarchy is based on the *similarity-in-topography* (SIT) principle. SIT argues that the distance between neurons within a region of cortex reflects how similar the features are that each neuron codes for. Neurons that lie close together will code highly similar features, whilst those further away code less similar features. Using the SIT principle, Simmons & Barsalou argued that, within the visual system, neurons responsible for conjoining features into more complex configurations should lie just downstream from areas that bind features of a specific type (i.e., feature detectors). Within this architecture, then, Simmons & Barsalou argue for modality CZs that lie at the end-point of visual processing in the ventral pathway, likely to be situated in anterior inferior temporal cortex or in parts of perirhinal and/or entorhinal cortices based on their projections from inferior temporal cortex (Tanaka, 1997) and reciprocally with other polymodal brain areas (Murray & Richmond, 2001). These CZs then capture information about different object categories because they code for the pattern of neuronal firing across conjunctive areas, and the topography of these conjunctive areas reflects informational structure based on SIT (importantly, modality CZs integrate the properties of a category on a single modality; e.g., visual information). This organisational principle has been used to explain the over-representation of living-things deficits in the category-specific literature (see Chapter 1), and also to explain the nature of errors exhibited by these patients as described at the outset of this chapter. For object categories that share many features (e.g., animals, see Chapter 1), damage to the region in the CZ containing their conjunctive neurons will produce a selective impairment for that type of knowledge, because those neurons will occupy a fairly circumscribed region of cortex based on SIT. For object categories having low similarity (e.g., tools), the resultant dispersion of conjunctive neurons will result in intact recognition.

In addition to modality CZs, Simmons & Barsalou (2003) argue for the existence of cross-modal CZs, which serve to integrate information across the different modalities. The most likely candidate location for cross-modal CZs is in perirhinal cortex (e.g., Bussey, Saksida, & Murray, 2002; Higuchi & Miyashita, 1996; Murray, Gaffan, & Mishkin, 1993;

FIGURE 6.1.1. Elements of the Conceptual Topography Theory and Proposed Neural Locations.



Schematic showing elements of the Conceptual Topography theory as posited by Simmons & Barsalou (2003), illustrating posterior to anterior visual object processing along the ventral stream. Boundaries of important processing areas should be interpreted as rough approximations, and serve as illustration only. FD=Feature Detectors; Areas V1, V2, V3, V4, MT, and TEO are posited to have neurons coding for specific visual features of an object. An CZ=Analytic Convergence Zones; This area corresponds to area TE and neurons in inferior temporal cortex. Hol CZ=Holistic Convergence Zones; Includes areas of the lateral occipital complex (LOC) and fusiform gyrus. Mod CZ=Modality Convergence Zones; Posited to occupy anterior inferior temporal cortex and parts of perirhinal and/or entorhinal cortices. C-M CZ=Cross-Modal Convergence Zones; Proposed neural location includes perirhinal cortex.

Parker & Gaffan, 1998). For example, Bussey et al. (2002) proposed that the ventromedial temporal region of the brain, specifically the perirhinal cortex, might play a crucial role in object identification based on their finding in monkeys that lesions to this area disrupt discrimination amongst objects that require access to conjunctions of features. In addition, Parker & Gaffan (1998) had monkeys learn a conditional discrimination problem using flavours and visual stimuli. The monkeys were first trained by presenting them with a food item that signalled they should displace 1 of 2 objects in order to receive an additional food reward. After the monkeys could perform this task in either lighted or dark conditions, the researchers lesioned perirhinal cortex and found that the monkeys could no longer use the flavour properties of the food to guide their choice, and they were at chance performance levels. Thus, they were unable to use the conjunctive information to perform the task. Finally, perirhinal lesions have been shown to impair the ability to link both auditory and tactile properties of a stimulus with both visual and gustatory properties (e.g., Higuchi & Miyashita 1996; Murray, et al., 1993). These findings have led some researchers to argue that the role of perirhinal cortex in primates is analogous to the conceptual knowledge system store accessed for semantic memory in humans (e.g., Murray & Richmond, 2001).

The idea that anterior temporal cortex, specifically perirhinal cortex, might play a crucial role in object identification in humans generally, and semantic memory specifically,

was tested using functional brain imaging by Tyler et al. (2004). They imaged 19 healthy subjects whilst they silently named a series of objects at either the basic (e.g, "dog") or domain (e.g., "living") level. For both tasks, posterior inferior temporal cortex was recruited bilaterally. However, when the task required access to more detailed information to differentiate between objects (i.e., basic-level naming), anteromedial temporal regions of the left hemisphere were recruited (see also Moss et al., 2005). When the task did not require such fine-grained differentiation (i.e., domain-level naming), activation was limited to bilateral posterior regions of the fusiform gyrus (a similar finding was reported by Joseph & Gathers, 2003 when they manipulated structural similarity directly). In addition, Tyler et al. overlaid their fMRI findings on anatomical scans from four herpes simplex encephalitis (HSE) patients and found close correspondence between the patient lesion sites and the fMRI activation of their normal participants. Two of these HSE patients were also run behaviourally on the fMRI task Tyler et al. used with their normal participants. The HSE patients were found to perform at relatively normal levels on the domain-level naming task (94 and 99% correct), but were significantly impaired on the basic-level naming task (34 and 30% correct). To subsequently test the claim that anterior temporal cortex should show greater activation for naming living than nonliving things at the basic level (due to higher similarity for living things), Moss et al. (2005) scanned 12 normal participants using fMRI whilst they silently named pictures of living and nonliving objects at either the basic or domain level in two blocked runs. Based on Tyler et al.'s previous findings, Moss et al. investigated activation in left perirhinal and entorhinal cortices only, and therefore set a threshold for significance at p=0.001 uncorrected. Direct comparison of basic-level naming of living and nonliving objects produced a cluster of significant activation in entorhinal cortex (BA 28). No differences were found for domain-level naming. Moss et al. also compared anatomical scans from 3 patients with HSE showing category-specific impairments for living things with 3 patients diagnosed with semantic dementia. Based on this analysis, they argue that damage to anteromedial temporal cortex produces selective deficits for living things.

We set out to test object processing along the ventral stream using a MEG task in which we varied the level of processing required to identify objects, either asking participants to name items at the basic level or the domain level. Based on the previous evidence, we predicted that we should see a divergence of visual processing along the ventral stream, with basic-level naming producing greater and more extensive anterior ventral temporal cortex activity compared with domain-level naming. In more posterior regions of the ventral stream, we predicted equal activation for both levels of processing. We opted to use MEG for the task because it allowed us to see the time-course of object processing along this ventral stream, whilst providing us the opportunity to localise the sources of differential activation.

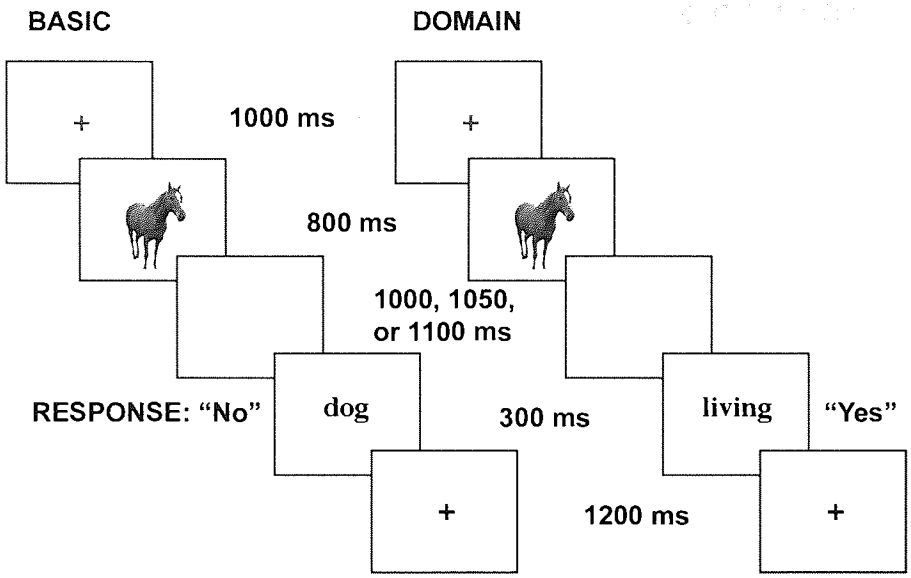
6.2. Methods

6.2.1. Study Procedure. Nine right-handed volunteers (Mean Age=31.3 years, range=22-41 years, 5 males) participated in the MEG study. During scanning, participants performed a categorisation task in which they were asked to categorise pictures of objects at either the basic level or the domain level (see Figure 6.2.1). Participants were first shown

a picture of a target object, and after a brief variable delay, they were presented with either a basic-level object name or a domain-level name. Participants were instructed to respond by button press as quickly and accurately as possible, indicating whether the basic or domain-level name matched the target object. Participants responded using a 2-button response box held in their right hand. After piloting an event-related design on a separate group of participants (N=10) where both level of processing and category membership were randomised across the entire run, we decided that a purely random design would not be appropriate for this study. Specifically, we found significantly faster reaction times when participants categorised objects at the basic level (mean=622.0 ms, SD=159.7 ms; acc=106.7/120, 88.9%) versus the domain level (mean=843.8 ms, SD=209.2 ms; acc=89.9/120, 74.9%) [$F(1,9)=82.618$, $p<0.001$]. We assume that this effect is a consequence of word frequency. For example, Rosch et al. (1976) showed that basic-level naming is one of the first categorisations made of the environment, in addition to being one of the earliest to be named by children. Rosch and colleagues also have shown that adults are faster at categorising most objects at the basic level compared with the superordinate or subordinate level (Mervis & Rosch, 1981; Rosch, 1978). Our findings are contrary to the results reported by Moss et al. (2005), who found faster reaction times for naming at the domain level compared with the basic level. This difference might have to do with variations in the task, as Moss et al. used a naming task, whilst we used a categorisation task. Irregardless of the cause of this discrepancy, we felt the need to try to vary the MEG design in order to try and balance the overall difficulty of basic and domain-level naming. Thus, to control for this task difference, we opted to block trials by level of processing, whilst allowing category membership to vary within each block. Therefore, participants were first shown a screen indicating which level of specificity they would be required to categorise the subsequent pictures at (i.e., "basic-level name" or "living/nonliving"), followed by a series of 20 pictures. This was done so that participants would be prepared for the level of processing required. In this way, even though basic naming is more natural, participants would at least be prepared for domain naming, and this should reduce differences between the two conditions. A total of six blocks were shown during the entire scan, with blocks alternating between the basic and domain level. Across participants, we then counterbalanced the presentation order of basic and domain-level blocks to minimise any potential practise and/or timing effects. Participants were instructed to respond by pressing the left button with their right index finger for "yes" (i.e., congruent) and the right button with their right middle finger for "no" (i.e., incongruent).

Target objects included 60 exemplars drawn from 3 living (plants, animals, fruits and vegetables) and 3 nonliving (tools, transport, furniture) categories (see Table 1 for a list of exemplars). For this study, we again ensured that stimuli were matched on pre-test naming speed (Living Mean=1220.7 ms, SD=274.4 ms; Nonliving Mean=1222.8, SD=278.4 ms), familiarity (Living Mean 3.56/5, SD=0.61; Nonliving Mean=3.72/5, SD=0.59), typicality (Living Mean=3.86/5, SD=0.39; Nonliving Mean=3.96/5, SD=0.34), and visual complexity (Living Mean=2.69/5, SD=0.37; Nonliving Mean=2.52/5, SD=0.30) (see Table 2). During scanning, each target object was presented four times. On 2 occasions, the target object was shown with a domain-level label, and on 2 occasions it was shown with a

FIGURE 6.2.1. Example Trial from Study 2.



Participants were shown a 1000 ms red fixation cross, signalling the beginning of a trial. They then saw a target object for 800 ms, followed by a variable delay (1000, 1050, or 1100 ms). Participants then saw a 300 ms probe at either the basic level (i.e., "dog") or domain level (i.e., "living"), followed by a black fixation cross for 1200 ms. They were instructed to decide as quickly and accurately as possible if the probe matched the target object and respond via button press.

basic-level label. For both of these conditions, the target object was congruently presented with its appropriate label (e.g., dog picture presented with either "dog" or "living" label) once, and incongruently presented with another label (e.g., dog picture presented with either "lily" or "nonliving" label) once. For incongruent trials at the basic-level, we ensured that the non-matching label did not come from the same general category. So, for example, a picture of an item from the animal category would be presented with a label drawn from either plants or fruits and vegetables. We did this to ensure that participants were still required to access the semantic system at the same level for basic-level congruent and incongruent trials, whilst not increasing the difficulty for incongruent trials by having the label come from the same general category (e.g., dog picture presented with an animal exemplar name). We also felt that presenting an across-domain non-matching exemplar name (e.g., dog picture with an exemplar name from tools, transport or furniture) might require less processing along the ventral stream, and thus we wanted to equate the difficulty of the task. A total of 240 trials were shown during the scan, half of which included a living target object and the other half a nonliving target object. The order of trial presentation was randomised across participants.

6.2.2. MEG Data Acquisition and Analyses. Neuromagnetic data were recorded at a 600 Hz sampling rate with a bandwidth of 0-150 Hz using a CTF 275 MEG system (VSM MedTech Ltd., Canada). We again used synthetic 3rd gradient balancing to remove background noise on-line. Fiducial coils were placed on the nasion, left preauricular, and right preauricular sites for each participant, and these coils were energised before each run to localise the participant's head with respect to the MEG sensors. Total head displacement was measured after each run and could not exceed 5 mm for inclusion in the source analyses. Prior to scanning, participants' head shapes and the location of fiducial coils

TABLE 1. Living and Nonliving Object Exemplars from Study 2.

LIVING			NONLIVING		
Plants	Animals	Fruits/Vegetables	Tools	Transport	Furniture
Clover	Cow	Apple	Axe	Aeroplane	Armchair
Daffodil	Deer	Cucumber	Drill	Bicycle	Bed
Dandelion	Eagle	Lemon	Garden Fork	Boat	Bunk beds
Grass	Goat	Lettuce	Hammer	Limousine	Chair
Palm	Hippo	Orange	Saw	London Bus	Chest
Rose	Penguin	Peach	Scissors	Lorry	Chest of Drawers
Sunflower	Pike	Pear	Screwdriver	Taxi	Deck Chair
Tree	Rabbit	Pepper	Spanner	Train	Desk
Water-lily	Raccoon	Potato	Tape Measure	Tram	Table
Wheat	Wolf	Strawberry	Workbench	Van	Wardrobe

TABLE 2. Naming Speed, Familiarity, Typicality, and Complexity Ratings for Living and Nonliving Objects from Study 2.

Measure	N	Living Mean (SD)	Nonliving Mean (SD)
Naming Speed (ms)	23	1220.7 (274.4)	1222.8 (278.4)
Familiarity (/5)	21	3.56 (0.61)	3.72 (0.59)
Typicality (/5)	21	3.86 (0.39)	3.96 (0.34)
Complexity (/5)	20	2.69 (0.37)	2.52 (0.30)

For all tasks, participants were instructed to respond as quickly and accurately as possible. For the Naming Speed task, participants were presented pictures of objects in random order and were asked to name each item aloud. For Familiarity, Typicality, and Complexity, participants were asked to rate each picture on a scale from 1 (Low) to 5 (High). Paired samples t-tests showed that there were no significant differences between living and nonliving objects on any measure.

were digitised using a Polhemus Isotrak 3D digitiser (Kaiser Aerospace Inc.). These were again coregistered to high-resolution T1-weighted anatomical images for each participant acquired with a 3-Tesla whole-body scanner (3T Trio, Siemens Medical Systems) using in-house coregistration software.

Data for each participant were edited and filtered to remove environmental and physiological artefacts. Again, we applied a beamforming technique to assess sources of differences in processing living and nonliving objects at the basic and domain levels. For a first set of analyses to address differences in processing objects at either the basic or domain level, we utilised overlapping SAM frequency bins (1-10, 5-15, 10-20, 15-25, 20-30, 25-35, and 30-60 Hz) and directly contrasted basic-level ('active') compared to domain-level ('passive') naming from target object onset to 1 second after, collapsing across category membership. Spectral power changes between the 'active' and 'passive' periods were again calculated as a pseudo t-statistic (Vrba & Robinson, 2001). Each participant's data were then normalised and converted to Talairach space using statistical parametric mapping

(SPM99, Wellcome Department of Imaging Neuroscience, London, UK) for group-level comparisons.

For group-level analyses, we again utilised peakomatic to assess the distribution of image peaks across our participants. We tested a range of P values from 2 to 40 and after multiple comparisons correction were left with a number of significant clusters of positive and negative peaks. As with our previous analyses, if a region was identified as showing a significant difference across a range of P values, we chose the region for reporting purposes that yielded the largest N. In cases where several P values yielded the same N, we then chose the volume that had the smallest spatial extent. In addition, because we used overlapping frequency bins, a region could be identified as showing a significant effect across a range of frequency bins. In this case, we again chose to report the region that yielded the largest N, however, we also reported the entire frequency range over which the region showed a significant difference.

We used virtual electrodes to probe the time-frequency characteristics of areas showing group-level effects in our peakomatic analyses. These virtual electrodes were based on a covariance matrix constructed using a 2 second window from 1 s prior to target picture onset, to 1 s after the target object, using a wide band (1-65 Hz). Time-frequency plots were then computed on the virtual electrodes using the Stockwell Transform (Stockwell, Mansinha, & Lowe, 1996) for a window beginning 1 second prior to 1 second after target picture onset. Percent power change from baseline (the 1 s preceding target object onset) was computed at each frequency from 0-60 Hz for both basic and domain-level naming to assess mean (across epochs and participants) power increases and decreases for objects named at the basic level and those same objects named at the domain level. In addition, basic and domain-level target objects were directly contrasted at each region of interest across participants for a window from 100 ms prior to 1 second after target object onset, thresholded at $p<0.01$ uncorrected.

6.3. Results

6.3.1. Behavioural Findings. Behaviourally, we found a significant advantage for classifying items at the basic level [$F(1,8)=43.543$, $p<0.001$]. Thus, although we attempted to account for our pre-test findings of faster reaction times when classifying at the basic level by having participants categorise in blocks, we were ultimately not successful in equating performance between the two conditions. Participants continued to show a significant advantage for basic-level naming (mean=801.4 ms, SD=198.6 ms; accuracy rate=90.0%) compared with domain-level naming (mean RT=961.3 ms, SD=238.2 ms; accuracy rate=86.7%) when categorising items in a blocked fashion. Importantly, this should have little effect on the results of the basic versus domain-level analysis, per se, as the response occurred following the target object onset. The participants responded to a domain or basic-level label shown from 1000-1100 ms *after* the target object was displayed.

6.3.2. Source-Level and Time-Frequency Findings. We used SAM to identify sources of differential activity between basic and domain-level naming during the 1 s window after target object onset. We then used peakomatic to define significantly clustered

TABLE 3. Regions Showing Significant Differences Between Basic and Domain-Level Object Naming.

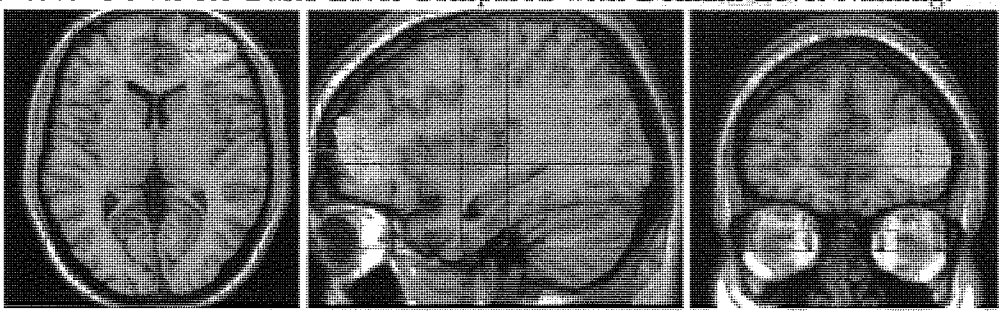
Location	N	P	Coordinates of Centre (x, y, z) [MNI]	Max Radius (mm)	Absolute Mean Value	Sign	Frequency Range (Hz)
Right Superior to Middle Frontal Gyrus	9	24	36.7, 51.3, 6.0	19.6	1.38	p	1-20
Right Superior Temporal Gyrus to Inferior Parietal Lobule	8	23	55.5, -43.5, 29.3	16.3	1.29	p	10-35
Right Inferior Frontal Gyrus	8	19	54.0, 1.5, 22.9	18.3	0.8	p	30-60
Left Occipito-Parietal Cortex	5	8	-25.8, -61.8, 30.0	13.7	1.5	p	25-35
Left Inferior Frontal Gyrus	5	22	-36.0, 23.4, 3.0	8.7	1.2	p	10-20
Right Inferior to Middle Occipital Gyrus	9	16	31.7, -79.0, 3.0	22.0	1.0	n	1-30
Left Precentral Gyrus	6	5	-52.5, -11.5, 39.5	27.3	1.4	n	15-30
Left Inferior Frontal Gyrus	6	10	-44.0, 26.5, 9.0	16.9	1.0	n	25-35
Right Inferior Frontal Gyrus	5	6	48.6, 34.2, 9.6	20.0	1.1	n	25-35
Left Postcentral Gyrus	5	6	-38.4, -19.8, 52.2	21.6	1.1	n	30-60

All regions identified as showing a significant group-level difference between basic and domain-level object naming during the 1 s window following target object onset. N=number of participants (out of 9) identified as having a peak within the volume. P=number of peaks used to identify the region. For regions identified in several of the overlapping bins, we chose the region yielding the largest N and report the associated P value. The sign column indicates the peak polarity: p=positive, n=negative. Positive values indicate those regions showing significantly greater power for basic-level object naming, and negative values indicate those showing significantly greater power for domain-level object naming. Frequency range indicates the range of frequencies (in 10 Hz bins) over which each region was identified as showing a significant difference.

peaks across our group of participants. We found ten distinct regions showing significant differences between basic and domain-level object naming (see Table 3). These included 5 regions showing significantly greater power for basic-level naming and 5 regions showing significantly greater power for domain-level naming during this 1 s time window.

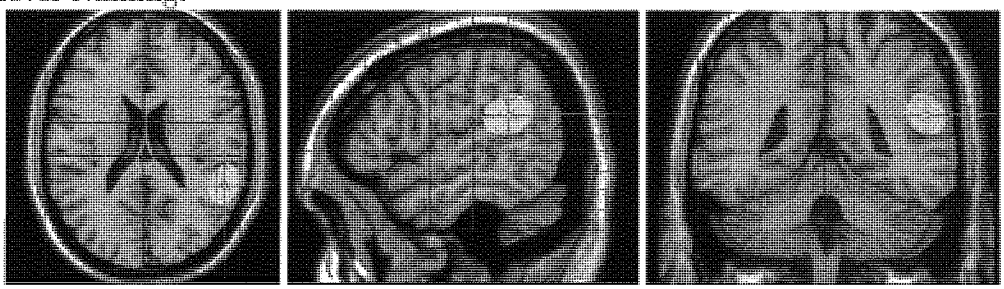
The analysis of positive peaks using peakomatic identified a region in right superior to middle frontal gyrus showing greater power for basic compared with domain-level object

FIGURE 6.3.1. Region in Right Superior to Middle Frontal Gyrus Showing Greater Power for Basic-Level Compared with Domain-Level Naming.



Axial, Sagittal, and Coronal views of the region in right superior to middle frontal gyrus identified as showing a significant group effect from 1-20 Hz in our SAM comparison of basic to domain-level object naming. The green crosshairs point to the centre of the sphere (Talairach coordinates= 37.1, 51.2, 6.0). This volume was identified with P set to the top 24 positive peaks for each participant; all 9 of our participants had a peak falling within this region (maximum radius=19.6 mm).

FIGURE 6.3.2. Region in Right Superior Temporal Gyrus to Inferior Parietal Lobule Showing Greater Power for Basic-Level Compared with Domain-Level Naming.

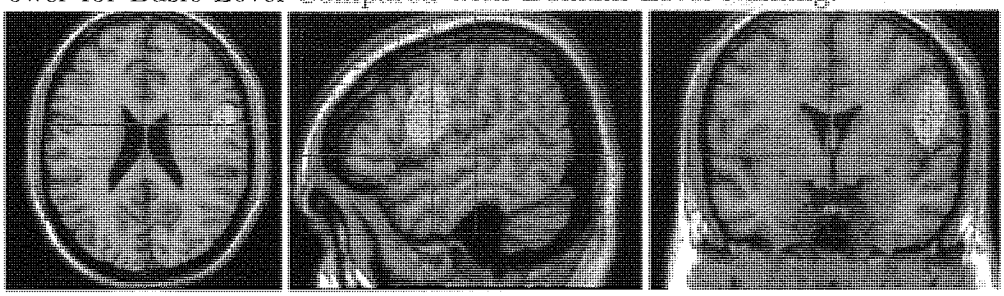


Axial, Sagittal, and Coronal views of the region in right superior temporal gyrus to inferior parietal lobule identified as showing a significant group effect from 10-35 Hz in our SAM comparison of basic to domain-level object naming. The green crosshairs point to the centre of the sphere (Talairach coordinates= 55.5, -43.5, 29.3). This volume was identified with P set to the top 23 positive peaks for each participant; 8 of 9 participants had a peak falling within this region (maximum radius=16.3 mm).

naming (see Figure 6.3.1). Using the top 24 positive peaks in each image, all 9 of our participants were found to have a peak falling within this region (maximum radius=19.6 mm, mean value=1.38). In addition to this region, we also found a region in right superior temporal to inferior parietal lobule (maximum radius=16.3, mean value=1.29) showing a peak for 8 participants, when using the top 23 peaks in an image (see Figure 6.3.2). A region in right inferior frontal gyrus (maximum radius=18.3, mean value=0.8) was also found to have a peak for 8 participants when using the top 19 peaks in an image (see Figure 6.3.3). Two additional regions were also found in left occipito-parietal cortex and left inferior frontal gyrus for 5 participants when using the top 8 and 22 peaks respectively (see Figure 6.3.4).

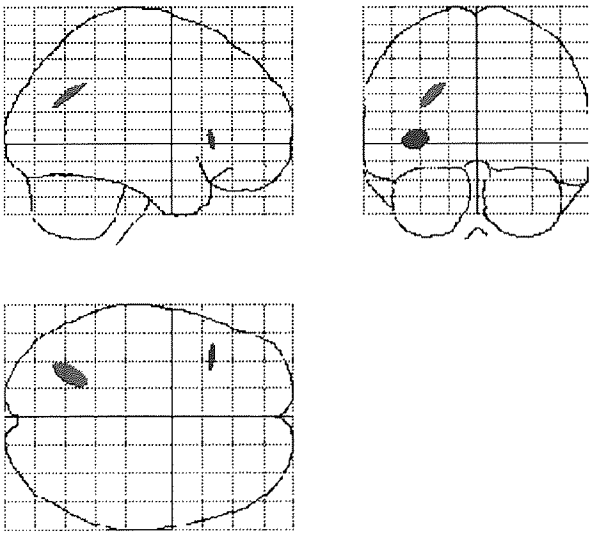
We constructed virtual electrodes to map the time-frequency characteristics of the regions in right superior to middle frontal gyrus, right superior temporal gyrus to inferior parietal lobule, and right inferior frontal gyrus for the subgroup of participants identified as having a peak in each volume. We chose these regions to focus on for further analysis because of the large number of participants having a peak in each region. Whilst this

FIGURE 6.3.3. Region in Right Inferior Frontal Gyrus Showing Greater Power for Basic-Level Compared with Domain-Level Naming.



Axial, Sagittal, and Coronal views of the region in right inferior frontal gyrus identified as showing a significant group effect from 30-60 Hz in our SAM comparison of basic to domain-level object naming. The green crosshairs point to the centre of the sphere (Talairach coordinates= 54.0, 1.5, 22.9). This volume was identified with P set to the top 19 positive peaks for each participant; 8 of 9 participants had a peak falling within this region (maximum radius=18.3 mm).

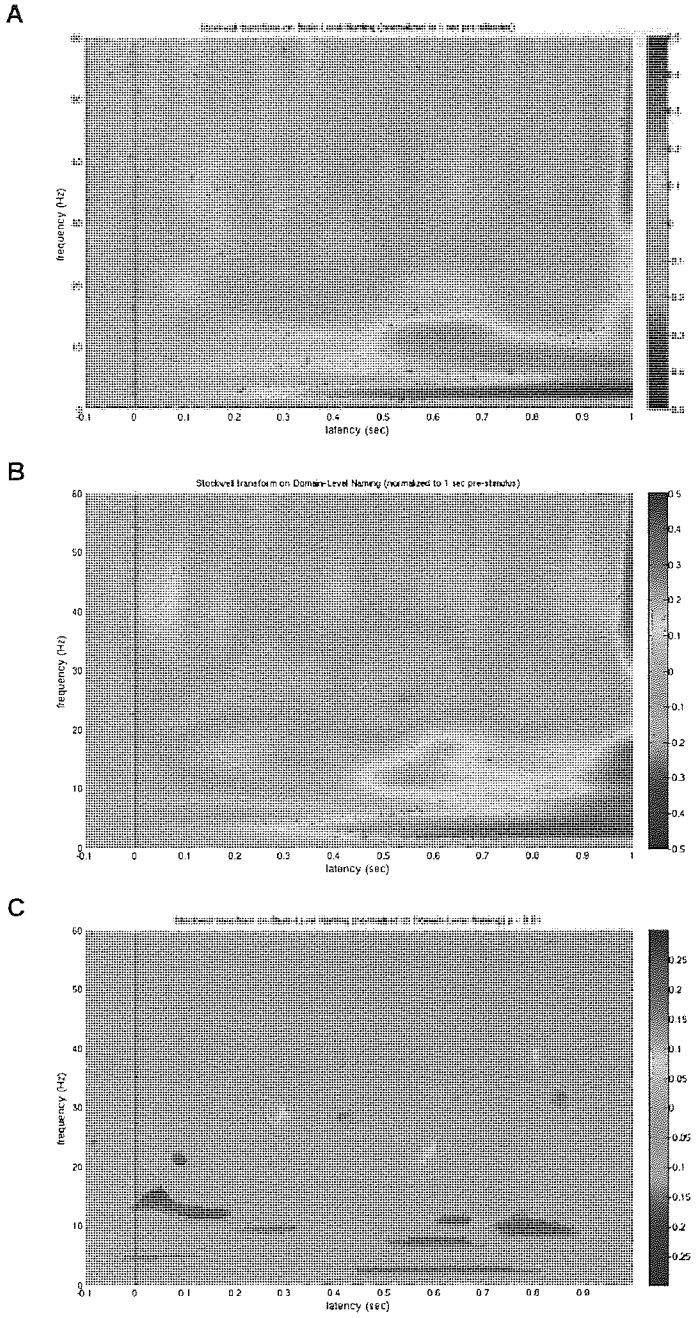
FIGURE 6.3.4. Two Regions Identified by Peakomatic as Showing Greater Power for Basic-Level Naming of Objects in Five Participants.



The two regions identified by peakomatic as showing significantly greater power for basic compared with domain-level object naming in 5 of 9 participants. Red=Left Occipito-Parietal Cortex; Blue=Left Inferior Frontal Gyrus.

might seem rather arbitrary, the larger number of participants suggests that these regions show greater consistency across our group of participants. In the region in right superior to middle frontal gyrus, we found early, significant differences between basic and domain-level objects (see Figure 6.3.5). Within 100 ms of seeing an object, there was greater low-frequency (approximately 1-20 Hz) power for basic-level compared with domain-level naming. Some of this activation occurred prior to stimulus onset. The early difference (prior to 300 ms) seems driven by a slight increase in power for basic-level naming, coupled with a slight desynchronisation (i.e., loss of power) for domain-level naming. After roughly

FIGURE 6.3.5. Time-Frequency Findings from Right Superior to Middle Frontal Gyrus.

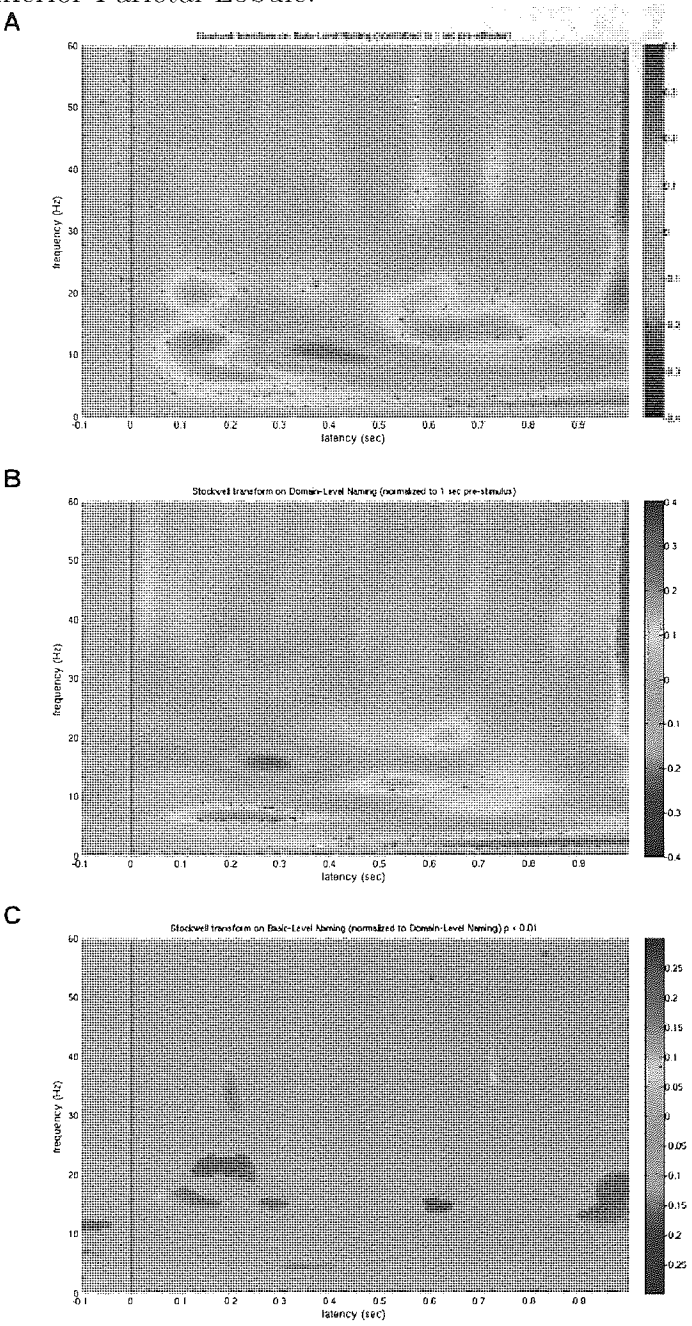


Time-frequency findings in right superior to middle frontal gyrus for all 9 participants. Target object onset is denoted by the solid line. A) Basic-level object naming compared to baseline; B) Domain-level object naming compared to baseline; C) Direct comparison of basic to domain-level object naming thresholded at $p<0.01$. Note the early difference in C (within 100 ms of target object onset, approximately 0-20 Hz) showing increased power for basic compared to domain-level object naming.

300 ms, this difference seems driven by increased power for basic-level object naming, with both basic and domain-level naming showing increased power in the low-frequency ranges at this later time.

In the region in right superior temporal gyrus to inferior parietal lobule, we found early, significant differences between basic and domain-level objects (see Figure 6.3.6). Beginning at roughly 100 ms after seeing an object, there was greater mid-frequency (approximately 10-40 Hz) power for basic-level compared with domain-level naming. This

FIGURE 6.3.6. Time-Frequency Findings from Right Superior Temporal Gyrus to Inferior Parietal Lobule.

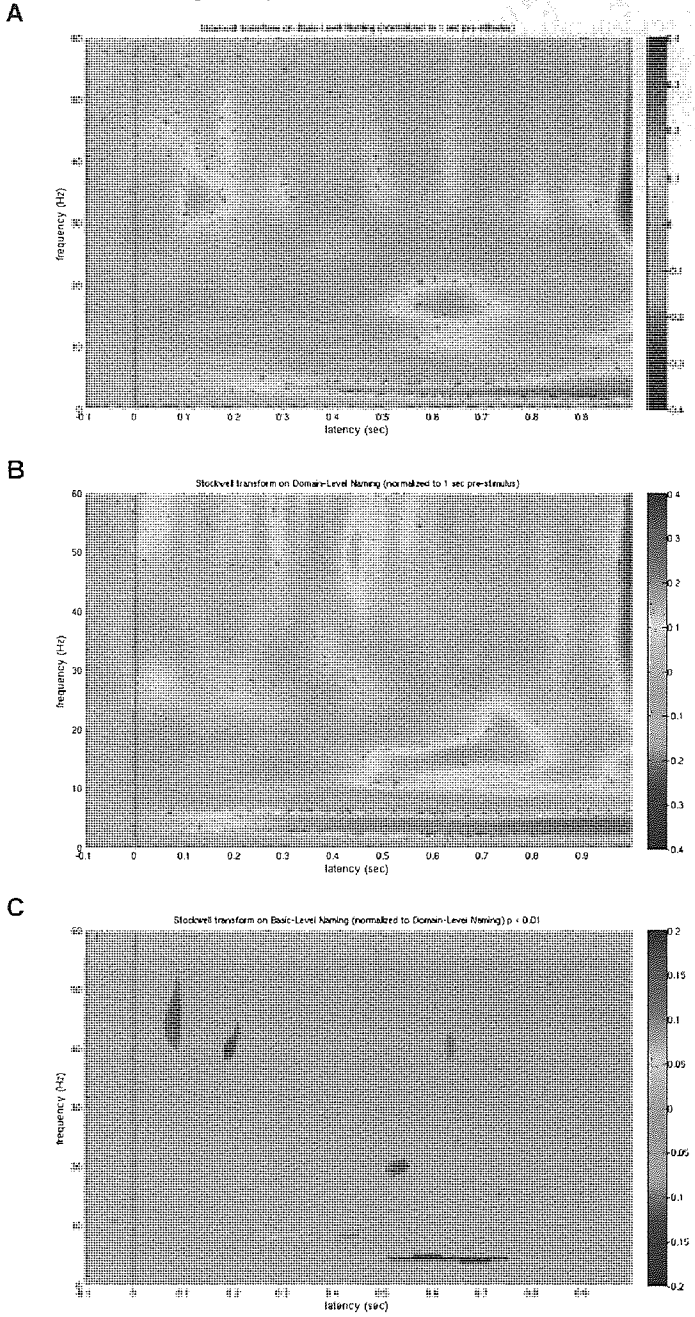


Time-frequency findings in right superior temporal gyrus to inferior parietal lobule for the subgroup of 8 participants identified as having a peak in the volume in our peakomatic analysis. Target object onset is denoted by the solid line. A) Basic-level object naming compared to baseline; B) Domain-level object naming compared to baseline; C) Direct comparison of basic to domain-level object naming thresholded at $p<0.01$. Note the early difference in C (within 100-300 ms of target object onset, approximately 10-40 Hz) showing increased power for basic compared to domain-level object naming.

difference seems driven by a larger increase in power for basic-level naming, coupled with a beta (approximately 20 Hz) desynchronisation for domain-level naming. In addition to this difference, there is another increase in power for basic-level naming compared to domain-level naming at a slightly later time (approximately 600 ms).

In the region in right inferior frontal gyrus, we also found early, significant differences between basic and domain-level objects (see Figure 6.3.7). Beginning at roughly 100 ms

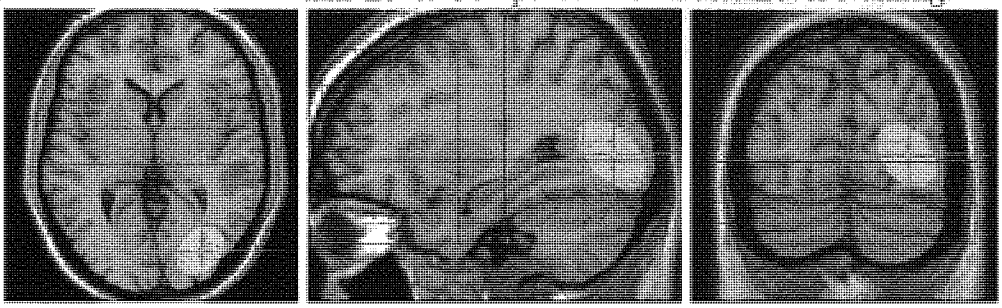
FIGURE 6.3.7. Time-Frequency Findings from Right Inferior Frontal Gyrus.



Time-frequency findings in right inferior frontal gyrus for the subgroup of 8 participants identified as having a peak in the volume in our peakomatic analysis. Target object onset is denoted by the solid line. A) Basic-level object naming compared to baseline; B) Domain-level object naming compared to baseline; C) Direct comparison of basic to domain-level object naming thresholded at $p<0.01$. Note the early difference in C (within 100-200 ms of target object onset, approximately 40-60 Hz) showing increased power for basic compared to domain-level object naming.

after seeing an object, there was greater high frequency (approximately 40-60 Hz) power for basic-level compared with domain-level naming. This difference seems driven by an increase in power for basic-level naming, with no increase for domain-level naming. In addition to this early difference, there is also another, later (approximately 600 ms after target object onset) difference between basic and domain-level object naming. This later difference also appears to result from an increase in power for basic-level naming, with no increase for domain-level naming.

FIGURE 6.3.8. Region in Right Inferior to Middle Occipital Gyrus Showing Greater Power for Domain-Level Compared with Basic-Level Naming.



Axial, Sagittal, and Coronal views of the region in right inferior to middle occipital gyrus identified as showing a significant group effect from 1-30 Hz in our SAM comparison of basic to domain-level object naming. The green crosshairs point to the centre of the sphere (Talairach coordinates= 31.7, -79.0, 3.0). This volume was identified with P set to the top 16 negative peaks for each participants; all 9 of our participants had a peak falling within this region (maximum radius=22 mm).

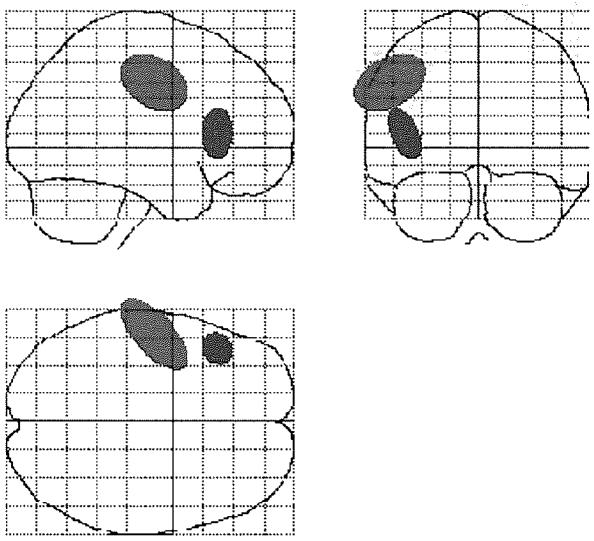
The analysis of negative peaks using peakomatic identified five regions showing greater power for domain-level object naming. This included a region in right inferior to middle occipital gyrus (maximum radius=22.0 mm, mean value=1.0), with all 9 participants having a peak falling within this region (see Figure 6.3.8). This region was identified when using the top 16 negative peaks within each image. In addition to this region, we also found a region in left precentral gyrus (maximum radius=27.3 mm, mean value=1.4) and left inferior frontal gyrus (maximum radius=16.9 mm, mean value=1.0), with both of these regions having 6 participants with a peak in the region (see Figure 6.3.9). These regions were identified using the top 5 and 10 peaks respectively. Finally, we also found regions in right inferior frontal gyrus (maximum radius=20.0 mm, mean value=1.1) and left postcentral gyrus (maximum radius=21.6, mean value=1.1), with 5 participants having a peak in each region (see Figure 6.3.10). Both of these were identified using the top 6 negative peaks within each image.

We constructed virtual electrodes to map the time-frequency characteristics of the region in right inferior to middle occipital gyrus for all of our participants. We again chose this region to focus on because of the large number of participants having a peak in the region. In this region, we found late, significant differences between basic and domain-level objects (see Figure 6.3.11). Beginning at roughly 800 ms after seeing an object, there was greater low to mid-frequency (approximately 1-30 Hz) power for domain-level compared with basic-level naming. This difference seems driven by a more sustained desynchronisation for basic-level naming compared with domain-level naming.

6.4. Discussion

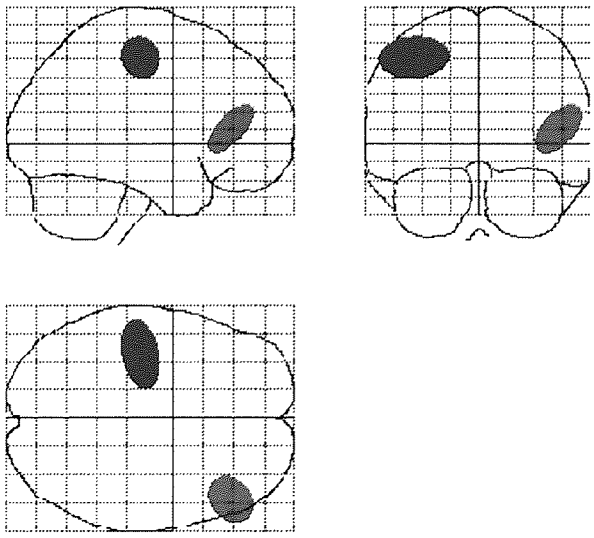
We set out to examine whether we could measure divergence of object-processing along the ventral stream as a function of the level at which participants were asked to identify an object. Based on previous research, we hypothesised that we should detect greater anterior ventral temporal cortex activation for basic-level object naming compared with domain-level naming. In addition, we hypothesised that we should see similar levels of activation in posterior ventral temporal cortex for both basic and domain-level object naming. Our

FIGURE 6.3.9. Two Regions Identified by Peakomatic as Showing Greater Power for Domain-Level Naming of Objects in Six Participants.



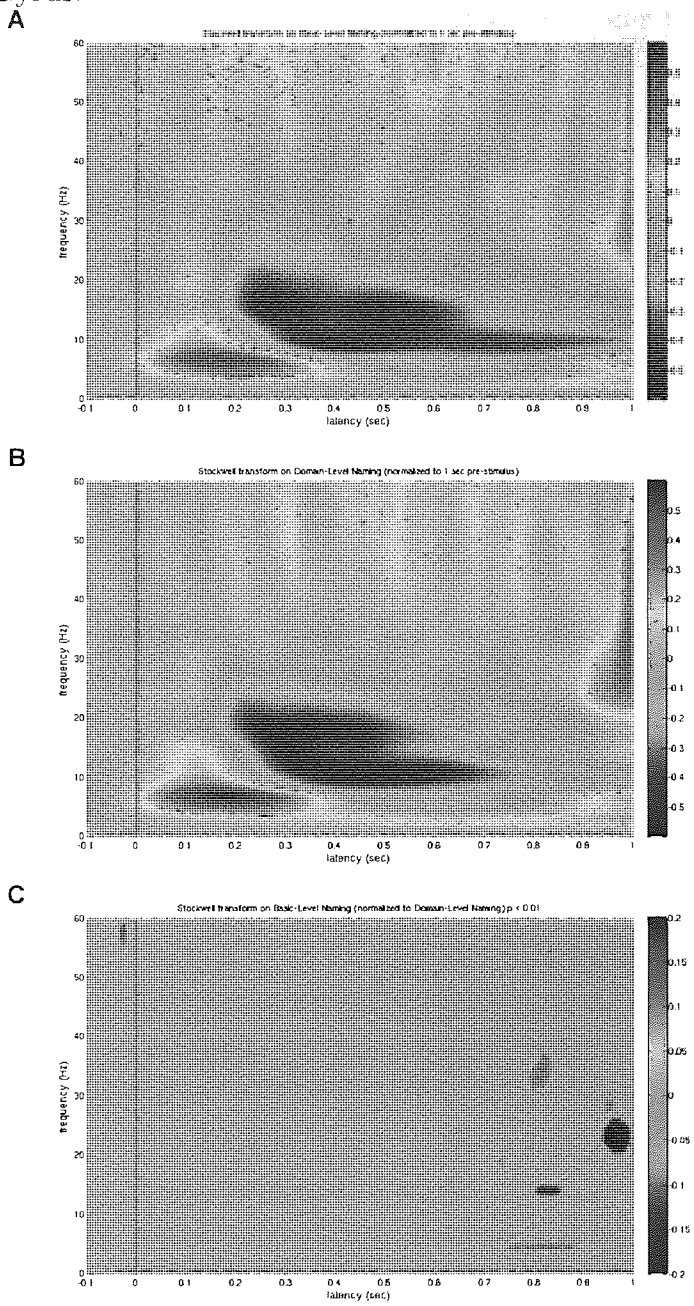
The two regions identified by peakomatic as showing significantly greater power for domain compared with basic-level object naming in 6 of 9 participants. Red=Left Precentral Gyrus; Blue=Left Inferior Frontal Gyrus.

FIGURE 6.3.10. Two Regions Identified by Peakomatic as Showing Greater Power for Domain-Level Naming of Objects in Five Participants.



The two regions identified by peakomatic as showing significantly greater power for domain compared with basic-level object naming in 5 of 9 participants. Red=Right Inferior Frontal Gyrus; Blue=Left Postcentral Gyrus.

FIGURE 6.3.11. Time-Frequency Findings from Right Inferior to Middle Occipital Gyrus.



Time-frequency findings in right inferior to middle occipital gyrus for all 9 participants. Target object onset is denoted by the solid line. A) Basic-level object naming compared to baseline; B) Domain-level object naming compared to baseline; C) Direct comparison of basic to domain-level object naming thresholded at $p<0.01$. Note the late difference in C (800 ms and later, approximately 1-30 Hz) showing increased power for domain compared to basic-level object naming.

analysis using long (picture onset to 1 second) time windows where we directly contrasted basic to domain-level naming did not show any support for our predictions. Specifically, we found no significant anterior ventral temporal activation for basic-level naming, but we did find a region in more posterior ventral temporal cortex (right inferior to middle occipital gyrus) showing greater power for domain-level naming compared with basic-level naming. Intriguingly, when we probed this region further by constructing virtual electrodes at the peak locations for each participant, we found the difference in this posterior region was driven by significantly greater desynchronisation (i.e., a greater loss

of power) for basic-level naming compared with domain-level naming in a time window beginning around 800 ms after an object was displayed. Due to the late timing of this difference, it appears that this posterior region is driven by some top-down influence.

In addition to the region in posterior ventral temporal cortex, we found a range of regions showing increased power for basic-level naming, including right superior to middle frontal gyrus, right superior temporal gyrus to inferior parietal lobule, and right inferior frontal gyrus. When we probed these regions further by constructing virtual electrodes at the peak locations for each participant, we found very early (in most cases, well within 100 ms of seeing an object) differences, suggesting some anticipatory influence or modulation in these regions. This finding is not surprising, as we blocked items by the level at which objects were to categorised, so that participants knew prior to the object appearing whether they were required to name it at the basic or domain level. Research has indicated that prefrontal cortex, in particular, is routinely activated during the delay period in match-to-category tasks (e.g., Freedman et al., 2003; Freedman & Miller, 2008; Meyers et al., 2008). For example, Meyers et al. (2008) recorded from neurons in prefrontal cortex (PFC) whilst monkeys engaged in a delayed match-to-category task in which they indicated whether a morphed target stimulus belonged to the same category as a previously presented sample stimulus. The researchers found that PFC neurons showed increased activation for the category membership of the sample stimulus during the delay period preceding target stimulus onset, suggesting that PFC was retaining category membership information online. Our findings in both right superior to middle frontal gyrus and right inferior frontal gyrus might therefore reflect some kind of task-set difference between basic-level and domain-level categorisation. In particular, basic-level naming would require fine-grained differentiation amongst exemplars, and thus more attention, than indicating whether an exemplar belonged to the living or nonliving category. Certainly research has indicated that attention operates in a top-down manner. For example, Buffalo et al. (2010) recorded from receptor fields of neurons in monkey V1, V2, and V4 that were tuned to a particular location in the visual field. They showed using a change detection task that attentional effects operated in a top-down manner preceding serially from V4 to V2 to V1. Thus these findings would lead us to predict later effects of attention in earlier regions of the visual stream, in line with our findings.

Does this mean that anterior ventral temporal cortex is not recruited for fine-grained object differentiation, contrary to the theories outlined at the outset of this chapter? Whilst our results show no evidence of recruitment of anterior regions of ventral temporal cortex when naming at the basic level, concluding that this region is not activated at all would be premature. One limiting factor is the nature of the task, itself. One idea is that perhaps participants always named items at the basic level, irregardless of the block cue. Certainly, there was ample time between target object onset and the onset of the label, so participants had no real time pressure and could very easily perform the task in this manner. Target objects were displayed for 800 ms, followed by an additional 1000-1100 ms before the label was displayed. It could well be the case that participants always identified objects at the basic level, then categorised objects as either living or nonliving in order to complete the domain-level task. If this were the case, then we would expect late timing differences between basic and domain-level naming, which is in

fact our finding in the ventral stream. A solution to this problem would have been to ask participants to silently name items at either the basic or domain level, rather than perform a categorisation task. However the behavioural consequence of this design has already been discussed previously. That is, participants would show significantly faster reaction times for the basic-level naming of objects, as this is the most familiar way in which people label or categorise objects (Mervis & Rosch, 1981; Rosch, 1978; Rosch et al., 1976).

A second criticism has to do with the source localisation approach taken, with comparison of relatively long active and passive windows. As discussed previously (Chapter 5), one benefit of MEG above other neuroimaging techniques such as PET and fMRI is its high temporal resolution. A second benefit above EEG is its ability to localise sources of activity without having to account for bone conductivity, as magnetic signals pass unimpeded through the skull. Therefore, MEG should be seen as a tool for source localisation and retrieval of the time course at a given voxel. As a first pass, we must decide what voxels warrant additional probing through construction of virtual electrodes, and the nature in which we decide upon voxels using MEG has a certain set of limitations. Using the SAM algorithm (and beamformers generally), the limitation is that if we do not include enough data in the covariance matrix construction, our source localisation could be inaccurate (e.g., Brookes et al., 2008). However, averaging over a long time window does not allow us to assess the full temporal evolution of the signal in the brain. In essence, we could be missing differences in how the brain processes objects at the basic compared with the domain level based on using a long covariance window to assess sources of differential power.

One other criticism that reduces the firm conclusion that anterior ventral temporal cortex is not recruited for basic-level naming has to do with the source localisation ability of MEG for deep sources generally. That is, the signal to noise ratio of a given source declines with depth, so that by the time you reach the centre of the head, noise power predominates. Therefore, sources such as perirhinal and entorhinal cortex, which are located medially, might not be detectable. This localisation deficit for deep sources aside, we should still find divergence at some point along the ventral stream for more fine-grained versus less fine-grained differentiation, and the only point at which we see it using this analysis approach is anatomically early in the processing stream.

CHAPTER 7

On the Time-Course of Categorising Objects at the Basic Versus Domain Level.

7.1. Introduction

In the previous chapter, we described a theory of object naming which attempts to explain the effect of high levels of similarity on naming performance, the "convergence zone" (CZ) hypothesis (initially proposed by Damasio, 1989, and elaborated by Simmons & Barsalou, 2003). We then described one approach to data analysis in which we contrasted long windows of activity between domain and basic-level object naming. Using this analysis approach, we did not find differential anterior ventral temporal cortex involvement for naming objects at the basic compared with the domain level, as would be predicted by the elaborated CZ hypothesis. However, this result could be interpreted in a number of ways. For example, one interpretation, which we discussed previously, is that participants always named items at the basic level during the task. Certainly there was no time pressure for responding, and the target object was displayed well before the basic or domain-level probe. A second interpretation is that there is a temporal shift in the pattern of activation between basic and domain-level naming, which we cannot resolve given the relatively large window in which we directly contrasted the two conditions. A similar set of ideas have already been discussed previously in Chapter 5 when comparing living and nonliving object-processing. Thus, in order to clarify these potential confounds, we set out using a separate analysis method to more generally explore the time-course of categorising objects at the basic compared with the domain level.

Many behavioural studies of object naming have shown that high levels of similarity can have a detrimental impact on performance (e.g., Humphreys, Riddoch, & Quinlan, 1988; Shapiro & Olson, 2005; Vitkovitch, Humphreys, & Lloyd-Jones, 1991). This effect of high similarity should only impair performance when participants are asked to identify objects at a basic level, but not at either a superordinate or domain-level. This phenomenon has been explained according to the elaborated CZ hypothesis (e.g., Simmons & Barsalou, 2003; Tyler et al., 2004). That is, because the ventral visual object-processing stream is organised hierarchically, enhanced competition from structural similarity will impact on the fine-grained differentiation of specific objects at the end point of this stream. Proposed regions that would be activated for highly similar items include perirhinal and entorhinal cortices (Tyler et al., 2004). This idea of higher similarity has been used to explain the overwhelming incidence of category-specific deficits for living compared to nonliving things. Certainly behavioural evidence has demonstrated that high levels of similarity can influence normal processing (e.g., Shapiro & Olson, 2005). In addition, Humphreys et al. (1988) showed that living things have higher within-category perceptual/visual similarity than nonliving things. According to the elaborated CZ hypothesis,

the similarity-in-topography (SIT) principle (a proposed organising principle for elaborative processing) results in an organisation whereby objects that share many features are processed by neurons that are located proximally within the cortex (Simmons & Barsalou, 2003). For objects that have low similarity (i.e., most nonliving things), the dispersion of neurons which process their specific features will result in intact recognition generally. A similar proposition is made by other theories of category-specificity that argue for a unitary, distributed semantic system (e.g., Conceptual Structure Account: Moss, Tyler, & Devlin, 2002).

Given this theoretical framework, MEG is a candidate neuroimaging strategy to test the prediction that similarity will influence elaborative (i.e., basic-level naming) processing of objects within the perirhinal or entorhinal cortices. One caveat, mentioned in the previous chapter, is that sources that are located deep within the cortex will not be as visible as sources located near the surface of the cortex. This is a limitation of MEG generally, as the signal to noise ratio of source estimates declines as you move deeper into the head. It is the case that as you move to the centre of the brain, noise power dominates over true source power. Thus, whilst MEG may suffer some problem with localising perirhinal or entorhinal cortex proper, we would still expect to see divergence along the ventral stream based on the level at which an object is identified. That is, basic level object naming should recruit more anterior regions of the ventral stream than domain-level naming, according to the elaborated CZ hypothesis (Damasio, 1989; Simmons & Barsalou, 2003).

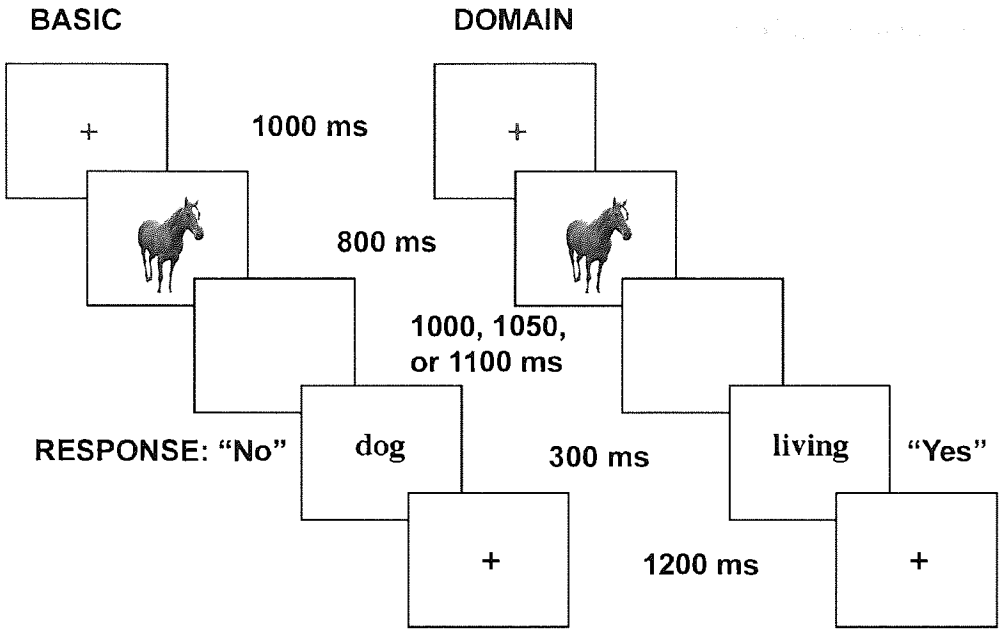
As our previous analysis method did not demonstrate anterior ventral temporal cortex recruitment for basic compared with domain-level naming over a long time window, we altered our analysis strategy to assess the temporal sequence of basic versus domain-level naming. Thus, as predicted before, if the elaborated CZ hypothesis is correct, we should see greater power for basic-level naming compared with domain-level naming in more anterior regions of ventral temporal cortex.

7.2. Methods

The study procedures reported in this chapter are identical to those described in the previous chapter (Chapter 6). In addition, the MEG data acquisition is identical to those previously reported, however the MEG analyses differ from those described previously. For clarity of reading and understanding, all methods used are reported again in this chapter.

7.2.1. Study Procedure. Nine right-handed volunteers (Mean Age=31.3 years, range=22-41 years, 5 males) participated in the MEG study. During scanning, participants performed a categorisation task in which they were asked to categorise pictures of objects at either the basic level or the domain level (see Figure 7.2.1) Participants were first shown a picture of a target object, and after a brief variable delay, they were presented with either a basic-level object name or a domain-level name. Participants were instructed to respond by button press as quickly and accurately as possible, indicating whether the basic or domain-level name matched the target object. Participants responded using a 2-button response box held in their right hand. We blocked trials by level of processing,

FIGURE 7.2.1. Example Trial from Study 2.



Participants were shown a 1000 ms red fixation cross, signalling the beginning of a trial. They then saw a target object for 800 ms, followed by a variable delay (1000, 1050, or 1100 ms). Participants then saw a 300 ms probe at either the basic level (i.e., "dog") or domain level (i.e., "living"), followed by a black fixation cross for 1200 ms. They were instructed to decide as quickly and accurately as possible if the probe matched the target object and respond via button press.

whilst allowing category membership to vary within each block. Therefore, participants were first shown a screen indicating which level of specificity they would be required to categorise the subsequent pictures at (i.e., "basic-level name" or "living/nonliving"), followed by a series of 20 pictures. A total of six blocks were shown during the entire scan, with blocks alternating between the basic and domain level. Across participants, we then counterbalanced the presentation order of basic and domain-level blocks to minimise any potential practise and/or timing effects. Participants were instructed to respond by pressing the left button with their right index finger for "yes" (i.e., congruent) and the right button with their right middle finder for "no" (i.e., incongruent).

Target objects included 60 exemplars drawn from 3 living (plants, animals, fruits and vegetables) and 3 nonliving (tools, transport, furniture) categories. For this study, we ensured that all selected images had a pre-test naming consistency rate of greater than 65%. In addition, stimuli were matched on pre-test naming speed, familiarity, typicality, and visual complexity. During scanning, each target object was presented four times. On 2 occasions, the target object was shown with a domain-level label, and on 2 occasions it was shown with a basic-level label. For both of these conditions, the target object was congruently presented with its appropriate label (e.g., dog picture presented with either "dog" or "living" label) once, and incongruently presented with another label (e.g., dog picture presented with either "lily" or "nonliving" label) once. For incongruent trials at the basic-level, we ensured that the non-matching label did not come from the same general category. So, for example, a picture of an item from the animal category would be presented with a label drawn from either plants or fruits and vegetables. We did this to ensure that participants were still required to access the semantic system at the same

level for basic-level congruent and incongruent trials, whilst not increasing the difficulty for incongruent trials by having the label come from the same general category (e.g., dog picture presented with an animal exemplar name). We also felt that presenting an across-domain non-matching exemplar name (e.g., dog picture with an exemplar name from tools, transport, or furniture) might require less processing along the ventral stream, and thus we wanted to equate the difficulty of the task. A total of 240 trials were shown during the scan, half of which included a living target object and the other half a nonliving target object. The order of trial presentation was randomised across participants.

7.2.2. MEG Data Acquisition and Analyses. Neuromagnetic data were recorded at a 600 Hz sampling rate with a bandwidth of 0-150 Hz using a CTF 275 MEG system (VSM MedTech Ltd., Canada). Synthetic 3rd gradient balancing was used to remove background noise on-line. Fiducial coils were placed on the nasion, left preauricular, and right preauricular sites for each participant, and these coils were energised before each run to localise the participant's head with respect to the MEG sensors. Total head displacement was measured after each run and could not exceed 5 mm for inclusion in the source analyses. Prior to scanning, participants' head shaped and the location of fiducial coils were digitised using a Polhemus Isotrak 3D digitiser (Kaiser Aerospace Inc.). These were coregistered to high-resolution T1-weighted anatomical images for each participant acquired with a 3-Tesla whole-body scanner (3T Trio, Siemens Medical Systems) using in-house coregistration software.

Data for each participant were edited and filtered to remove environmental and physiological artefacts. We then applied a beamforming technique to assess sources of differences in processing living and nonliving objects at the basic and domain levels. For this analysis, we aimed to identify the time-course of processing objects at either the basic or domain level. In order to do this, we used 100 ms windows in which we directly contrasted basic-level ('active') to domain-level ('passive') object processing using a wide frequency range (1-80 Hz), collapsing across category membership. Our first window began at target object onset, and we then slid this window every 50 ms until 400-500 ms after target object onset. Spectral power changes between the 'active' and 'passive' periods were calculated as a pseudo t-statistic (Vrba & Robinson, 2001). Each participant's data were then normalised and converted to Talairach space using statistical parametric mapping (SPM99, Wellcome Department of Imaging Neuroscience, London, UK) for group-level comparisons.

For group-level analyses, we utilised peakomatic to assess the distribution of image peaks across our participants. We tested a range of P values from 2 to 40 and after multiple comparisons correction were left with a number of significant clusters of positive and negative peaks. As with our previous analyses, if a region was identified as showing a significant difference across a range of P values, we chose the region for reporting purposes that yielded the largest N. In cases where several P values yielded the same N, we then chose the volume that had the smallest spatial extent.

We used virtual electrodes to probe the time-frequency characteristics of areas showing group-level effects in our peakomatic analyses. Based on *a priori* predictions regarding differential effects of basic compared with domain-level item naming, we probed only

those regions showing an effect within the ventral object-processing stream. These virtual electrodes were based on a covariance matrix constructed using a 1 second window from 500 ms prior to target picture onset, to 500 s after the target object, using a wide band (1-80 Hz). Time-frequency plots were then computed on the virtual electrodes using the Stockwell Transform (Stockwell, Mansinha, & Lowe, 1996) for a window beginning 500 ms prior to 500 ms after target picture onset. Percent power change from baseline (the 500 ms preceding target object onset) was computed at each frequency from 0-60 Hz for both basic and domain-level naming to assess mean (across epochs and participants) power increases and decreases for objects named at the basic level and those same objects named at the domain level. In addition, basic and domain-level target objects were directly contrasted at each region of interest across participants for a window from 100 ms prior to 500 ms after target object onset, thresholded at $p<0.01$ uncorrected.

7.3. Results

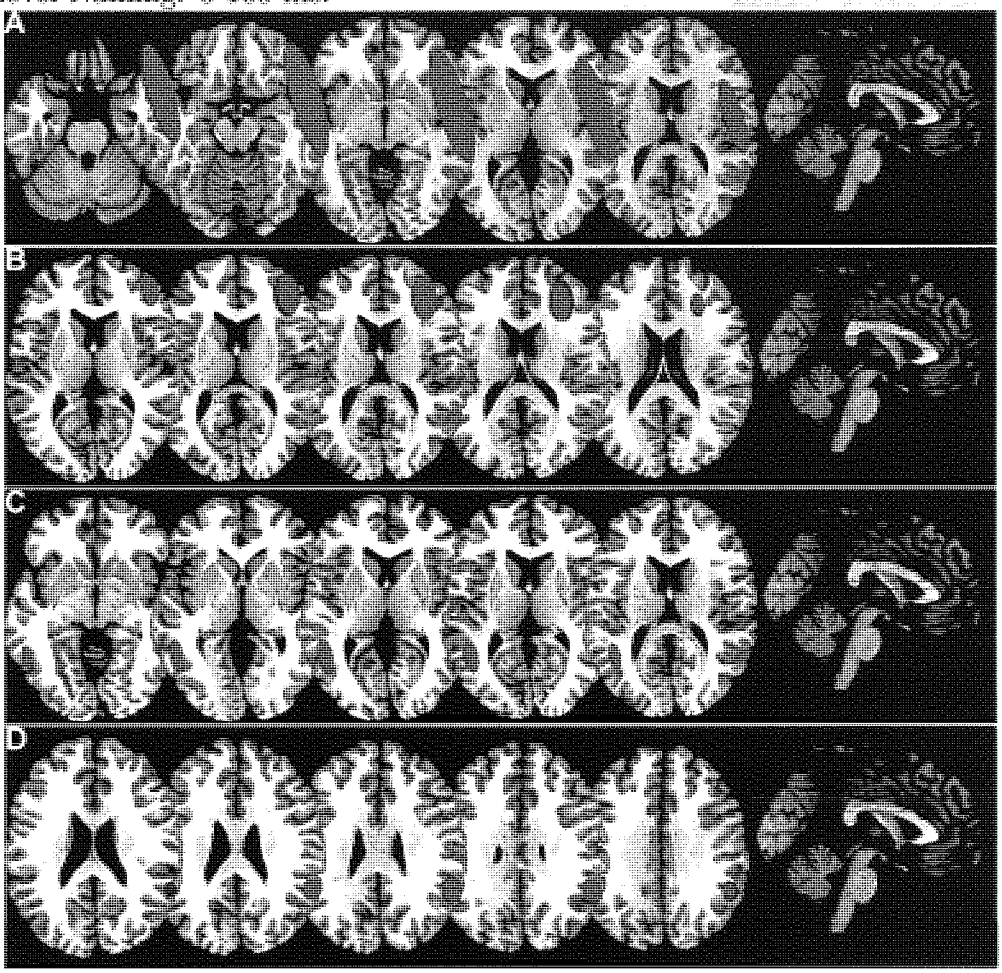
7.3.1. Behavioural Findings. As reported previously, we found a significant behavioural advantage for classifying items at the basic level (see Chapter 6). Participants showed a significant advantage for basic-level naming compared with domain-level naming even when they were cued at the beginning of a block of items at which level of specificity they would be required to categorise objects. Importantly, this should have little effect on the results of the basic versus domain-level analysis, per se, as the response occurred following target object onset, and we are only analysing source differences during the target object.

7.3.2. Source-Level Findings. We used SAM to identify sources of differential activity between basic and domain-level naming using a 100 ms window slid every 50 ms. The first window began at target object onset, and the right-hand edge of the last window was at 500 ms after target object onset. Thus, we assessed differences in basic and domain-level object processing within 500 ms of seeing a picture. Source differences in each of these 100 ms windows are discussed separately below.

Within the first 100 ms (time window: 0-100 ms) of identifying an object at either the basic or domain level, our peakomatic analyses identified four regions showing significant differences. All four of these regions showed greater power for basic-level naming compared with domain-level naming. The first region was rather extensive spatially, and it was centred on the right insula (N=8, P=3, peak activation=2.45) (see Figure 7.3.1). In addition, a region in right frontal cortex showed greater power for basic-level compared with domain-level naming (N=8, P=13, peak activation=1.55) (see Figure 7.3.1). A region in left posterior superior temporal gyrus also showed greater power for basic-level compared with domain-level naming (N=7, P=17, peak activation=1.66) (see Figure 7.3.1). Finally, a region centred on the right angular gyrus showed greater power for basic-level compared with domain-level naming (N=7, P=26, peak activation=1.22) (see Figure 7.3.1).

From 50-150 ms after identifying an object at either the basic or domain level, our peakomatic analysis identified two regions showing significant differences. Both of these regions showed greater power for basic-level naming compared with domain-level naming. The first region showing greater power for basic-level naming was centred on the right

FIGURE 7.3.1. Regions Showing Significantly Greater Power for Basic-Level Naming: 0-100 ms.

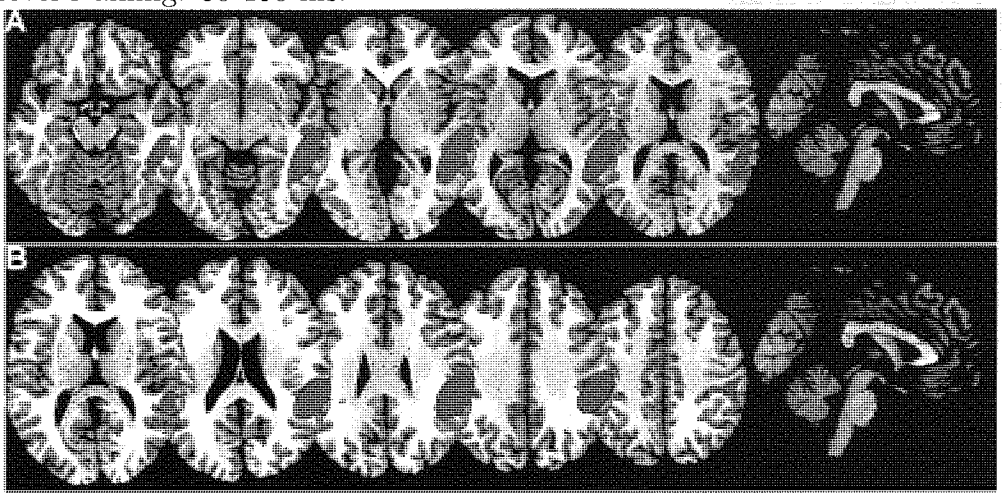


Regions identified as showing significantly greater power for basic-level compared to domain-level naming from 0-100 ms. A) Right insula (centre=54.3, 5.3, -9.0). This region was identified using the top 3 positive peaks per image; 8 of 9 participants had a peak in the volume (maximum radius=49.6 mm). B) Right frontal cortex (centre=35.3, 39.4, 14.6). This region was identified using the top 13 positive peaks per image; 8 of 9 participants had a peak in the volume (maximum radius=19.4 mm). C) Left posterior superior temporal gyrus (centre= -48.0, -53.6, 6.0). This region was identified using the top 17 positive peaks per image; 7 of 9 participants had a peak in the volume (maximum radius=16.2 mm). D) Right angular gyrus (centre=54.9, -47.1, 29.1). This region was identified using the top 26 positive peaks per image; 7 of 9 participants had a peak in the volume (maximum radius=9.9 mm).

middle temporal gyrus (N=7, P=7, peak activation=2.3) (see Figure 7.3.2). In addition, a region centred on the right angular gyrus showed greater power for basic-level compared with domain-level naming (N=7, P=10, peak activation=1.76) (see Figure 7.3.2).

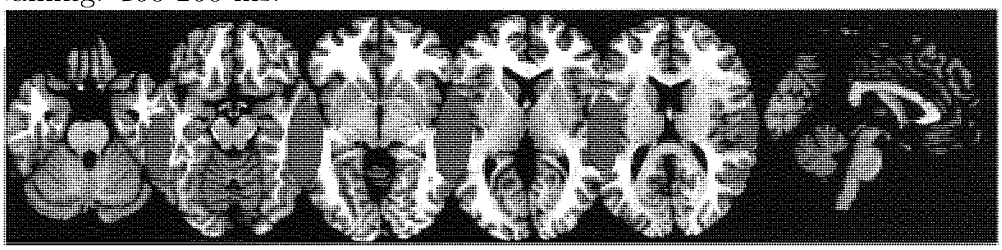
From 100-200 ms after identifying an object at either the basic or domain level, our peakomatic analysis identified two regions showing significant differences. One of these regions showed greater power for basic-level naming, whilst the other region showed greater power for domain-level naming. The region showing greater power for basic-level naming was located in right anterior inferior temporal cortex (N=8, P=5, peak activation=2.02) (see Figure 7.3.3). The region showing greater power for domain-level naming was located in left occipito-temporal cortex (N=7, P=3, peak activation=1.78) (see Figure 7.3.4).

FIGURE 7.3.2. Regions Showing Significantly Greater Power for Basic-Level Naming: 50-150 ms.



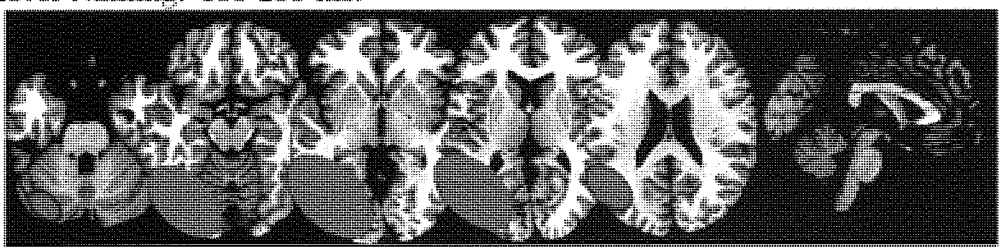
Regions identified as showing significantly greater power for basic-level compared to domain-level naming from 50-150 ms. A) Right middle temporal gyrus (centre=53.1, -36.9, -0.4). This region was identified using the top 7 positive peaks per image; 7 of 9 participants had a peak in the volume (maximum radius=25.6 mm). B) Right angular gyrus (centre=52.7, -34.3, 28.7). This region was identified using the top 10 positive peaks per image; 7 of 9 participants had a peak in the volume (maximum radius=21.0 mm).

FIGURE 7.3.3. Region Showing Significantly Greater Power for Basic-Level Naming: 100-200 ms.



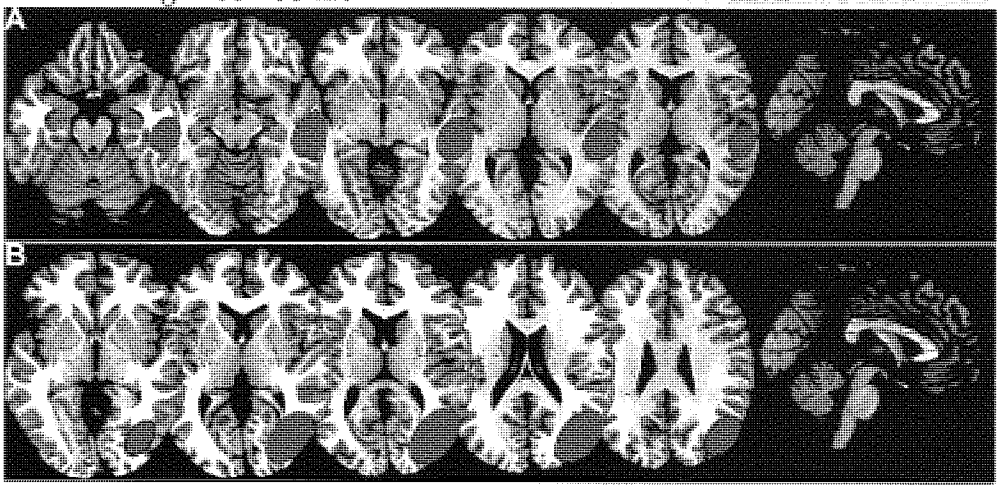
Region in right anterior inferior temporal cortex (centre=57.8, -23.6, -6.8) identified as showing significantly greater power for basic-level compared with domain-level naming from 100-200 ms. This region was identified using the top 5 positive peaks per image; 8 of 9 participants had a peak in the volume (maximum radius=36.6 mm).

FIGURE 7.3.4. Region Showing Significantly Greater Power for Domain-Level Naming: 100-200 ms.



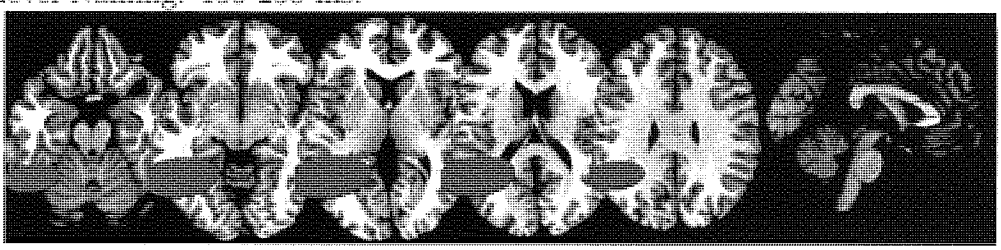
Region in left occipito-temporal cortex (centre= -40.7, -67.7, -1.3) identified as showing significantly greater power for domain-level compared with basic-level naming from 100-200 ms. This region was identified using the top 3 negative peaks per image; 7 of 9 participants had a peak in the volume (maximum radius=43.0).

FIGURE 7.3.5. Regions Showing Significantly Greater Power for Basic-Level Naming: 150-250 ms.



Regions identified as showing significantly greater power for basic-level compared to domain-level naming from 150-250 ms. A) Right anterior inferior temporal cortex (centre=57.3, -25.0, -6.0). This region was identified using the top 9 positive peaks per image; all 9 of our participants had a peak in the volume (maximum radius=24.9 mm). B) Right posterior middle temporal gyrus (centre=39.0, -71.7, 13.3). This region was identified using the top 13 positive peaks per image; all 9 of our participants had a peak in the volume (maximum radius=26.6 mm).

FIGURE 7.3.6. Region Showing Significantly Greater Power for Domain-Level Naming: 150-250 ms.

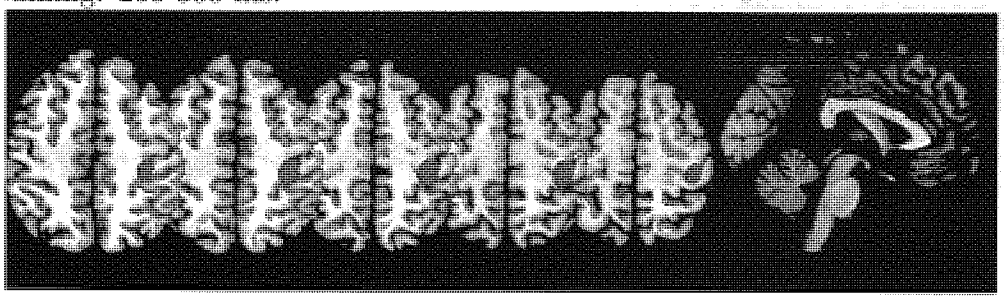


Region in left occipito-temporal cortex (centre= -47.6, -53.6, 5.3) identified as showing significantly greater power for domain-level compared with basic-level naming from 150-250 ms. This region was identified using the top 5 negative peaks per image; 8 of 9 participants had a peak in the volume (maximum radius=34.6 mm).

From 150-250 ms after identifying an object at either the basic or domain level, our peakomatic analysis identified three regions showing significant differences. Two of these regions showed greater power for basic-level naming, whilst the other region showed greater power for domain-level naming. The first region showing greater power for basic-level naming was located in right anterior inferior temporal cortex (N=9, P=9, peak activation=1.81) (see Figure 7.3.5). In addition, a region centred on right posterior middle temporal gyrus showed greater power for basic-level compared with domain-level naming (N=9, P=13, peak activation=1.54) (see Figure 7.3.5). The region showing greater power for domain-level naming was located in left occipito-temporal cortex (N=8, P=5, peak activation=1.46) (see Figure 7.3.6).

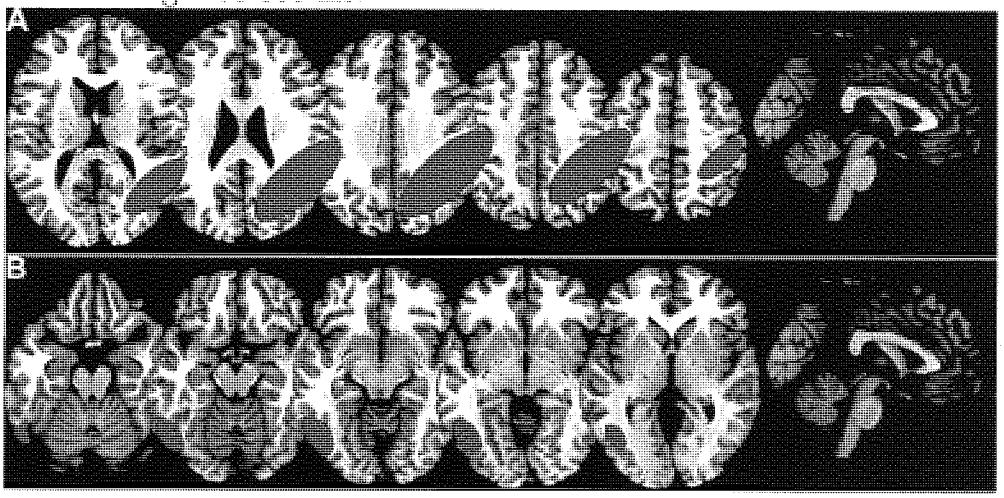
From 200-300 ms after identifying an object at either the basic or domain level, our peakomatic analysis identified three regions showing significant differences. One of these regions showed greater power for basic-level naming, whilst 2 regions showed greater power

FIGURE 7.3.7. Region Showing Significantly Greater Power for Basic-Level Naming: 200-300 ms.



Region in right primary cortex (centre=36.0, =28.5, 55.0) identified as showing significantly greater power for basic-level compared with domain-level naming from 200-300 ms. This region was identified using the top 32 positive peaks per image; 6 of 9 participants had a peak in the volume (maximum radius=9.4 mm).

FIGURE 7.3.8. Regions Showing Significantly Greater Power for Domain-Level Naming: 200-300 ms.

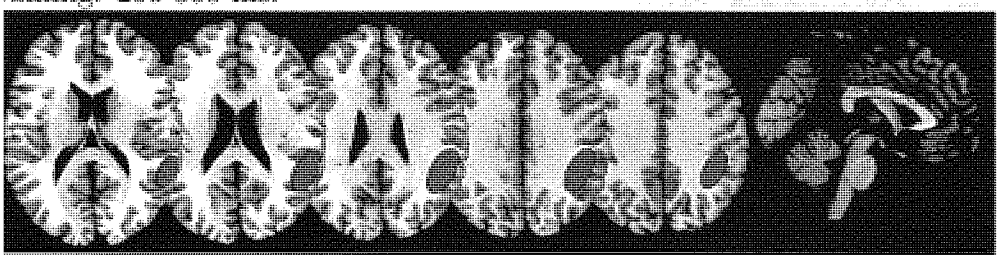


Regions identified as showing significantly greater power for domain-level compared to basic-level naming from 200-300 ms. A) Right angular gyrus (centre=40.3, -46.0, 33.7). This region was identified using the top 5 negative peaks per image; all 9 of our participants had a peak in the volume (maximum radius=45.6 mm). B) Left occipito-temporal cortex (centre= -49.3, -63.4, -9.4). This region was identified using the top 12 negative peaks per image; 7 of 9 participants had a peak in the volume (maximum radius=18.4 mm).

for domain-level naming. The region showing greater power for basic-level naming was located in right primary motor cortex (N=6, P=32, peak activation=1.59) (see Figure 7.3.7). The first region showing greater power for domain-level naming was centred on the right angular gyrus (N=9, P=5, peak activation=1.63) (see Figure 7.3.8). In addition, a region located in left occipito-temporal cortex showed greater power for domain-level compared with basic-level naming (N=7, P=12, peak activation=1.47) (see Figure 7.3.8).

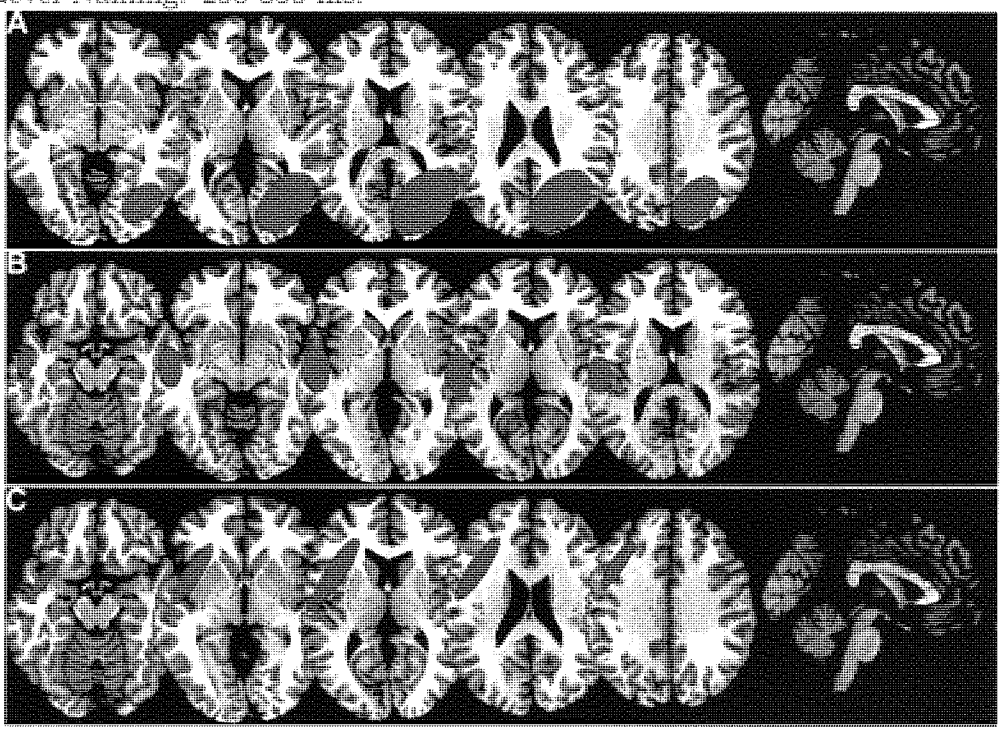
From 250-350 ms after identifying an object at either the basic or domain level, our peakomatic analysis identified four regions showing significant differences. One of these regions showed greater power for basic-level naming, whilst 3 regions showed greater power for domain-level naming. The region showing greater power for basic level naming was centred on the right angular gyrus (N=7, P=9, peak activation=1.98). (see Figure 7.3.9). The first region showing greater power for domain-level naming was rather extensive

FIGURE 7.3.9. Region Showing Significantly Greater Power for Basic-Level Naming: 250-350 ms.



Region in right angular gyrus (centre=46.7, -43.3, 28.7) identified as showing significantly greater power for basic-level compared with domain-level naming from 250-350 ms. This region was identified using the top 9 positive peaks per image; 7 of 9 participants had a peak in the volume (maximum radius=22.8 mm).

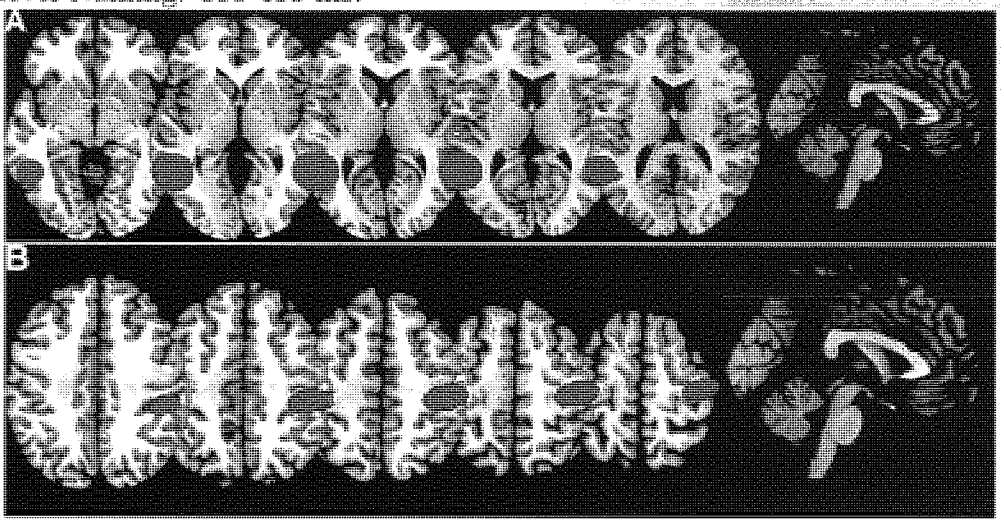
FIGURE 7.3.10. Regions Showing Significantly Greater Power for Domain-Level Naming: 250-350 ms.



Regions identified as showing significantly greater power for domain-level compared to basic-level naming from 250-350 ms. A) Right occipital cortex (centre=26.7, -70.0, 16.7). This region was identified using the top 8 negative peaks per image; all 9 of our participants had a peak in the volume (maximum radius=32.9 mm). B) Left anterior temporal cortex (centre= -57.0, -16.1, 2.6). This region was identified using the top 13 negative peaks per image; 8 of 9 participants had a peak in the volume (maximum radius=22.5 mm). C) Left frontal cortex (centre=45.5, 7.5, 27.5). This region was identified using the top 3 negative peaks per image; 6 of 9 participants had a peak in the volume (maximum radius=38.7 mm).

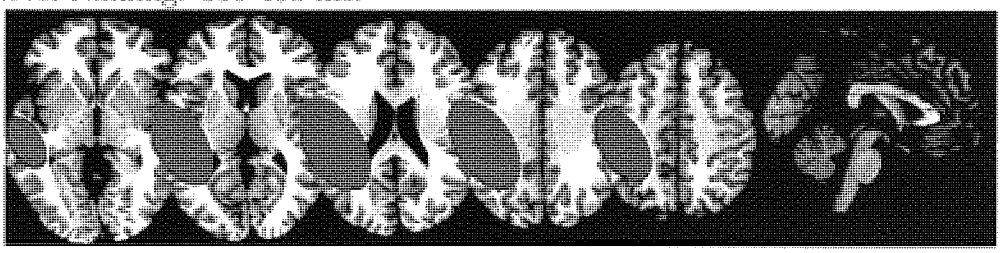
spatially, and was located in right occipital cortex (N=9, P=8, peak activation=1.47) (see Figure 7.3.10). In addition, a region in left anterior temporal cortex showed greater power for domain-level compared with basic-level naming (N=8, P=13, peak activation=1.35) (see Figure 7.3.10). Finally, a region located in left frontal cortex showed greater power for domain-level compared with basic-level naming (N=6, P=3, peak activation=1.64) (see Figure 7.3.10).

FIGURE 7.3.11. Regions Showing Significantly Greater Power for Basic-Level Naming: 350-450 ms.



Regions identified as showing significantly greater power for basic-level compared to domain-level naming from 350-450 ms. A) Left posterior middle temporal gyrus (centre= -55.1, -50.3, 5.6). This region was identified using the top 14 positive peaks per image; 8 of 9 participants had a peak in the volume (maximum radius=19.7 mm). B) Right parietal cortex (centre=43.0, -25,0, 53.5). This region was identified using the top 7 positive peaks per image; 6 of 9 participants had a peak in the volume (maximum radius=19.0 mm).

FIGURE 7.3.12. Region Showing Significantly Greater Power for Domain-Level Naming: 350-450 ms.

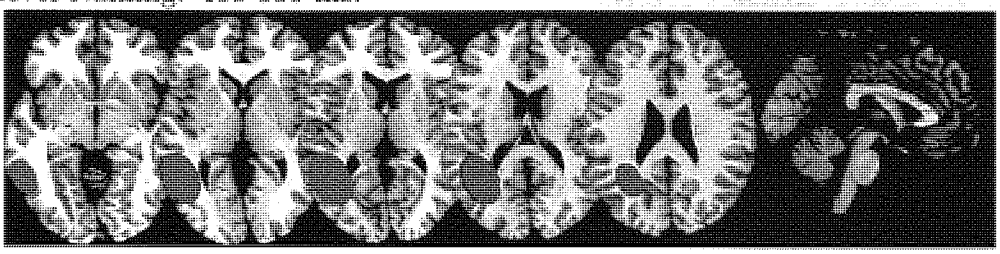


Region in left temporal to parietal cortex (centre= -48.3, -27.0, 25.7) identified as showing significantly greater power for domain-level compared with basic-level naming from 350-450 ms. This region was identified using the top 5 negative peaks per image; all 9 of our participants had a peak in the volume (maximum radius=42.1 mm).

From 300-400 ms after identifying an object at either the basic or domain level, our peakomatic analysis found no regions showing significant differences.

From 350-450 ms after identifying an object at either the basic or domain level, our peakomatic analysis identified three regions showing significant differences. Two of these regions showed greater power for basic-level naming, whilst the other region showed greater power for domain-level naming. The first region showing greater power for basic-level naming was located in left posterior middle temporal gyrus (N=8, P=14, peak activation=1.37) (see Figure 7.3.11). In addition, a region in right parietal cortex showed greater power for basic-level compared with domain-level naming (N=6, P=7, peak activation=1.89) (see Figure 7.3.11). The region showing greater power for domain level naming was rather extensive spatially, and was located in left superior temporal to inferior parietal cortex (N=9, P=5, peak activation=1.71) (see Figure 7.3.12).

FIGURE 7.3.13. Region Showing Significantly Greater Power for Basic-Level Naming: 400-500 ms.



Region in left posterior middle temporal gyrus (centre= -43.3, -53.7, 10.0) identified as showing significantly greater power for basic-level compared with domain-level naming from 400-500 ms. This region was identified using the top 10 positive peaks per image; all 9 of our participants had a peak in the volume (maximum radius=29.2 mm).

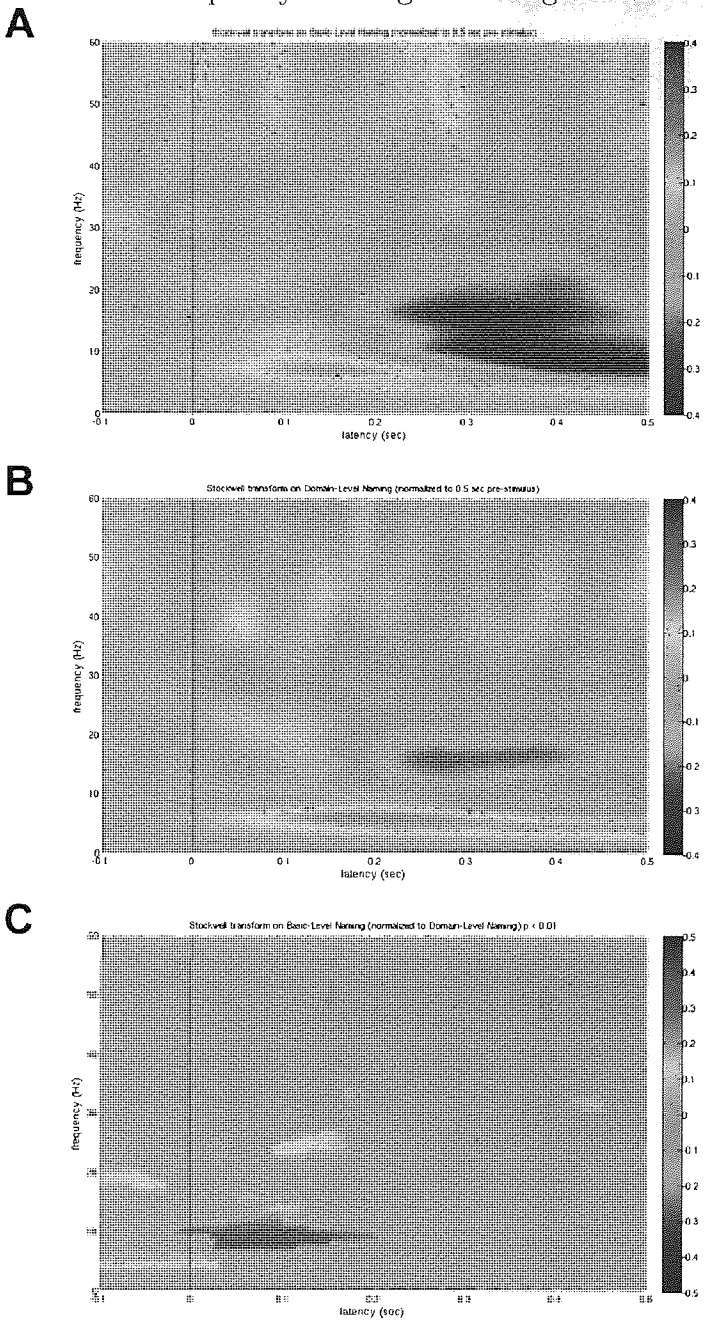
From 400-500 ms after identifying an object at either the basic or domain level, our peakomatic analysis identified a single region showing significant differences. This region showed greater power for basic-level naming and was located in left posterior middle temporal gyrus (N=9, P=10, peak activation=1.88) (see Figure 7.3.13).

7.3.3. Time-Frequency Findings. We constructed virtual electrodes to map the time-frequency characteristics of the seven regions in the ventral object-processing stream showing significant group-level effects. These included: right middle temporal gyrus, occipito-temporal cortex bilaterally, anterior inferior temporal cortex bilaterally, and posterior middle temporal gyrus bilaterally. The virtual electrodes were constructed for the subgroup of participants identified as having a peak in each volume. These regions were selected to assess the timecourse of living and nonliving object-processing in the ventral stream. Specifically, we wanted to test the prediction that anterior ventral temporal cortex would be recruited to a greater extent for basic-level object-naming, whilst more posterior regions of ventral temporal cortex would show no difference between basic and domain-level object-naming.

Within the region in right middle temporal gyrus (see Figure 7.3.2A for source location), we found very early differences between basic and domain-level object naming (see Figure 7.3.14). At this location in the brain, there was an increase in power in the low-frequencies (approximately 5-10 Hz) for both basic and domain-level object naming immediately after target object onset, peaking at roughly 150 ms. For basic-level naming compared with domain-level naming, however, there was greater low-frequency (approximately 10 Hz) power at this location within 100 ms of target object onset. In fact, there was greater low-frequency power at this region for basic-level naming even prior to target object onset.

Within the region in right occipito-temporal cortex (see Figure 7.3.10A for source location), we again found very early differences between basic and domain-level object naming (see Figure 7.3.15). At this location in the brain, there was an increase in power in the low frequencies (approximately 5-10 Hz) for both basic and domain-level object naming immediately after target object onset, peaking at approximately 150-200 ms. For basic-level naming compared with domain-level naming, however, there was greater low-frequency (approximately 10 Hz) power at this location at roughly 100 ms after target object onset. At this location in the brain, there was also a decrease in power in beta

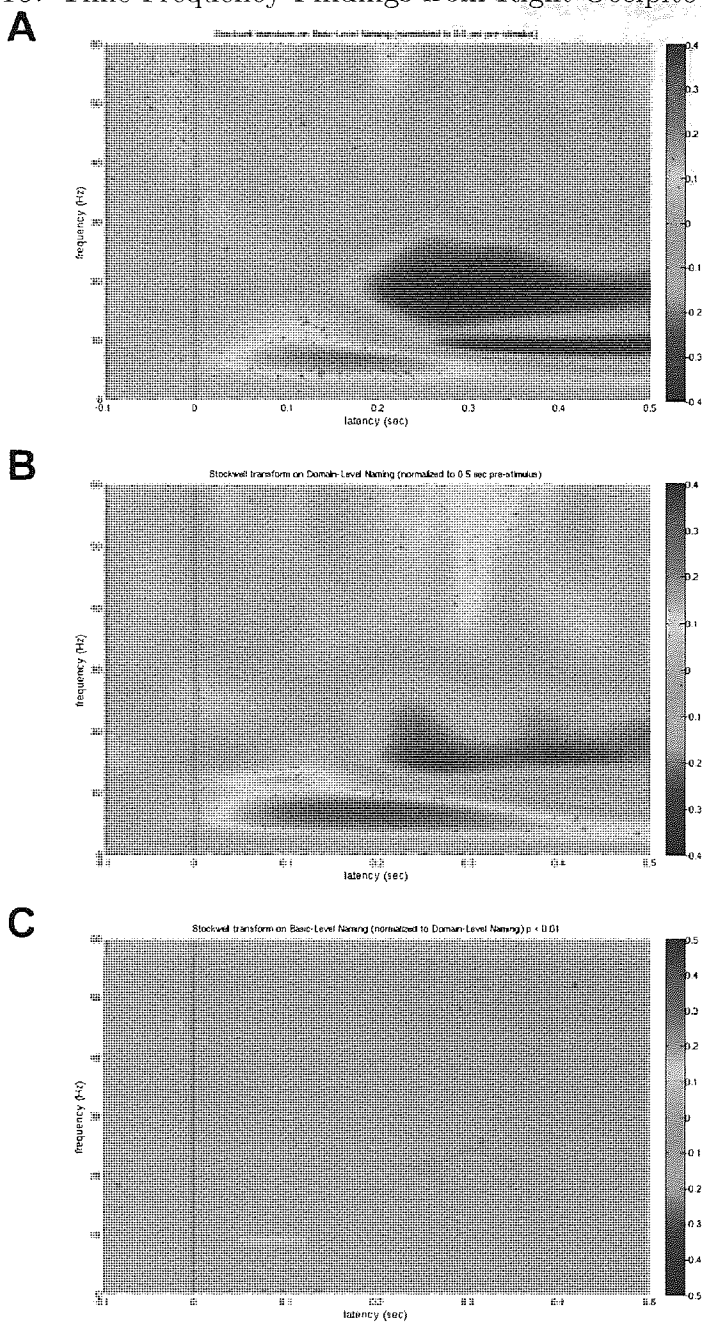
FIGURE 7.3.14. Time-Frequency Findings from Right Middle Temporal Gyrus.



Time-frequency findings in right middle temporal gyrus for the group of 7 participants identified as showing greater power for basic-level naming from 50-150 ms. Target object onset is denoted by the solid line. A) Basic-level object naming compared to baseline; B) Domain-level object naming compared to baseline; C) Direct comparison of basic to domain-level object naming thresholded at $p<0.01$ uncorrected. Note the early difference in C (within 100 ms of target object onset, approximately 10 Hz) showing increased power for basic compared to domain-level object naming.

frequencies (approximately 10-30 Hz) for both basic and domain-level object naming after the initial power increase, beginning at approximately 200 ms after target object onset. For basic-level naming compared with domain-level naming, however, there was a larger decrease in beta-frequency (approximately 20 Hz) power at this location, beginning at roughly 250 ms after target object onset. In addition, there was greater gamma-frequency (approximately 50-60 Hz) power for domain-level naming compared with basic-level naming at roughly the same time.

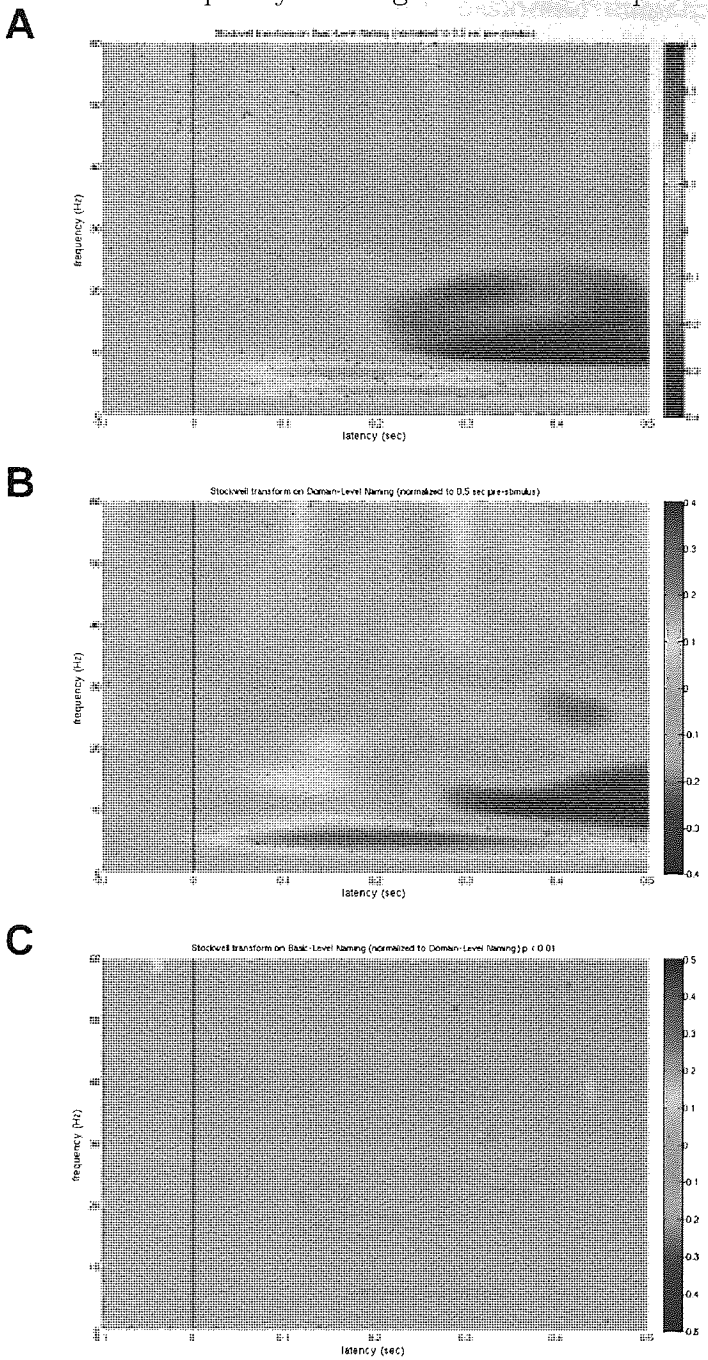
FIGURE 7.3.15. Time-Frequency Findings from Right Occipito-Temporal Cortex.



Time-frequency findings in right occipito-temporal cortex for all 9 participants identified as showing greater power for domain-level naming from 250-350 ms. Target object onset is denoted by the solid line. A) Basic-level object naming compared to baseline; B) Domain-level object naming compared to baseline; C) Direct comparison of basic to domain-level object naming thresholded at $p<0.01$ uncorrected. Note the early difference in C (approximately 100 ms after target object onset, approximately 10 Hz) showing increased power for basic compared to domain-level object naming. Also note the later (approximately 300 ms after target object onset, approximately 20 Hz and 50-60Hz) difference showing increased power for domain compared to basic-level object naming.

Within the region in left occipito-temporal cortex (see Figure 7.3.6 for source location), we found differences between basic and domain-level object naming beginning around 100 ms after target object onset (see Figure 7.3.16). At this location in the brain, there was an increase in power in the low frequencies (approximately 5-10 Hz) for both basic and domain-level object naming immediately after target object onset, peaking at

FIGURE 7.3.16. Time-Frequency Findings from Left Occipito-Temporal Cortex.



Time-frequency findings in left occipito-temporal cortex for the group of 8 participants identified as showing greater power for domain-level naming from 150-250 ms. Target object onset is denoted by the solid line. A) Basic-level object naming compared to baseline; B) Domain-level object naming compared to baseline; C) Direct comparison of basic to domain-level object naming thresholded at $p<0.01$ uncorrected. Note the difference in C (beginning at approximately 100 ms of target object onset, approximately 15-25 Hz) showing increased power for domain compared to basic-level object naming.

approximately 150-200 ms. In addition, there was a decrease in power in beta frequencies (approximately 10-30 Hz) for both basic and domain-level object naming beginning at approximately 200-300 ms after target object onset. For basic-level naming compared with domain-level naming, however, there was a larger decrease in beta-frequency (approximately 15-25 Hz) power at this location, beginning at roughly 100 ms after target object onset.

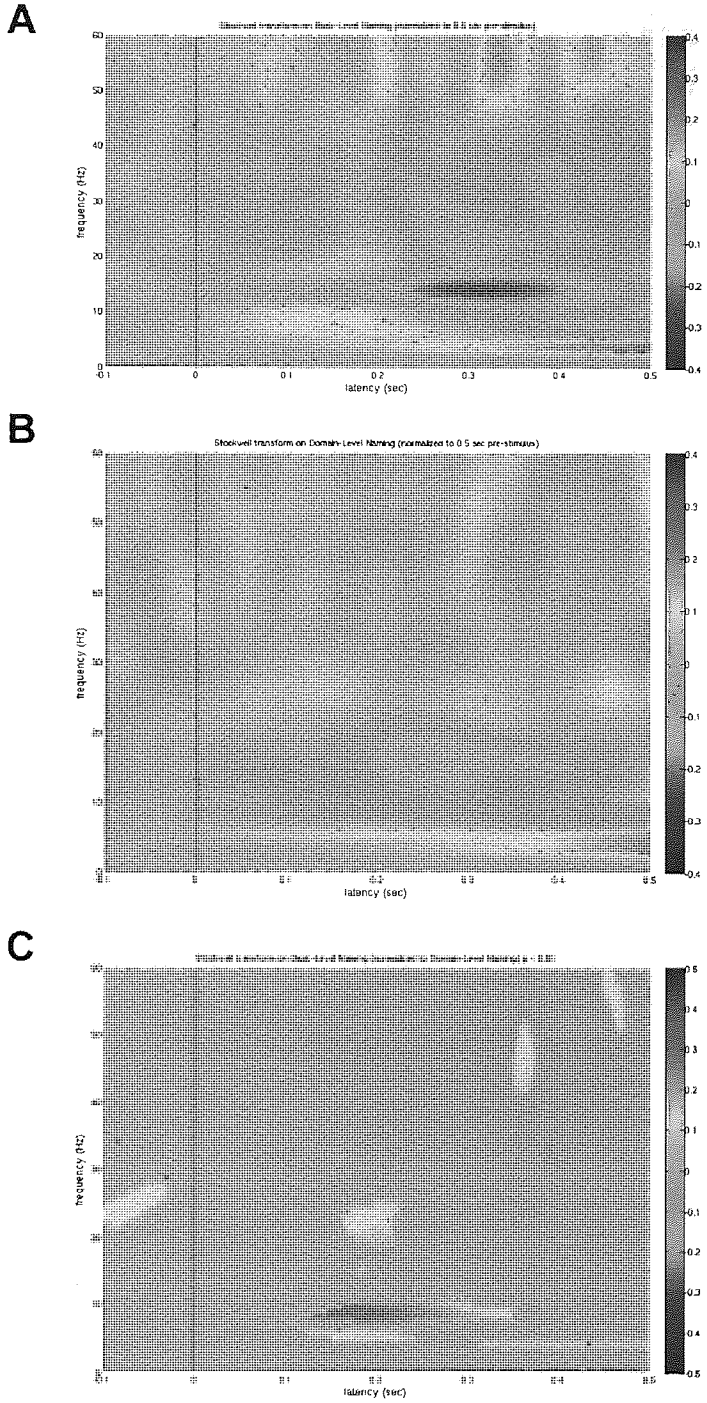
Within the region in right anterior inferior temporal cortex (see Figure 7.3.5A for source location), we found differences between basic and domain-level object naming beginning around 100 ms after target object onset (see Figure 7.3.17). At this location in the brain, there was an increase in power in the low frequencies (approximately 5-10 Hz) for basic-level object naming beginning around 100 ms after target object onset, in addition to an increase in power at a slightly higher frequency (approximately 20 Hz). For domain-level object naming, there was no increase in power in these frequency ranges during this time period.

Within the region in left anterior inferior temporal cortex (see Figure 7.3.10B for source location), we found differences between basic and domain-level object naming beginning around 100 ms after target object onset (see Figure 7.3.18). At this location in the brain, there was an increase in power in the low frequencies (approximately 5-10 Hz) for both basic and domain-level object naming beginning around 100 ms after target object onset. This was followed by a decrease in power in beta frequencies (approximately 10-30 Hz) for both basic and domain-level object naming beginning around 200-300 ms after target object onset. For basic-level naming compared with domain-level naming, however, there was a larger decrease in beta-frequency (approximately 15-25 Hz) power at this location, beginning at roughly 100 ms after target object onset and again at roughly 250 ms after target object onset.

Within the region in right posterior middle temporal gyrus (see Figure 7.3.5B for source location), we found differences between basic and domain-level object naming beginning around 100 ms after target object onset (see Figure 7.3.19). At this location in the brain, there was an increase in power in the low frequencies (approximately 5-10 Hz) for both basic and domain-level object naming immediately after target object onset, peaking at roughly 150-200 ms. In addition, for both basic and domain-level object naming there was a slight increase in power at approximately 100 ms in high beta frequency (approximately 25-30 Hz). For basic-level naming compared with domain-level naming, however, there was greater beta-frequency (approximately 30 Hz) power at this location at approximately 100 ms of target object onset. This was followed by a loss of beta frequency (approximately 10-30 Hz) power for both basic and domain-level object naming. However, in the comparison of basic and domain-level naming, there was a greater loss of beta frequency power beginning at approximately 200 ms after target object onset.

Within the region in left posterior middle temporal gyrus (see Figure 7.3.13 for source location), we found an increase in power in the low frequencies (approximately 5-10 Hz) for both basic and domain-level object naming immediately after target object onset, peaking at roughly 150-200 ms (see Figure 7.3.20). This was followed by a loss of power in the beta frequency (approximately 10-30 Hz) at a slightly later time (beginning approximately 200-300 ms after target object onset). For basic-level naming compared with domain-level naming, there was an increase in power in the gamma frequency (approximately 40-60 Hz) at approximately 300 ms after target object onset. At approximately 400 ms after target object onset, there was an increase in power for basic-level object naming in the alpha to beta frequency (approximately 10 and 15 Hz respectively), caused by a larger decrease for domain-level naming compared with basic-level naming).

FIGURE 7.3.17. Time-Frequency Findings from Right Anterior Inferior Temporal Cortex.

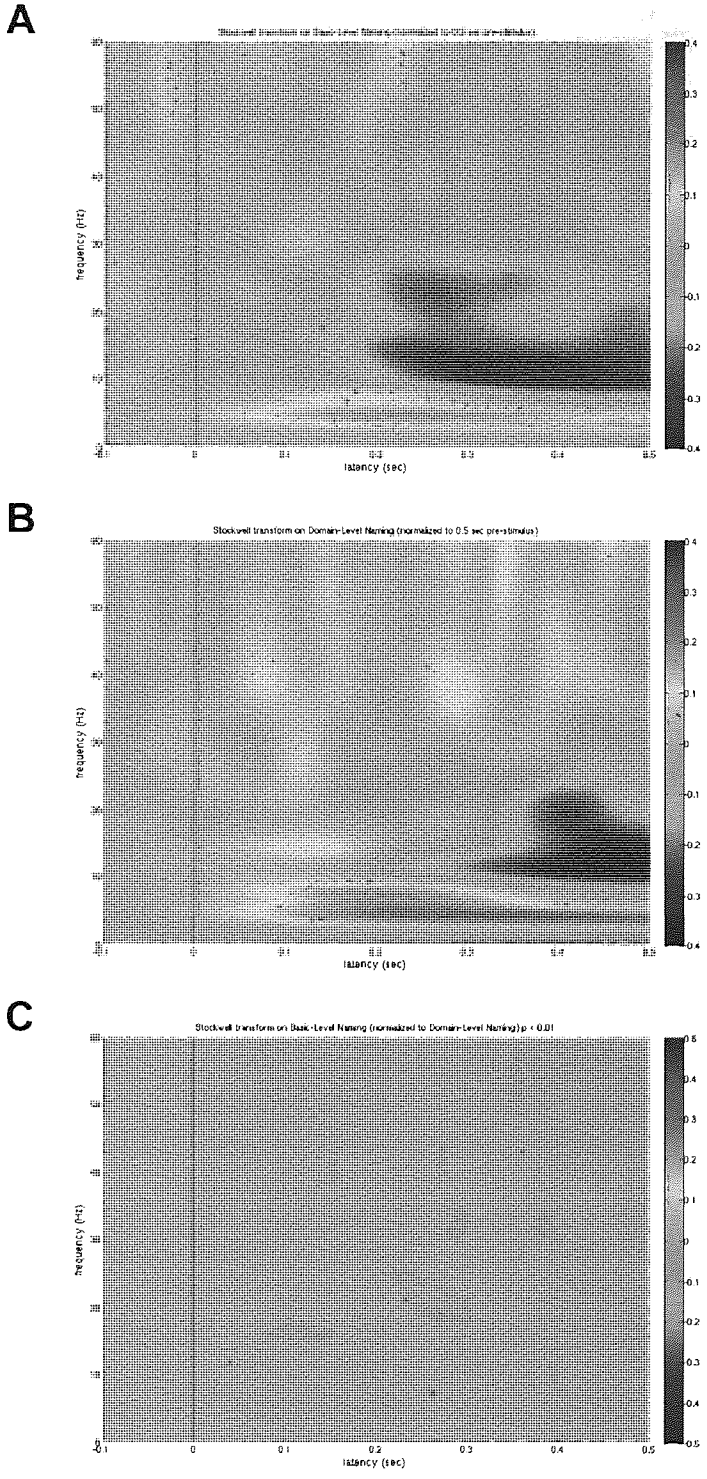


Time-frequency findings in right anterior inferior temporal cortex for all 9 participants identified as showing greater power for basic-level naming from 150-250 ms. Target object onset is denoted by the solid line. A) Basic-level object naming compared to baseline; B) Domain-level object naming compared to baseline; C) Direct comparison of basic to domain-level object naming thresholded at $p<0.01$ uncorrected. Note the difference in C (beginning at approximately 100 ms of target object onset, approximately 5-10 Hz and 20 Hz) showing increased power for basic compared to domain-level object naming.

7.4. Discussion

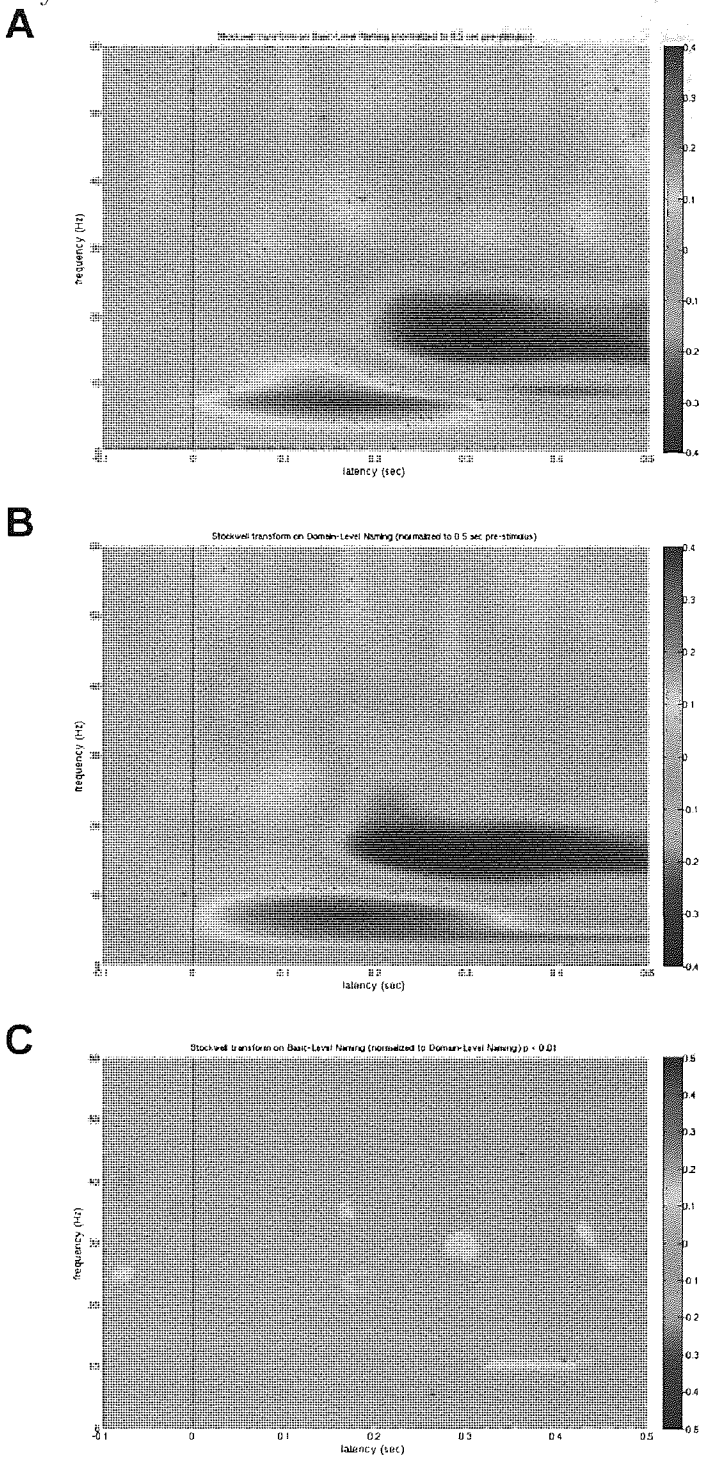
We found a range of regions in the brain showing significant differences between basic and domain-level object naming. In contrast to our analyses presented previously, these

FIGURE 7.3.18. Time-Frequency Findings from Left Anterior Inferior Temporal Cortex.



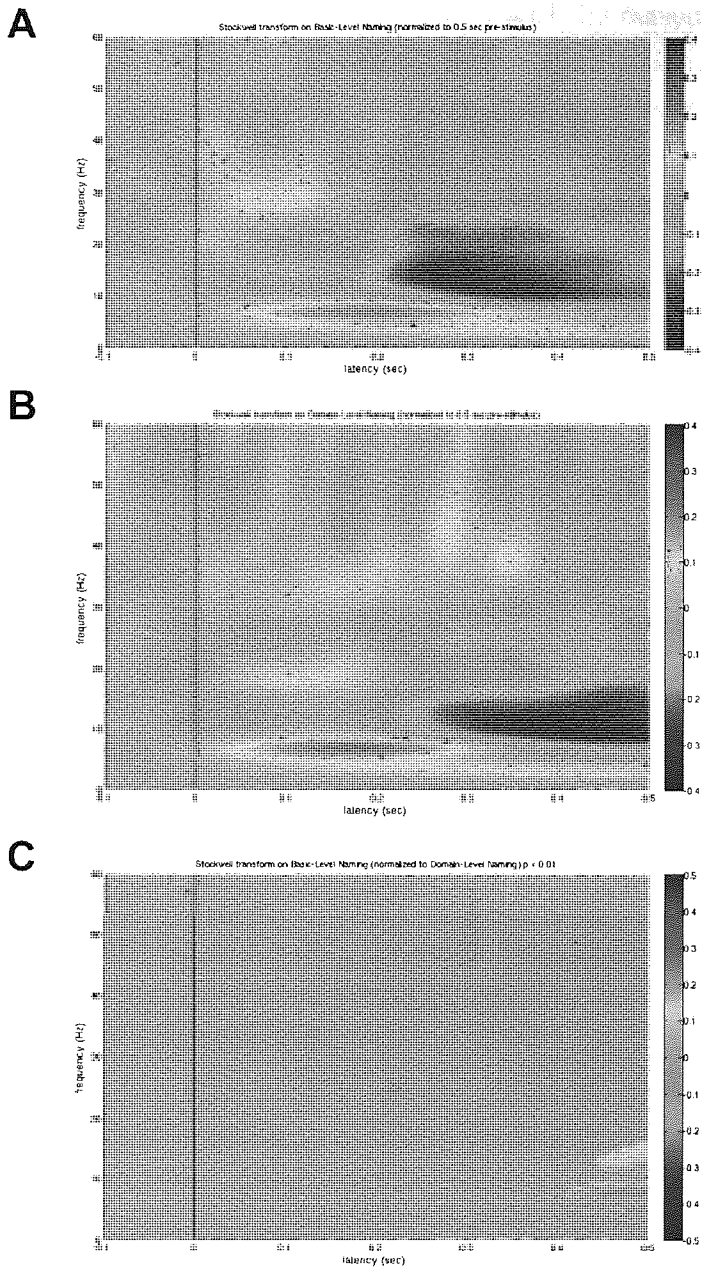
Time-frequency findings in left anterior inferior temporal cortex for the group of 8 participants identified as showing greater power for domain-level naming from 250-350 ms. Target object onset is denoted by the solid line. A) Basic-level object naming compared to baseline; B) Domain-level object naming compared to baseline; C) Direct comparison of basic to domain-level object naming thresholded at $p<0.01$ uncorrected. Note the difference in C (beginning at approximately 100 ms of target object onset, approximately 15-25 Hz) showing increased power for domain compared to basic-level object naming.

FIGURE 7.3.19. Time-Frequency Findings from Right Posterior Middle Temporal Gyrus.



Time-frequency findings in right posterior middle temporal gyrus for all 9 participants identified as showing greater power for domain-level naming from 150-250 ms. Target object onset is denoted by the solid line. A) Basic-level object naming compared to baseline; B) Domain-level object naming compared to baseline; C) Direct comparison of basic to domain-level object naming thresholded at $p<0.01$ uncorrected. Note the early difference in C (approximately 100 ms after target object onset, approximately 30 Hz) showing increased power for domain compared to basic-level object naming. Also note the later (approximately 200 ms after target object onset, approximately 20-30 Hz) difference showing increased power for basic compared to domain-level object naming.

FIGURE 7.3.20. Time-Frequency Findings from Left Posterior Middle Temporal Gyrus.



Time-frequency findings in left posterior middle temporal gyrus for all 9 participants identified as showing greater power for basic-level naming from 400-500 ms. Target object onset is denoted by the solid line. A) Basic-level object naming compared to baseline; B) Domain-level object naming compared to baseline; C) Direct comparison of basic to domain-level object naming thresholded at $p<0.01$ uncorrected. Note the difference in C at approximately 300 ms after target object onset (at approximately 40-60 Hz) showing increased power for domain compared to basic-level naming. Also note the later (approximately 400 ms after target object onset, approximately 10 Hz) difference showing increased power for basic compared to domain-level object naming.

included a selection of regions within the ventral object-processing stream, including regions in middle temporal gyrus, occipito-temporal cortex, and anterior inferior temporal cortex. These findings suggest that there are differences between basic and domain-level object naming in the ventral stream, and these differences reflect a temporal shift in processing between living and nonliving objects, rather than an amplitude difference.

Our findings suggest early differences in right middle temporal gyrus between basic and domain-level object naming. Within this region of the brain, our time-frequency findings show differences within 100 ms of seeing an object, with increased power for basic-level compared with domain-level naming at around 10 Hz. In addition, our findings indicate that there is greater power for basic-level naming in this region even prior to target object onset, suggesting perhaps anticipatory effects in this region. Given that participants had already been cued as to what level of specificity they would be required to name a picture at, it is not surprising that we would see effects even prior to stimulus onset.

Within early anatomical regions of the ventral stream (i.e., occipito-temporal cortex) we find differences between basic and domain-level object naming beginning slightly later than the timing in right middle temporal gyrus. The first differences here occur at roughly 100-200 ms after target object onset, with greater power for domain-level compared with basic-level naming within the beta frequency range in left occipito-temporal cortex. Both left and right occipito-temporal cortex then show differences between basic and domain-level naming around 300 ms after target object onset in the beta frequency range. These differences reflect greater desynchronisation (i.e., a greater loss of power) for basic-level compared with domain-level object naming, suggesting greater processing demands for naming items at the basic compared with the domain level (Singh et al., 2002). What is interesting about this finding is that the behavioural performance suggests that, if anything, domain-level naming is harder than basic-level naming. Therefore, this effect cannot simply be attributed to greater processing demands for basic-level naming per se.

Within anterior inferior temporal cortex we find differences between basic and domain-level object naming beginning at roughly the same time period as in earlier anatomical regions of the ventral stream. The first differences here occur around 100 ms after target object onset, with greater power for basic-level compared with domain-level naming within the alpha frequency range in right anterior inferior temporal cortex. In addition, we find greater power for basic-level naming in the beta frequency range beginning at roughly 200 ms after target object onset. In left anterior inferior temporal cortex we find greater power for domain-level naming at around 100 ms after target object onset in a low beta frequency. In addition, beginning around 200 ms after target object onset, we find greater power for domain-level object naming in the beta frequency range, which is a consequence of greater desynchronisation for basic compared with domain-level object naming. Again, these findings suggest greater processing demands for naming items at the basic compared with domain level (Singh et al., 2002), contrary to the behavioural performance results.

Within posterior middle temporal gyrus, we find differences between basic and domain-level object naming beginning at roughly 200 ms after target object onset in the right hemisphere. This region showed greater desynchronisation for domain-level compared to basic-level naming in the beta frequency. In left posterior middle temporal gyrus, we found late differences (after 400 ms) between basic and domain-level object naming. Again, this region was driven by greater desynchronisation for domain-level compared with basic-level object naming. Both of these effects suggest greater processing demands for naming items at the domain compared with the basic level (Singh et al., 2002).

If we look at the left lateralised regions coming out of the analysis, as this task involves a sort of covert naming which should recruit the left hemisphere, it appears as if two

separate phenomenon account for the pattern of activation we find. Initially, at around 100 ms after target object onset, there is greater power in low beta (approximately 15-20 Hz) for domain compared with basic-level naming in both left occipito-temporal cortex and left anterior inferior temporal cortex. In both these regions, this is then followed at a later time (at around 300-400 ms after target object onset) by greater desynchronisation for basic compared with domain-level naming in a slightly higher beta frequency (around 18-25 Hz). In left posterior middle temporal gyrus, there is a late effect of level of object-processing on activation. There is greater desynchronisation at this region for domain than basic-level naming around 400-500 ms after target object onset. These findings suggest that both occipito-temporal cortex and anterior ventral temporal cortex show an initial increase in power for domain-level naming. Then, these regions are recruited to a greater extent for basic compared with domain-level naming at around 300-400 ms after naming. Then, at around 400-500 ms after target object onset, middle temporal gyrus is recruited to a greater extent for domain compared with basic-level naming.

Taken together, these findings suggest that anterior ventral temporal cortex is recruited to a greater extent for basic-level object naming. In addition, in more posterior regions in middle temporal gyrus, we find greater recruitment for domain compared with basic-level object naming. These findings are generally in line with predictions made by the elaborated CZ hypothesis (Damasio, 1989; Simmons & Barsalou, 2003). In addition, in both posterior and anterior regions of the ventral stream, we find initially greater power for domain-level naming. Perhaps these findings can be accounted for by differing strategies used to classify objects than to name them. For example, research indicates that there are differences in normal participants use of local and global shape in identifying living or nonliving things (e.g., Gerlach, 2001; Lloyd-Jones & Luckhurst, 2002). It might be the case that when participants know they will be categorising objects rather than naming them, they pay attention to different features. Certainly the initial greater activation in occipito-temporal cortex for domain-level naming would support these findings, if accessing the structural descriptions of objects depends largely on the the type of object you are identifying.

What is interesting is that our findings suggest posterior middle temporal gyrus might show a later response to domain-level naming than the more anterior regions to basic-level naming. That is, there appears to be greater recruitment of posterior middle temporal gyrus for domain-level naming at a fairly late time point. Perhaps this finding can be explained, however, by the behavioural results. Namely, our behavioural results indicate that domain-level naming is a harder task to perform than basic-level naming.

In line with the elaborated CZ hypothesis, our MEG findings suggest recruitment of anterior ventral temporal cortex for basic compared with domain-level naming. In addition, there is some indication that more posterior regions are recruited for domain-level naming. These findings lend support to the elaborated convergence zone hypothesis.

CHAPTER 8

Exploring Perceptual Differences in Object-Processing in a Patient with a Category-Specific Deficit for Living Things

8.1. Introduction

All of the research reported in this thesis thus far has been carried out using normal participants. This is because our primary research interest has to do with category-specific processing under normal circumstances. Certainly the use of normal participants allows us to understand category-specific processing in the normal brain, however there are certain limitations. For example, we do not know if findings such as increased perceptual processing for living than nonliving objects could account for patterns of difficulty shown in patients. That is, category-specific patients do not all have damage to regions involved in perceptual processing, So, although we have shown that perceptual processing is important, that does not rule out the possibility of some later specialisation as well. In the cascade model of picture naming, Humphreys et al. (1988) argue that there is interaction between the different stages involved in naming objects. These interactions then can have knock-on effects into the semantic system (Humphreys & Forde, 2001). These knock-on effects occur because structurally similar items to a target are co-activated during an initial feedforward pass. Once structurally similar items are co-activated, there is enhanced competition between a target and other activated representations, and this competition results in longer reaction times or decision making for items that share many features. Therefore, living things tend to be disadvantaged relative to nonliving things because of the higher degree of similarity (and thus greater competition) amongst category members. The critical argument is that our normal participants show enhanced activation of structural descriptions for living things, and this difference is perceptually-driven. That is, it is not being driven by differences within the semantic system (i.e., feedback connections). According to the cascade model, structural similar items would be subject to greater competition effects at various stages of the processes. Initially, structural similarity effects naming at the level of accessing structural descriptions because a greater set of items share these features. Structural similarity can also cause competition again at the semantic level because many items are co-activated alongside the target object. Humphreys et al. noted that living things are especially effected because of enhanced competition from both the structural and semantic similarity amongst living things.

We therefore set out to explore early, perceptually-driven category-specific effects in object processing in a single patient having a documented category-specific deficit for living things. This patient's deficit is of particular interest, as behavioural testing has indicated that his deficit appears to effect his semantic knowledge about objects, but not his access to perceptual information (e.g., Humphreys & Riddoch, 2003). In addition, the location of his anatomical lesion is within a region of the ventral stream that is anterior

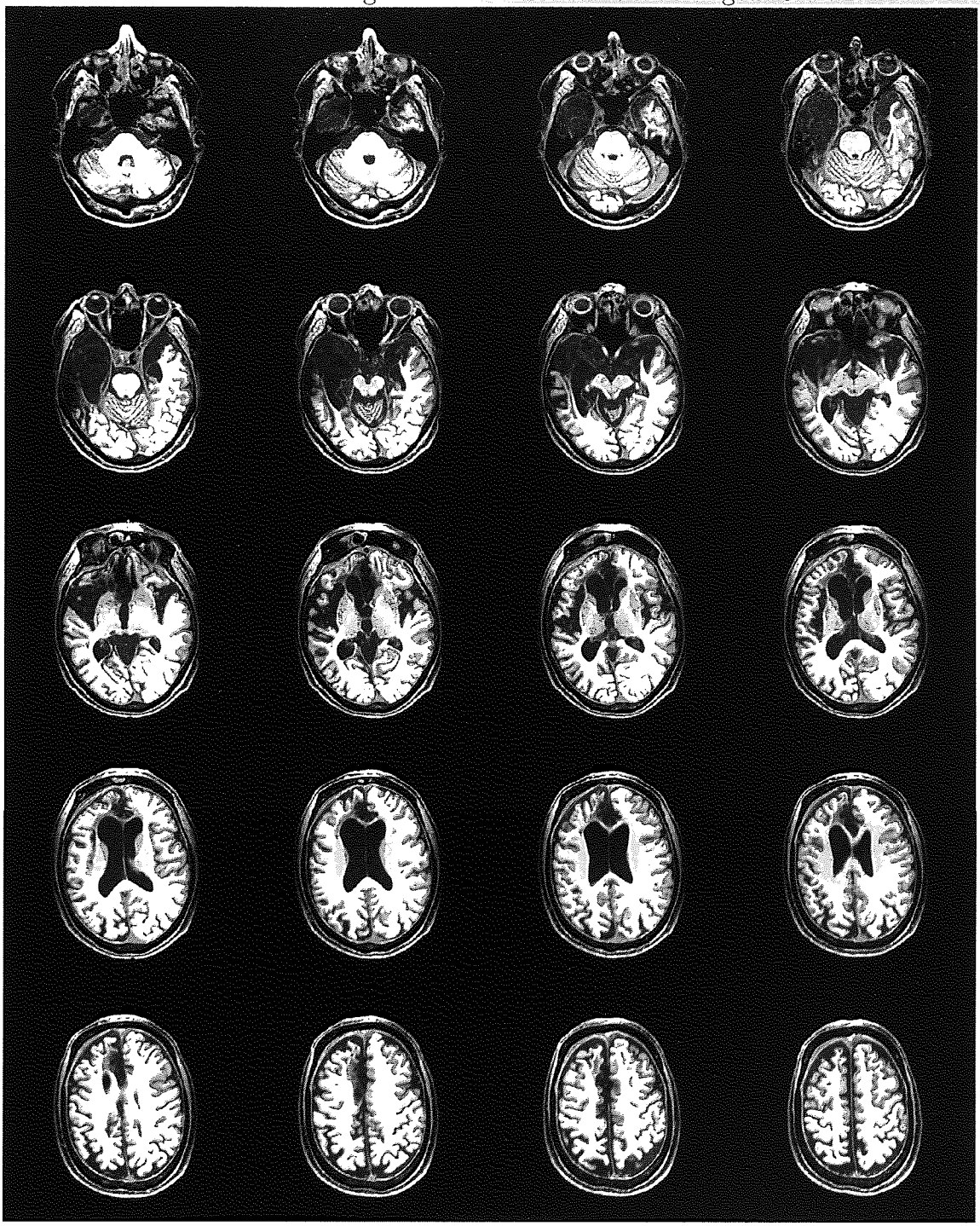
to the region showing category-specific perceptual effects for our normal participants (see Chapter 3). Thus, our aim was to determine whether the early, perceptual differences between living and nonliving objects reported previously (i.e., Chapter 3) could occur in a patient whose deficit encompasses a later stage of object-processing. Findings of enhanced processing for living objects in early regions of the ventral stream would support models of picture naming that suggest deficits could occur at different levels of the object-processing system. (e.g., cascade model of picture naming: Humphreys et al., 1988; HIT account: Humphreys & Forde, 2001). That is, we could demonstrate that perceptual differences between living and nonliving objects still exist in patients whose damage is at the level of the semantic system. In addition, for normal participants, we could rule out that this early activation is a consequence of top-down, feedback projections from the semantic system. However, further research with a range of patients having deficits at different levels in the system would be necessary to fully test the predictions of the model. This research was carried out in collaboration with Professor Glyn Humphreys at the University of Birmingham.

8.2. Methods

8.2.1. Study Procedures. We tested G.A. on a battery of tests to characterise his category-specific deficit and to confirm that he would be able to perform the neuroimaging task appropriately. A brief patient history and description of his performance are discussed below. In addition, we scanned a healthy, age-matched control (A.B.) on the MEG task. This was to confirm there were no age-related differences between G.A. and our previous normal participants (see Chapter 3) that might explain the findings. The experimental design and MEG procedures were identical for both G.A. and A.B., but varied from those utilised in our previously-reported findings with healthy participants. That is, we varied the stimulus set that was presented so that items were matched on naming speed, familiarity, typicality, and visual complexity. Therefore, we utilised the set of items presented in Chapter 3, Study 2, but only showed each item twice. A full description of the experimental design is reported below. Thus, we compare G.A.'s neuroimaging findings to both an age-matched control and the findings from our normal participants reported in Chapter 3.

8.2.1.1. *Patient History.* G.A., a right-handed male, was 54 years old at the time of testing. He suffered herpes simplex encephalitis infection in 1990, at the age of 36. High-resolution anatomical MRI images showed his main lesion sites to occupy the bilateral medial and anterior temporal lobes, extending into the left medial frontal region (see Figure 8.2.1). Major clinical manifestation of his damage included a general aphasia, amnesia, and a dysexecutive syndrome. A detailed description of his case history and general category-specific performance is reported in Humphreys & Riddoch (2003). G.A. was selected for MEG testing because previous behavioural and MRI evidence suggested that his category-specific deficit involved accessing his semantic knowledge store (e.g., Humphreys & Riddoch, 2003). As we were interested in seeing whether enhanced perceptual processing for living objects (see Chapter 3) would still occur in a patient whose deficit is anatomically anterior to the more 'early' region we identified previously, we set out to measure early, perceptual processing differences between living and nonliving

FIGURE 8.2.1. High-Resolution Anatomical Images: G.A.



A montage of axial slices through G.A.'s brain, showing clear bilateral medial and anterior temporal lobe damage (primarily left-lateralised), extending into the left medial frontal region. Slices are in neuroanatomical orientation (Left is Left).

objects in this patient. In particular, we hypothesised that if we still find a region in occipito-temporal cortex responding more for living than nonliving objects in G.A., this might rule out the effect being driven by top-down modulation.

8.2.1.2. *Behavioural Piloting of MEG Study Design.* We aimed to utilise the design of study 1 (i.e., superordinate categorisation task) to probe category-specific activations in our patient. We made some modifications to the stimuli that were utilised from study 1, to ensure that items were fully matched on name agreement, familiarity, frequency, and visual complexity (see Table 1 for a list of items used in the final MEG study). In

TABLE 1. Living and Nonliving Object Exemplars.

LIVING			NONLIVING		
Plants	Animals	Fruits/Vegetables	Tools	Transport	Furniture
Clover	Cow	Apple	Axe	Aeroplane	Armchair
Daffodil	Deer	Cucumber	Drill	Bicycle	Bed
Dandelion	Eagle	Lemon	Garden Fork	Boat	Bunk beds
Grass	Goat	Lettuce	Hammer	Limousine	Chair
Palm	Hippo	Orange	Saw	London Bus	Chest
Rose	Penguin	Peach	Scissors	Lorry	Chest of Drawers
Sunflower	Pike	Pear	Screwdriver	Taxi	Deck Chair
Tree	Rabbit	Pepper	Spanner	Train	Desk
Water-lily	Raccoon	Potato	Tape Measure	Tram	Table
Wheat	Wolf	Strawberry	Workbench	Van	Wardrobe

addition, we increased the timing of the category label, to allow sufficient time for our patient to read each category. Also, because we initially felt that responding on matching and non-matching trials might be too challenging for the patient, we initially modified that task so that he was instructed to respond only when the category label and target object were congruently-matched. We then piloting this altered procedure on a laptop computer using a 2-button mouse to collect responses. For the piloting, we did not want to use the stimuli from the MEG experiment, so we chose other stimuli from each of the six categories simply to avoid repetition effects while allowing us to assess G.A.'s ability to perform the task.

In initial testing of our modified superordinate-level categorisation task, we found G.A.'s performance to be fairly impaired. Across all trials, we counted items as correct where he either correctly pressed the left-hand mouse button to indicate a matching trial, or where he withheld response when the target object did not match the superordinate label. His percent correct were 65.0% and 56.7% for living and nonliving items respectively (see Table 2) during initial piloting. This performance was achieved only with continuous prompting about the nature of the task during the entire experimental run. Also, G.A. seemed to get confused during the experimental run as to when the next trial began. In our initial task, we had utilised a red fixation cross to demarcate the beginning of another trial, but this visual signal did not seem to help G.A. in deciphering the presentation order. He became confused on several trials, using the target object from a previous trial and responding as to whether it matched a category label from the subsequent trial. Therefore, we made a modification to the initial procedure by altering the red fixation cross so that the screen said 'next...' in red letters, as a signal for the next trial. We then pre-tested G.A. on this modified task a week after initial testing. During his second test, we did not prompt G.A. as frequently as we had during the initial testing. However, his performance did not improve significantly this second time around. He correctly responded on 63.3% of the living target object trials and 56.7% on the nonliving target object trials (see Table

TABLE 2. Behavioural Piloting of MEG Procedures: G.A.'s Performance.

	Session 1 Performance (/20) [%]	Session 2 Performance (/20) [%]	Session 3 Performance (/20) [%]
Animal	12 [60]	16 [80]	17 [85]
Fruit/Vegetable	13 [65]	11 [55]	13 [65]
Plant	14 [70]	11 [55]	16 [80]
Furniture	10 [50]	9 [45]	16 [80]
Tool	11 [55]	8 [40]	10 [50]
Transport	13 [65]	17 [85]	16 [80]

2). One improvement that was noted during this second pilot was that the substitution of the word 'next...' seemed to alleviate G.A.'s trial order confusion.

Given G.A.'s performance on the two behavioural pilots, we felt that altering the task to allow G.A. to respond on every trial might serve to improve his accuracy. Specifically, we noted that during the previous testing, G.A. would often respond to non-matching trials by pressing the right-hand mouse button. We would correct him at that point, reminding him that the task required him to only respond during matching trials. Since he seemed to want to respond on every trial, we altered the task back to its initial design. That is, we asked G.A. to respond with the left-hand mouse button for matching trials and with the right-hand mouse button for non-matching trials in a third pilot run a week after the second. In this design variation, G.A. achieved his best piloting performance. He accurately responded on 76.7% of living trials and on 70.0% of nonliving trials (see Table 2). It is interesting to note that G.A.'s performance is better for living than nonliving items across all three testing sessions. This performance is probably a reflection of the task being a superordinate-level categorisation task. In fact, when G.A. was tested on a semantic verification task (mentioned in the next section) for the actual items used in the MEG experiment, his performance indicated a significant impairment for living compared with nonliving objects. We felt that G.A.'s performance on this pilot procedure was reasonable in that his performance was comparable for both living and nonliving objects. Thus we were satisfied with the new design procedures and G.A.'s general ability to execute the task appropriately.

8.2.1.3. *Semantic Verification Task.* We created a semantic verification task to assess G.A.'s semantic impairments on the set of items we used in our MEG experiment. This task was modelled after an attribute verification task created by Samson & Pillon (2003). In the task, G.A. was first presented with the name of an item, followed by four probe questions. Two of these questions probed visual knowledge about each object, and 2 probed non-visual knowledge. Non-visual knowledge probes included questions about how items were typically used, where they were typically found, and other non-visual attributes specific to the type of category (e.g., how items were typically eaten for items from the fruits and vegetables category). For each of these types of knowledge, 1 question was constructed to be true and 1 question was constructed to be false. Many of the questions were based on a set of feature norms collected by Cree & McRae (2003).

TABLE 3. Semantic Verification Task: G.A.'s Overall Performance.

Category	Items Correct (/10) [%]
Animals	3 [30]
Fruits/Vegetables	3 [30]
Plants	1 [10]
Furniture	8 [80]
Tools	4 [40]
Transport	4 [40]

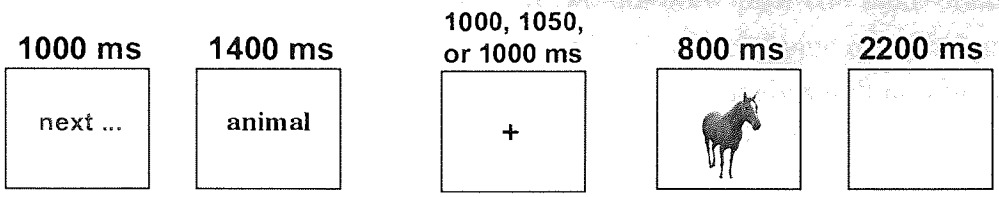
G.A. had to answer all 4 probe questions correctly in order for an item to be considered correct.

We presented G.A. with a paper and pencil version of the task, which was read aloud to him (see Appendix D). He was asked to respond "yes" or "no" to each question, and this was noted via a tick mark placed on his answer sheet. Following the scoring procedure used by Samson & Pillon (2003), an item was scored as correct if G.A. answered all the probe questions correctly (i.e., "yes" to the 2 true statements and "no" to the 2 false statements). We found G.A.'s performance to be more impaired for living items (23.3%) compared with nonliving items (53.3%) (see Table 3). In a second analysis, we assessed G.A.'s performance for each of the visual and non-visual probe questions. For living things, his performance on the visual-knowledge questions (71.7%) was better than his performance on the non-visual knowledge questions (65.0%). His performance for the visual and non-visual knowledge questions for the nonliving items was relatively similar, and better than his performance on the living probe questions. For the nonliving questions he scored 80.0% and 83.3% for the visual and non-visual knowledge questions respectively.

Thus we felt that G.A.'s performance on this semantic verification task highlighted his specific deficit for living compared to nonliving object knowledge. A similar pattern of performance was reported for G.A. on visual/perceptual and verbal/functional knowledge of living and nonliving objects using a property verification task administered by Humphreys & Riddoch (2003). That is, G.A. showed significant impairment for both visual and verbal knowledge of living relative to nonliving things. Given that G.A.'s performance on our task was both poorer for living than nonliving objects, and approximately equal for both visual and non-visual knowledge of living things compared with nonliving things, this performance suggests that G.A.'s impairment with living objects is either within the semantic system or at a location following accessing structural descriptions but prior to accessing semantic knowledge about objects. A similar conclusion was reached by Humphreys & Riddoch. We therefore felt that the stimulus set was adequate to test G.A.'s category-specific activations, and proceeded with the set of items that had been selected.

8.2.1.4. *MEG Experimental Design.* As mentioned previously, a modified version of the task described in Chapter 3, Study 1 was administered to both G.A. and A.B. We obtained written informed consent following Aston University ethical guidelines for both participants. During scanning, both G.A. and A.B. were first shown a superordinate category name as a probe, followed by a target object (see Figure 8.2.2). Both G.A. and

FIGURE 8.2.2. Example Trial from Patient Study.



G.A. and A.B. were shown 'next...' in red font colour for 1000 ms, followed by a 1400 ms category probe. After a variable (1000, 1050, or 1100 ms) delay interval, they were shown a target object for 800 ms. They were instructed to decide as quickly and accurately as possible if the target object was a member of the previously presented category probe by pressing a button.

A.B. were instructed to respond by button press as quickly and accurately as possible, identifying whether the target object matched the category probe. They responded using a 2-button response box held in their right hand. They were instructed to respond by pressing the left button with their right index finger for "yes" (i.e., congruent trial) and the right button with their middle finger for "no" (i.e., incongruent trial).

Target objects included 60 exemplars drawn from 3 living (plants, animals, fruits and vegetables) and 3 nonliving (tools transport, and furniture) categories (see Table 1 for a list of exemplars). Previous behavioural piloting of these items on a separate group of normal participants indicated that they had high name agreement (greater than 65 percent). In addition, the selected items were matched across domain on naming speed, familiarity, typicality, and visual complexity (see Chapter 3, Study 2 for ratings of the selected items). During scanning, each target object was presented twice, once as a congruent trial and once as an incongruent trial. A total of 120 trials were shown during the scan, half of which included a living target object and the other half a nonliving target object. The order of trial presentation was randomised.

8.2.2. MEG Data Acquisition and Analyses. Neuromagnetic data were recorded at a 600 Hz sampling rate with a bandwidth of 0-150 Hz using a CTF 275 MEG system (VSM MedTech Ltd., Canada) composed of a whole-head array of 275 radial 1st order gradiometer channels housed in a magnetically shielded room (Vacuumschmelze, Germany). Synthetic 3rd gradient balancing was used to remove background noise on-line. Fiducial coils were placed on the nasion, left preauricular, and right preauricular sites of each participant. These coils were energised before each run to localise the participant's head with respect to the MEG sensors. Prior to scanning, participants' head shapes and the location of fiducial coils were digitised using a Polhemus Isotrak 3D digitiser (Kaiser Aerospace Inc.). These were then coregistered to high-resolution T1-weighted anatomical images for each participant acquired with a 3-Tesla whole-body scanner (3T Trio, Siemens Medical Systems) using in-house coregistration software.

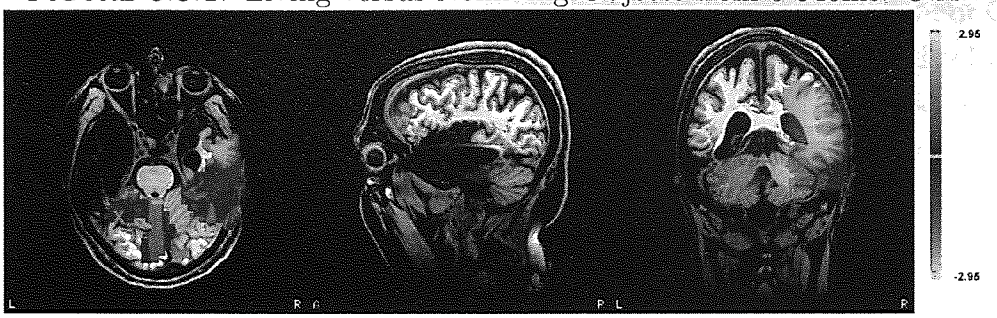
For A.B., but not G.A., total head displacement was measured after the run and could not exceed 5 mm for inclusion in the source analysis. G.A., however, experienced significant difficulty keeping still during the entire experimental run. As significant movement can have detrimental effects on beamformer performance, we attempted to re-start the scanning procedures several times. This did not alleviate the issue, as G.A. would forget to remain still and start moving around to try to keep comfortable. Therefore, we

ultimately decided to continue running him for a single experimental run. Once head movement exceeded 5 mm within the scan, we would wait until the next break in the experiment, at which time we would re-localise his head and continue on. This procedure resulted in 3 'blocks' of data being collected, each with a relatively small number of trials, and each having a separate head localisation. Since a separate head localisation is used for each 'block', it is difficult to combine these three sessions into a single run. This is primarily due to differences in sensor locations above the surface of the head during each of these blocks, which results in a different set of weighting parameters of the sensors in the covariance matrix. Therefore, we will only report a subset of G.A.'s data, which had the smallest movement (maximum head movement=6.8 mm) and most trials of living (N=19) and nonliving (N=19) target objects.

Data for each participant were edited and filtered to remove environmental and physiological artefacts. A beamforming technique was used to assess sources of early, category-specific differences in processing living and nonliving objects. Synthetic Aperture Magnetometry (SAM) was again used to produce 3-dimensional images of cortical power changes. For this study, separate source localisation procedures were utilised for G.A. and A.B. For A.B., a wide-band (1-80 Hz) SAM analysis was computed using a 100 ms window surrounding the M170 (120-220 ms) for living ('active') compared to nonliving ('control') target objects. This is a similar procedure to that adopted in Chapter 3. To accommodate the smaller number of trials collected for G.A., we altered the source localisation procedure so that a wide-band (1-80 Hz) SAM analysis was computed during a 340 ms window (0-340 ms) for living ('active') compared to nonliving ('control') target objects. The lengthening of this window allows more data to be used in constructing the covariance matrix. Spectral power changes between the 'active' and 'passive' periods were calculated as a pseudo t-statistic (Vrba & Robinson, 2001). No group-level analyses could be computed on the data, however we qualitatively compare our source-level findings for G.A. and A.B. with findings reported in Chapter 3.

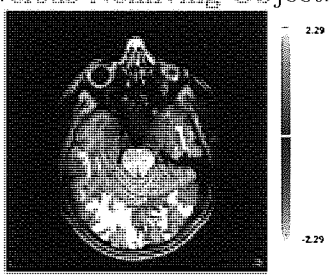
In order to determine whether occipito-temporal cortex in G.A. is responding to the stimulus (i.e., showing event-related, oscillatory activity as a function of visual input), we constructed virtual electrodes at peak locations identified in the SAM analysis. These virtual electrodes were based on a covariance matrix constructed using a 1 second window from 500 ms prior to target picture onset, to 500 ms after the target object, using a wide band (1-80 Hz). Time-frequency plots were then computed on the virtual electrodes using the Stockwell Transform (Stockwell, Mansinha, & Lowe, 1996) for a window beginning 100 ms prior to 500 ms after target picture onset. Power change from baseline (the 500 ms preceding target object onset) was computed at each frequency from 0-60 Hz for both living and nonliving target objects to assess mean (across epochs) power increases and decreases for all objects. A direct comparison of living and nonliving target objects was computed, without any statistical thresholding. This analysis was used as a means to assess whether occipito-temporal cortex was showing a similar pattern of activation to objects for both G.A. and A.B.

FIGURE 8.3.1. Living versus Nonliving Objects from 0-340ms: G.A.



Axial, Sagittal, and Coronal views showing greater bilateral occipital and inferior temporal lobe involvement for living compared with nonliving objects for G.A. Note that in the left hemisphere, greater power for living objects extends from primary visual cortex to just prior to the lesion site. The green 'x' denotes the approximate location of the virtual electrode shown in Figure 8.3.3).

FIGURE 8.3.2. Living versus Nonliving Objects from 120-220 ms: A.B.



Axial view showing several foci in occipito-temporal cortex showing greater power for living compared with nonliving objects for A.B. The green 'x' denotes the approximate location of the virtual electrode shown in Figure 8.3.4).

8.3. Results

We used SAM to identify sources of differential activity between living and nonliving objects. For G.A., we utilised a 340 ms window beginning at target object onset. For A.B., we utilised a 100 ms window surrounding the M170. For both of these analyses, we used a wide frequency band (1-80 Hz). We then constructed virtual electrodes within areas of occipito-temporal cortex for both G.A. and A.B. to assess the timecourse of activation within these regions for all objects. As no group-level statistics were computed, we qualitatively describe category-specific activation in occipito-temporal cortex for living and nonliving objects for both G.A. and A.B.

For G.A., our SAM analysis showed greater power in occipital into temporal regions bilaterally for living compared to nonliving objects (see Figure 8.3.1). Activity was more extensive in the right hemisphere than left. Within the left hemisphere, greater power for living than nonliving objects extended from early visual cortex to just prior to the lesion site. Within the lesion site, there was no difference in power for either living or nonliving objects, suggesting that the beamformer was doing an adequate job of constructing source locations even with the small number of trials included in the sample.

For A.B. our SAM analysis showed several foci within the occipito-temporal cortex showing greater power for living than nonliving objects (see Figure 8.3.2).

We mapped the time-frequency characteristics of region in left occipito-temporal cortex for both G.A. and A.B. These regions were chosen because they were located in the

left hemisphere and were in close approximation to the regions identified in our study of perceptual differences between living and nonliving objects (see Chapter 3). For G.A., our time-frequency analysis was based on 19 trials of living objects and 19 trials of nonliving objects (see Figure 8.3.3). Note that because of the limited number of trials included, the virtual electrode is noisy. Therefore, we need to be cautious in our interpretation of the findings. Generally, for living objects, our time-frequency analysis identified an increase in low frequency (approximately 10 Hz) power at approximately 200 ms post target-object onset. For nonliving objects, a similar increase in low-frequency power did not occur until a later time period (approximately 300 ms post target-object onset). In the direct comparison of living to nonliving objects, in the low frequency, there was greater power for living than nonliving objects, peaking just after 200 ms post target-object onset.

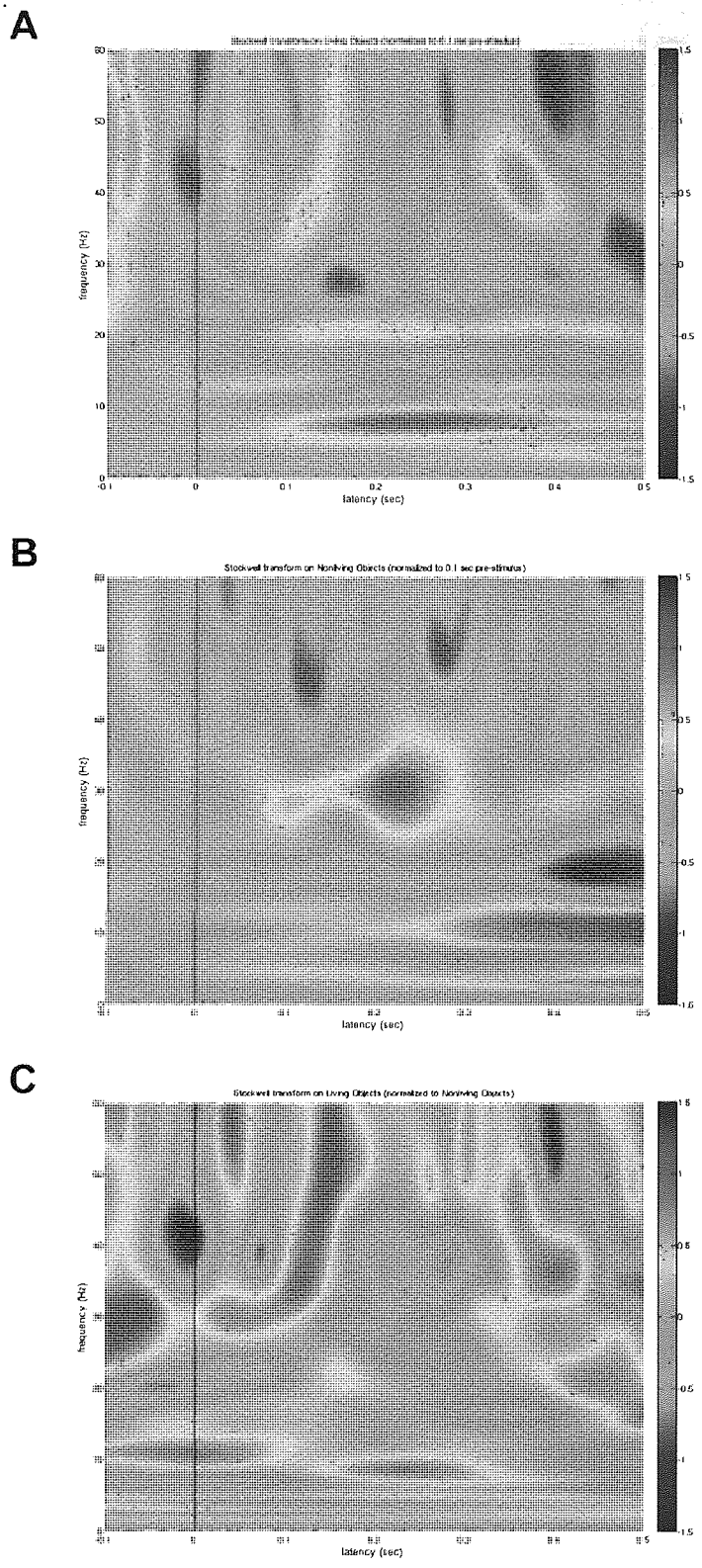
For A.B., our time-frequency analysis was based on 60 trials of living objects and 60 trials of nonliving objects (see Figure 8.3.4). For living objects, our time-frequency analysis identified an increase in low frequency (approximately 7 Hz) power beginning immediately after target-object onset. For nonliving objects, the increase in power was for a shorter time period. In the direct comparison of living to nonliving objects, in the low frequency, there was a sustained increase in power for living compared to nonliving objects.

8.4. Discussion

We set out to determine whether we could detect perceptual differences between living and nonliving object-processing in a patient with a documented category-specific deficit for living things. Our patient, G.A., was selected for testing based on evidence from previous behavioural work that indicated that his deficit for living things encompassed his semantic knowledge rather than his perceptual knowledge of objects (e.g., Humphreys & Riddoch, 2003). Using the cascade model of picture naming (Humphreys et al., 1988) as a theoretical framework then, G.A.'s deficit would exist either somewhere between accessing the structural description system and accessing the semantic representations of objects, or his deficit would reside purely within the semantic system. Therefore, given our previous findings of early, perceptual differences between living and nonliving objects, we hypothesised that G.A. should still show early processing differences between living and nonliving objects, as his deficit reflects impaired retrieval of stored semantic knowledge.

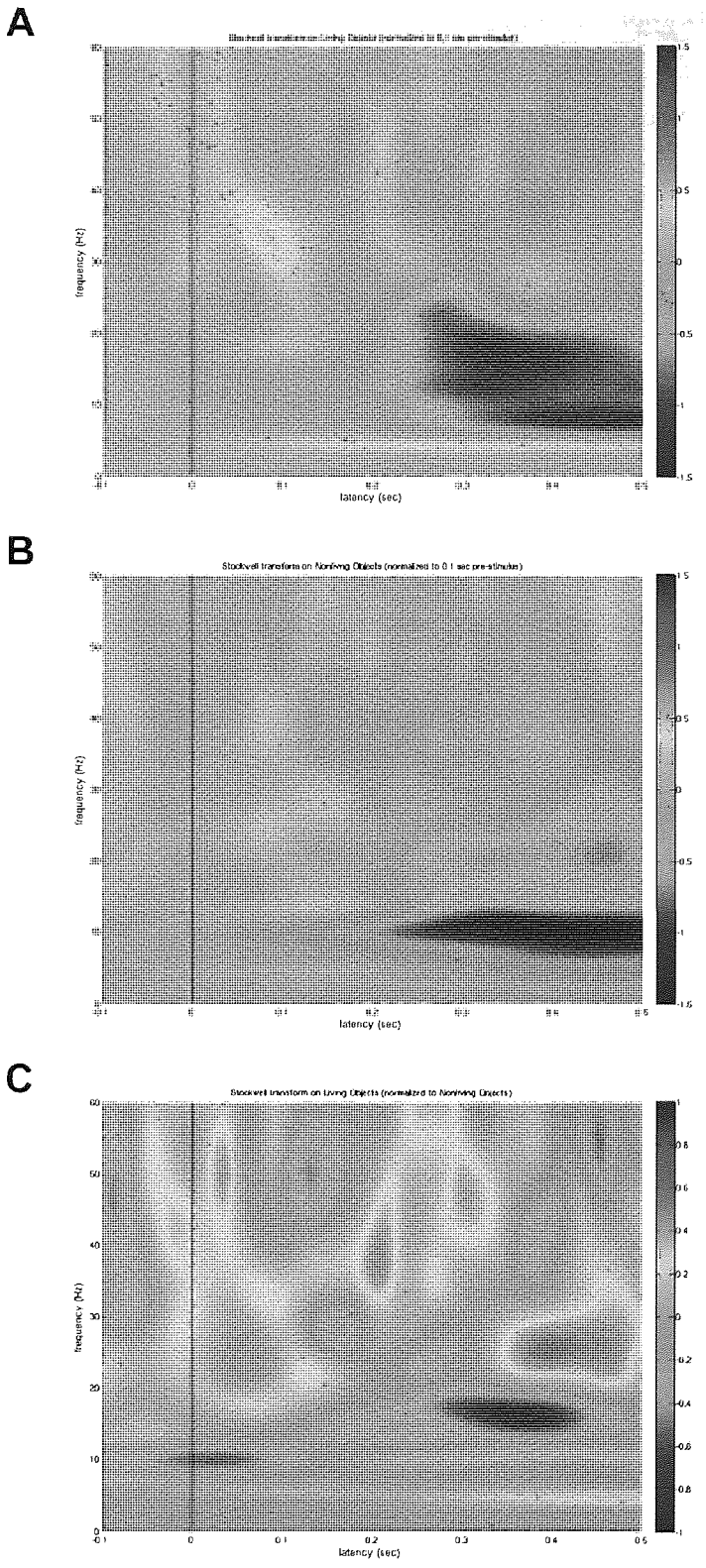
In behavioural piloting, we demonstrated that G.A. could perform a superordinate categorisation task with living and nonliving things. Using a similar experimental design to our previous work with normal participants (see Chapter 3), we altered the presentation speed of each trial in order to give G.A. adequate time to perform the task. After several piloting sessions, we were satisfied that G.A. was performing the task as expected, and we found approximately equal impairment for living and nonliving objects. That is, although G.A.'s deficit is selective for living rather than nonliving things, he could adequately categorise living objects at their superordinate level. In fact, his performance was slightly better for categorising living than nonliving things. Our semantic verification task, however, clearly indicated that G.A.'s deficit was more pronounced for living than nonliving things. He could correctly identify information for only 7 (out of 30) living things compared with 16 (out of 30) nonliving things.

FIGURE 8.3.3. Time-Frequency Findings in Left Occipito-Temporal Cortex: G.A.



Time-frequency findings in left occipito-temporal cortex for G.A. Target object onset is denoted by the solid line. A) Living objects compared to baseline; B) Nonliving objects compared to baseline; C) Direct comparison of living to nonliving objects. Note the increased low-frequency power for living compared to nonliving objects at approximately 200 ms post-stimulus.

FIGURE 8.3.4. Time-Frequency Findings in Left Occipito-Temporal Cortex: A.B.



Time-frequency findings in left occipito-temporal cortex for A.B. Target object onset is denoted by the solid line. A) Living objects compared to baseline; B) Nonliving objects compared to baseline; C) Direct comparison of living to nonliving objects. Note the slight increase in low-frequency power for living compared to nonliving objects beginning around 100 ms post-stimulus.

Our MEG findings lend tentative support to the idea that G.A.'s deficit is at a time point in object-recognition that is later than accessing the structural descriptions of objects. That is, our MEG analysis showed increased power for living than nonliving objects throughout the early anatomical regions of the ventral stream. In the left hemisphere, greater power for living objects extended to just prior to the lesion site. In the right hemisphere, greater power for living objects extended into anterior regions of ventral temporal cortex. In addition, time-frequency findings from a region in left occipito-temporal cortex showed a pattern of activation that is comparable to the pattern we found in our earlier study of perceptual differences with normal participants. That is, there was greater power for living objects at around 200 ms after target object onset. This timing is slightly later than the timing seen in our normal participant group, but given that this patient has extensive damage to his brain from herpes simplex encephalitis, the timing in this region is reasonable.

Our findings, then, are fairly provocative. They suggest that patients with damage to the semantic system rather than perceptual system might still show perceptual processing differences between living and nonliving objects. Thus, these findings indicate that the region we have identified is driven bottom-up rather than top-down. Unfortunately, we were only able to test a single patient with a category-specific deficit. Had we been able to test more patients, it would have been interesting to examine perceptual processing differences in a range of patients whose damage is at different stages in the process.

It should be noted that our findings should be interpreted with caution. This is because we have based our source localisation and time-frequency findings from our patient on a limited number of trials of living and nonliving objects. This is regrettable, but was unavoidable. The limited data available for constructing the covariance matrix and source projections could result in inaccuracies of the beamformer reconstruction (Brookes et al., 2008). Even so, it is reasonable to note that the source projection did not identify any sources of differential activation within the site of G.A.'s lesion in left anterior ventral temporal cortex. Thus, it appears that even with the limited data, the beamformer did an adequate job of source reconstruction.

CHAPTER 9

Conclusions

In a series of four studies, we explored how the brain responds to objects. In particular, we were motivated by the literature on category-specific agnosias and category-specific processing differences in normal participants to examine whether there are specialised regions in the brain for processing different types of objects. In addition, we were interested in whether category-specific processing differences could be detected at different levels within the visual object-processing system.

In a first study, we explored the time course of naming objects (see Chapter 2). This study was motivated to test different models of object-naming, particularly to test whether the serial or cascade model of picture naming could be supported by the pattern of activation found in the brain across time. Generally, our findings showed that activation in the brain did not proceed serially, as many regions were identified as showing significant activation at each time point. In addition, the general pattern of activation was fairly consistent across time, with some regions being activated consistently over several time points, thus suggesting that activation at a given region did not need to be resolved in order for activation to occur at the next important location. Therefore, our findings support a model of picture naming that proposes parallel processing of objects (e.g., cascade model: Humphreys et al., 1988; HIT account: Humphreys & Forde, 2001).

In a set of three studies, we explored perceptual differences between living and nonliving objects (see Chapter 3). Each of these studies were designed to ask different questions about object-processing in the brain, yet each presented living and nonliving objects, so that we could compare processing across these three studies. The analysis was motivated by reports in the literature of early differences between living and nonliving objects (e.g., Kiefer, 2001; VanRullen & Thorpe, 2001). Given the temporal benefits of MEG, as well as adequate source localisation, we set out to determine whether we could detect differences in processing living and nonliving objects within the ventral object-processing stream. Our findings showed very early differences between living and nonliving objects (i.e., 120-220 ms post-stimulus), which localised to a region in left occipito-temporal cortex across all three studies. Time-frequency findings showed this difference reflected greater power for living than nonliving objects within a relatively low frequency band (approximately 10-20 Hz). These findings show very early category-specific processing differences, suggesting that there are differences in the accessing of structural descriptions between living and nonliving objects. Our findings indicate greater processing for living objects at this early time window.

In the next study, we contrasted living to nonliving objects during a 1 s window immediately following target object onset (see Chapter 4). This study was motivated to determine regions in the brain showing semantic differences between living and nonliving objects. Specifically, we wanted to assess whether MEG could detect differences in

the semantic processing of living and nonliving objects. Given the range of studies of category-specificity using either PET or fMRI, we could assess how MEG findings during this 1 s window compared. In particular, we hypothesised that if theories which propose an amodal semantic store are correct, we should find no differences for living compared to nonliving objects. Our findings indicated a range of regions showing category-specific differences, with a number of these regions having been reported in the literature previously. Our findings lend tentative support to the sensory/motor model of object naming (Martin, 1998), as regions that show activation during motor tasks and biological motion tasks showed differential activation for living and nonliving objects.

We then contrasted living to nonliving objects in small, overlapping time windows (see Chapter 5). This analysis was motivated to assess the time-course of category-specific differences in the brain. Our findings indicated very early differences between living and nonliving objects, with regions in frontal and superior temporal gyrus showing selective power for either living or nonliving objects. A more general assessment of differences in the ventral versus dorsal stream suggested that there are both early and late differences between living and nonliving objects. Our results indicate support again for the sensory/motor model of object naming (Martin, 1998), as regions that have been indicated in motor and biological motion tasks were again activated during our picture categorisation task. In addition, in support of the cascade model (Humphreys et al., 1988), we found early and late differences within the ventral stream. According to the model, early perceptual differences between living and nonliving things will cause increased competition within the semantic system. This increased competition then causes re-activation of early regions in order to resolve the identity of the item that is presented. Our results indicate support for this idea, as we found both early and later differences within the ventral stream.

In another study, we set out to measure differences in processing objects at either the basic or domain level (see Chapter 6). This study was motivated to test the convergence zone (CZ) hypothesis (Damasio, 1989; Simmons & Barsalou, 2003), which indicates that anterior ventral temporal cortex is involved in more elaborative processing of objects. Therefore, we hypothesised that anterior ventral temporal cortex should show greater activation for basic compared with domain-level naming. Using a 1 s window of time, we directly contrasted basic to domain-level naming. Our analysis did not indicate any involvement of anterior ventral temporal cortex in basic-level compared with domain-level naming. However, a range of factors could have influenced this finding, and thus we could not resolve whether the hypothesis is correct given only this set of findings.

We then contrasted basic to domain-level object naming in small, overlapping time windows (see Chapter 7). This analysis was motivated to assess the time-course of the level at which you are asked to identify an object on activation patterns in the brain. Again, we hypothesised that if the CZ hypothesis is correct, we should find increased power for basic compared with domain-level naming in anterior ventral temporal cortex. Our results indicated differences between basic and domain-level naming, with greater involvement of more anterior regions in basic level naming. In addition, we found greater involvement of more posterior regions in domain-level naming, suggesting tentative support for the CZ hypothesis.

In a final study we assessed perceptual differences in neural processing between living and nonliving objects in a patient with a documented category-specific semantic deficit for living things (see Chapter 8). This study was motivated to assess whether we would still detect perceptual differences between objects for patients whose deficits reside within the semantic system. This finding would indicate that the perceptual difference we detected in normal participants (see Chapter 3) is a consequence of bottom-up processing of a stimulus. Our results suggest perceptually-driven differences between living and nonliving objects in the patient. This finding supports our assertion that the differences found in our normal participants are a consequence of bottom-up processing, and probably reflect differences in accessing the structural descriptions of objects, with living things requiring greater processing. Thus again, our findings support the cascade model of object naming (Humphreys et al., 1988).

In sum, our findings clearly indicate that living and nonliving object-processing diverges at an earlier time-point than previously assumed. This early divergence is a consequence of greater perceptual processing for living than nonliving objects, supporting behavioural evidence that perceptual processing differences can cause apparent category-specific deficits. In addition, our findings indicate that these effects are likely to be bottom-up, reflecting differences in initial feedforward processing in relatively early regions of the ventral stream. The claim that this initial processing difference reflects feedforward processing is supported by our patient data, whose lesion affects his access to semantic information about objects. This divergence needs to be taken into account in any theory of category-specificity, as this could have knock-on effects for semantic processing. In addition, our analysis of later differences between living and nonliving objects indicates support for distributed representations of object knowledge (sensory/motor model; Martin, 1998).

Our set of experiments are the first to systematically assess perceptual and semantic differences in processing objects. Our findings clearly indicate the benefit of utilising a technique such as MEG to measure the time-course of object processing. Temporal information is critically important, as it allows us to test models of naming explicitly. We have clearly shown early and late differences between objects, both between living and nonliving objects and between categorising objects at the basic and domain levels. These differences have not been systematically measured previously, and thus our findings are the first to provide a comprehensive assessment of the time-course of processing objects. In addition, our study of a patient with a category-specific deficit seems to be the first report using MEG to assess the time-course of object processing. These findings are especially relevant, as they demonstrate intact, early perceptual differences between living and nonliving objects.

In terms of future work, one fruitful direction would be to assess differential processing of objects at a finer scale. All of our research has utilised living and nonliving objects broadly (and basic versus domain-level object naming), but clearly the patient literature and even some neuroimaging evidence using normal participants suggest that there are finer-grained differences between objects. Thus, it would be beneficial to increase the number of items within each category, in order to measure differences in processing for each type of object. For example, manipulable objects (i.e., tools) should make demands

on the motor system, whilst animals should activate regions associated with biological motion according to the sensory/motor model (Martin, 1998). In addition, much research has focused on other factors which could influence category-specificity. One obvious direction is to measure the influence of similarity directly, as this has been indicated to be crucial in explaining some of the category-specific deficits exhibited in patients, in addition to being shown to influence normal processing generally. Thus, a study designed to assess the influence of similarity on early and later processing is vital to a more complete understanding of object-processing generally. Again, the temporal information available using MEG is critical for differentiating early and late processing differences.

In addition, another fruitful direction would be combining neuroimaging methods to gain a greater understanding of object-processing. For example, it would be beneficial to scan participants using both fMRI and MEG. Although the mechanisms behind the hemodynamic and magnetic fields are not identical, and the relationship is not well understood, both techniques have advantages that can be exploited. For example, the greater spatial localisation of fMRI could aid in determining the sources of activation in MEG. In addition, it might be useful to utilise EEG to bridge the fMRI and MEG data. That is, you could scan the same participants using fMRI and EEG combined and MEG and EEG combined, then use the EEG information as a measure to bring together the fMRI and MEG signals. A study such as this would allow you to directly relate the two signals being measured.

Another fruitful direction would be to utilise functional connectivity measures to assess differences in living and nonliving object processing. Many interesting methods for assessing functional connectivity in MEG have developed over the last several years (e.g., DICS: Gross et al., 2001; nulling beamformer: Hui et al., 2010; for a recent review see Schnitzler & Gross, 2005). These techniques are especially useful, as they allow one to assess how cortical interactions change across time. Thus, it would be advantageous to utilise a technique such as these to understand the dynamic change in the pattern of activation for living and nonliving objects. For example, a crucial question that remains unanswered in how early differences between living and nonliving objects influence later differences. This type of question might best be answered by looking at the functional connectivity in the brain dynamically.

Finally, one other fruitful direction would be to assess the time-course of object processing in a range of patients having category-specific deficits. This follows on from our findings that a patient with a category-specific deficit for living things still showed early processing differences between living and nonliving objects. Our patient had a deficit that was thought to occupy the semantic system based on behavioural testing. Our MEG findings confirmed this, as the patient still showed early differences between living and nonliving objects, in line with our normal participants. Assessing the time-course of object processing in a range of patients with damage at different levels in the object-naming system will allow us to better understand the interaction between perceptual and semantic information in identifying living and nonliving objects.

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Appendix

Appendix A.

Methodological Considerations for Peakomatic. There is one arbitrary parameter P which determines how many of the top-ranked peaks from each subject will be used in the analysis. In this section, we set out to examine the dependence of our results on this parameter in more detail and to propose an approximate heuristic for dealing with it in future.

Figure A1 shows the dependence of 95% percentile of the confidence radius (R) (maximum radius in mm of the ellipsoid defining the confidence volume) on P for positive peaks in the analysis reported in Chapter 3 using the data from Study 1. Statistics are automatically produced for all subgroups from (N=) 5-10 participants, but only N=5, 7, and 10 are shown here for clarity. Intuitively, the larger the N, the larger the size of the cluster one would expect to occur by chance.

The parameter P determines the trade off between the importance assigned to rank order and the importance assigned to tight clustering of peaks across participants. If there is high importance assigned to rank order (smaller P), then relatively larger clusters of peaks across participants will be acceptable (although these may have little anatomical consistency). However, if the effect in question does not reach the top P peaks in most participants, it will be completely missed by the analysis. By contrast, if P is set to be too large, then the inclusion of many superfluous (i.e., low rank) peaks will mean that a

Figure A1.

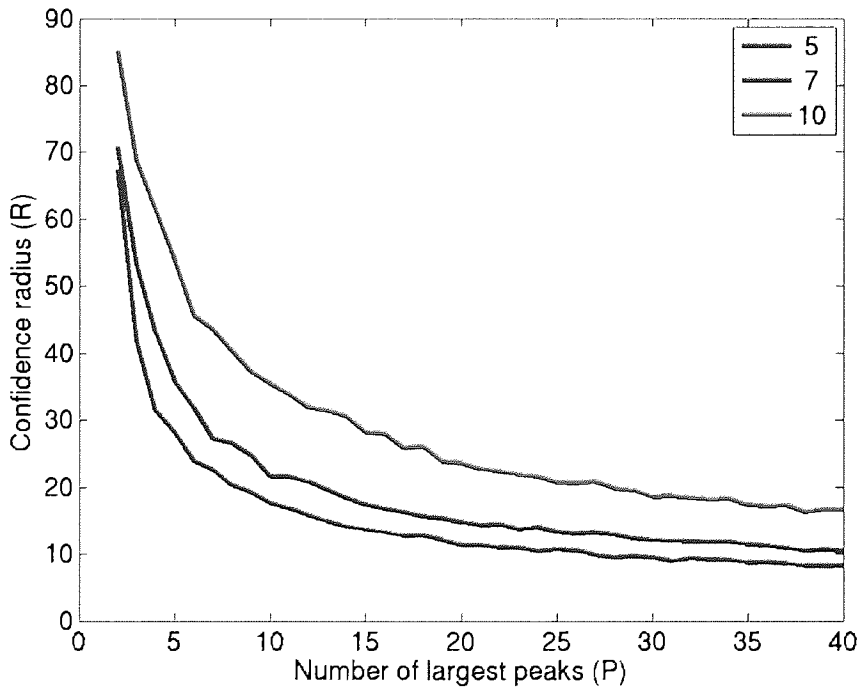
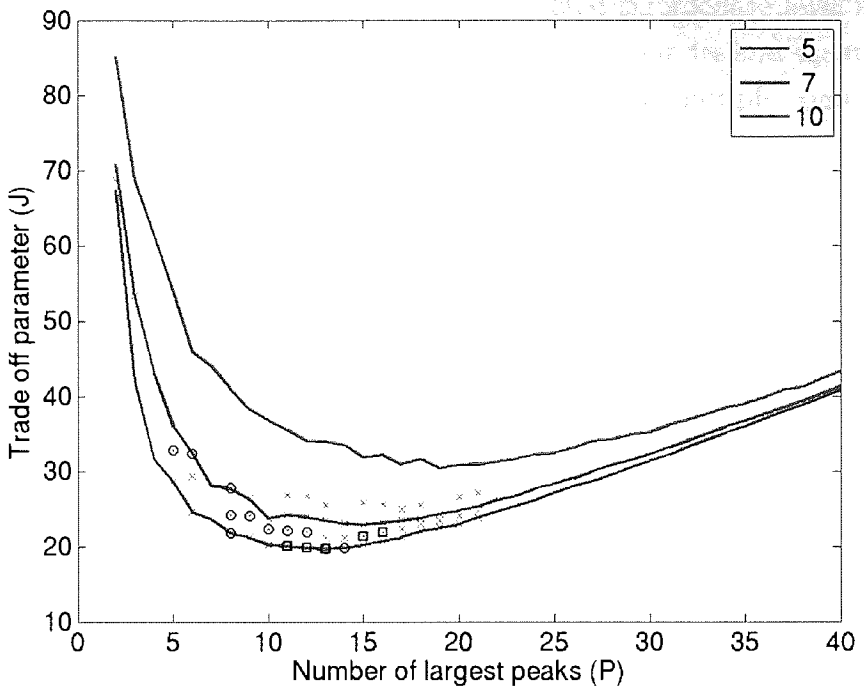


Figure A2.



very tight spatial distribution is required to distinguish a functionally meaningful cluster from one occurring by chance.

We propose a simple heuristic in order to choose a value of P which balances dependence on peak rank against cluster size. If we take the knee of the curve to represent some optimal balance between dependence on peak magnitude (i.e., small P) and anatomical consistency across subjects (i.e., small R), we can compute a parameter J which quantifies the distance of the curves from the knee.

$J = \sqrt{P^2 + R^2}$

Where P and R are the number of peaks and the confidence radius respectively. Now plotting J against P gives a curve (Figure A2) with a clear minimum. For each subgroup (N), crosses on the curve indicate that at least one significant ($p<0.05$) cluster was found for this choice of P when analysing positive peaks. Importantly, these significant excursions predominate around the minimum of the heuristic function.

The next problem is how to set an appropriate significance level given that there will be a multiple comparisons problem. One simple solution would be to only examine the function minima at each value of N. One problem here is that the minima are relatively flat and the smoothness depends on the number of random permutation steps performed, which is processing intensive. Also, one can see from A2 that each subgroup curve N has a different optimal P value (the larger the number of subjects in the group, the larger the optimal number of peaks).

Another possibility is to consider the range of P which defines this minimum. This approach does not rely on the identification of minima (so it is more robust) and can be computed for all N at once. However, there is a multiple comparison penalty. It is important to note however that a completely new (i.e., independent) set of data is only introduced each time the number of peaks is doubled.

Making a Bonferroni correction, the significance level should be decreased by a factor

$$p_{corr} = \frac{0.05}{log_2(\frac{P_{end}}{P_{start}})}$$

Where $\log_2$ is log to the base 2, p_{corr} is the corrected significance level and P_{start} and P_{end} define the range of P we pre-specify an interest in. The circles and squares around the crosses in A2 show the two significant ellipsoids found after multiple comparison correct (for P_{start}=2 and P_{end}=30) for positive peaks.

Appendix B.

Ethical Guidelines Followed in All Studies.

Our research using both normal participants and the patient with a category-specific deficit were reviewed and approved by the Ethics Committee at Aston University. Prior to scanning, all participants reviewed an information sheet detailing the procedures for the study. In addition, detailed information about MEG and MRI were provided. Information sheets were provided that described the type of information available in scans, the procedures employed when collecting data, and assurance that data obtained would remain confidential. In addition, the information sheets described risks associated with the procedures and benefits to be gained. Importantly, all participants were asked if they had any questions upon reading the information sheets. If questions existed, these were answered by the experimenter. If all questions had been answered, and the participants were still happy to volunteer to take part, they were asked to sign a consent form to participate in the study. In addition, there were specific consent forms for both the MEG and MRI procedures, which were reviewed in detail with each participant. In addition, for the MRI procedure, there were screening forms that were completed prior to entering the scan room. These screening forms ensured that no metal was on the person that could harm them during scanning. In addition, the screening forms were used to ensure that participants would not be harmed based on other factors during scanning, such as history of seizures, heart disease, and potential pregnancy. After all paperwork was completed indicating the participants were clear to be scanned, and consent was provided, the participants were placed in the scanner.

Appendix C.

Event-Related Time-Frequency Information From Regions Active During Picture Naming.

For each region identified in our ER-SAM analysis of silent picture naming, we constructed virtual electrodes to map the time-frequency characteristics across the group of participants identified as having a peak in the volume. The virtual electrodes were constructed using all pictures, normalised to a 100 ms window prior to picture onset. We then averaged the virtual electrodes across trials to assess event-related activity at each location. We used the time points at which the largest number of participants were identified as having a peak at each location for constructing the virtual electrodes. The corresponding time point and number of participants having a peak in each volume are given below.

Figure A3. Right Middle Frontal Gyrus, 65 ms, N=9.

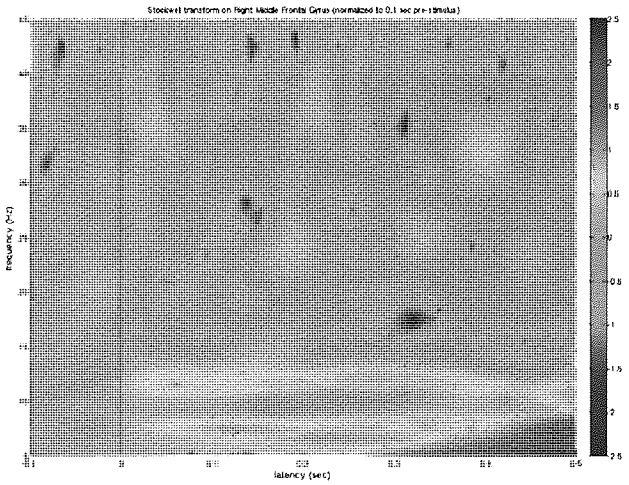


Figure A4. Left Lingual Gyrus, 165 ms, N=9.

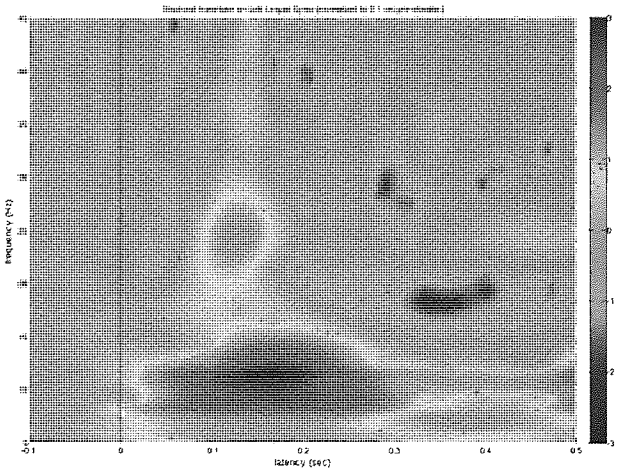


Figure A5. Right Middle Temporal Gyrus, 195 ms, N=7.

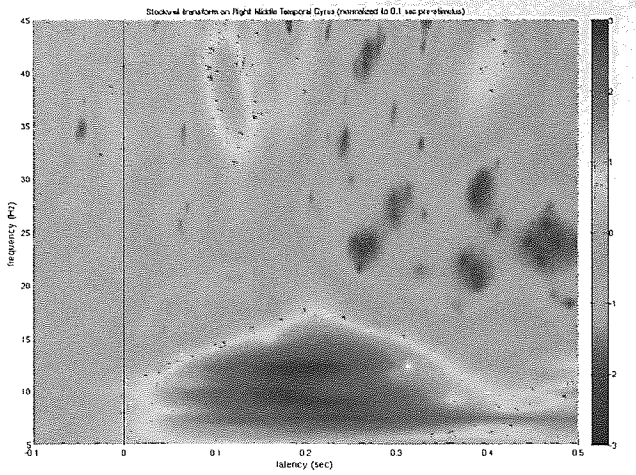


Figure A6. Right Inferior Frontal Gyrus, 235 ms, N=9.

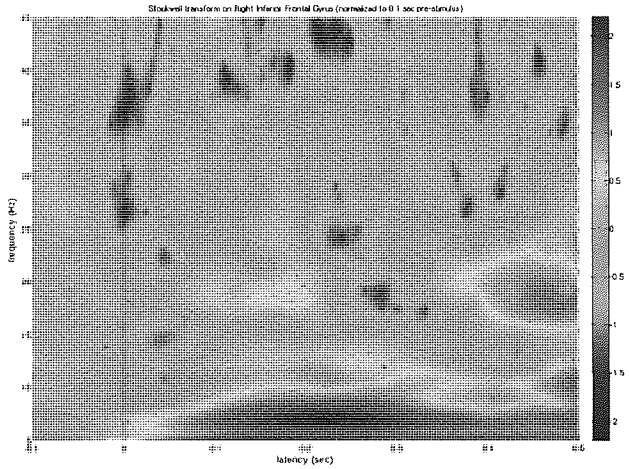


Figure A7. Left Inferior Parietal Lobule, 295 ms, N=9.

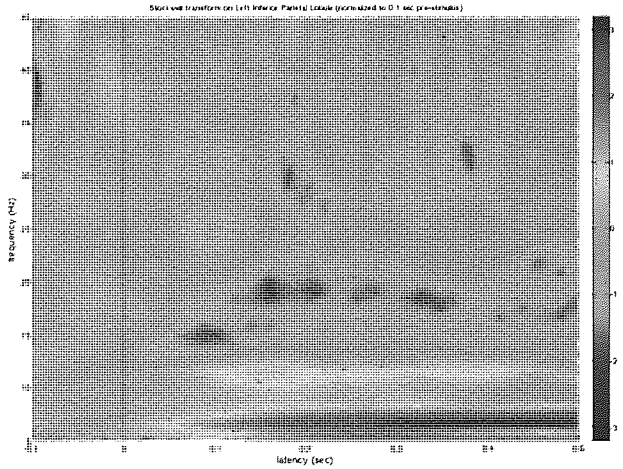


Figure A8. Left Superior Temporal Gyrus, 365 ms, N=6.

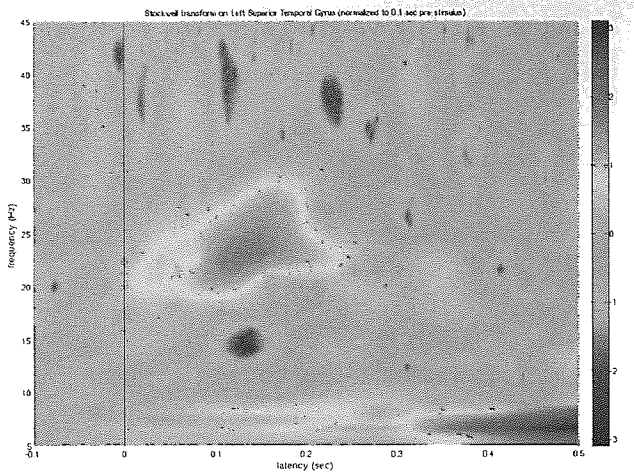
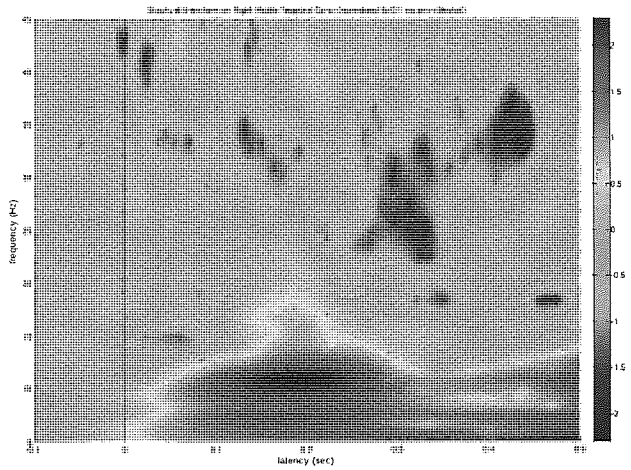


Figure A9. Right Middle Temporal Gyrus, 390 ms, N=10.



Appendix D.

Semantic Verification Task.

Instructions: You will see the same of several objects listed below, followed by a series of questions. Please indicate YES or NO whether each question is correct or not as it relates to each object listed above.

SAW
Is it used for cutting?
Is it used for hitting?
Does it have sharp teeth?
Does it have numbers?

AEROPLANE
Does it have tracks?
Does it have a nose?
Does it have a conductor?
Does it fly in the air?

COW
Does it climb trees?
Does it have an udder?
Does it produce milk?
Does it have a mask?

GARDEN FORK
Is it used for moving leaves?
Is it used for gripping?
Does it have prongs?
Does it have numbers?

RACCOON
Does it hop?
Does it climb trees?
Does it have long ears?
Does it have a mask

WOLF
Does it have an udder?
Does it swim?
Does it have a furry tail?
Does it howl?

DEER
Does it have antlers?
Does it howl?
Is it used for meat?
Is it black and white?

TAXI

Does it require money?
Does it run on tracks?
Does it have a sign on top?
Is it two-story?

BUNKBEDS
Does it have a lid?
Does it have a mattress?
Is it found in office buildings?
It is used for sleeping?

CHEST OF DRAWERS
Does it have knobs?
Does it have a mattress?
Is it used for sitting?
Is it used for storing clothes?

WORKBENCH
Is it used for gripping?
Does it have legs?
Does it have a handle?
Is it used when cutting?

DANDELION
Does it cause allergies?
Is it used to make cooking oil?
Is it yellow?
Does it have bark?

BICYCLE
Does it have a motor?
Does it require money?
Is it used by riding?
Does it have pedals?

LORRY
Is it used to transport things?
Does it have wheels?
Does it have a track?
Does it have a conductor?

WARDROBE
Is it used for eating?
Is it used for storing clothes?
Does it have handles?
Does it have a mattress?

RABBIT
Does it have scales?
Does it have long ears?
Does it live in the Arctic?
Does it hop?

DRILL
Is it used for making holes?
Is it used for distance?
Does it have bits?

Does it have a rounded head?

CLOVER
Does it have rounded leaves?
Is it used for luck?
Is it used in bouquets?
Does it have a trunk?

DESK
Is it found in an office?
Does it have a flat surface?
Is it found outside?
Does it have a lid?

LONDON BUS
Is it used for cargo?
Is it two-story?
Does it require money?
Does it run on tracks?

CHEST
Is it used for storing things?
Is it used for eating?
Does it have a lid?
Does it have a mattress?

WATER-LILY
Does it have a trunk?
Does it have flowers?
Does it provide shade?
Is it found in a pond?

LIMOUSINE
Does it require a driver?
Is it long?
Is it used for fishing?
Does it run on tracks?

EAGLE
Does it produce milk?
Does it have a furry tail?
Does it have wings?
Does it fly?

PALM TREE
Is it red?
Does it have a trunk?
Does it require mowing?
Does it grow in Tropical climates?

ROSE
Is it red?
Is it fragrant?
Is it a type of weed?
Does it have bark?

HAMMER

Is it used for hitting?
Is it used for cutting?
Does it have a rounded head?
Does it have bits?

LEMON
Is it sour?
Is it yellow?
Is it used in salad?
Is it green?

STRAWBERRY
Does it have a core?
Is it used in salad?
Is it sweet?
Is it red?

TRAIN
Does it run on tracks?
Does it have wheels?
Does it have a conductor?
Does it fly in the air?

GRASS
Is it used in bread?
Is it green?
Does it have flowers?
Does it require mowing?

TREE
Does it provide shade?
Does it have bark?
Is it found in a pond?
Is it yellow?

PENGUIN
Does it have horns?
Is it black and white?
Is it found on a farm?
Does it live in the Arctic?

WHEAT
Is it used in bouquets?
Does it have round leaves?
Does it have a stalk?
Is it used in bread?

SPANNER
Does it have a handle?
Is it used for making holes?
Does it have a sharp edge?
Is it used for gripping?

APPLE
Is it used in pies?
Does it have a core?
Is it sour?

Is it orange?

TRAM
Does it require money?
Does it have wheels?
Is it used for fishing?
Does it run on tracks?

DAFFODIL
Is it used in bread?
Does it have flowers?
Is it red?
Is it used in bouquets?

LETTUCE
Is it used in salad?
Is it leafy?
Is it juiced?
Does it have a stone?

PEPPER
Is it used in pies?
Does it grow on a bush?
Is it brown?
Does it have seeds?

SCREWDRIVER
Is it used for turning?
Is it used for cutting?
Does it have legs?
Does it have a head?

TABLE
Is it used for sleeping?
Does it have knobs?
Does it have a flat surface?
Is it used for eating?

PEAR
Does it grow on trees?
Is it sour?
Does it have skin?
Is it leafy?

AXE
Does it have prongs?
Does it have a sharp edge?
Is it used for turning things?
Is it used for cutting?

CHAIR
Is it used for storing things?
Is it two-story?
Is it used for sitting?
Does it have four legs?

SUNFLOWER

Is it yellow?
Does it have bark?
Does it require mowing?
Is it used for making cooking oil?

HIPPO
Is it found in a zoo?
Does it have antlers?
Does it have four legs?
Is it hunted for meat?

BED
Is it found outside?
Does it have a mattress?
Is it used for sleeping?
Does it have knobs?

SCISSORS
Does it have a head?
Does it have a sharp edge?
Is it used for turning things?
Is it used for cutting?

CUCUMBER
Is it eaten raw?
Is it eaten mashed?
Is it green?
Is it yellow?

ORANGE
Is it used in pies?
Is it round?
Is it leafy?
Is it juiced?

POTATO
Is it eaten raw?
Is it brown?
Does it have a stone?
Is it eaten mashed?

VAN
Is it used for cargo?
Does it have a nose?
Does it have wheels?
Does it fly in the air?

GOAT
Does it have horns?
Is it found on a farm?
Does it fly?
Does it have wings?

TAPE MEASURE
Does it have sharp edges?
Is it used for cutting?
Is it used for distance?

Does it have numbers?

ARMCHAIR
Does it have a lid?
Is it used for sitting?
Is it used for storing things?
Does it have four legs?

DECK CHAIR
Does it have knobs?
Does it have a seat?
Is it used for sleeping?
Is it found outside?

PEACH
Is it eaten mashed?
Is it used in pies?
Does it have a stone?
Is it red?

PIKE
Is it found in a zoo?
Does it have four legs?
Does it swim?
Does it have scales?

BOAT
Does it have a motor?
Does it run on tracks?
Does it fly in the air?
Is it used for fishing?